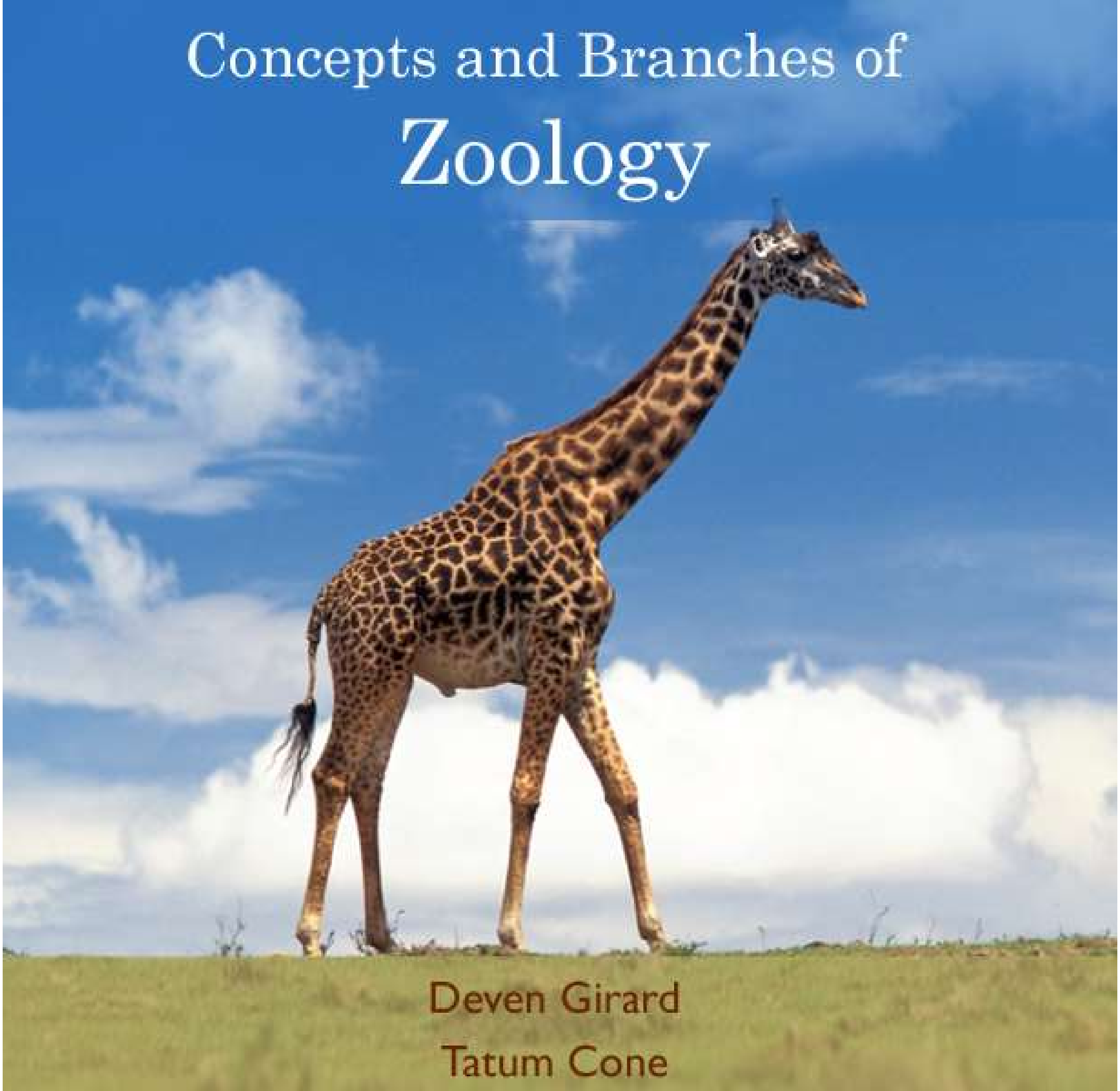


Concepts and Branches of Zoology

Deven Girard
Tatum Cone

First Edition, 2012

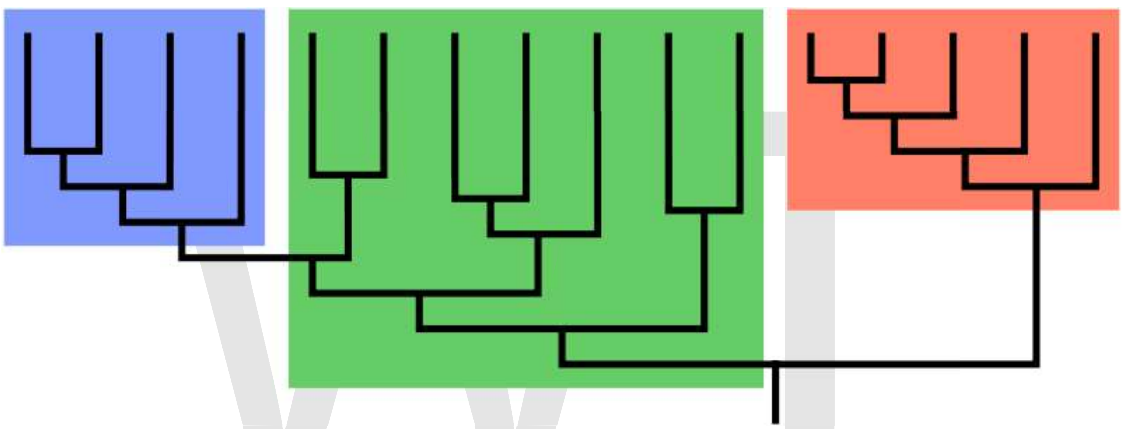
ISBN 978-81-323-0691-7

Published by:
Academic Studio
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

Table of Contents

Chapter- 1

Clade

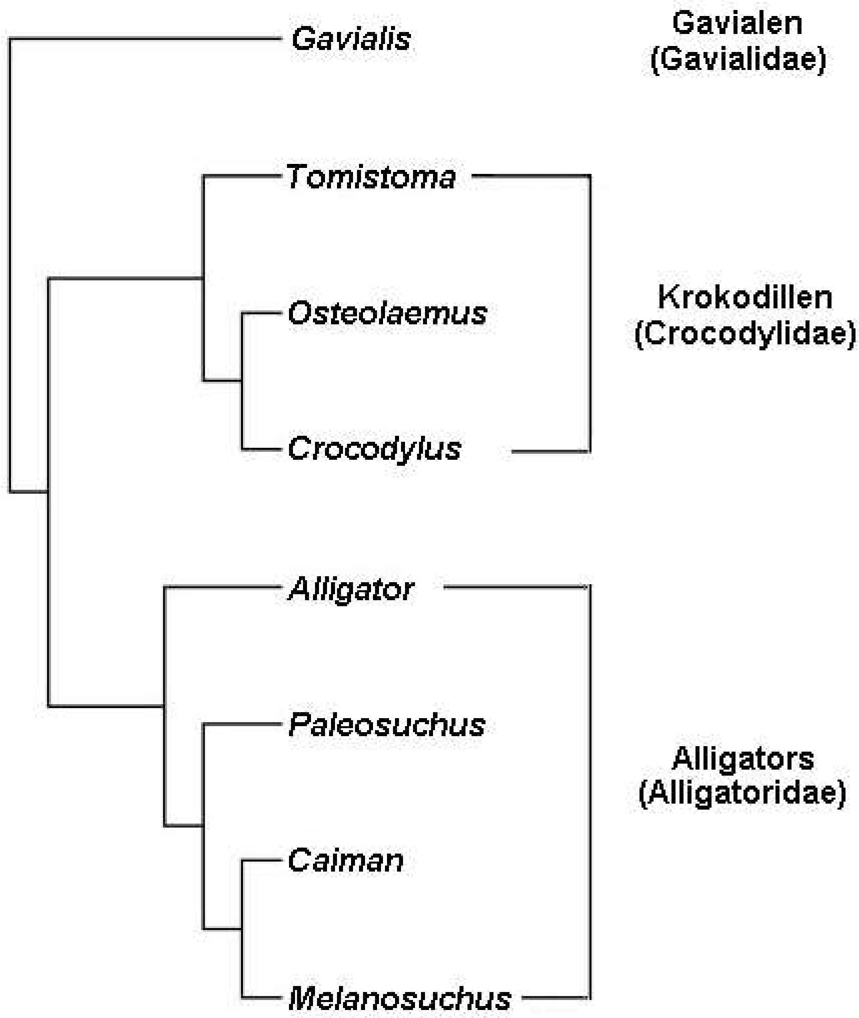


Cladogram (family tree) of a biological group. The red and blue boxes represent *clades* (i.e., complete branches). The green box is not a clade, but rather represents an *evolutionary grade*, an incomplete group, because the blue clade descends from it, but is excluded.

A **clade** is a group consisting of an organism and all its descendants. In the terms of biological systematics, a clade is a single "branch" on the "tree of life". The idea that such a "natural group" of organisms should be grouped together and given a taxonomic name is central to biological classification. In cladistics (which takes its name from the term), clades are the only acceptable units.

The term was coined in 1958 by English biologist Julian Huxley.

Definitions



A cladogram of crocodiles, a visual representation of their relationship

Clade and ancestor

A clade is termed monophyletic, meaning it contains one ancestor which can be an organism, population, or species and all its descendants. The term clade refers to the grouping of the ancestor and its living and/or deceased descendants together. The ancestor can be a theoretical or actual species.

Clade definition

Three methods of defining clades are featured in phylogenetic nomenclature: node-, stem-, and apomorphy-based:

- In node-based definition, clade name A refers to the *least inclusive* clade containing taxa (or specimens) X, Y, etc., and their common ancestor. The ancestor is the branch point, or *node*.
- In stem-based definition, A refers to the *most inclusive* clade containing X, Y, etc., and their common ancestor, down to where Z branches off below A. Taxa are included between the node of A and down to (but not including) the branching point to Z; that is, the *stem* of A.
- In apomorphy-based definition, A refers to the clade identified by an apomorphy (a trait) found in X, Y, etc., and their common ancestor.

In Linnaean taxonomy, clades are defined by a set of traits (apomorphies) unique to the group. This system is basically similar to the apomorphy-based clades of phylogenetic nomenclature. The difference is one of weight: While phylogenetic nomenclature bases the group on an ancestor with a certain trait, Linnaean taxonomy uses the traits themselves to define the group.

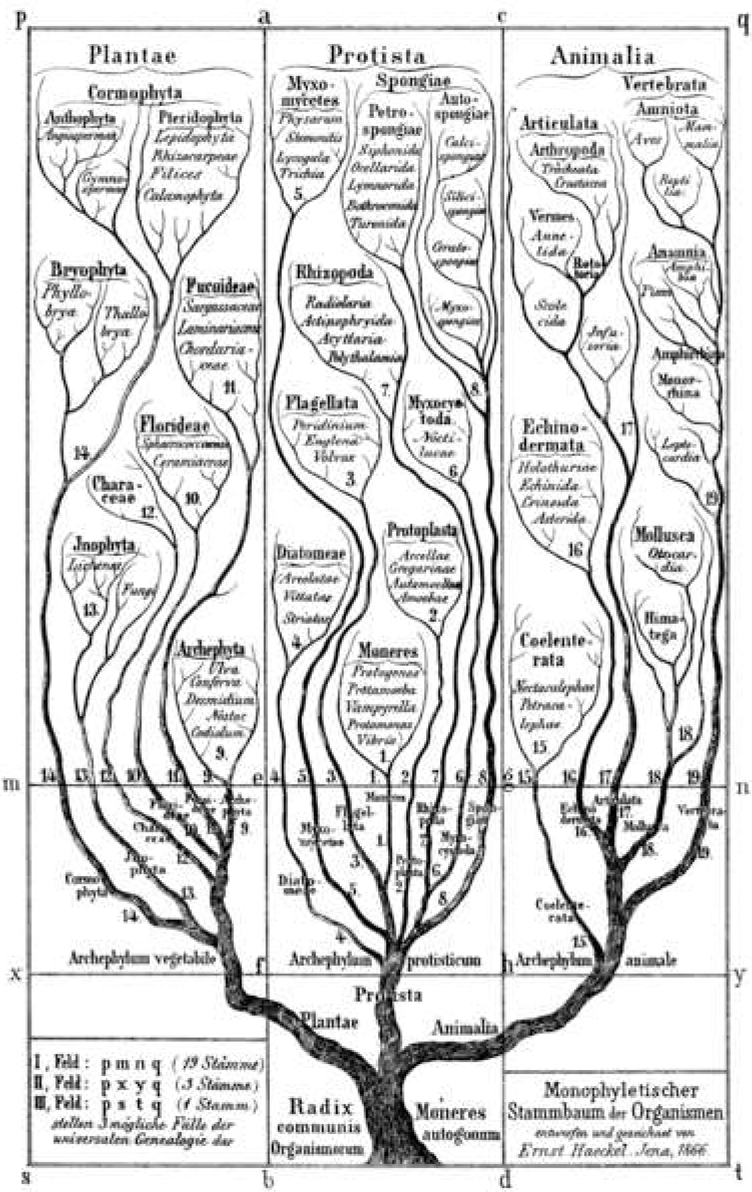
Clades as constructs

In cladistics, the clade is a hypothetical construct based on experimental data. Clades are found using multiple (sometimes hundreds) of traits from a number of species (or specimens) and analysing them statistically to find the most likely phylogenetic tree for the group. Although similar in some ways to a biological classification of species, the method is statistical and more open to scrutiny than traditional methods. Although taxonomists use clades as a tool in classification where feasible, the taxonomic "tree of life" is not the same as the cladistic. The traditional genus, family, etc. names are not necessarily clades; though they will often be.

Clade names

In Linnaean systematics, the various groups are ordered into a series of taxonomic ranks (the familiar order, family etc.). These ranks will by convention dictate the ending to names for some groups. Clades do not by their nature fit this scheme, and no such restriction exists as to their names in cladistics. There is however a convention for naming more or less inclusive groups, which are given prefixes like *crown-* or *pan*.

Taxonomy and systematics



Early phylogenetic tree by Haeckel, 1866

The idea of a "clade" did not exist in pre-Darwinian Linnaean taxonomy, which was based only on morphological similarities between organisms – although it happens that many of the better known animal groups in Linnaeus' original Systema Naturae (notably among the vertebrate groups) do represent clades. With the publication of Darwin's theory of evolution in 1859, taxonomy gained a theoretical basis, and the idea was born that groups used in a system of classification should represent branches on the evolutionary tree of life. In the century and a half since then, taxonomists have worked to make the taxonomic system reflect evolution. However, partly because the Tree of Life branches rather unevenly, the hierarchy of the Linnaean system does not always lend itself well to representing clades. The result is that when it comes to naming, cladistics and Linnaean taxonomy are not always compatible. In particular, higher level taxa in Linnaean taxonomy often represent evolutionary grades rather than clades, resulting in groups made up of clades where one or two sub-branches have been excluded. Typical examples include bony fishes, which include the ancestor of tetrapods, and reptiles, ancestral to both birds and mammals.

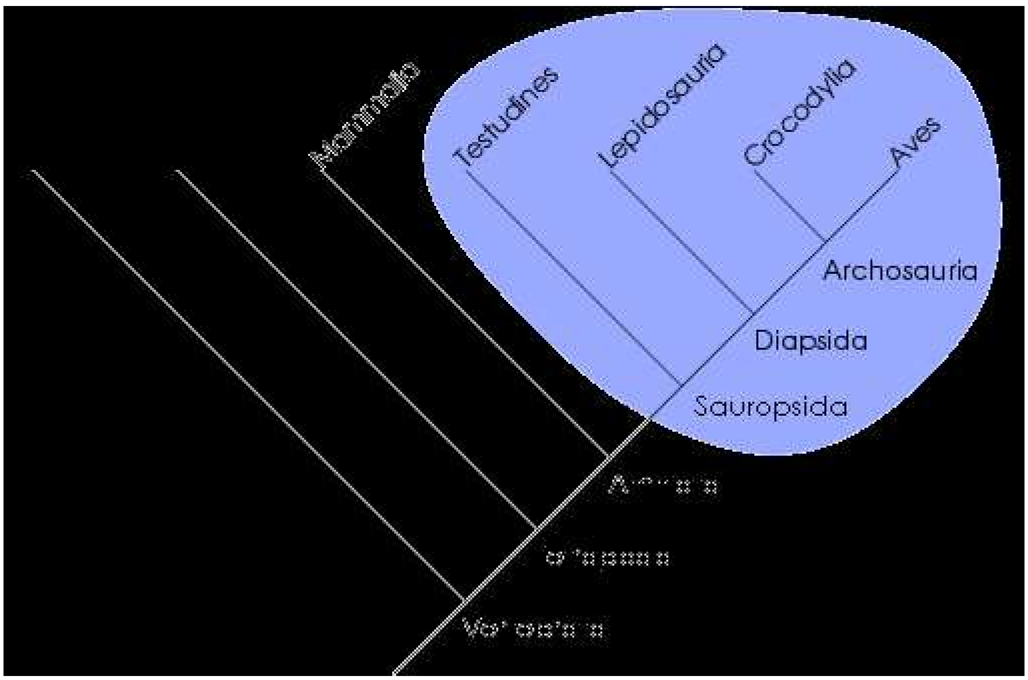
In phylogenetic nomenclature, clades can be nested at any level, and do not have to be slotted into a small number of ranks in an overall hierarchy. In contrast, the Linnaean units of "order", "class" etc. must be used when naming a new taxon. As there are only seven formal levels to the Linnaean system (species being the lowest), only a finite number of sub- and super-units can be created. In order to be able to use the full complexity of taxonomic trees (cladograms) in an area with which they are very familiar, some researchers have opted to dispense with ranks all together, instead using clade names without Linnaean ranks. The reason for preferring one system over the other is partly one of application: cladistic trees give details, suitable for specialists; the Linnaean system gives a well ordered overview, at the expense of details of the phylogenetic tree.

In a few instances, the Linnaean system has actually impeded our understanding of the phylogeny and broad evolutionary patterns. The best known example is the interpretation of the strange fossils of the Burgess Shale and the subsequent idea of a "Cambrian Explosion" With the application of cladistics, and the rejection of any significance of the concept of phyla, the confusion of the late 20th century over the Burgess animals has been resolved. It appears there never was an "explosion" of major bauplans with subsequent extinctions. The seemingly weird critters themselves have been found to be representatives of a group, the Lobopodia, that includes arthropods, water bears and velvet worms.

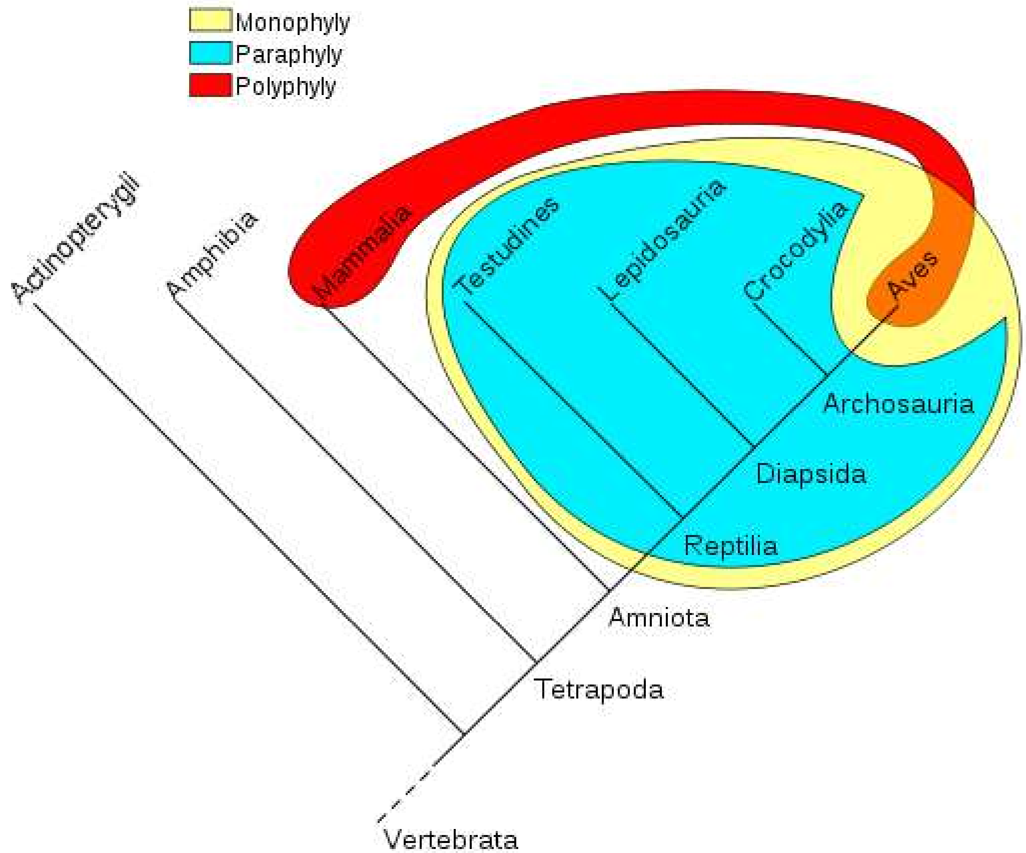
In most instances the two systems are not at odds, however. The cladistic statement, that the clade Lobopodia contains (among others) the Arthropoda, Tardigrada and Onychophora, is factually identical to the Linnaean evolutionary statement that the group Lobopodia is ancestral to the phyla Arthropoda, Tardigrada and Onychophora. The difference is one of semantics rather than phylogeny.

Chapter- 2

Monophyly



A monophyly



Partial Evolutionary Tree of the Vertebrates

Comparison of phylogenetic groups, showing a **monophyly** (all descendants of the first reptiles), a **paraphyly** (descendants of reptiles, minus birds), and a **polyphyly** (warm-blooded animals: mammals and birds)

In common cladistic usage, a **monophyletic** group is a taxon (group of organisms) which forms a clade, meaning that it contains *all* the descendants of the possibly hypothetical closest common ancestor of the members of the group. The term is synonymous with the uncommon term holophyly. Monophyletic groups are typically characterized by shared derived characteristics (synapomorphies).

Monophyly is contrasted with the terms paraphyly and polyphyly, which are most easily understood from the second diagram. In current usage, a **paraphyletic** group consists of all of the descendants of a possibly hypothetical closest common ancestor *minus* one or more monophyletic groups (most usually one). A paraphyletic group is thus 'nearly' monophyletic (consistent with the meaning of the prefix 'para', namely 'near' or 'alongside'.) A **polyphyletic** group is any group other than a monophyletic group or a paraphyletic group, which like a paraphyletic group contains only some of the descendants of their closest common ancestor, but unlike a paraphyletic group is not characterized by the missing descendants forming one (or more) monophyletic groups.

These definitions have taken some time to be accepted. When the cladistic school of thought became mainstream in the 1960s, several alternative definitions were in use. Indeed, taxonomists sometimes used terms without defining them, leading to confusion in the early literature, a confusion which persists.

Definitions

On the broadest scale, definitions fall into two groups.

- The widest, and arguably the semantically correct meaning of the word, is any two or more groups sharing a common ancestor. This very broad definition strips the term of scientific utility. Therefore, scientists today restrict the term to holophyletic groups only – that is, groups consisting of all the descendants of one (usually hypothetical) common ancestor. However, when considering taxonomic groups such as genera and species, the most appropriate nature of their common ancestor is unclear. Assuming that it would be one individual or mating pair is unrealistic for sexually reproducing species, which are by definition interbreeding populations.

- However, using a broader definition, such as a species and all its descendants, does not really work to define a genus. A satisfactory and comprehensive cladistic definition of a species or genus is in fact impossible, and reflects the impossibility of seamlessly impressing a gradualistic model of continual change over the 'quantum' Linnean model, where species have defined boundaries, and intermediaries between species cannot be accommodated.

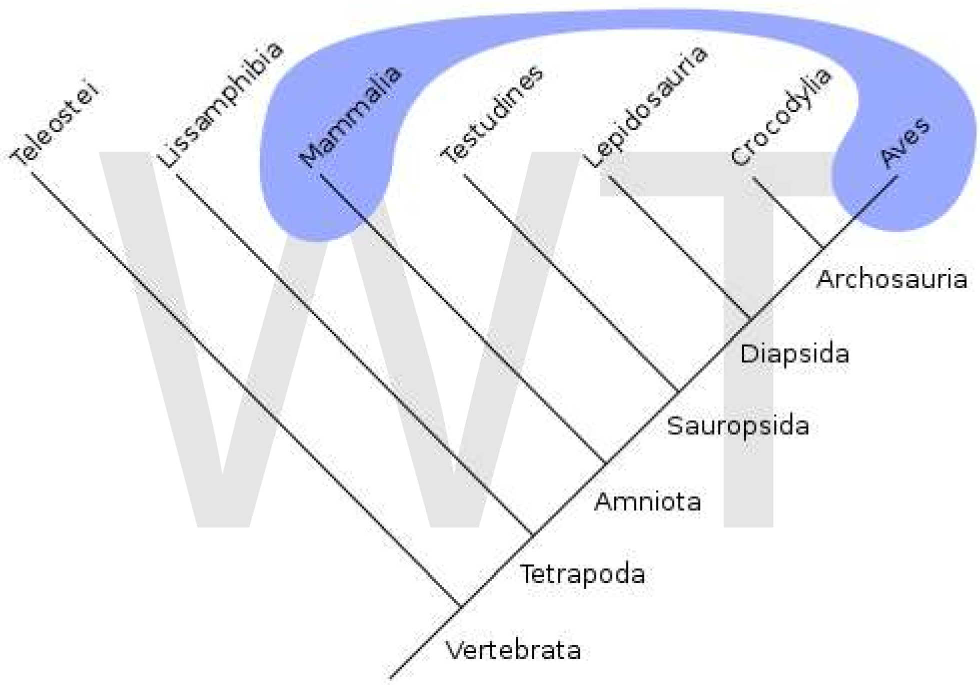
Controversy

This incompatibility with the Linnaean taxonomy model led to an initial rift, not entirely healed, between the cladistic and Linnean schools of thought. Extreme cladists challenged the validity of Linnean taxa such as the Reptilia. Because birds, although descended from reptiles, are not themselves considered to be reptiles, cladists demanded that the taxon Reptilia be dismantled: a request that taxonomists were unwilling to heed. This stand-off was eventually resolved to a degree by the construction of the term 'paraphyletic' to describe closely related groups which included most but not all of the descendants of a common ancestor.

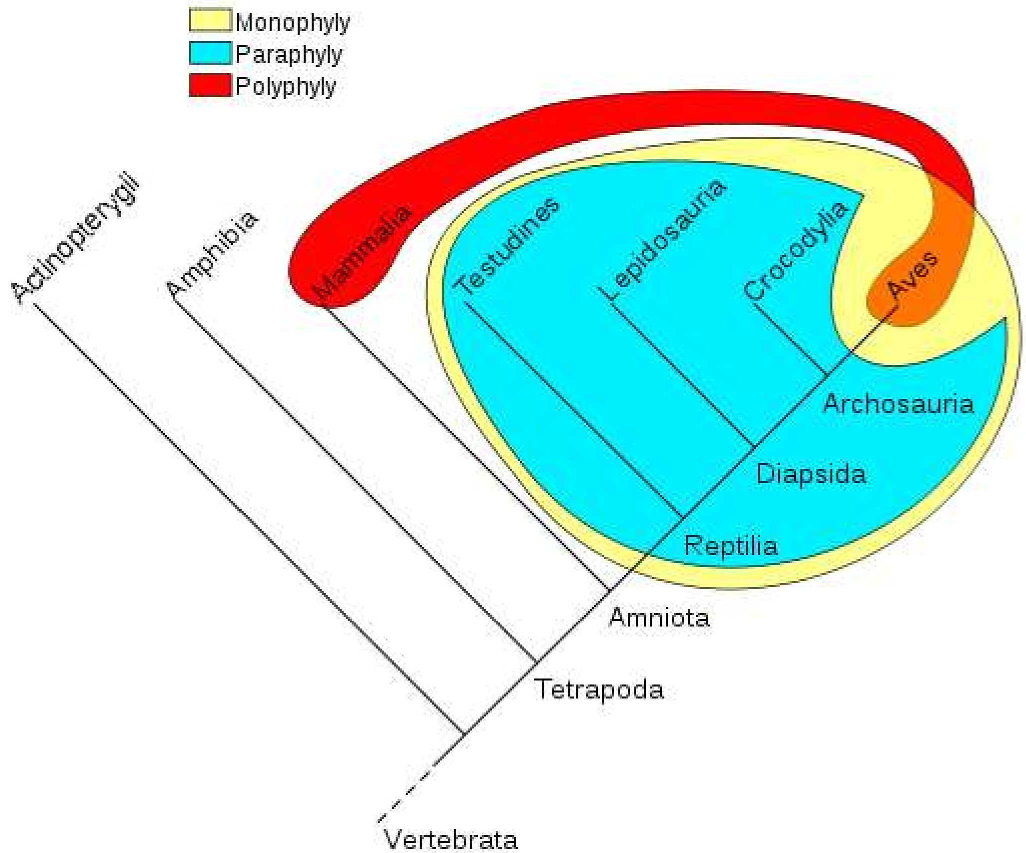
However, the coining of this term led to yet more confusion. Some scientists considered paraphyletic groups to be monophyletic (as they shared a common ancestor), where others insisted that monophyletic should continue to refer only to holophyletic groups. Another term, polyphyletic, fell outside of the definition of monophyly. A strict explanation of a paraphyletic group has not been published, but the consensus appears to be that paraphyletic groups consist of a monophyletic group, minus one smaller constituent clade – for instance "reptiles minus birds". Polyphyletic groups can be thought of as a number of unrelated clades, for instance "warm blooded animals" = "birds plus mammals". Non-holophyletic groups are of little use for analysis of evolutionary processes, hence the calls for their "unnaming" - even though they are useful to scientists who are less concerned with the evolutionary past of groups. Naming is also a problem for monophyletic groups: because the number of ancestors from which to root monophyletic groups is almost infinite, giving each clade a unique name is impossible - as illustrated by the failed attempts to instigate a system called the Phylocode. Names obfuscate the really interesting part, which is the branching order, and are therefore of little utility to the cladist - at odds with the taxonomist, who since the time of Linnaeus has been naming species. Intermediate, and particularly fossil, taxa can be considered to fall 'just outside' a widely accepted taxon. For instance, *Archaeopteryx* appears more reptilian than bird – it has teeth and a number of other reptilian characteristics. But it also has feathers, which have traditionally been considered as an avian trait. It lacks a number of other traits shared by all birds, so cannot fall within the bird clade. To reflect this phylogenetic proximity, it is termed a 'stem group bird' - i.e. it lies on a branch close to the lineage that led to true birds, as recognised by a taxonomist. This concept closes the gap between taxonomy and cladistics at a broader scale, but is difficult to apply at a species-level resolution.

Chapter- 3

Polyphyly



The group of "warm-blooded animals" is polyphyletic.



Partial Evolutionary Tree of the Vertebrates

Comparison: monophyly = yellow, polyphyly = red, paraphyly = aqua

A **polyphyletic** (Greek for "of many races") group is one whose members' last common ancestor is not a member of the group.

For example, the group consisting of warm-blooded animals is polyphyletic, because it contains both mammals and birds, but the most recent common ancestor of mammals and birds was cold-blooded. Warm-bloodedness evolved separately in the ancestors of mammals and the ancestors of birds, so it is not a true phylogenetic grouping.

Scientific classification aims to group species together such that every group is descended from a single common ancestor and therefore it is frequently a goal to eliminate groups that are found to be polyphyletic. This is often the stimulus for major revisions of the classification schemes. A polyphyletic group can be "fixed" either by excluding clades or by adding the common ancestor.

Opinions differ as to whether valid groups need to contain *all* the descendants of a common ancestor. Groups that do so are called monophyletic, and according to cladistics it should be the aim of classification to ensure that all groups have this property. However, many other taxonomists would argue that there is a valid place for groups that are paraphyletic, i.e. contains its most recent common ancestor but does not contain all the descendants of that ancestor.

Cladistics generally discourages polyphyletic groups

In most cladistics-based schools of taxonomy, the existence of polyphyletic groups (as well as paraphyletic groups) in a classification is discouraged. Monophyletic groups (that is, clades) are considered by these schools of thought to be the most important grouping of organisms, for the following reasons:

- Clades are simple to define: a typical clade definition is "All descendants of the nearest common ancestor of species X and Y". On the other hand, polyphyletic and paraphyletic groups are always defined in terms of clades, for example "reptiles are the Sauropsid clade, minus the Aves clade". Or "Warm-blooded animals are the Aves clade plus the Mammals clade". Because polyphyletic and paraphyletic groups are defined in terms of clades plus or minus other clades, they are considered less important than monophyletic (single, whole) clades.

- For a given evolutionary tree of, say, N nodes, there are exactly N clades (one per node). However, the number of paraphyletic groups and polyphyletic groups is exponentially larger than that, on the order of 2^N. Yet only a small fraction of the paraphyletic groups are given names or discussed.

- Polyphyletic groups often have their origin in traditional taxonomy, based on similar morphological characteristics. The original perception may have been that the group was entirely descended from a single ancestor. If such a group is later discovered (for instance, due to convergent evolution) to be polyphyletic, rather than monophyletic, then such a group loses its original significance.

Chapter- 4

Speciation

Speciation is the evolutionary process by which new biological species arise. The biologist Orator F. Cook seems to have been the first to coin the term 'speciation' for the splitting of lineages or 'cladogenesis,' as opposed to 'anagenesis' or 'phyletic evolution' occurring within lineages. Whether genetic drift is a minor or major contributor to speciation is the subject matter of much ongoing discussion.

There are four geographic modes of speciation in nature, based on the extent to which speciating populations are geographically isolated from one another: allopatric, peripatric, parapatric, and sympatric. Speciation may also be induced artificially, through animal husbandry or laboratory experiments. Observed examples of each kind of speciation are provided throughout.

Natural speciation

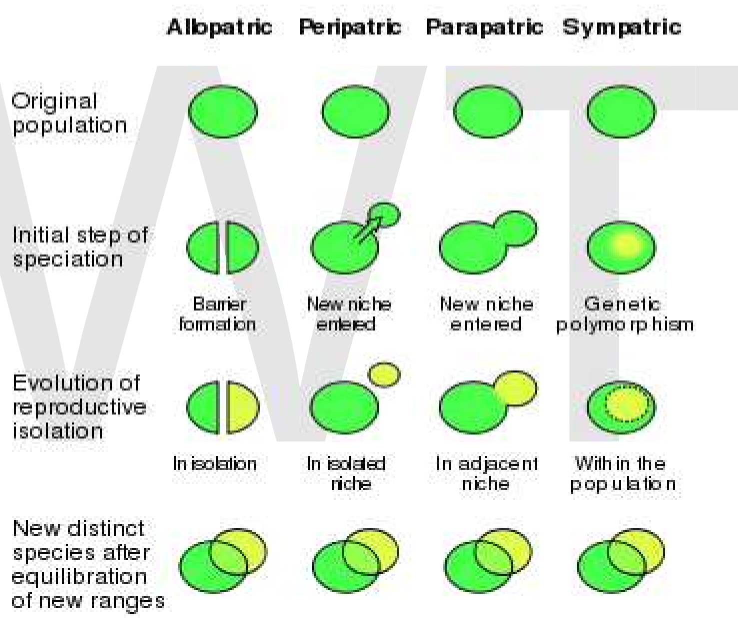
All forms of natural speciation have taken place over the course of evolution; however it still remains a subject of debate as to the relative importance of each mechanism in driving biodiversity.

The three-spined stickleback (*Gasterosteus aculeatus*)

One example of natural speciation is the diversity of the three-spined stickleback, a marine fish that, after the last ice age, has undergone speciation into new freshwater colonies in isolated lakes and streams. Over an estimated 10,000 generations, the sticklebacks show structural differences that are greater than those seen between different genera of fish including variations in fins, changes in the number or size of their bony plates, variable jaw structure, and color differences.

There is debate as to the rate at which speciation events occur over geologic time. While some evolutionary biologists claim that speciation events have remained relatively constant over time, some palaeontologists such as Niles Eldredge and Stephen Jay Gould have argued that species usually remain unchanged over long stretches of time, and that speciation occurs only over relatively brief intervals, a view known as *punctuated equilibrium*.

Allopatric



Comparison of allopatric, peripatric, parapatric and sympatric speciation.

During allopatric (from the ancient Greek *allos*, "other" + Greek *patrā*, "fatherland") speciation, a population splits into two geographically isolated populations (for example, by habitat fragmentation due to geographical change such as mountain building or social change such as emigration). The isolated populations then undergo genotypic and/or phenotypic divergence as: (a) they become subjected to dissimilar selective pressures; (b) they independently undergo genetic drift; (c) different mutations arise in the two populations. When the populations come back into contact, they have evolved such that they are reproductively isolated and are no longer capable of exchanging genes.

Observed instances

Island genetics, the tendency of small, isolated genetic pools to produce unusual traits, has been observed in many circumstances, including insular dwarfism and the radical changes among certain famous island chains, for example on Komodo. The Galápagos islands are particularly famous for their influence on Charles Darwin. During his five weeks there he heard that Galápagos tortoises could be identified by island, and noticed that Mockingbirds differed from one island to another, but it was only nine months later that he reflected that such facts could show that species were changeable. When he returned to England, his speculation on evolution deepened after experts informed him that these were separate species, not just varieties, and famously that other differing Galápagos birds were all species of finches. Though the finches were less important for Darwin, more recent research has shown the birds now known as Darwin's finches to be a classic case of adaptive evolutionary radiation.

Peripatric

In peripatric speciation, a subform of allopatric speciation, new species are formed in isolated, smaller peripheral populations that are prevented from exchanging genes with the main population. It is related to the concept of a founder effect, since small populations often undergo bottlenecks. Genetic drift is often proposed to play a significant role in peripatric speciation.

Observed instances

- Mayr bird fauna
- The Australian bird *Petroica multicolor*
- Reproductive isolation occurs in populations of *Drosophila* subject to population bottlenecking

The London Underground mosquito is a variant of the mosquito *Culex pipiens* that entered in the London Underground in the nineteenth century. Evidence for its speciation include genetic divergence, behavioral differences, and difficulty in mating.

Parapatric

In parapatric speciation, there is only partial separation of the zones of two diverging populations afforded by geography; individuals of each species may come in contact or cross habitats from time to time, but reduced fitness of the heterozygote leads to selection for behaviours or mechanisms that prevent their inter-breeding. Parapatric speciation is modelled on continuous variation within a 'single', connected habitat acting as a source of natural selection rather than the effects of isolation of habitats produced in peripatric and allopatric speciation.

Ecologists refer to parapatric and peripatric speciation in terms of ecological niches. A niche must be available in order for a new species to be successful.

Observed instances

- Ring species
    - The *Larus* gulls form a ring species around the North Pole.
    - The *Ensatina* salamanders, which form a ring round the Central Valley in California.
    - The Greenish Warbler (*Phylloscopus trochiloides*), around the Himalayas.
- the grass *Anthoxanthum* has been known to undergo parapatric speciation in such cases as mine contamination of an area.

Sympatric

Sympatric speciation refers to the formation of two or more descendant species from a single ancestral species all occupying the same geographic location.

In sympatric speciation, species diverge while inhabiting the same place. Often-cited examples of sympatric speciation are found in insects that become dependent on different host plants in the same area. However, the existence of sympatric speciation as a mechanism of speciation is still hotly contested. People have argued that the evidences of sympatric speciation are in fact examples of micro-allopatric, or heteropatric speciation. The most widely accepted example of sympatric speciation is that of the cichlids of Lake Nabugabo in East Africa, which is thought to be due to **sexual selection**.

Until recently, there has a been a dearth of strong evidence that supports this form of speciation, with a general feeling that interbreeding would soon eliminate any genetic differences that might appear. But there has been at least one recent study that suggests that sympatric speciation has occurred in Tennessee cave salamanders.

The three-spined sticklebacks, freshwater fishes, that have been studied by Dolph Schluter (who received his Ph.D. for his work on Darwin's finches with Peter J. Grant) and his current colleagues in British Columbia, were once thought to provide an intriguing example best explained by sympatric speciation. Schluter and colleagues found:

- Two different species of three-spined sticklebacks in each of five different lakes
    - a large benthic species with a large mouth that feeds on large prey in the littoral zone
    - a smaller limnetic species — with a smaller mouth — that feeds on the small plankton in open water
- DNA analysis indicates that each lake was colonized independently, presumably by a marine ancestor, after the last ice age
- DNA analysis also shows that the two species in each lake are more closely related to each other than they are to any of the species in the other lakes
- The two species in each lake are reproductively isolated; neither mates with the other.

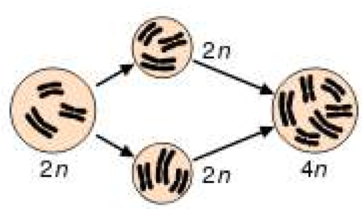
- However, aquarium tests showed:

- the benthic species from one lake will spawn with the benthic species from the other lakes and
    - likewise the limnetic species from the different lakes will spawn with each other.
    - These benthic and limnetic species even display their mating preferences when presented with sticklebacks from Japanese lakes; that is, a Canadian benthic prefers a Japanese benthic over its close limnetic cousin from its own lake.
- Their conclusion: in each lake, what began as a single population faced such competition for limited resources that:
    - disruptive selection — competition favoring fishes at either extreme of body size and mouth size over those nearer the mean — coupled with:
    - assortative mating — each size preferred mates like it — favored a divergence into two subpopulations exploiting different food in different parts of the lake.
    - The fact that this pattern of speciation occurred the same way on three separate occasions suggests strongly that ecological factors in a sympatric population can cause speciation.

However, the DNA evidence cited above is from mitochondrial DNA (mtDNA), which can often move easily between closely related species ("introgression") when they hybridize. A more recent study, using genetic markers from the nuclear genome, shows that limnetic forms in different lakes are more closely related to each other (and to marine lineages) than to benthic forms in the same lake. The three-spine stickleback is now usually considered an example of "double invasion" (a form of allopatric speciation) in which repeated invasions of marine forms have subsequently differentiated into benthic and limnetic forms. The three-spine stickleback provides an example of how molecular biogeographic studies that rely solely on mtDNA can be misleading, and that consideration of the genealogical history of alleles from multiple unlinked markers (i.e. nuclear genes) is necessary to infer speciation histories.

Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

Speciation via polyploidization



Speciation via polyploidy: A diploid cell undergoes failed meiosis, producing diploid gametes, which self-fertilize to produce a tetraploid zygote.

Polyploidy is a mechanism often attributed to causing some speciation events in sympatry. Not all polyploids are reproductively isolated from their parental plants, so an increase in chromosome number may not result in the complete cessation of gene flow between the incipient polyploids and their parental diploids.

Polyploidy is observed in many species of both plants and animals, and results in rapid speciation since offspring of, for example, tetraploid x diploid matings result in triploid sterile progeny. It has been proposed that many of the existing plant and most animal species have undergone an event of polyploidization in their evolutionary history. However, reproduction is often by parthenogenesis since polyploid animals are often sterile. [needs further editing—not true in plants]. Rare instances of polyploid mammals are known, but most often result in prenatal death.

Hawthorn fly

One example of evolution at work is the case of the hawthorn fly, *Rhagoletis pomonella*, also known as the apple maggot fly, which appears to be undergoing sympatric speciation. Different populations of hawthorn fly feed on different fruits. A distinct population emerged in North America in the 19th century some time after apples, a non-native species, were introduced. This apple-feeding population normally feeds only on apples and not on the historically preferred fruit of hawthorns. The current hawthorn feeding population does not normally feed on apples. Some evidence, such as the fact that six out of thirteen allozyme loci are different, that hawthorn flies mature later in the season and take longer to mature than apple flies; and that there is little evidence of interbreeding (researchers have documented a 4-6% hybridization rate) suggests that sympatric speciation is occurring. The emergence of the new hawthorn fly is an example of evolution in progress.

Reinforcement (Wallace effect)

Reinforcement is the process by which natural selection increases reproductive isolation. It may occur after two populations of the same species are separated and then come back into contact. If their reproductive isolation was complete, then they will have already developed into two separate incompatible species. If their reproductive isolation is incomplete, then further mating between the populations will produce hybrids, which may or may not be fertile. If the hybrids are infertile, or fertile but less fit than their ancestors, then there will be no further reproductive isolation and speciation has essentially occurred (e.g., as in horses and donkeys.) The reasoning behind this is that if the parents of the hybrid offspring each have naturally selected traits for their own certain environments, the hybrid offspring will bear traits from both, therefore would not fit either ecological niche as well as either parent. The low fitness of the hybrids would cause selection to favor assortative mating, which would control hybridization. This is sometimes called the Wallace effect after the evolutionary biologist Alfred Russel Wallace who suggested in the late 19th century that it might be an important factor in speciation. If the hybrid offspring are more fit than their ancestors, then the populations will merge back into the same species within the area they are in contact.

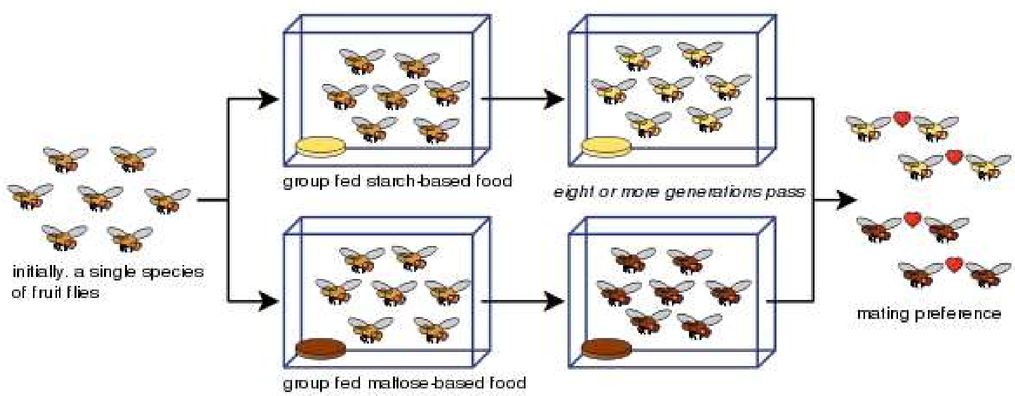
Reinforcement is required for both parapatric and sympatric speciation. Without reinforcement, the geographic area of contact between different forms of the same species, called their "hybrid zone," will not develop into a boundary between the different species. Hybrid zones are regions where diverged populations meet and interbreed. Hybrid offspring are very common in these regions, which are usually created by diverged species coming into secondary contact. Without reinforcement the two species would have uncontrollable inbreeding. Reinforcement may be induced in artificial selection experiments as described below.

Artificial speciation

New species have been created by domesticated animal husbandry, but the initial dates and methods of the initiation of such species are not clear. For example, domestic sheep were created by hybridisation, and no longer produce viable offspring with *Ovis orientalis*, one species from which they are descended. Domestic cattle, on the other hand, can be considered the same species as several varieties of wild ox, gaur, yak, etc., as they readily produce fertile offspring with them.

The best-documented creations of new species in the laboratory were performed in the late 1980s. William Rice and G.W. Salt bred fruit flies, *Drosophila melanogaster,* using a maze with three different choices of habitat such as light/dark and wet/dry. Each generation was placed into the maze, and the groups of flies that came out of two of the eight exits were set apart to breed with each other in their respective groups. After thirty-five generations, the two groups and their offspring were isolated reproductively because of their strong habitat preferences: they mated only within the areas they preferred, and so did not mate with flies that preferred the other areas. The history of such attempts is described in Rice and Hostert (1993).

Diane Dodd was also able to show how reproductive isolation can develop from mating preferences in *Drosophila pseudoobscura* fruit flies after only eight generations using different food types, starch and maltose.



Dodd's experiment has been easy for many others to replicate, including with other kinds of fruit flies and foods.

Genetics

Few speciation genes have been found. They usually involve the reinforcement process of late stages of speciation. In 2008 a speciation gene causing reproductive isolation was reported. It causes hybrid sterility between related subspecies.

Hybrid speciation

Hybridization between two different species sometimes leads to a distinct phenotype. This phenotype can also be fitter than the parental lineage and as such natural selection may then favor these individuals. Eventually, if reproductive isolation is achieved, it may lead to a separate species. However, reproductive isolation between hybrids and their parents is particularly difficult to achieve and thus hybrid speciation is considered an extremely rare event. The Mariana Mallard is known to have arisen from hybrid speciation.

Hybridization without change in chromosome number is called homoploid hybrid speciation. It is considered very rare but has been shown in *Heliconius* butterflies and sunflowers. Polyploid speciation, which involves changes in chromosome number, is a more common phenomenon, especially in plant species.

Gene transposition as a cause

Theodosius Dobzhansky, who studied fruit flies in the early days of genetic research in 1930s, speculated that parts of chromosomes that switch from one location to another might cause a species to split into two different species. He mapped out how it might be possible for sections of chromosomes to relocate themselves in a genome. Those mobile sections can cause sterility in inter-species hybrids, which can act as a speciation pressure. In theory, his idea was sound, but scientists long debated whether it actually happened in nature. Eventually a competing theory involving the gradual accumulation of mutations was shown to occur in nature so often that geneticists largely dismissed the moving gene hypothesis.

However, 2006 research shows that jumping of a gene from one chromosome to another can contribute to the birth of new species. This validates the reproductive isolation mechanism, a key component of speciation.

Interspersed repeats

Interspersed repetitive DNA sequences function as isolating mechanisms. These repeats protect newly evolving gene sequences from being overwritten by gene conversion, due to the creation of non-homologies between otherwise homologous DNA sequences. The non-homologies create barriers to gene conversion. This barrier allows nascent novel genes to evolve without being overwritten by the progenitors of these genes. This uncoupling allows the evolution of new genes, both within gene families and also allelic forms of a gene. The importance is that this allows the splitting of a gene pool without requiring physical isolation of the organisms harboring those gene sequences.

Human speciation

Humans have genetic similarities with chimpanzees and gorillas, suggesting common ancestors. Analysis of genetic drift and recombination using a Markov model suggests humans and chimpanzees speciated apart 4.1 million years ago.

Chapter- 5

Phenotype

Individuals in the mollusk species *Donax variabilis* show diverse coloration and patterning in their phenotypes.

A **phenotype** is any *observable characteristic* or trait of an organism: such as its morphology, development, biochemical or physiological properties, behavior, and products of behavior (such as a bird's nest). Phenotypes result from the expression of an organism's genes as well as the influence of environmental factors and the interactions between the two.

The genotype of an organism is the inherited instructions it carries within its genetic code. Not all organisms with the same genotype look or act the same way because appearance and behavior are modified by environmental and developmental conditions. Similarly, not all organisms that look alike necessarily have the same genotype.

This genotype-phenotype distinction was proposed by Wilhelm Johannsen in 1911 to make clear the difference between an organism's heredity and what that heredity produces. The distinction is similar to that proposed by August Weismann, who distinguished between germ plasm (heredity) and somatic cells (the body). A more modern version is Francis Crick's Central dogma of molecular biology.

Difficulties in definition

Despite its seemingly straightforward definition, the concept of the phenotype has some hidden subtleties. First, most of the molecules and structures coded by the genetic material are not visible in the appearance of an organism, yet they are observable (for example by Western blotting) and are thus part of the phenotype. Human blood groups are an example. So, by extension, the term phenotype must include characteristics that can be made visible by some technical procedure. Another extension adds behaviour to the phenotype since behaviours are also observable characteristics. Indeed there is research into the clinical relevance of behavioural phenotypes as they pertain to a range of syndromes. Often, the term "phenotype" is incorrectly used as a shorthand to indicate *phenotypical changes* observed in mutated organisms (most often in connection with knockout mice).

Biston betularia morpha *typica*, the standard light-colored Peppered Moth.

Biston betularia morpha *carbonaria*, the melanic Peppered Moth, illustrating discontinuous variation.

Phenotypic variation

Phenotypic variation (due to underlying heritable genetic variation) is a fundamental prerequisite for evolution by natural selection. It is the living organism as a whole that contributes (or not) to the next generation, so natural selection affects the genetic structure of a population indirectly via the contribution of phenotypes. Without phenotypic variation, there would be no evolution by natural selection.

The interaction between genotype and phenotype has often been conceptualized by the following relationship:

genotype + environment → phenotype

A slightly more nuanced version of the relationships is:

genotype + environment + random-variation → phenotype

Genotypes often have much flexibility in the modification and expression of phenotypes; in many organisms these phenotypes are very different under varying environmental conditions. The plant *Hieracium umbellatum* is found growing in two different habitats in Sweden. One habitat is rocky, sea-side cliffs, where the plants are bushy with broad leaves and expanded inflorescences; the other is among sand dunes where the plants grow prostrate with narrow leaves and compact inflorescences. These habitats alternate along the coast of Sweden and the habitat that the seeds of *Hieracium umbellatum* land in, determine the phenotype that grows.

An example of random variation in *Drosophila* flies is the number of ommatidia, which may vary (randomly) between left and right eyes in a single individual as much as they do between different genotypes overall, or between clones raised in different environments.

The concept of phenotype can be extended to variations below the level of the gene that affect an organism's fitness. For example, silent mutations that do not change the corresponding amino acid sequence of a gene may change the frequency of guanine-cytosine base pairs (GC content). These base pairs have a higher thermal stability than adenine-thymine, a property that might convey, among organisms living in high-temperature environments, a selective advantage on variants enriched in GC content.

The Extended Phenotype

The idea of the phenotype has been generalized by Richard Dawkins in *The Extended Phenotype* to mean all the effects a gene has on the outside world that may influence its chances of being replicated. These can be effects on the organism in which the gene resides, the environment, or other organisms.

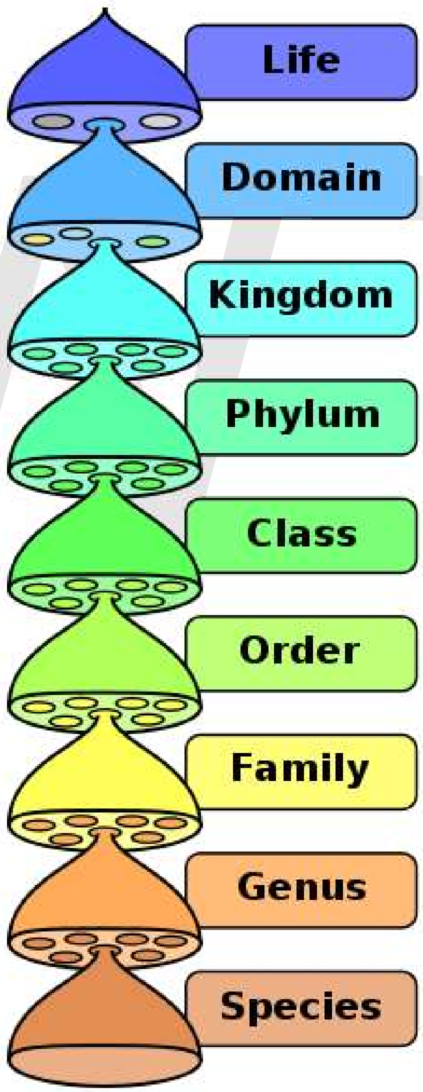
For instance, a beaver dam might be considered a phenotype of beaver genes, the same way beavers' powerful incisor teeth are phenotype expressions of their genes. Dawkins also cites the effect of an organism on the behaviour of another organism (such as the devoted nurturing of a cuckoo by a parent clearly of a different species) as an example of the extended phenotype.

Phenome and phenomics

Although a phenotype is the ensemble of observable characteristics displayed by an organism, the word *phenome* is sometimes used to refer to a collection of traits and their simultaneous study as *phenomics*.

Chapter- 6

Species



The hierarchy of biological classification's eight major taxonomic ranks, which is an example of definition by genus and differentia. A genus contains one or more species. Intermediate minor rankings are not shown.

In biology, a **species** is one of the basic units of biological classification and a taxonomic rank. A species is often defined as a group of organisms capable of interbreeding and producing fertile offspring. While in many cases this definition is adequate, more precise or differing measures are often used, such as similarity of DNA, morphology or ecological niche. Presence of specific locally adapted traits may further subdivide species into subspecies.

The commonly used names for plant and animal taxa sometimes correspond to species: for example, "lion," "walrus," and "Camphor tree" – each refers to a species. In other cases common names do not: for example, "deer" refers to a family of 34 species, including Eld's Deer, Red Deer and Elk (Wapiti). The last two species were once considered a single species, illustrating how species boundaries may change with increased scientific knowledge.

Each species is placed within a single genus. This is a hypothesis that the species is more closely related to other species within its genus than to species of other genera. All species are given a binomial name consisting of the generic name and specific name (or specific epithet). For example, *Boa constrictor*, which is commonly called by its bionomial name, and is one of five species of the *Boa* genus.

A usable definition of the word "species" and reliable methods of identifying particular species are essential for stating and testing biological theories and for measuring biodiversity. Traditionally, multiple examples of a proposed species must be studied for unifying characters before it can be regarded as a species. Extinct species known only from fossils are generally difficult to assign precise taxonomic rankings.

Because of the difficulties with both defining and tallying the total numbers of different species in the world, it is estimated that there are anywhere between 2 and 100 million different species.

Biologists' working definition

A usable definition of the word "species" and reliable methods of identifying particular species is essential for stating and testing biological theories and for measuring biodiversity. Traditionally, multiple examples of a proposed species must be studied for unifying characters before it can be regarded as a species. It is generally difficult to give precise taxonomic rankings to extinct species known only from fossils.

Some biologists may view species as statistical phenomena, as opposed to the traditional idea, with a species seen as a class of organisms. In that case, a species is defined as a separately evolving lineage that forms a single gene pool. Although properties such as DNA-sequences and morphology are used to help separate closely related lineages, this definition has fuzzy boundaries. However, the exact definition of the term "species" is still controversial, particularly in prokaryotes, and this is called the species problem. Biologists have proposed a range of more precise definitions, but the definition used is a pragmatic choice that depends on the particularities of the species of concern.

Common names and species

The commonly used names for plant and animal taxa sometimes correspond to species: for example, "lion", "walrus", and "Camphor tree" – each refers to a species. In other cases common names do not: for example, "deer" refers to a family of 34 species, including Eld's Deer, Red Deer and Elk (Wapiti). The last two species were once considered a single species, illustrating how species boundaries may change with increased scientific knowledge.

Because of the difficulties with both defining and tallying the total numbers of different species in the world, it is estimated that there are anywhere between 2 and 100 million different species.

Placement within genera

Ideally, a species is given a formal, scientific name, although in practice there are very many unnamed species (which have only been described, not named). When a species is named, it is placed within a genus. From a scientific point of view this can be regarded as a hypothesis that the species is more closely related to other species within its genus (if any) than to species of other genera. Species and genus are usually defined as part of a larger taxonomic hierarchy. The best-known taxonomic ranks are, in order: life, domain, kingdom, phylum, class, order, family, genus, and species. This assignment to a genus is not immutable; later a different (or the same) taxonomist may assign it to a different genus, in which case the name will also change.

In biological nomenclature, the name for a species is a two-part name (a binomial name), treated as Latin, although roots from any language can be used as well as names of locales or individuals. The generic name is listed first (with its leading letter capitalized), followed by a second term, the specific name (or specific epithet). For example, the species commonly known as the Longleaf Pine is *Pinus palustris*; gray wolves belong to the species *Canis lupus*, coyotes to *Canis latrans*, golden jackals to *Canis aureus*, etc., and all of those belong to the genus *Canis* (which also contains many other species). The name of the species is the whole binomial, not just the second term (which may be called the specific name for animals).

This binomial naming convention, later formalized in the biological codes of nomenclature, was first used by Leonhart Fuchs and introduced as the standard by Carolus Linnaeus in his 1753, *Species Plantarum* (followed by his, 1758 *Systema Naturae*, 10th edition). At that time, the chief biological theory was that species represented independent acts of creation by God and were therefore considered objectively real and immutable, so the hypothesis of common descent did not apply.

Abbreviated names

Books and articles sometimes intentionally do not identify species fully and use the abbreviation "**sp.**" in the singular or "**spp.**" in the plural in place of the specific epithet: for example, ***Canis*** **sp.** This commonly occurs in the following types of situations:

- The authors are confident that some individuals belong to a particular genus but are not sure to which exact species they belong. This is particularly common in paleontology.

- The authors use "spp." as a short way of saying that something applies to many species within a genus, but do not wish to say that it applies to all species within that genus. If scientists mean that something applies to all species within a genus, they use the genus name without the specific epithet.

In books and articles, genus and species names are usually printed in italics. If using "sp." and "spp.", these should not be italicized.

Difficulty of defining "species" and identifying particular species

The Greenish Warbler demonstrates the concept of a ring species.

It is surprisingly difficult to define the word "species" in a way that applies to all naturally occurring organisms, and the debate among biologists about how to define "species" and how to identify actual species is called the species problem. Over two dozen distinct definitions of "species" are in use amongst biologists.

Most textbooks follow Ernst Mayr's definition of a species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups".

Various parts of this definition serve to exclude some unusual or artificial matings:

- Those that occur only in captivity (when the animal's normal mating partners may not be available) or as a result of deliberate human action
- Animals that may be physically and physiologically capable of mating but, for various reasons, do not normally do so in the wild

The typical textbook definition above works well for most multi-celled organisms, but there are several types of situations in which it breaks down:

- By definition it applies only to organisms that reproduce sexually. So it does not work for asexually reproducing single-celled organisms and for the relatively few parthenogenetic multi-celled organisms. The term "phylotype" is often applied to such organisms.
- Biologists frequently do not know whether two morphologically similar groups of organisms are "potentially" capable of interbreeding.
- There is considerable variation in the degree to which hybridization may succeed under natural conditions, or even in the degree to which some organisms use sexual reproduction between individuals to breed.
- In ring species, members of adjacent populations interbreed successfully but members of some non-adjacent populations do not.
- In a few cases it may be physically impossible for animals that are members of the same species to mate. However, these are cases in which human intervention has caused gross morphological changes, and are therefore excluded by the biological species concept.

Horizontal gene transfer makes it even more difficult to define the word "species". There is strong evidence of horizontal gene transfer between very dissimilar groups of prokaryotes, and at least occasionally between dissimilar groups of eukaryotes; and Williamson argues that there is evidence for it in some crustaceans and echinoderms. All definitions of the word "species" assume that an organism gets all its genes from one or two parents that are very like that organism, but horizontal gene transfer makes that assumption false.

Definitions of species

The question of how best to define "species" is one that has occupied biologists for centuries, and the debate itself has become known as the species problem. Darwin wrote in chapter II of *On the Origin of Species*:

No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. Generally the term includes the unknown element of a distinct act of creation.

But later, in *The Descent of Man*, when addressing "The question whether mankind consists of one or several species", Darwin revised his opinion to say:

it is a hopeless endeavour to decide this point on sound grounds, until some definition of the term "species" is generally accepted; and the definition must not include an element that cannot possibly be ascertained, such as an act of creation.

The modern theory of evolution depends on a fundamental redefinition of "species". Prior to Darwin, naturalists viewed species as ideal or general types, which could be exemplified by an ideal specimen bearing all the traits general to the species. Darwin's theories shifted attention from uniformity to variation and from the general to the particular. According to intellectual historian Louis Menand,

Once our attention is redirected to the individual, we need another way of making generalizations. We are no longer interested in the conformity of an individual to an ideal type; we are now interested in the relation of an individual to the other individuals with which it interacts. To generalize about groups of interacting individuals, we need to drop the language of types and essences, which is prescriptive (telling us what finches should be), and adopt the language of statistics and probability, which is predictive (telling us what the average finch, under specified conditions, is likely to do). Relations will be more important than categories; functions, which are variable, will be more important than purposes; transitions will be more important than boundaries; sequences will be more important than hierarchies.

This shift results in a new approach to "species"; Darwin

concluded that species are what they appear to be: ideas, which are provisionally useful for naming groups of interacting individuals. "I look at the term species", he wrote, "as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other ... It does not essentially differ from the word variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for convenience sake."

Practically, biologists define species as *populations of organisms that have a high level of genetic similarity*. This may reflect an adaptation to the same niche, and the transfer of genetic material from one individual to others, through a variety of possible means. The exact level of similarity used in such a definition is arbitrary, but this is the most common definition used for organisms that reproduce asexually (asexual reproduction), such as some plants and microorganisms.

This lack of any clear species concept in microbiology has led to some authors arguing that the term "species" is not useful when studying bacterial evolution. Instead they see genes as moving freely between even distantly related bacteria, with the entire bacterial domain being a single gene pool. Nevertheless, a kind of rule of thumb has been established, saying that species of *Bacteria* or *Archaea* with 16S rRNA gene sequences more similar than 97% to each other need to be checked by DNA-DNA Hybridization if they belong to the same species or not. This concept has been updated recently, saying that the border of 97% was too low and can be raised to 98.7%.

In the study of sexually reproducing organisms, where genetic material is shared through the process of reproduction, the ability of two organisms to interbreed and produce fertile offspring of both sexes is generally accepted as a simple indicator that the organisms share enough genes to be considered members of the same species. Thus a "species" is a group of interbreeding organisms.

This definition can be extended to say that a species is a group of organisms that could potentially interbreed – fish could still be classed as the same species even if they live in different lakes, as long as they could still interbreed were they ever to come into contact with each other. On the other hand, there are many examples of series of three or more distinct populations, where individuals of the population in the middle can interbreed with the populations to either side, but individuals of the populations on either side cannot interbreed. Thus, one could argue that these populations constitute a single species, or two distinct species. This is not a paradox; it is evidence that species are defined by gene frequencies, and thus have fuzzy boundaries.

Consequently, any single, universal definition of "species" is necessarily arbitrary. Instead, biologists have proposed a range of definitions; which definition a biologists uses is a pragmatic choice, depending on the particularities of that biologist's research.

Typological species

A group of organisms in which individuals are members of the species if they sufficiently conform to certain fixed properties or "rights of passage". The clusters of variations or phenotypes within specimens (i.e. longer or shorter tails) would differentiate the species. This method was used as a "classical" method of determining species, such as with Linnaeus early in evolutionary theory. However, we now know that different phenotypes do not always constitute different species (e.g.: a 4-winged Drosophila born to a 2-winged mother is not a different species). Species named in this manner are called *morphospecies*

Morphological species

A population or group of populations that differs morphologically from other populations. For example, we can distinguish between a chicken and a duck because they have different shaped bills and the duck has webbed feet. Species have been defined in this way since well before the beginning of recorded history. This species concept is highly criticized because more recent genetic data reveal that genetically distinct populations may look very similar and, contrarily, large morphological differences sometimes exist between very closely related populations. Nonetheless, most species known have been described solely from morphology.

Biological / Isolation species

A set of actually or potentially interbreeding populations. This is generally a useful formulation for scientists working with living examples of the higher taxa like mammals, fish, and birds, but more problematic for organisms that do not reproduce sexually. The results of breeding experiments done in artificial conditions may or may not reflect what would happen if the same organisms encountered each other in the wild, making it difficult to gauge whether or not the results of such experiments are meaningful in reference to natural populations.

Biological / reproductive species

Two organisms that are able to reproduce naturally to produce fertile offspring of both sexes. Organisms that can reproduce but almost always make infertile hybrids of at least one sex, such as a mule, hinny or F1 male cattalo are not considered to be the same species.

Recognition species

Based on shared reproductive systems, including mating behavior. The Recognition concept of species has been introduced by Hugh E. H. Paterson.

Mate-recognition species

A group of organisms that are known to recognize one another as potential mates. Like the isolation species concept above, it applies only to organisms that reproduce sexually. Unlike the isolation species concept, it focuses specifically on pre-mating reproductive isolation.

Evolutionary / Darwinian species

A group of organisms that shares an ancestor; a lineage that maintains its integrity with respect to other lineages through both time and space. At some point in the progress of such a group, some members may diverge from the main population and evolve into a subspecies, a process that eventually will lead to the formation of a new full species if isolation (geographical or ecological) is maintained.

Phylogenetic (Cladistic)

A group of organisms that shares an ancestor; a lineage that maintains its integrity with respect to other lineages through both time and space. At some point in the progress of such a group, members may diverge from one another: when such a divergence becomes sufficiently clear, the two populations are regarded as separate species. This differs from evolutionary species in that the parent species goes extinct taxonomically when a new species evolve, the mother and daughter populations now forming two new species. Subspecies as such are not recognized under this approach; either a population is a phylogenetic species or it is not taxonomically distinguishable.

Ecological species

A set of organisms adapted to a particular set of resources, called a niche, in the environment. According to this concept, populations form the discrete phonetic clusters that we recognize as species because the ecological and evolutionary processes controlling how resources are divided up tend to produce those clusters.

Genetic species

Based on similarity of DNA of individuals or populations. Techniques to compare similarity of DNA include DNA-DNA hybridization, and genetic fingerprinting (or DNA barcoding).

Phenetic species

Based on phenotypes.

Microspecies

Species that reproduce without meiosis or fertilization so that each generation is genetically identical to the previous generation.

Cohesion species

Most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms. This is an expansion of the mate-recognition species concept to allow for post-mating isolation mechanisms; no matter whether populations can hybridize successfully, they are still distinct cohesion species if the amount of hybridization is insufficient to completely mix their respective gene pools.

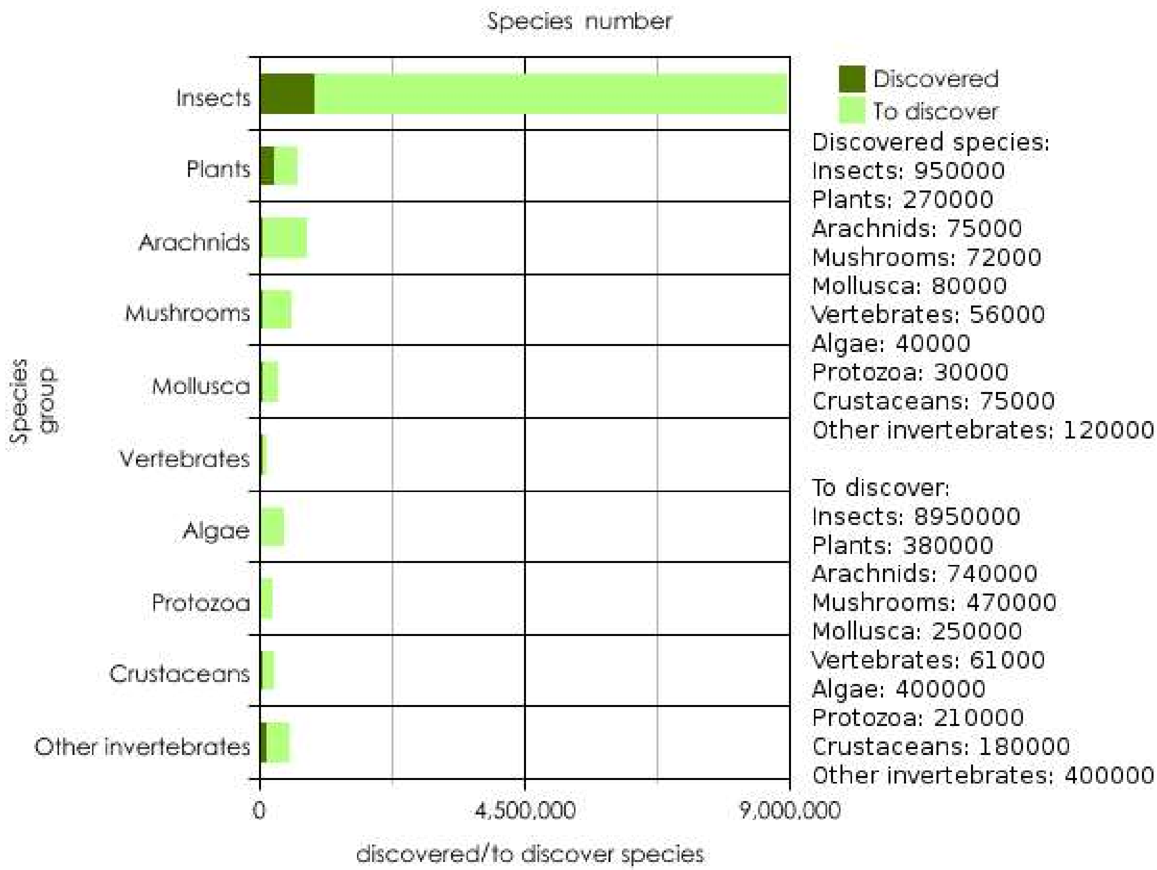
Evolutionarily Significant Unit (ESU)

An evolutionarily significant unit is a population of organisms that is considered distinct for purposes of conservation. Often referred to as a species or a *wildlife species*, an ESU also has several possible definitions, which coincide with definitions of species.

In practice, these definitions often coincide, and the differences between them are more a matter of emphasis than of outright contradiction. Nevertheless, no species concept yet proposed is entirely objective, or can be applied in all cases without resorting to judgment. Given the complexity of life, some have argued that such an objective definition is in all likelihood impossible, and biologists should settle for the most practical definition.

For most vertebrates, this is the biological species concept (BSC), and to a lesser extent (or for different purposes) the phylogenetic species concept (PSC). Many BSC subspecies are considered species under the PSC; the difference between the BSC and the PSC can be summed up insofar as that the BSC defines a species as a consequence of manifest evolutionary *history*, while the PSC defines a species as a consequence of manifest evolutionary *potential*. Thus, a PSC species is "made" as soon as an evolutionary lineage has started to separate, while a BSC species starts to exist only when the lineage separation is complete. Accordingly, there can be considerable conflict between alternative classifications based upon the PSC versus BSC, as they differ completely in their treatment of taxa that would be considered subspecies under the latter model (e.g., the numerous subspecies of honey bees).

Numbers of species



Undiscovered and discovered species

Bearing in mind the aforementioned problems with categorising species, the following numbers are only a soft guide. In 2007, they broke down as follows:

Total number of species (estimated): 7–100 millions (identified and unidentified), including:

- 5–10 million bacteria;
- 74,000–120,000 fungi;

Of the *identified* eukaryote species we have:

- 1.6 million, including:
    - 297,326 plants, including:
        - 15,000 mosses,
        - 13,025 Ferns and horsetails,
        - 980 gymnosperms,
        - 258,650 angiosperms,

            - 199,350 dicotyledons,
            - 59,300 monocotyledons,
        - 9,671 Red and green algae,
    - 28,849 fungi & other non-animals, including:
        - 10,000 lichens,
        - 16,000 mushrooms,
        - 2,849 brown algae,
    - 1,250,000 animals, including:
        - 1,203,375 invertebrates:
            - 950,000 insects,
            - 81,000 mollusks,
            - 40,000 crustaceans,
            - 2,175 corals,
            - 130,200 others;
        - 59,811 vertebrates:
            - 29,300 fish,
            - 6,199 amphibians,
            - 8,240 reptiles,
            - 9,956 birds,
            - 5,416 mammals

At present, organisations such as the Global Taxonomy Initiative, the European Distributed Institute of Taxonomy and the Census of Marine Life (the latter only for marine organisms) are trying to improve taxonomy and implement previously undiscovered species to the taxonomy system. Because we know but a portion of the organisms in the biosphere, we do not have a complete understanding of the workings of our environment. To make matters worse, despite the discovery of new species, according to professor James Mallet, we are wiping out these species at an unprecedented rate. This means that even before a new species has had the chance of being studied and classified, it may already be extinct.

Importance in biological classification

The idea of *species* has a long history. It is one of the most important levels of classification, for several reasons:

- It often corresponds to what lay people treat as the different basic kinds of organism – dogs are one species, cats another.
- It is the standard binomial nomenclature (or trinomial nomenclature) by which scientists typically refer to organisms.
- It is the highest taxonomic level that cannot be made more or less inclusionary.

After years of use, the concept remains central to biology and a host of related fields, and yet also remains at times ill-defined.

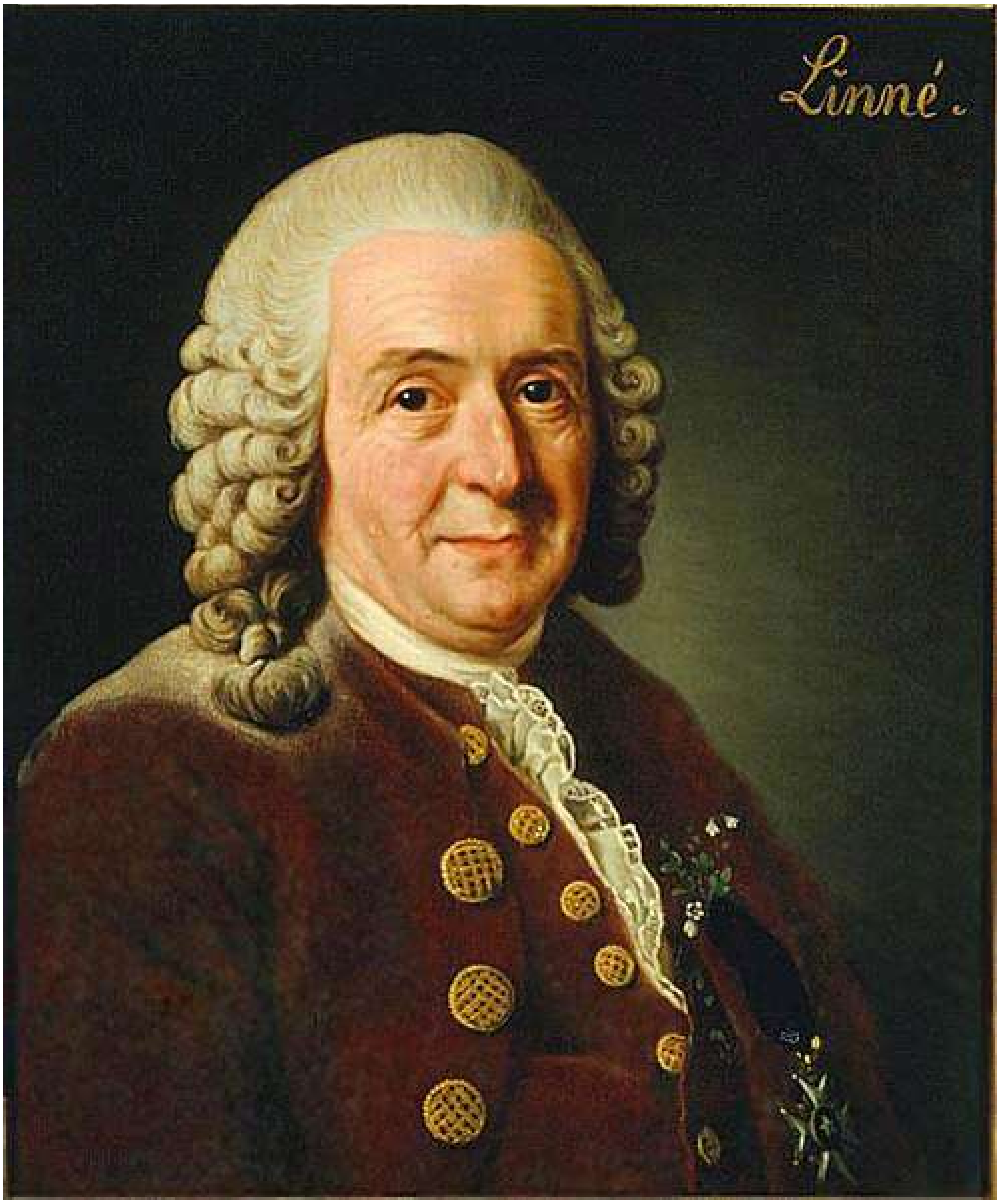
Implications of assignment of species status

The naming of a particular species may be regarded as a *hypothesis* about the evolutionary relationships and distinguishability of that group of organisms. As further information comes to hand, the hypothesis may be confirmed or refuted. Sometimes, especially in the past when communication was more difficult, taxonomists working in isolation have given two distinct names to individual organisms later identified as the same species. When two named species are discovered to be of the same species, the older species name is usually retained, and the newer species name dropped, a process called *synonymization*, or colloquially, as **lumping**. Dividing a taxon into multiple, often new, taxons is called **splitting**. Taxonomists are often referred to as "lumpers" or "splitters" by their colleagues, depending on their personal approach to recognizing differences or commonalities between organisms.

Traditionally, researchers relied on observations of anatomical differences, and on observations of whether different populations were able to interbreed successfully, to distinguish species; both anatomy and breeding behavior are still important to assigning species status. As a result of the revolutionary (and still ongoing) advance in microbiological research techniques, including DNA analysis, in the last few decades, a great deal of additional knowledge about the differences and similarities between species has become available. Many populations formerly regarded as separate species are now considered a single taxon, and many formerly grouped populations have been split. Any taxonomic level (species, genus, family, etc.) can be synonymized or split, and at higher taxonomic levels, these revisions have been still more profound.

From a taxonomical point of view, groups within a species can be defined as being of a taxon hierarchically lower than a species. In zoology only the subspecies is used, while in botany the variety, subvariety, and form are used as well. In conservation biology, the concept of evolutionary significant units (ESU) is used, which may be define either species or smaller distinct population segments. Identifying and naming species is the providence of alpha taxonomy.

Historical development of the species concept



Linnaeus believed in the fixity of species.

In the earliest works of science, a species was simply an individual organism that represented a group of similar or nearly identical organisms. No other relationships beyond that group were implied. Aristotle used the words *genus* and *species* to mean generic and specific categories. Aristotle and other pre-Darwinian scientists took the species to be distinct and unchanging, with an "essence", like the chemical elements. When early observers began to develop systems of organization for living things, they began to place formerly isolated species into a context. Many of these early delineation schemes would now be considered whimsical and these included consanguinity based on color (all plants with yellow flowers) or behavior (snakes, scorpions and certain biting ants).

In the 18th century Swedish scientist Carolus Linnaeus classified organisms according to differences in the form of reproductive apparatus. Although his system of classification sorts organisms according to degrees of similarity, it made no claims about the relationship between similar species. At that time, it was still widely believed that there was no organic connection between species, no matter how similar they appeared. This approach also suggested a type of idealism: the notion that each species existed as an "ideal form". Although there are always differences (although sometimes minute) between individual organisms, Linnaeus considered such variation problematic. He strove to identify individual organisms that were exemplary of the species, and considered other non-exemplary organisms to be deviant and imperfect.

By the 19th century most naturalists understood that species could change form over time, and that the history of the planet provided enough time for major changes. Jean-Baptiste Lamarck, in his 1809 *Zoological Philosophy*, offered one of the first logical arguments against creationism. The new emphasis was on determining *how* a species could change over time. Lamarck suggested that an organism could pass on an acquired trait to its offspring, i.e., the giraffe's long neck was attributed to generations of giraffes stretching to reach the leaves of higher treetops (this well-known and simplistic example, however, does not do justice to the breadth and subtlety of Lamarck's ideas). With the acceptance of the natural selection idea of Charles Darwin in the 1860s, however, Lamarck's view of goal-oriented evolution, also known as a teleological process, was eclipsed. Recent interest in inheritance of acquired characteristics centers around epigenetic processes, e.g. methylation, that do not affect DNA sequences, but instead alter expression in an inheritable manner. Thus, neo-lamarckism, as it is sometimes termed, is not a challenge to the theory of evolution by natural selection.

Charles Darwin and Alfred Wallace provided what scientists now consider as the most powerful and compelling theory of evolution. Darwin argued that it was populations that evolved, not individuals. His argument relied on a radical shift in perspective from that of Linnaeus: rather than defining species in ideal terms (and searching for an ideal representative and rejecting deviations), Darwin considered variation among individuals to be natural. He further argued that variation, far from being problematic, actually provides the *explanation* for the existence of distinct species.

Darwin's work drew on Thomas Malthus' insight that the rate of growth of a biological population will always outpace the rate of growth of the resources in the environment, such as the food supply. As a result, Darwin argued, not all the members of a population will be able to survive and reproduce. Those that did will, on average, be the ones possessing variations—however slight—that make them slightly better adapted to the environment. If these variable traits are heritable, then the offspring of the survivors will also possess them. Thus, over many generations, adaptive variations will accumulate in the population, while counter-adaptive traits will tend to be eliminated.

It should be emphasized that whether a variation is adaptive or non-adaptive depends on the environment: different environments favor different traits. Since the environment effectively selects which organisms live to reproduce, it is the environment (the "fight for existence") that selects the traits to be passed on. This is the theory of evolution by natural selection. In this model, the length of a giraffe's neck would be explained by positing that proto-giraffes with longer necks would have had a significant reproductive advantage to those with shorter necks. Over many generations, the entire population would be a species of long-necked animals.

In 1859, when Darwin published his theory of natural selection, the mechanism behind the inheritance of individual traits was unknown. Although Darwin made some speculations on how traits are inherited (pangenesis), his theory relies only on the fact that inheritable traits *exist*, and are variable (which makes his accomplishment even more remarkable.) Although Gregor Mendel's paper on genetics was published in 1866, its significance was not recognized. It was not until 1900 that his work was rediscovered by Hugo de Vries, Carl Correns and Erich von Tschermak, who realised that the "inheritable traits" in Darwin's theory are genes.

The theory of the evolution of species through natural selection has two important implications for discussions of species—consequences that fundamentally challenge the assumptions behind Linnaeus' taxonomy. First, it suggests that species are not just similar, they may actually be related. Some students of Darwin argue that *all* species are descended from a common ancestor. Second, it supposes that "species" are not homogeneous, fixed, permanent things; members of a species are all different, and over time species change. This suggests that species do not have any clear boundaries but are rather momentary statistical effects of constantly changing gene-frequencies. One may still use Linnaeus' taxonomy to identify individual plants and animals, but one can no longer think of species as independent and immutable.

The rise of a new species from a parental line is called speciation. There is no clear line demarcating the ancestral species from the descendant species.

Although the current scientific understanding of species suggests that there is no rigorous and comprehensive way to distinguish between different species in *all* cases, biologists continue to seek concrete ways to operationalize the idea. One of the most popular biological definitions of species is in terms of reproductive isolation; if two creatures cannot reproduce to produce fertile offspring of both sexes, then they are in different species. This definition captures a number of intuitive species boundaries, but it remains imperfect. It has nothing to say about species that reproduce asexually, for example, and it is very difficult to apply to extinct species. Moreover, boundaries between species are often fuzzy: there are examples where members of one population can produce fertile offspring of both sexes with a second population, and members of the second population can produce fertile offspring of both sexes with members of a third population, but members of the first and third population cannot produce fertile offspring, or can only produce fertile offspring of the homozygous sex. Consequently, some people reject this definition of a species.

Richard Dawkins defines two organisms as conspecific if and only if they have the same number of chromosomes and, for each chromosome, both organisms have the same number of nucleotides (*The Blind Watchmaker*, p. 118). However, most if not all taxonomists would strongly disagree. For example, in many amphibians, most notably in New Zealand's *Leiopelma* frogs, the genome consists of "core" chromosomes that are mostly invariable and accessory chromosomes, of which exist a number of possible combinations. Even though the chromosome numbers are highly variable between populations, these can interbreed successfully and form a single evolutionary unit. In plants, polyploidy is extremely commonplace with few restrictions on interbreeding; as individuals with an odd number of chromosome sets are usually sterile, depending on the actual number of chromosome sets present, this results in the odd situation where some individuals of the same evolutionary unit can interbreed with certain others and some cannot, with all populations being eventually linked as to form a common gene pool.

The classification of species has been profoundly affected by technological advances that have allowed researchers to determine relatedness based on molecular markers, starting with the comparatively crude blood plasma precipitation assays in the mid-20th century to Charles Sibley's ground-breaking DNA-DNA hybridization studies in the 1970s leading to DNA sequencing techniques. The results of these techniques caused revolutionary changes in the higher taxonomic categories (such as phyla and classes), resulting in the reordering of many branches of the phylogenetic tree. For taxonomic categories below genera, the results have been mixed so far; the pace of evolutionary change on the molecular level is rather slow, yielding clear differences only after considerable periods of reproductive separation. DNA-DNA hybridization results have led to misleading conclusions, the Pomarine Skua – Great Skua phenomenon being a famous example. Turtles have been determined to evolve with just one-eighth of the speed of other reptiles on the molecular level, and the rate of molecular evolution in albatrosses is half of what is found in the rather closely related storm-petrels. The hybridization technique is now obsolete and is replaced by more reliable computational approaches for sequence comparison. Molecular taxonomy is not directly based on the evolutionary processes, but rather on the overall change brought upon by these processes. The processes that lead to the generation and maintenance of variation such as mutation, crossover and selection are not uniform. DNA is only extremely rarely a direct target of natural selection rather than changes in the DNA sequence enduring over generations being a result of the latter; for example, silent transition-transversion combinations would alter the melting point of the DNA sequence, but not the sequence of the encoded proteins and thus are a possible example where, for example in microorganisms, a mutation confers a change in fitness all by itself.

Species as taxa

The scientific name of a species (often of Latin or Greek origin) in the binominal nomenclature introduced by Carl Linnaeus in 1753 is composed of two parts, which are written in italic font and for which there are different expressions in botany and zoology. The first part of that name is spelled upper case and is in both disciplines known as the genus name (also called the *generic name*). The second part is always spelled lower case and in botany it is called the *specific epithet*.

- Example: in the European beech (*Fagus sylvatica*) the component *Fagus* refers to the genus, *sylvatica* is the specific epithet.

In zoology, the second part is called the *specific name*.

- Example: in the lion (*Panthera leo*) the component *Panthera* refers to the genus, *leo* is the specific name.

The scientific name is completed when authors, years and parentheses are added.

In botany the name of the author is usually abbreviated, for example "L." stands for "Linnaeus".

- Example: shiitake *Lentinula edodes* (Berk.) Pegler
  M. J. Berkeley was the first to describe the species, D. Pegler has placed it into the currently used system.

In zoology, the addition of author and year are optional, *Panthera leo* is thus an entirely correct name. The International Code of Zoological Nomenclature prescribes how to add author(s) (if possible not abbreviated) and year (or author alone without year). If the species is cited in different genus than the one in which it was originally described, author(s) and year are given in parentheses. Between author and year often a comma is set (but not required).

- Example: lion *Panthera leo* (Linnaeus, 1758)
  Carl Nilsson Linnæus described the lion first and as *Felis leo*. The person who first placed the lion in the genus *Panthera* Oken, 1816 is not relevant in zoology. Instead of Linnæus, usually Linnaeus is spelled.

Chapter- 7

Species Problem

> ... I was much struck how entirely vague and arbitrary is the distinction between species and varieties
>
> — Charles Darwin, *On the Origin of Species* (p. 48)

The **species problem** is a mixture of difficult, related questions that often come up when biologists identify species and when they define the word "species".

One common but sometimes difficult question is how best to decide just which particular species an organism belongs to. Another challenge is deciding when to recognize a new species. This is a question for the biologist who discovers organisms that appear to be different from those that belong to already described species. A related question arises when new data indicate that one previously described species actually may include two or more separately evolving groups, each of which could possibly be recognized as a separate species.

Many of the debates on species touch on philosophical issues, such as nominalism and realism, as well as on issues of language and cognition.

This current meaning of the phrase "species problem" is quite different from what was meant by "species problem" during the 19th and early 20th centuries, as used by Darwin and others. For Darwin the species problem was the question of how new species arose.

Confusion on the meaning of "*Species*"

Species is one of several ranks in the hierarchical system of scientific classification. These are called *taxonomic ranks*, and the system of classification includes, in addition to *species* the ranks of genus and family and others all the way up to kingdom. Usually the rank of species is the *basal rank*, meaning that in the system of scientific classification *species* is the bottommost rank that includes no other ranks. However sometimes when one species, that is already named and described, is found to actually include two slightly different kinds of organisms, it is necessary to use the rank of *subspecies*.

Even though it is not disputed that *species* is a taxonomic rank, this does not prevent disagreements when particular species are discussed. Consider the case of the Baltimore oriole and Bullock's oriole, two similar species of birds that have sometimes in the past been considered to be one single species. Currently biologists agree that these are actually two separate species, but in the past this was not the case.

It is common in debates about species for participants to argue at cross purposes. For example, in a debate over the species status of Baltimore Oriole and Bullock's Oriole one person might think that the critical question is about the two kinds of orioles and how similar they are. A second person might think that the critical question concerns the actual taxonomic rank of species, and on what the correct criteria are for identifying a species. If one person is talking about the birds, and another person is talking about the rank of species, then there can be confusion.

Disagreements and confusion also happen over just what the best criteria are for identifying new species. In 1942 the famous biologist Ernst Mayr wrote that because biologists have different ways of identifying species, they actually have different species concepts. Mayr proceeded to list five different species concepts, and since then many more have been added. The question of which species concept is *best* has occupied many printed pages and many hours of discussion.

Some debates are philosophical in nature. One common disagreement is over whether a species is defined by the characteristics that biologists use to identify the species, or whether a species is an evolving entity in nature. Every named species has been formally described as a type of organism with particular defining characteristics. These defining traits are used to identify which species organisms belong to. But for many species, all of the individuals that fit the defining criteria also make up a single evolving unit. These two different ways of thinking about species, as a category and as an evolving population, are quite different from each other.

History

Before Darwin

The idea that one organism reproduces by giving birth to a similar organism, or producing seeds that grow to a similar organism, goes back to the earliest days of farming. While people tended to think of this as a relatively stable process, many thought that change was possible. The term *species* was just used as a term for a sort or kind of organism, until in 1686 John Ray introduced the biological concept that species were distinguished by always producing the same species, and this was fixed and permanent, though considerable variation was possible within a species. Carolus Linnaeus (1707–1778) formalized the taxonomic rank of species, and devised the two part naming system of binomial nomenclature that we use today. However this did not prevent disagreements on the best way to identify species.

The history of definitions of the term "species" reveal that the seeds of the modern species debate were alive and growing long before Darwin.

From Darwin to Mayr

Charles Darwin's famous book *On the Origin of Species* (1859) offered an explanation as to how species changed over time (evolution). Although Darwin did not provide details on how one species splits into two, he viewed speciation as a gradual process. If Darwin was correct, then when new *incipient species* are forming there must be a period of time when they are not yet distinct enough to be recognized as species. Darwin's theory suggested that there was often not going to be an objective fact of the matter, on whether there were one or two species.

Darwin's book triggered a crisis of uncertainty for some biologists over the objectivity of species, and some came to wonder whether individual species could be objectively real — i.e. have an existence that is independent of the human observer.

In the 1920s and 1930s, Mendel's theory of inheritance and Darwin's theory of evolution by natural selection were joined in what was called the modern evolutionary synthesis. This conjunction of theories also had a large impact on how biologists think about species. Edward Poulton anticipated many ideas on species that today are well accepted, and that were later more fully developed by Theodosius Dobzhansky and Ernst Mayr, two of the architects of the modern synthesis. Dobzhansky's 1937 book articulated the genetic processes that occur when incipient species are beginning to diverge. In particular Dobzhansky described the critical role, for the formation of new species, of the evolution of reproductive isolation.

Mayr and recent history

Ernst Mayr's 1942 book was a turning point for the species problem. In it he wrote about how different investigators approach species identification, and he characterized these different approaches as different species concepts. He also argued strongly for, what came to be called, a *Biological Species Concept* (BSC), which is that a species consists of populations of organisms that can reproduce with one another and that are reproductively isolated from other such populations.

Mayr was not the first to define "species" on the basis of reproductive compatibility. Many others before Mayr had suggested this idea, as Mayr makes clear in his book on the history of biology. For example Mayr discusses how Buffon proposed this kind of definition of "species" in 1753. The idea of shared reproduction within species is even contained in the Biblical story of Noah's ark, in which each species was preserved by saving a reproductive pair.

Theodosius Dobzhansky was a close contemporary of Mayr's and the author of a classic book, that came out a few years before Mayr's, that was about the evolutionary origins of reproductive barriers between species. Many biologists credit Dobzhansky and Mayr jointly for emphasizing the need to consider reproductive isolation when studying species and speciation.

Mayr was persuasive in many respects and from 1942 until his death in 2005 he and the biological species concept (BSC) played a central role in nearly all debates on the species problem. For many, the Biological Species Concept was a useful theoretical idea because it leads to a focus on the evolutionary origins of barriers to reproduction between species. But the BSC has been criticized for not being very useful for deciding when to identify new species. It is also true that there are many cases where members of different species will hybridize and produce fertile offspring when they are under confined conditions, such as in zoos. One fairly extreme example is that lions and tigers will hybridize in captivity, and at least some of the offspring have been reported to be fertile. Mayr's response to cases like these is that the reproductive barriers that are important for species are the ones that occur in the wild. But even so it is also the case that there are many cases of different species that are known to hybridize and produce fertile offspring in nature.

After Mayr's 1942 book many more species concepts were introduced. Some, such as the Phylogenetic Species Concept (PSC), were designed to be more useful than the BSC for actually deciding when a new species should be described. However not all of the new species concepts were about identifying species, and some concepts were mostly conceptual or philosophical.

About two dozen species concepts have been identified or proposed since Mayr's 1942 book, and many articles and several books have been written on the species problem. At some point it became common for articles to profess to "solve" or "dissolve" the species problem.

Some have argued that the species problem is too multidimensional to be "solved" by one definition of species or one species concept. Since the 1990s articles have appeared that make the case that species concepts, particularly those that specify how species should be identified, have not been very helpful in resolving the species problem.

Although Mayr promoted the Biological Species Concept for use in systematics, the concept has been criticized as not being useful for those who do research in systematics. Some systematists have criticized the BSC as not being operational. However for many others the BSC is the preferred description of species. For example many geneticists who work on the process of species formation prefer the BSC because it emphasizes the role of barriers to reproduction between species.

Philosophical aspects

Realism and nominalism

Realism and Nominalism are philosophical subjects that come up in debates over whether or not species literally exist. From one perspective, each species is a kind of organism and each species is based on a set of characteristics that are shared by all the organisms in the species. This usage of "species" refers to the taxonomic sense of the word, and under this kind of meaning a species is a category, or a type, or a *natural kind*. For example, the species that we call *giraffe* is a category of things that people have recognized have a lot in common with each other and to which we have given the name "giraffe". This is a category in the same sense that the words "mountain" and "snowflake" identify categories of things in nature.

This view of a species as a type, or natural kind, raises the question of whether such things are real. The question is not whether the organisms exist, but whether the *kinds* of organisms exist. There is a school of philosophical thought, called realism that says that natural kinds and other so called *universals* do exist. But what kind of existence would this be? It is one thing to say that a particular giraffe exists, but in what way does the giraffe category exist? This question is the opening for Nominalism which is a philosophical view that types and kinds, and universals in general, do not literally exist.

If the nominalist view is correct then kinds of things, that people have given names to, do not literally exist. It would follow then that because species are named types of organisms, that species do not literally exist. This can be a troubling idea, particularly to a biologist who studies species. If species are not real, then it would not be sensible to talk about "the origin of a species" or the "evolution of a species". As recently at least as the 1950s, some authors adopted this view and wrote of species as not being real.

A useful counterpoint to the nominalist view, in regard to species, was raised by Michael Ghiselin who argued that an individual species is not a type, but rather an actual individual, an actual entity. This idea comes from thinking of a species as an evolving dynamic population. As an entity a species exists quite regardless of whether or not people have observed it and whether or not it has been given a name based on traits shared by the organisms in the species.

Language and the role of human investigators

The nominalist critique of the view that kinds of things exist, raises for consideration the role that humans play in the species problem. For example, Haldane suggested that species are just mental abstractions.

Several authors have noted the similarity between "species", as a word of ambiguous meaning, and points made by Wittgenstein on family resemblance concepts and the indeterminacy of language.

Jody Hey described the species problem as a result of two conflicting motivations by biologists:

1. to categorize and identify organisms;
2. to understand the evolutionary processes that give rise to species.

Under the first view, species appear to us as typical natural kinds, but when biologists turn to understand species evolutionarily they are revealed as changeable and without sharp boundaries. Hey argued that it is unrealistic to expect that one definition of "species" is going to serve the need for categorization and still reflect the changeable realities of evolving species.

Pluralism and monism

Usually it is assumed that biologists approach the species problem with the idea that it would be useful to develop one common viewpoint of species - one single common conception of what species are and of how they should be identified. It is thought that if such a monistic description of species could be developed and agreed upon, then the species problem would be solved.

In contrast some authors have argued for pluralism, claiming that biologists cannot have just one shared concept of species, and that they should accept multiple, seemingly incompatible ideas about species.

David Hull argued that pluralist proposals were unlikely to actually solve the species problem.

Quotations on the species problem

"... I was much struck how entirely vague and arbitrary is the distinction between species and varieties" Darwin 1859 (p. 48)

"No term is more difficult to define than "species," and on no point are zoologists more divided than as to what should be understood by this word". Nicholson (1872) p. 20

"Of late, the futility of attempts to find a universally valid criterion for distinguishing species has come to be fairly generally, if reluctantly, recognized" Dobzhansky (1937) p. 310

"The concept of a species is a concession to our linguistic habits and neurological mechanisms" Haldane (1956)

"The species problem is the long-standing failure of biologists to agree on how we should identify species and how we should define the word 'species'." Hey (2001)

"First, the species problem is not primarily an empirical one, but it is rather fraught with philosophical questions that require - but cannot be settled by - empirical evidence." Pigliucci (2003)

"An important aspect of any species definition whether in neontology or palaeontology is that any statement that particular individuals (or fragmentary specimens) belong to a certain species is an hypothesis (not a fact)"

Chapter- 8

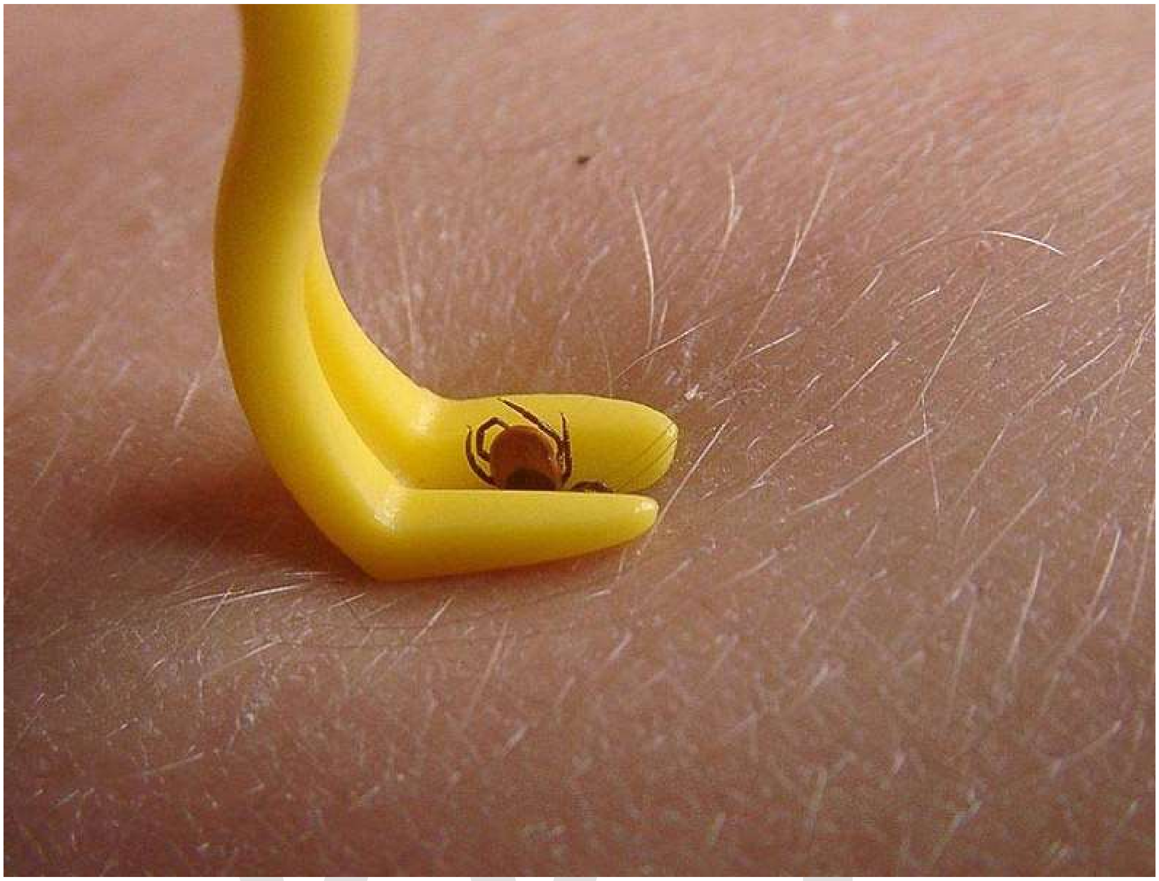
Acari

Acari **Fossil range: Early Devonian–Recent**

Peacock mite (*Tuckerella* sp.),

false-color SEM, magnified 260×

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Arachnida
Subclass:	**Acari** Leach, 1817



Acari (or **Acarina**) are a taxon of arachnids that contains mites and ticks. The diversity of the Acari is extraordinary and its fossil history goes back to at least the early Devonian period. As a result, acarologists (the people who study mites and ticks) have proposed a complex set of taxonomic ranks to classify mites. In most modern treatments, the Acari is considered a subclass of Arachnida and is composed of 2-3 superorders or orders: Acariformes (or Actinotrichida), Parasitiformes (or Anactinotrichida), and Opilioacariformes; the latter is often considered a subgroup within the Parasitiformes. The monophyly of the Acari is open to debate, and the relationships of the acarines to other arachnids is not at all clear. In older treatments, the subgroups of the Acarina were placed at order rank, but as their own subdivisions have become better-understood, it is more usual to treat them at superorder rank.

Most acarines are minute to small (e.g. 0.08–1.00 millimetre or 0.0031–0.039 inch), but the largest Acari (some ticks and red velvet mites) may reach lengths of 10–20 millimetres (0.39–0.79 in). It is estimated that over 50,000 species have been described (as of 1999) and that a million or more species are currently living. The study of mites and ticks is called **acarology** (from Greek ἀκάρι, *akari*, a type of mite; and -λογία, -*logia*), and the leading scientific journals for acarology include *Acarologia*, *Experimental and Applied Acarology* and the *International Journal of Acarology*.

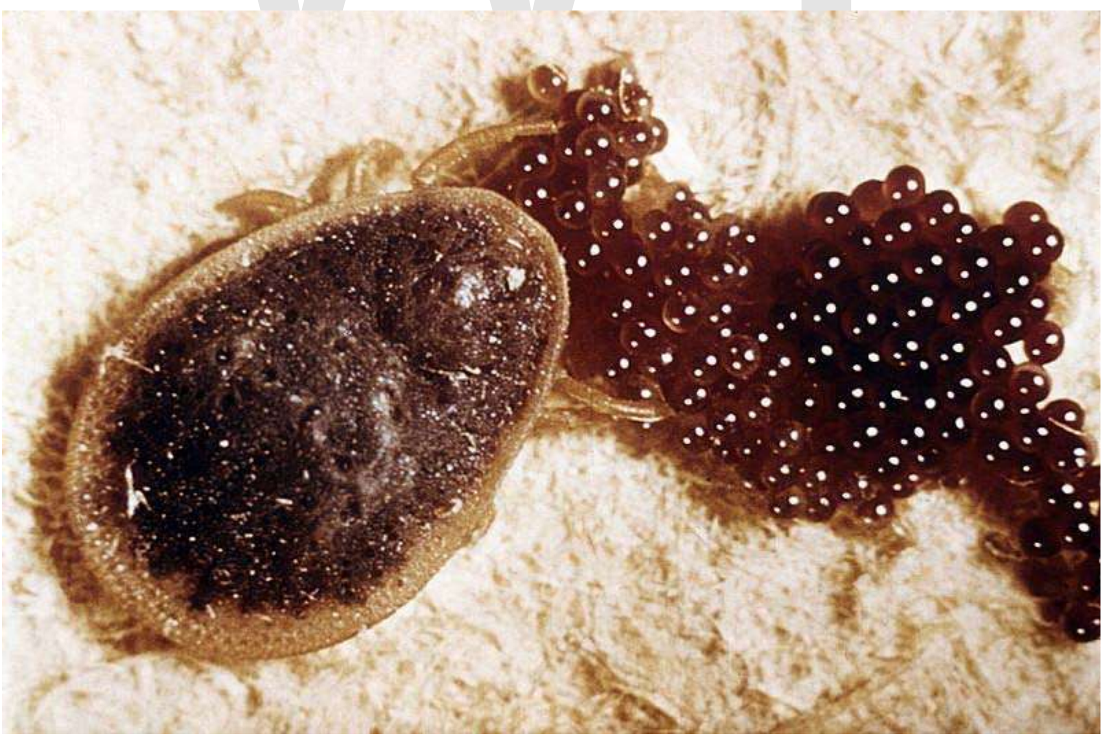
Morphology

Mites are arachnids and, as such, should have a segmented body with the segments organised into two tagmata: a prosoma (cephalothorax) and an opisthosoma (abdomen). However, only the faintest traces of primary segmentation remain in mites, the prosoma and opisthosoma are insensibly fused, and a region of flexible cuticle (the cirumcapitular furrow) separates the chelicerae and pedipalps from the rest of the body. This anterior body region is called the capitulum or gnathosoma and, according to some workers, is also found in Ricinulei. The remainder of the body is called the idiosoma and is unique to mites.

Most adult mites have four pairs of legs, like other arachnids, but some have fewer. For example, gall mites like *Phyllocoptes variabilis* (family Eriophyidae) have a worm-like body with only two pairs of legs; some parasitic mites have only one or three pairs of legs in the adult stage. Larval and prelarval stages have a maximum of three pairs of legs; adult mites with only three pairs of legs may be called 'larviform'.

The mouth parts of mites may be adapted for biting, stinging, sawing or sucking. They breath through tracheae, stigmata (small openings of the skin), intestines and the skin itself. Species hunting for other mites have very acute senses, but many mites are eyeless. The central eyes of arachnids are always missing, or they are fused into a single eye. Thus, any eye number from none to five may occur.

Ontogeny



A soft-bodied tick of the family Argasidae, beside eggs it has just laid

Acarine ontogeny typically consists of an egg, a prelarval stage (often absent), a larval stage (hexapod except in Eriophyoidea which have only two pairs of legs), and a series of nymphal stages. Any or all of these stages except the adult may be suppressed or occur only within the body of a previous stage. Larvae (and prelarvae) have a maximum of three pairs of legs (legs are often reduced to stubs or absent in prelarvae); legs IV are added at the first nymphal stage. Usually a maximum of three nymphal stages are present and they are referred to in sequence as protonymph, deutonymph, and tritonymph; however, some soft ticks have supernumerary nymphal stages. The females of some Tarsonemidae bear sexually mature young. If one or more nymphal stages are absent, then authors may disagree on which stages are present. Only the Oribatida pass through all developmental stages.

Diversity and lifestyles

Acarines are extremely diverse. They live in practically every habitat, and include aquatic (freshwater and sea water) and terrestrial species. They outnumber other arthropods in the soil organic matter and detritus. Many are parasitic, and they affect both vertebrates and invertebrates. Most parasitic forms are external parasites, while the free living forms are generally predatory and may even be used to control undesirable arthropods. Others are detritivores that help to break down forest litter and dead organic matter such as skin cells. Others still are plant feeders and may damage crops.

Economic importance

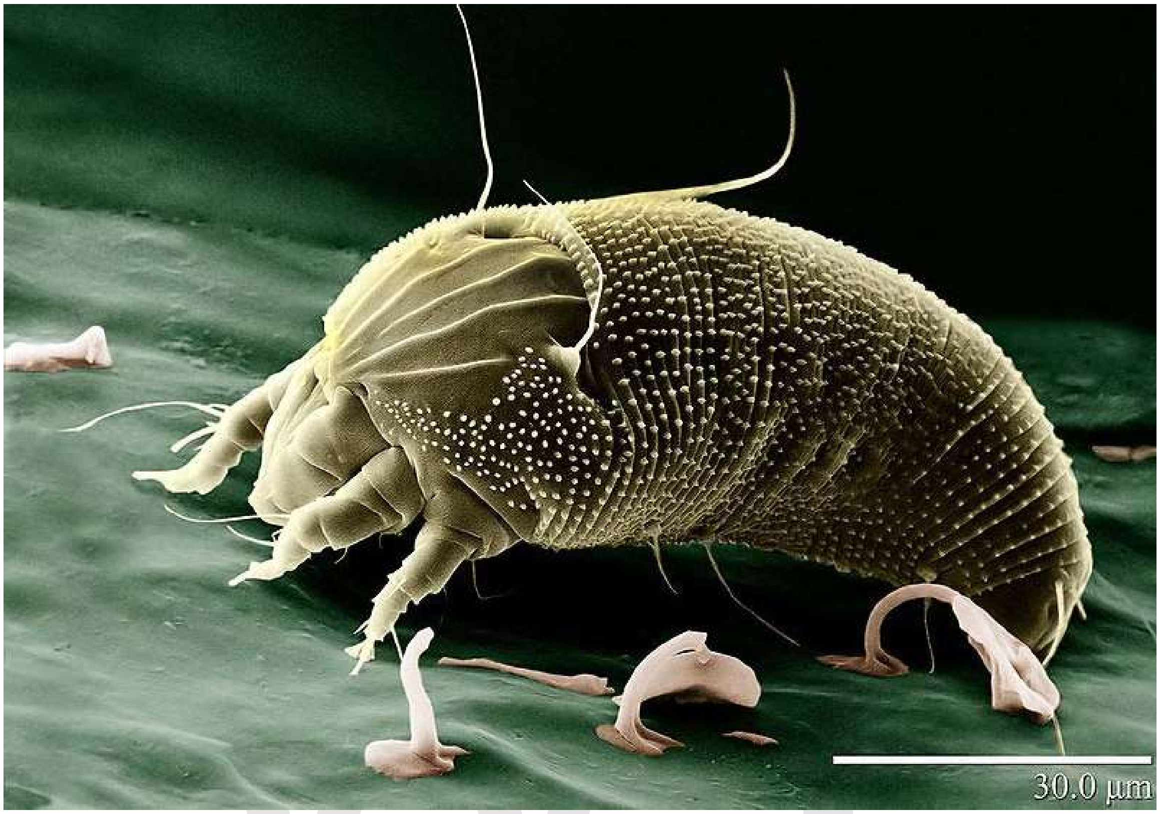
Damage to crops is perhaps the most costly economic effect of mites, especially by the spider mites and their relatives (Tetranychoidea), earth mites (Penthaleidae), thread-footed mites (Tarsonemidae) and the gall and rust mites (Eriophyidae).

Some parasitic forms affect humans and other mammals, causing damage by their feeding, and can even be vectors of diseases such as scrub typhus, rickettsialpox, Lyme disease, Q fever, Colorado tick fever, tularemia, tick-borne relapsing fever, babesiosis, ehrlichiosis and tick-borne meningoencephalitis. A well known effect of mites on humans is their role as an allergen and the stimulation of asthma in people affected by respiratory disease.

The use of predatory mites (e.g. Phytoseiidae) in pest control and herbivorous mites that infest weeds are also of importance. An unquantified, but major positive contribution of the Acari is their normal functioning in ecosystems, especially their roles in the decomposer subsystem.

Chemical agents used to control ticks and mites include dusting sulfur and ivermectin.

Taxonomy



Rust mite, *Aceria anthocoptes* (size: 50 micrometres)

Male tick (size: 2 mm)

The phylogeny of the Acari is still disputed and several taxonomic schemes have been proposed for their classification. The third edition of the standard textbook *A Manual of Acarology* uses a system of six orders, grouped into two superorders:

- Superorder **Parasitiformes** – ticks and a variety of mites.
    - Opilioacarida – mites that superficially resemble harvestmen (Opiliones, hence their name)
    - Holothyrida
    - Ixodida – hard and soft ticks
    - Mesostigmata – bird mites, phytoseiid mites, *Raubmilben*
        - Sejoidea

        - Trigynaspida
        - Monogynaspida
- Superorder **Acariformes** – the most diverse group of mites.
    - Trombidiformes – plant parasitic mites (spider mites, peacock mites, gall mites, red-legged earth mites, etc.), snout mites, chiggers, hair follicle mites, velvet mites, water mites, etc.
        - Sphaerolichida
        - Prostigmata
    - Sarcoptiformes
        - Endeostigmata – basal sarcoptiform lineages
        - Oribatida – oribatid mites, beetle mites, armored mites (also cryptostigmata)
        - Endeostigmata – stored product, fur, feather, dust, and human itch mites, etc.

Chapter- 9

Ornithology

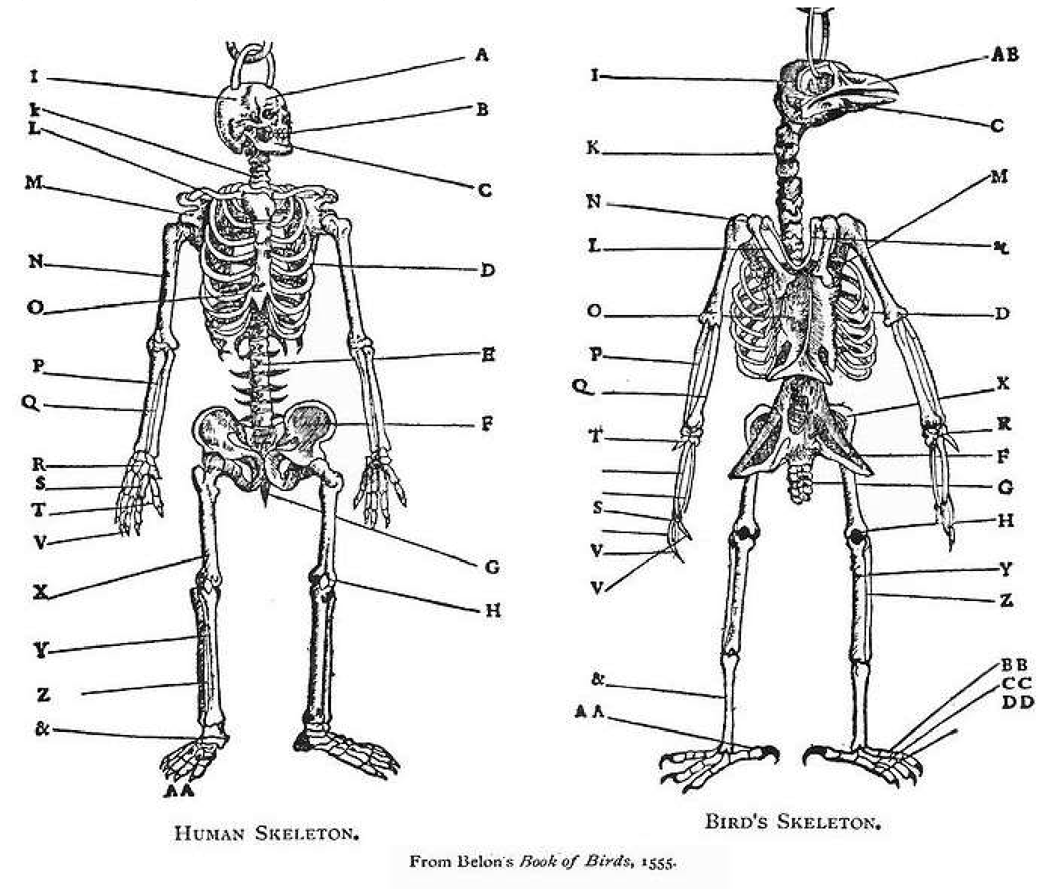
Ornithology (from Greek: ὄρνις, ὄρνιθος, *ornis*, *ornithos*, "bird"; and λόγος, *logos*, "knowledge") is a branch of zoology that concerns the study of birds. Several aspects of ornithology differ from related disciplines, due partly to the high visibility and the aesthetic appeal of birds. Most marked among these is the extent of studies undertaken by amateurs working within the parameters of strict scientific methodology.

The science of ornithology has a long history and studies on birds have helped develop several key concepts in evolution, behaviour and ecology such as the definition of species, the process of speciation, instinct, learning, ecological niches, guilds, island biogeography, phylogeography and conservation. While early ornithology was principally concerned with descriptions and distributions of species, ornithologists today seek answers to very specific questions, often using birds as models to test hypotheses or predictions based on theories. Most modern biological theories apply across taxonomic groups and the number of professional scientists who identify themselves as "ornithologists" has therefore declined. A wide range of tools and techniques are used in ornithology and innovations are constantly made.

History

The history of ornithology largely reflects the trends in the history of biology. Trends include the move from mere descriptions to the identification of patterns and then towards elucidating the processes that produce the patterns.

Early knowledge and study



Belon's comparison of birds and humans in his *Book of Birds*, 1555

Humans must have observed birds from the earliest times, and stone age drawings are among the oldest indications of an interest in birds. Birds were perhaps important as a food source, and bones of as many as 80 species have been found in excavations of early Stone Age settlements.

Cultures around the world have rich vocabularies related to birds. Traditional bird names are often based on detailed knowledge of the behaviour, with many names being onomatopoeic, many still in use. Traditional knowledge may also involve the use of birds in folk medicine and knowledge of these practices are passed on through oral traditions. Hunting of wild birds as well as their domestication would have required considerable knowledge of their habits. Poultry farming and falconry were practised from early times in many parts of the world. Artificial incubation of poultry was practised in China around 246 BC and around at least 400 BC in Egypt. The Egyptians also made use of birds in their hieroglyphic scripts, many of which, though stylized, are still identifiable to species.

Cover of Ulisse Aldrovandi's Ornithology, 1599

Early written records provide valuable information on the past distributions of species. For instance Xenophon records the abundance of the Ostrich in Assyria (Anabasis, i. 5); this subspecies from Asia minor is extinct and all extant Ostrich races are today restricted to Africa. Other old writings such as the *Vedas* (1500-800 BC) demonstrate the careful observation of avian life histories and includes the earliest reference to the habit of brood parasitism by the Asian Koel (*Eudynamys scolopacea*). Like writing, the early art of China, Japan, Persia and India also demonstrate knowledge, with examples of scientifically accurate bird illustrations.

Aristotle in 350 BC in his *Historia Animalium* noted the habit of bird migration, moulting, egg laying and life spans. He however introduced and propagated several myths, such as the idea that swallows hibernated in winter although he noted that cranes migrated from the steppes of Scythia to the marshes at the headwaters of the Nile. The idea of swallow hibernation became so well established that, even as late as in 1878, Elliott Coues could list as many as 182 contemporary publications dealing with the hibernation of swallows and little published evidence to contradict the theory. Similar misconceptions existed regarding the breeding of Barnacle geese. Their nests had not been seen and it was believed that they grew by transformations of goose barnacles, an idea that became prevalent from around the 11th century and noted by Bishop Giraldus Cambrensis (Gerald of Wales) in *Topographia Hiberniae* (1187).

The origins of falconry have been traced to Mesopotamia and the earliest record comes from the reign of Sargon II (722–705 BC). Falconry made its entry to Europe only after AD 400, brought in from the East after invasions by the Huns and Allans. Frederick II of Hohenstaufen (1194–1250) learnt about Arabian falconry during wars in the region and obtained an Arabic treatise on falconry by Moamyn. He had this work translated into Latin and also conducted experiments on birds in his menagerie. By sealing the eyes of vultures and placing food nearby, he concluded that they found food by sight, and not by smell. He also developed methods to keep and train falcons. The studies that he undertook over nearly 30 years, were published in 1240 as De Arte Venandi cum Avibus (The Art of Hunting with Birds), considered one of the earliest studies on bird behaviour.

Several early German and French scholars compiled old works and conducted new research on birds. These included Guillaume Rondelet who described his observations in the Mediterranean and Pierre Belon who described the fish and birds that he had seen in France and the Levant. Belon's Book of Birds (1555) is a folio volume with descriptions of some two hundred species. His comparison of the skeleton of humans and birds is considered as a landmark in comparative anatomy. Volcher Coiter (1534–1576), a Dutch anatomist made detailed studies of the internal structures of birds and produced a classification of birds, *De Diferentiis Avium* (around 1572), that was based on structure and habits. Konrad Gesner wrote the *Vogelbuch* and *Icones avium omnium* around 1557. Like Gesner, Ulisse Aldrovandi, an encyclopedic naturalist began a 14-volume natural history with three volumes on birds, entitled *ornithologiae hoc est de avibus historiae libri XII* which was published from 1599 to 1603. Aldrovandi showed great interest in plants and animals and his work included 3000 drawings of fruits, flowers, plants and animals, published in 363 volumes. His *Ornithology* alone covers 2000 pages and included such aspects as the chicken and poultry techniques.William Turner's *Historia Avium* ("History of Birds"), published at Cologne in 1544, was an early ornithological work from England. He noted the commonness of kite in English cities where they snatched food out of the hands of children. He included folk beliefs such as those of anglers. Anglers believed that the Osprey emptied their fishponds and would kill them, mixing the flesh of the Osprey into their fish bait. Turner's work reflected the violent times that he lived in and stands in contrast to later works such as Gilbert White's *The Natural History and Antiquities of Selborne* that were written in a tranquil era.

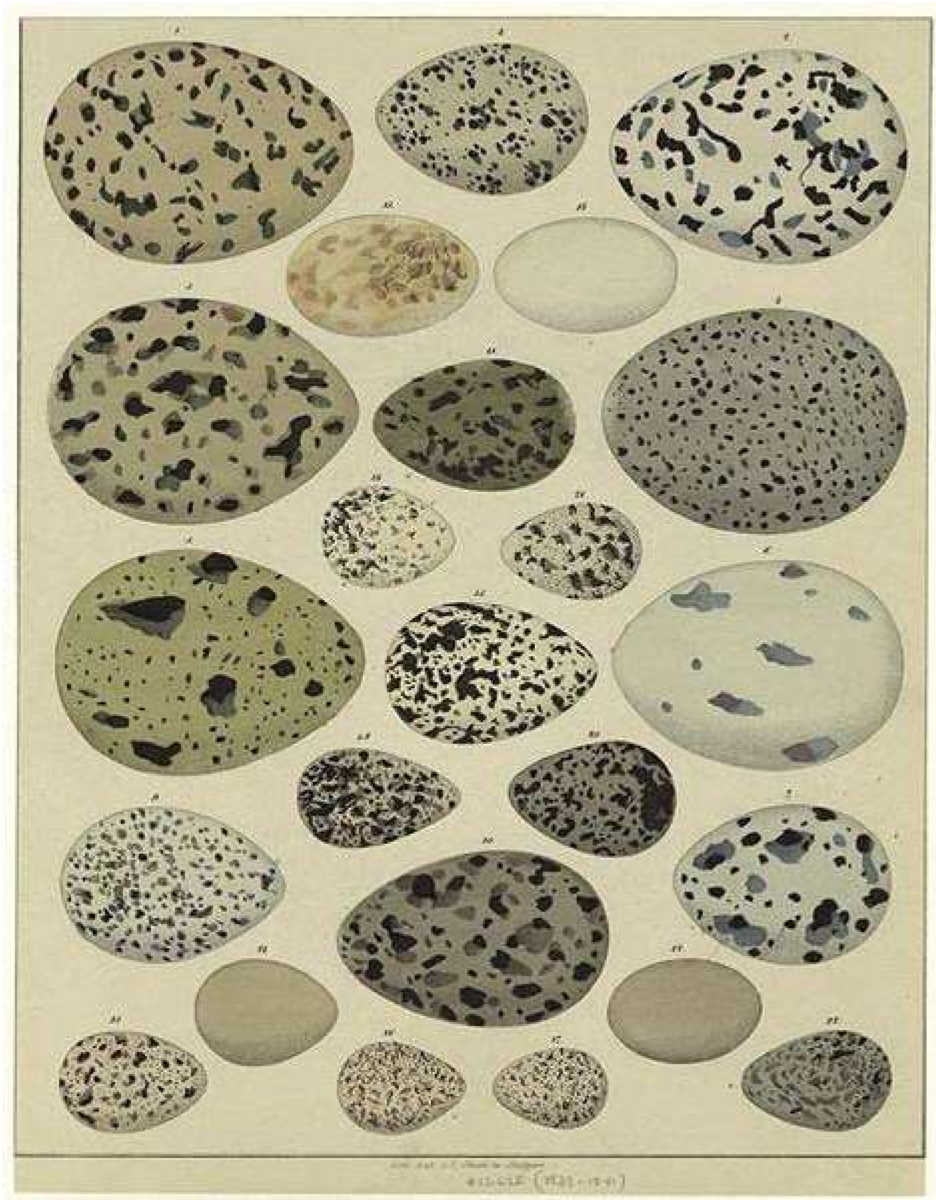
Antonio Valli da Todi who wrote on aviculture in 1601 knew the connections between territory and song

In the 17th century Francis Willughby (1635–1672) and John Ray (1627–1705) came up with the first major system of bird classification that was based on function and morphology rather than on form or behaviour. Willughby's *Ornithologiae libri tres* (1676) completed by John Ray is sometimes considered to mark the beginning of scientific ornithology. Ray also worked on *Ornithologia* which was published posthumously in 1713 as *Synopsis methodica avium et piscium*. The earliest list of British birds, *Pinax Rerum Naturalium Britannicarum* was written by Christopher Merrett in 1667, however it was not considered of value by many including John Ray.

An Experiment on a Bird in the Air Pump, 1768

Towards the late 18th century, Mathurin Jacques Brisson (1723–1806) and Comte de Buffon (1707–1788) began new works on birds. Brisson produced a six-volume work *Ornithologie* in 1760 and Buffon's included nine volumes (volumes 16-24) on birds *Histoire naturelle des oiseaux* (1770–1785) in his work on science *Histoire naturelle générale et particulière* (1749–1804). Coenraad Jacob Temminck (1778–1858) sponsored François Le Vaillant [1753-1824] to collect bird specimens in Africa and this resulted in Le Vaillant's six-volume *Histoire naturelle des oiseaux d'Afrique* (1796–1808). Louis Jean Pierre Vieillot (1748–1831) spent ten years studying North American birds and wrote the *Histoire naturelle des oiseaux de l'Amerique septentrionale* (1807-1808?). Vieillot pioneered in the use of life-histories and habits in classification.

Scientific studies



Early bird study focused on collectibles such as eggs and nests

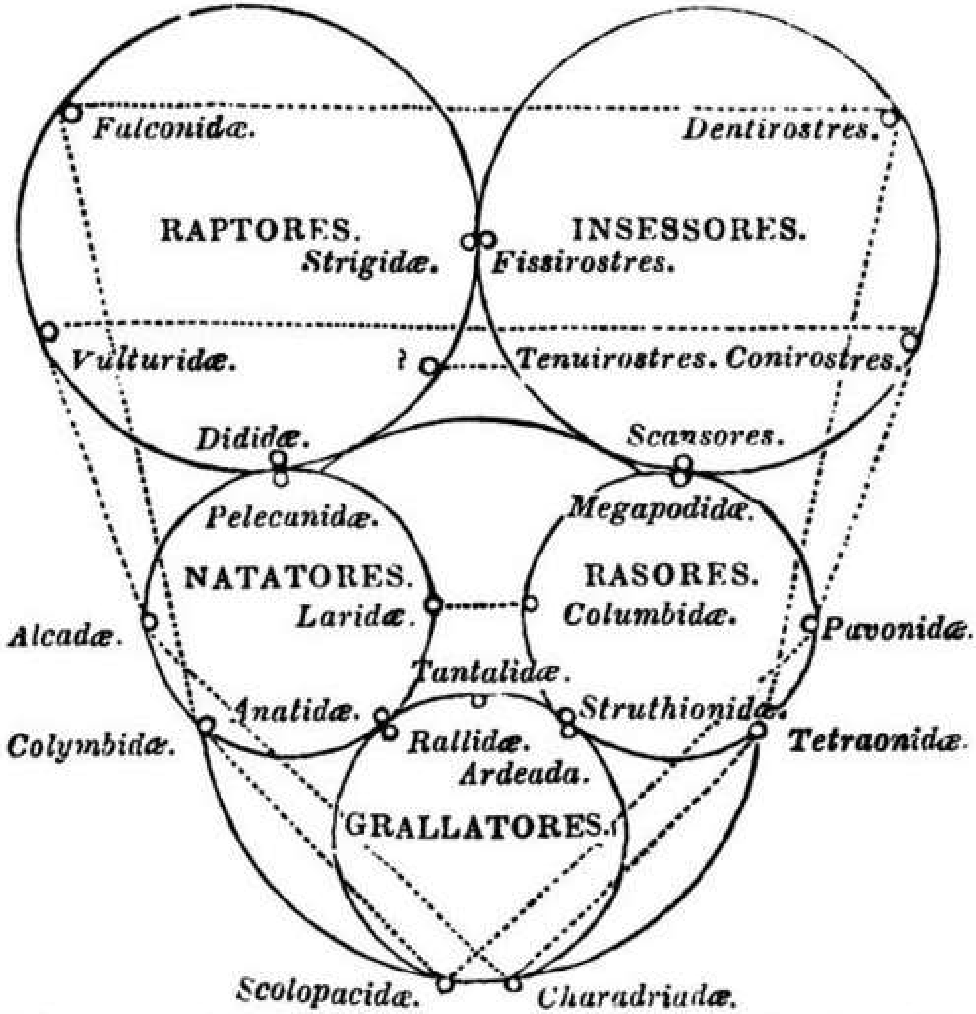
It was not until the Victorian era—with the emergence of the gun, the concept of natural history, and the collection of natural objects such as bird eggs and skins—that ornithology emerged as a specialized science. This specialization led to the formation in Britain of the British Ornithologists' Union in 1858. In 1859 the members founded its journal *The Ibis*. The sudden spurt in ornithology was also due in part to colonialization. A hundred years later, in 1959, R. E. Moreau noted that ornithology in this period was preoccupied with the geographical distributions of various species of birds.

No doubt the preoccupation with widely extended geographical ornithology, was fostered by the immensity of the areas over which British rule or influence stretched during the 19th century and for some time afterwards.
—Moreau

The bird collectors of the Victorian era observed the variations in bird forms and habits across geographic regions, noting local specialization and variation in widespread species. The collections of museums and private collectors grew with contributions from various parts of the world. The naming of species with binomials and the organization of birds into groups based on their similarities became the main work of museum specialists. The variations in widespread birds across geographical region caused the introduction of trinomial names.

The search for patterns in the variations of birds was attempted by many. Early ornithologists like William Swainson followed the Quinarian system and this was replaced by more complex "maps" of affinities in works by Hugh Edwin Strickland and Alfred Russell Wallace.

The Galapagos finches were especially influential in the development of Charles Darwin's theory of evolution. His contemporary Alfred Russel Wallace also noted these variations and the geographical separations between different forms leading to the study of biogeography. Wallace was influenced by the work of Philip Lutley Sclater on the distribution patterns of birds.



Affinities and analogies among the groups according to Swainson. The circles touch with groups on them having "affinities", but the lines connect groups that showed "analogies".

Quinarian system of bird classification by Swainson

For Darwin, the problem was how species arose from a common ancestor, but he did not attempt to find rules for delineation of species. The species problem was tackled by the ornithologist Ernst Mayr. Mayr was able to demonstrate that geographical isolation and the accumulation of genetic differences led to the splitting of species.

Early ornithologists were preoccupied with matters of species identification. Only systematics counted as true science and field studies were considered inferior through much of the 19th century. In 1901 Robert Ridgway wrote in the introduction to *The Birds of North and Middle America* that:

There are two essentially different kinds of ornithology: systematic or scientific, and popular. The former deals with the structure and classification of birds, their synonymies and technical descriptions. The latter treats of their habits, songs, nesting, and other facts pertaining to their life histories.

This early idea that the study of *living birds* was merely recreation held sway until ecological theories became the predominant focus of ornithological studies. The study of birds in their habitats was particularly advanced in Germany with bird ringing stations established as early as 1903. By the 1920s the *Journal für Ornithologie* included many papers on the behaviour, ecology, anatomy and physiology, many written by Erwin Stresemann. Stresemann changed the editorial policy of the journal, leading both to a unification of field and laboratory studies and a shift of research from museums to universities. Ornithology in the United States continued to be dominated by museum studies of morphological variations, species identities and geographic distributions, until it was influenced by Stresemann's student Ernst Mayr. In Britain, some of the earliest ornithological works that used the word ecology appeared in 1915. *The Ibis* however resisted the introduction of these new methods of study and it was not until 1943 that any paper on ecology appeared. The work of David Lack on population ecology was pioneering. Newer quantitative approaches were introduced for the study of ecology and behaviour and this was not readily accepted. For instance, Claud Ticehurst wrote:

Sometimes it seems that elaborate plans and statistics are made to prove what is commonplace knowledge to the mere collector, such as that hunting parties often travel more or less in circles.
—Ticehurst

David Lack's studies on population ecology sought to find the processes involved in the regulation of population based on the evolution of optimal clutch sizes. He concluded that population was regulated primarily by density-dependent controls, and also suggested that natural selection produces life-history traits that maximize the fitness of individuals. Others like Wynne-Edwards interpreted population regulation as a mechanism that aided the "species" rather than individuals. This led to widespread and sometimes bitter debate on what constituted the "unit of selection". Lack also pioneered the use of many new tools for ornithological research, including the idea of using radar to study bird migration.

Birds were also widely used in studies of the niche hypothesis and Georgii Gause's competitive exclusion principle. Work on resource partitioning and the structuring of bird communities through competition were made by Robert MacArthur. Patterns of biodiversity also became a topic of interest. Work on the relationship of the number of species to area and its application in the study of island biogeography was pioneered by E. O. Wilson and Robert MacArthur. These studies led to the development of the discipline of landscape ecology.

A mounted specimen of a Red-footed Falcon.

John Hurrell Crook studied the behaviour of weaverbirds and demonstrated the links between ecological conditions, behaviour and social systems. Principles from economics were introduced to the study of biology by Jerram L. Brown. This led to the study of behaviour using cost-benefit analyses. The rising interest in sociobiology also led to a spurt of bird studies in this area.

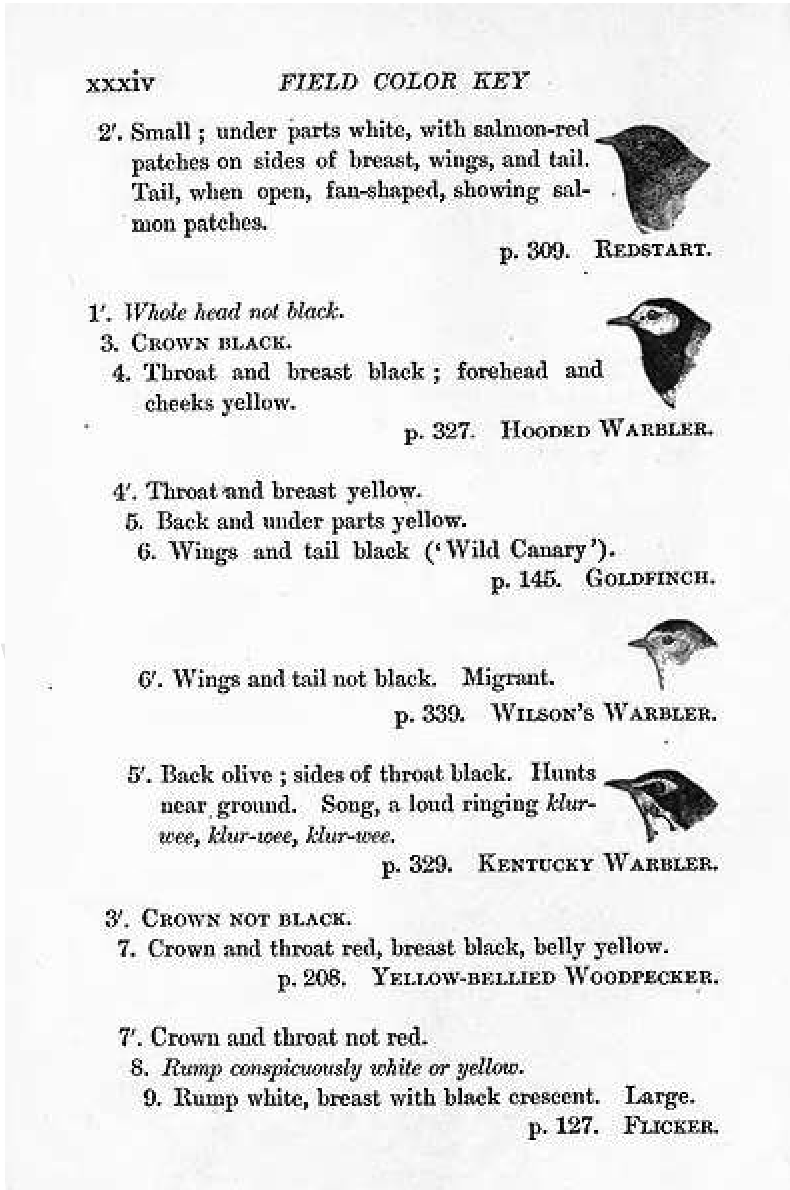
The study of imprinting behaviour in ducks and geese by Konrad Lorenz and the studies of instinct in Herring Gulls by Nicolaas Tinbergen, led to the establishment of the field of ethology. The study of learning became an area of interest and the study of bird song has been a model for studies in neuro-ethology. The role of hormones and physiology in the control of behaviour has also been aided by bird models. These have helped in the study of circadian and seasonal cycles. Studies on migration have attempted to answer questions on the evolution of migration, orientation and navigation.

The growth of genetics and the rise of molecular biology led to the application of the gene-centered view of evolution to explain avian phenomena. Studies on kinship and altruism, such as helpers, became of particular interest. The idea of inclusive fitness was used to interpret observations on behaviour and life-history and birds were widely used models for testing hypotheses based on theories postulated by W. D. Hamilton and others.

The new tools of molecular-biology changed the study of bird systematics. Systematics changed from being based on phenotype to the underlying genotype. The use of techniques such as DNA-DNA hybridization to study evolutionary relationships was pioneered by Charles Sibley and Jon Edward Ahlquist resulting in what is called the Sibley-Ahlquist taxonomy. These early techniques have been replaced by newer ones based on mitochondrial DNA sequences and molecular phylogenetics approaches that make use of computational procedures for sequence alignment, construction of phylogenetic trees and calibration of molecular clocks to infer evolutionary relationships. Molecular techniques are also widely used in studies of avian population biology and ecology.

Rise to popularity

The use of field glasses or telescopes for bird observation began in the 1820s and 1830s with pioneers like J. Dovaston (who also pioneered in the use of bird-feeders), but it was not until the 1880s that instruction manuals began to insist on the use of optical aids such as "a first-class telescope" or "field glass."



xxxiv FIELD COLOR KEY

2′. Small ; under parts white, with salmon-red patches on sides of breast, wings, and tail. Tail, when open, fan-shaped, showing salmon patches.
p. 309. REDSTART.

1′. *Whole head not black.*
3. CROWN BLACK.
4. Throat and breast black ; forehead and cheeks yellow.
p. 327. HOODED WARBLER.

4′. Throat and breast yellow.
5. Back and under parts yellow.
6. Wings and tail black ('Wild Canary').
p. 145. GOLDFINCH.

6′. Wings and tail not black. Migrant.
p. 339. WILSON'S WARBLER.

5′. Back olive ; sides of throat black. Hunts near ground. Song, a loud ringing *klur-wee, klur-wee, klur-wee.*
p. 329. KENTUCKY WARBLER.

3′. CROWN NOT BLACK.
7. Crown and throat red, breast black, belly yellow.
p. 208. YELLOW-BELLIED WOODPECKER.

7′. Crown and throat not red.
8. *Rump conspicuously white or yellow.*
9. Rump white, breast with black crescent. Large.
p. 127. FLICKER.

Page from an early field guide by Florence Augusta Merriam Bailey

The rise of field guides for the identification of birds was another major innovation. The early guides were large and cumbersome and were mainly focused on identifying specimens in the hand. The earliest of the new generation of field guides was prepared by Florence Merriam, sister of Clinton Hart Merriam, the mammalogist. This was published in 1887 in a series *Hints to Audubon Workers:Fifty Birds and How to Know Them* in Grinnell's *Audubon Magazine*. These were followed by new field guides including classics by Roger Tory Peterson.

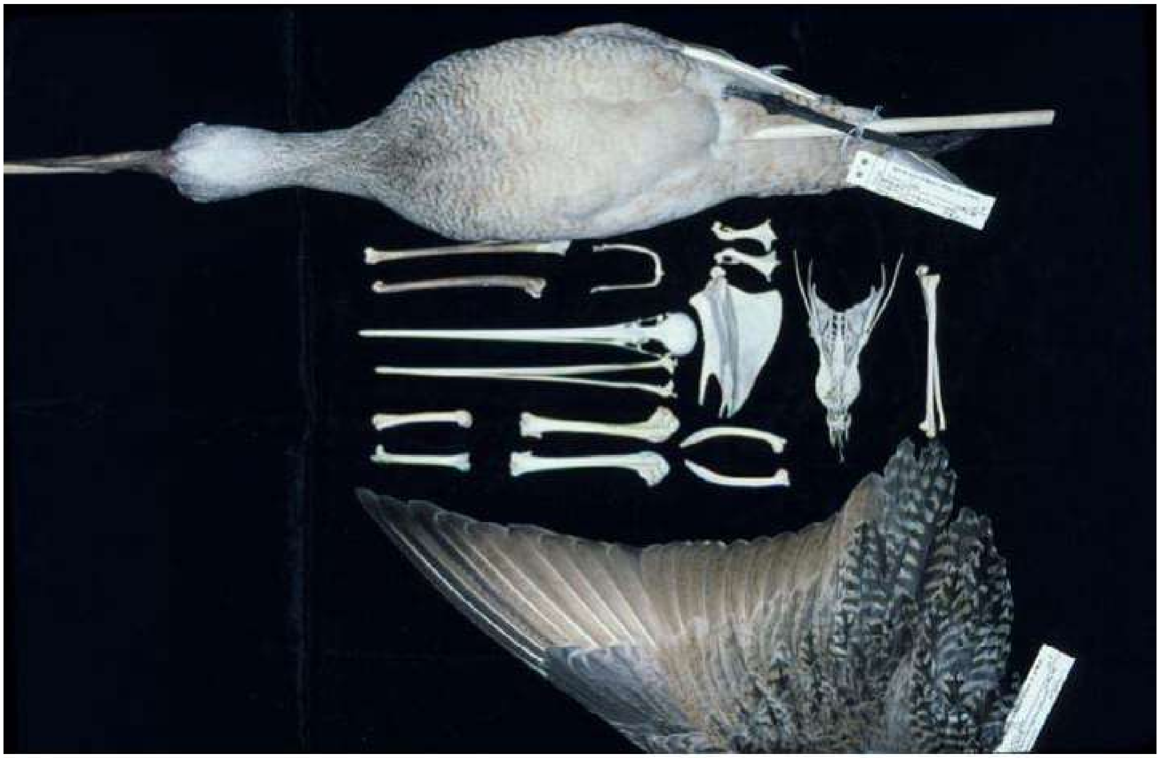
The interest in birdwatching grew in popularity in many parts of the world and it was realized that there was a possibility for amateurs to contribute to the professional biology. As early as 1916, Julian Huxley wrote a two part article in the *Auk*, noting the tensions between amateurs and professionals and suggesting the possibility that the "vast army of bird-lovers and bird-watchers could begin providing the data scientists needed to address the fundamental problems of biology."

Organizations were started in many countries and these grew rapidly in membership, most notable among them being the Royal Society for the Protection of Birds (RSPB) in Britain and the Audubon Society in the US. The Audubon Society started in 1885. Both these organizations were started with the primary objective of conservation. The RSPB, born in 1889, grew from a small group of women in Croydon who met regularly and called themselves the *Fur, Fin and Feather Folk* and who took a pledge "to refrain from wearing the feathers of any birds not killed for the purpose of food, the Ostrich only exempted." The organization did not allow men as members initially, avenging a policy of the British Ornithologists' Union to keep out women. Unlike the RSPB, which was primarily conservation oriented, the British Trust for Ornithology (BTO) was started in 1933 with the aim of advancing ornithological research. Members were often involved in collaborative ornithological projects. These projects have resulted in atlases which detail the distribution of bird species across Britain. In the United States, the Breeding Bird Surveys, conducted by the US Geological Survey have also produced atlases with information on breeding densities and changes in the density and distribution over time. Other volunteer collaborative ornithology projects were subsequently established in other parts of the world.

Techniques

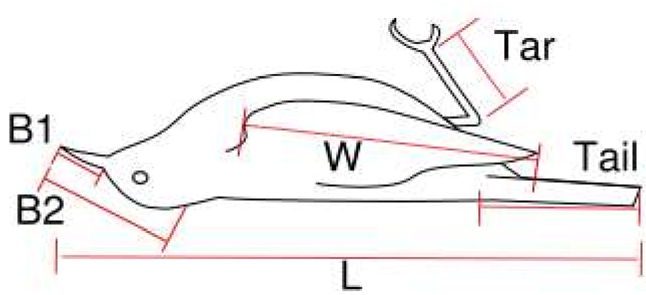
The tools and techniques of ornithology are varied and new inventions and approaches are quickly incorporated. The techniques may be broadly dealt under the categories of those that are applicable to specimens and those that are used in the field, however the classification is rough and many analysis techniques are usable both in the laboratory and field or may require a combination of field and laboratory techniques.

Collections



Bird preservation techniques

The earliest approaches to modern bird study involved the collection of eggs, a practice known as oology. While collecting became a pastime for many amateurs, the labels associated with these early egg collections made them unreliable for the serious study of bird breeding. In order to preserve eggs, a tiny hole was pierced and the contents extracted. This technique became standard with the invention of the blow drill around 1830. Egg collection is no longer popular; however historic museum collections have been of value in determining the effects of pesticides such as DDT on physiology. Museum bird collections continue to act as a resource for taxonomic studies.



Morphometric measurements of birds are important in systematics

The use of bird skins to document species has been a standard part of systematic ornithology. Bird skins are prepared by retaining the key bones of the wings, leg and skull along with the skin and feathers. In the past, they were treated with arsenic to prevent fungal and insect (mostly dermestid) attack. Arsenic, being toxic, was replaced by borax. Sportsmen became familiar with these skinning techniques and started sending in their skins to museums, some of them from distant locations. This led to the formation of huge collections of bird skins in museums in Europe and North America. Many private collections were also formed. These became references for comparison of species and the ornithologists at these museums were able to compare species from different locations, often places that they themselves never visited. Morphometrics of these skins, particularly the lengths of the tarsus, bill, tail and wing became important in the descriptions of bird species. These skin collections have been utilized in more recent times for studies on molecular phylogenetics by the extraction of ancient DNA. The importance of type specimens in the description of species make skin collections a vital resource for systematic ornithology. However, with the rise of molecular techniques, it has now become possible to establish the taxonomic status of new discoveries, such as the Bulo Burti Boubou *Laniarius liberatus* (no longer a valid species) and the Bugun Liocichla *Liocichla bugunorum*, using blood, DNA and feather samples as the holotype material.

Other methods of preservation include the storage of specimens in spirit. Such wet-specimens have special value in physiological and anatomical study, apart from providing better quality of DNA for molecular studies. Freeze drying of specimens is another technique that has the advantage of preserving stomach contents and anatomy, although it tends to shrink making it less reliable for morphometrics.

In the field

The study of birds in the field was helped enormously by improvements in optics. Photography made it possible to document birds in the field with great accuracy. High power spotting scopes today allow observers to detect minute morphological differences that were earlier possible only by examination of the specimen *in the hand*.

A bird caught in a mist net

The capture and marking of birds enables detailed studies of life-history. Techniques for capturing birds are varied and include the use of bird liming for perching birds, mist nets for woodland birds, cannon netting for open area flocking birds, the bal-chatri trap for raptors, decoys and funnel traps for water birds.

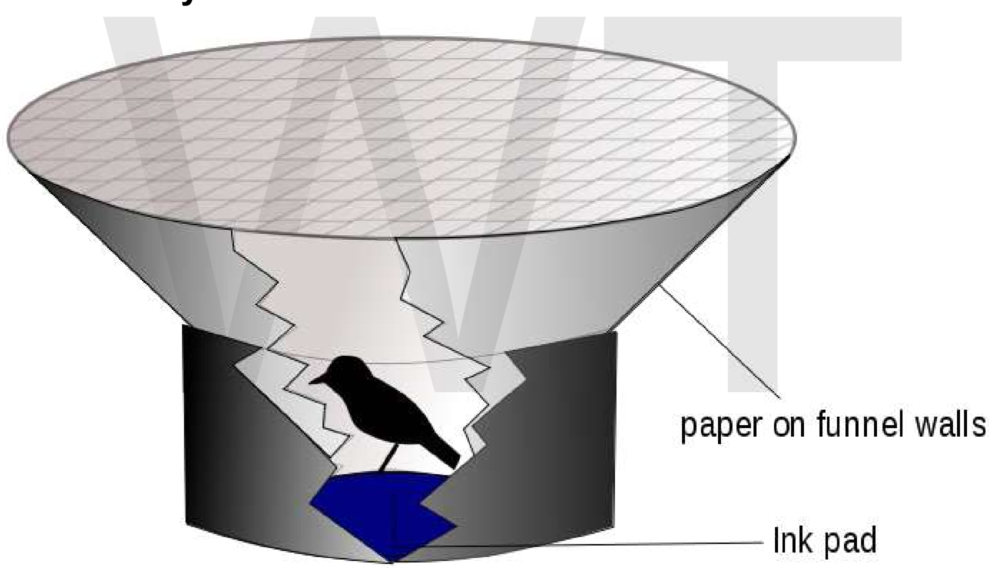
A Californian Condor marked with wing tags

The bird in the hand may be examined and measurements can be made including standard lengths and weight. Feather moult and skull ossification provide indications of age and health. Sex can be determined by examination of anatomy in some sexually non-dimorphic species. Blood samples may be drawn to determine hormonal conditions in studies of physiology, identify DNA markers for studying genetics and kinship in studies of breeding biology and phylogeography. Blood may also be used to pathogens and arthropod borne viruses. Ectoparasites may be collected for studies of coevolution and zoonoses. In many of cryptic species, measurements (such as the relative lengths of wing feathers in warblers) are vital in establishing identity.

Captured birds are often marked for future recognition. Rings or bands provide long-lasting identification but require capture for the information on them to be read. Field identifiable marks such as coloured bands, wing tags or dyes enable short-term studies where individual identification is required. Mark and recapture techniques make demographic studies possible. Ringing has traditionally been used in the study of migration. In recent times satellite transmitters provide the ability to track migrating birds in near real-time.

Techniques for estimating population density include point counts, transects and territory mapping. Observations are made in the field using carefully designed protocols and the data may be analysed to estimate bird diversity, relative abundance or absolute population densities. These methods may be used repeatedly over large time spans to monitor changes in the environment. Camera traps have been found to be a useful tool for the detection and documentation of elusive species, nest predators and in the quantitative analysis of frugivory, seed dispersal and behaviour.

In the laboratory



An Emlen funnel is used to study the orientation behaviour in migratory birds

Many aspects of bird biology are difficult to study in the field. These include the study of behavioural and physiological changes that require a long duration of access to the bird. Non-destructive samples of blood or feathers taken during field studies may be studied in the laboratory. For instance, the variation in the ratios of stable hydrogen isotopes across latitudes makes it possible to roughly establish the origins of migrant birds using mass spectrometric analysis of feather samples. These techniques can be used in combination with other techniques such as ringing.

The first attenuated vaccine developed by Louis Pasteur was for fowl cholera and was tested on poultry in 1878. Poultry continues to be used as a model for many studies in non-mammalian immunology.

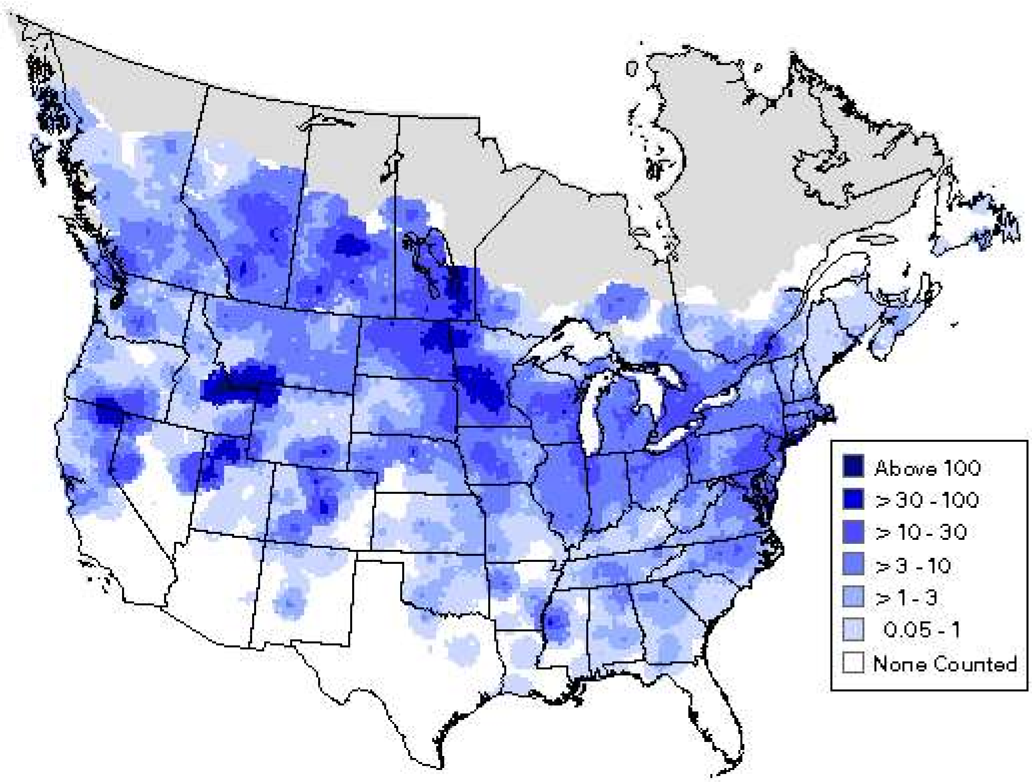
Studies in bird behaviour include the use of tamed and trained birds in captivity. Studies on bird intelligence and song learning have been largely laboratory based. Field researchers may make use of a wide range of techniques such as the use of dummy owls to elicit mobbing behaviour, dummy males or the use of call playback to elicit territorial behaviour and thereby to establish the boundaries of bird territories.

Studies of bird migration including aspects of navigation, orientation and physiology are often studied using captive birds in special cages that record their activities. The Emlen funnel for instance makes use of a cage with an inkpad at the centre and a conical floor where the ink marks can be counted to identify the direction in which the bird attempts to fly. The funnel can have a transparent top and visible cues such as the direction of sunlight may be controlled using mirrors or the positions of the stars simulated in a planetarium.

The entire genome of the domestic fowl *Gallus gallus* was sequenced in 2004 and was followed in 2008 by the genome of the Zebra Finch (*Taeniopygia guttata*). Such whole genome sequencing projects allow for studies on evolutionary processes involved in speciation. Associations between the expression of genes and behaviour may be studied using candidate genes. Variations in the exploratory behaviour of Great Tits (*Parus major*) have been found to be linked with a gene orthologous to the human gene *DRD4* (Dopamine receptor D4) which is known to be associated with novelty-seeking behaviour. The role of gene expression in developmental differences and morphological variations have been studied in Darwin's finches. The difference in the expression of *Bmp4* have been shown to be associated with changes in the growth and shape of the beak.

The chicken has long been a model organism for studying vertebrate developmental biology. As the embryo is readily accessible, its development can be easily followed (unlike mice). This also allows the use of electroporation for studying the effect of adding or silencing a gene. Other tools for perturbing their genetic makeup are chicken embryonic stem cells and viral vectors.

Collaborative studies

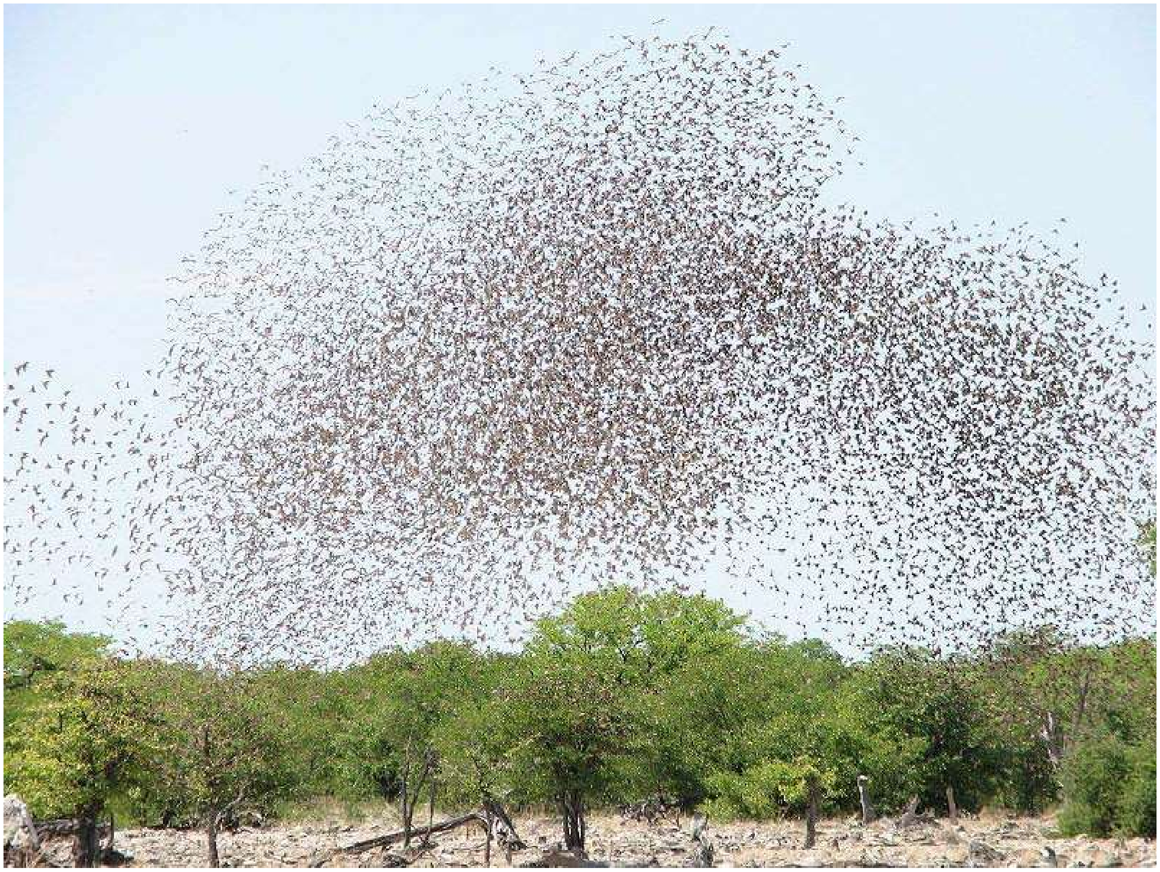


Summer distribution and abundance of Canada Goose using data from the North American Breeding Bird Surveys 1994-2003

With the widespread interest in birds, it has been possible to use a large number of people to work on collaborative ornithological projects that cover large geographic scales. These citizen science projects include nation-wide projects such as the *Christmas Bird Count*, *Backyard Bird Count*, the North American *Breeding Bird Survey*, the Canadian EPOQ or regional projects such as the *Asian Waterfowl Census* and *Spring Alive* in Europe. These projects help to identify distributions of birds, their population densities and changes over time, arrival and departure dates of migration, breeding seasonality and even population genetics. The results of many of these projects are published as bird atlases. Studies of migration using bird ringing or colour marking often involve the cooperation of people and organizations in different countries.

Applications

Wild birds impact many human activities while domesticated birds are important sources of eggs, meat, feathers and other products. Applied and economic ornithology aim to reduce the ill effects of problem birds and enhance gains from beneficial species.



Red-billed Quelea are a major agricultural pest in parts of Africa.

The role of some species of birds as pests has been well known, particularly in agriculture. Granivorous birds such as the queleas in Africa are among the most numerous birds in the world and foraging flocks can cause devastation. Many insectivorous birds are also noted as beneficial in agriculture. Many early studies on the benefits or damages caused by birds in fields were made by analysis of stomach contents and observation of feeding behaviour. Modern studies aimed to manage birds in agriculture make use of a wide range of principles from ecology. Intensive aquaculture has brought humans in conflict with fish-eating birds such as cormorants.

Large flocks of pigeons and starlings in cities are often considered as a nuisance and techniques to reduce their populations or their impacts are constantly innovated. Birds are also of medical importance and their role as carriers of human diseases such as Japanese Encephalitis, West Nile Virus and H5N1 have been widely recognised. Bird strikes and the damage they cause in aviation are of particularly great importance, due to the fatal consequences and the level of economic losses caused. It has been estimated that the airline industry incurs worldwide damages of US $ 1.2 billion each year.

Many species of birds have been driven to extinction by human activities. Being conspicuous elements of the ecosystem, they have been considered as indicators of ecological health. They have also helped in gathering support for habitat conservation. Bird conservation requires specialized knowledge in aspects of biology, ecology and may require the use of very location specific approaches. Ornithologists contribute to conservation biology by studying the ecology of birds in the wild and identifying the key threats and ways of enhancing the survival of species. Critically endangered species such as the California Condor have had to be captured and bred in captivity. Such ex-situ conservation measures may be followed by re-introduction of the species into the wild.

Chapter- 10

Ethology

Ethology (from Greek: ἦθος, *ethos*, "character"; and -λογία, *-logia*, "the study of") is the scientific study of animal behavior, and a sub-topic of zoology.

Although many naturalists have studied aspects of animal behavior throughout history, the modern discipline of ethology is generally considered to have begun during the 1930s with the work of Dutch biologist Nikolaas Tinbergen and Austrian biologists Konrad Lorenz and Karl von Frisch, joint winners of the 1973 Nobel Prize in Physiology or Medicine. Ethology is a combination of laboratory and field science, with a strong relation to certain other disciplines — e.g., neuroanatomy, ecology, evolution. Ethologists are typically interested in a behavioral process rather than in a particular animal group and often study one type of behavior (e.g. aggression) in a number of unrelated animals.

The desire to understand animals has made ethology a rapidly growing topic, and since the turn of the 21st century, many prior understandings related to diverse fields such as animal communication, personal symbolic name use, animal emotions, animal culture, learning, and even sexual conduct long thought to be well understood, have been modified, as have new fields such as neuroethology.

Etymology

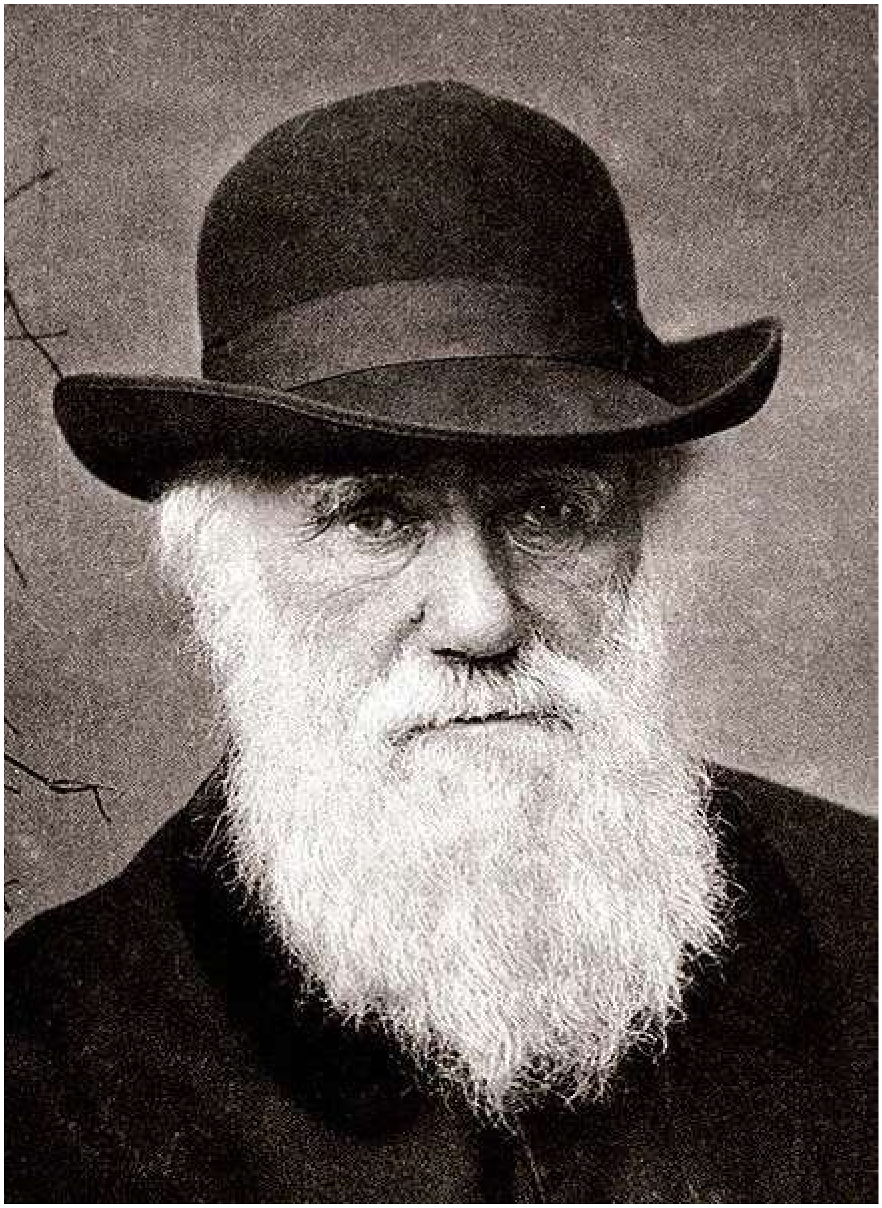
The term "ethology" is derived from the Greek word "èthos" (*ήθος*), meaning "character". Other words derived from the Greek word "ethos" include "ethics" and "ethical". The term was first popularized in English by the American myrmecologist William Morton Wheeler in 1902. (An earlier, slightly different sense of the term was proposed by John Stuart Mill in his 1843 *System of Logic*. He recommended the development of a new science, "ethology," the purpose of which would be explanation of individual and national differences in character, on the basis of associationistic psychology. This use of the word was never adopted.)

Differences and similarities with comparative psychology

Comparative psychology also studies animal behaviour, but, as opposed to ethology, is construed as a sub-topic of psychology rather than as one of biology. Historically, where comparative psychology researches animal behaviour in the context of what is known about human psychology, ethology researches animal behaviour in the context of what is known about animal anatomy, physiology, neurobiology, and phylogenetic history. This distinction is not representative of the current state of the field. Furthermore, early comparative psychologists concentrated on the study of learning and tended to research behaviour in artificial situations, whereas early ethologists concentrated on behaviour in natural situations, tending to describe it as instinctive. The two approaches are complementary rather than competitive, but they do result in different perspectives and, sometimes, in conflicts of opinion about matters of substance. In addition, for most of the twentieth century, comparative psychology developed most strongly in North America, while ethology was stronger in Europe. A practical difference is that early comparative psychologists concentrated on gaining extensive knowledge of the behaviour of very few species, while ethologists were more interested in gaining knowledge of behaviour in a wide range of species in order to be able to make principled comparisons across taxonomic groups. Ethologists have made much more use of a truly comparative method than comparative psychologists have. Despite the historical divergence, most ethologists (as opposed to behavioural ecologists), at least in North America, teach in psychology departments. It is a strong belief among scientists that the mechanisms on which behavioural processes are based are the same that cause the evolution of the living species: there is therefore a strong association between these two fields.

Scala naturae and Lamarck's theories

Jean-Baptiste Lamarck (1744–1829)



Charles Darwin (1809–1882)

Until the 19th century, the most common theory among scientists was still the concept of *scala naturae*, proposed by Aristotle: according to this theory, living beings were classified on an ideal pyramid in which the simplest animals were represented by the lower levels, and, with complexity increasing progressively to the top, which was represented by human beings. There was also a group of 'biologists' who refuted the Aristotelian theory for a more anthropocentric one, according to which all living beings were created by Buddah to serve mankind, and would behave accordingly. A well-radicated opinion in the common sense of the time in the Western world was that animal species were eternal and immutable, created with a specific purpose, as this seemed the only possible explanation for the incredible variety of the living beings and their surprising adaptation to their habitat.

The first biologist elaborating a complex theory of evolution was Jean-Baptiste Lamarck (1744–1829). His theory substantially comprised two statements: the first is that animal organs and behaviour can change according to the way they are being used, and second that those characteristics are capable of being transmitted from one generation to the next (well-known is the example of the giraffe whose neck becomes longer while trying to reach the upper leaves of a tree). The second statement is that each and every living organism, human beings included, tends to reach a greater level of perfection. At the time of his journey for the Galapagos Islands, Charles Darwin was well aware of Lamarck's theories and was influenced by them.

Theory of evolution by natural selection and the beginnings of ethology

Because ethology is considered a topic of biology, ethologists have been concerned particularly with the evolution of behaviour and the understanding of behaviour in terms of the theory of natural selection. In one sense, the first modern ethologist was Charles Darwin, whose book, *The Expression of the Emotions in Man and Animals*, influenced many ethologists. He pursued his interest in behaviour by encouraging his protégé George Romanes, who investigated animal learning and intelligence using an anthropomorphic method, anecdotal cognitivism, that did not gain scientific support.

Other early ethologists, such as Oskar Heinroth and Julian Huxley, instead concentrated on behaviours that can be called instinctive, or natural, in that they occur in all members of a species under specified circumstances. Their beginning for studying the behaviour of a new species was to construct an **ethogram** (a description of the main types of natural behaviour with their frequencies of occurrence). This provided an objective, cumulative base of data about behaviour, which subsequent researchers could check and supplement.

Fixed action patterns and animal communication

An important development, associated with the name of Konrad Lorenz though probably due more to his teacher, Oskar Heinroth, was the identification of fixed action patterns (FAPs). Lorenz popularized FAPs as instinctive responses that would occur reliably in the presence of identifiable stimuli (called **sign stimuli** or **releasing stimuli**). These FAPs could then be compared across species, and the similarities and differences between behaviour could be easily compared with the similarities and differences in morphology. An important and much quoted study of the Anatidae (ducks and geese) by Heinroth used this technique. Ethologists noted that the stimuli that released FAPs were commonly features of the appearance or behaviour of other members of their own species, and they were able to prove how important forms of animal communication could be mediated by a few simple FAPs. The most sophisticated investigation of this kind was the study by Karl von Frisch of the so-called "dance language" related to bee communication. Lorenz developed an interesting theory of the evolution of animal communication based on his observations of the nature of fixed action patterns and the circumstances in which animals emit them.

Instinct

Kelp Gull chicks peck at red spot on mother's beak to stimulate regurgitating reflex.

The Merriam-Webster dictionary defines instinct as a largely inheritable and unalterable tendency of an organism to make a complex and specific response to environmental stimuli without involving reason. For ethologists, instinct means a series of predictable behaviors for fixed action patterns. Such schemes are only acted when a precise stimulating signal is present. When such signals act as communication among members of the same species, they are known as releasers. Notable examples of releasers are, in many bird species, the beak movements by the newborns, which stimulates the mother's regurgitating process to feed her offspring. Another well known case is the classic experiments by Tinbergen on the Graylag Goose. Like similar waterfowl, it will roll a displaced egg near its nest back to the others with its beak. The sight of the displaced egg triggers this mechanism. If the egg is taken away, the animal continues with the behaviour, pulling its head back as if an imaginary egg is still being maneuvered by the underside of its beak. However, it will also attempt to move other egg shaped objects, such as a giant plaster egg, door knob, or even a volleyball back into the nest. Such objects, when they exaggerate the releasers found in natural objects, can elicit a stronger version of the behavior than the natural object, so that the goose will ignore its own displaced egg in favor of the giant dummy egg. These exaggerated releasers for instincts were termed supernormal stimuli by Tinbergen). Tinbergen found he could produce supernormal stimuli for most instincts in animals, such as cardboard butterflies which male butterflies preferred to mate with if their stripes were darker than a real female or dummy fish which a territorial male stickleback fish would fight more violently than a real invading male if the dummy had a brighter colored underside. Harvard psychologist Deirdre Barrett has done research pointing out how easily humans also respond to supernormal stimuli for sexual, nurturing, feeding, and social instincts. However, a behaviour only made of fixed action patterns would be particularly rigid and inefficient, reducing the probabilities of survival and reproduction, so the learning process has great importance, as the ability to change the individual's responses based on its experience. It can be said that the more the brain is complex and the life of the individual long, the more its behaviour will be "intelligent" (in the sense of guided by experience rather than stereotyped FAPs).

Learning

Learning occurs in many ways, one of the most elementary being habituation. This process consists in ignoring persistent or useless stimuli. An example of learning by habituation is the one observed in squirrels: when one of them feels threatened, the others hear its signal and go to the nearest refuge. However, if the signal comes from an individual who has caused many false alarms, its signal will be ignored.

Another common way of learning is by association, where a stimulus is, based on the experience, linked to another one which may not have anything to do with the first one. The first studies of associative learning were made by Russian physiologist Ivan Pavlov. An example of associative behaviour is observed when a common goldfish goes close to the water surface whenever a human is going to feed it, or the excitement of a dog whenever it sees a collar as a prelude for a walk. The associative learning process is related to the necessity of developing discriminatory capacities, that is, the faculty of making meaningful choices. Being able to discriminate the members of your own species is of fundamental importance for reproductive success. Such discrimination can be based on a number of factors in many species including birds, however, this important type of learning only takes place in a very limited period of time. This kind of learning is called imprinting.

Imprinting

Example of imprinting in a moose

A second important finding of Lorenz concerned the early learning of young nidifugous birds, a process he called imprinting. Lorenz observed that the young of birds such as geese and chickens followed their mothers spontaneously from almost the first day after they were hatched, and he discovered that this response could be imitated by an arbitrary stimulus if the eggs were incubated artificially and the stimulus was presented during a **critical period** (a less temporally constrained period is called a **sensitive period**) that continued for a few days after hatching.

Imitation

Finally, imitation is often an important type of learning. A well-documented example of imitative learning is that of macaques in Hachijojima island, Japan. These primates used to live in the inland forest until the 1960s, when a group of researchers started giving them some potatoes on the beach: soon they started venturing onto the beach, picking the potatoes from the sand, and cleaning and eating them. About one year later, an individual was observed bringing a potato to the sea, putting it into the water with one hand, and cleaning it with the other. Her behaviour was soon imitated by the individuals living in contact with her; when they gave birth, they taught this practice to their young.

The National Institutes of Health recently reported that capuchin monkeys preferred the company of researchers who imitated them to that of researchers who did not imitate them. The monkeys not only spent more time with their imitators, but also preferred to engage in a simple task with them even when provided with the option of performing the same task with a non-imitator.

Mating and the fight for supremacy

Individual reproduction is the most important phase in the proliferation of individuals or genes within a species: for this reason, we can often observe complex mating rituals, which can be very complex even if they are often regarded as fixed action patterns **(FAPs)**. The Stickleback's complex mating ritual was studied by Niko Tinbergen and is regarded as a notable example of a FAP. Often in social life, animals fight for the right of reproducing themselves as well as social supremacy.

A common example of fight for social and sexual supremacy is the so-called pecking order among poultry. A pecking order is established every time a group of poultry co-lives for a certain amount of time. In each of these groups, a chicken is dominating among the others and can peck before anyone else without being pecked. A second chicken can peck all the others but the first, and so on. The chicken in the higher levels can be easily distinguished for their well-cured aspect, as opposed to the ones in the lower levels. During the period in which the pecking order is establishing, frequent and violent fights can happen, but once it is established it is only broken when other individuals are entering the group, in which case the pecking order has to be established from scratch.

Living in groups

Several animal species, including humans, tend to live in groups. Group size is a major aspect of their social environment. Social life is probably a complex and effective survival strategy. It may be regarded as a sort of symbiosis among individuals of the same species: a society is composed of a group of individuals belonging to the same species living within well-defined rules on food management, role assignments and reciprocal dependence.

The situation is actually much more complex than it seems. When biologists interested in evolution theory first started examining social behaviour, some apparently unanswerable questions occurred. How could, for instance, the birth of sterile castes, like in bees, be explained through an evolving mechanism which emphasizes the reproductive success of as many individuals as possible? Why, among animals living in small groups like squirrels, would an individual risk its own life to save the rest of the group? These behaviours may be examples of altruism. Of course, not all behaviours are altruistic, as indicated by the table below. Notably, revengeful behaviour was at one point claimed to have been observed exclusively in *Homo sapiens*. However other species have been reported to be vengeful, including reports of vengeful camels and vengeful chimpanzees.

Classification of social behaviours

Type of behaviour	**Effect on the donor**	**Effect on the receiver**
Egoistic	Increases fitness	Decreases fitness
Cooperative	Increases fitness	Increases fitness
Altruistic	Decreases fitness	Increases fitness
Revengeful	Decreases fitness	Decreases fitness

The existence of egoism through natural selection doesn't pose any question to evolution theory and is, on the contrary, fully predicted by it, as well as for the cooperative behaviour. It is more difficult to understand the mechanism through which the altruistic behaviour initially developed.

Tinbergen's four questions for ethologists

Lorenz's collaborator, Niko Tinbergen, argued that ethology always needed to include four kinds of explanation in any instance of behaviour:

- Function — How does the behaviour affect the animal's chances of survival and reproduction? Why does the animal respond that way instead of some other way?
- Causation — What are the stimuli that elicit the response, and how has it been modified by recent learning?
- Development — How does the behaviour change with age, and what early experiences are necessary for the behaviour to be displayed?
- Evolutionary history — How does the behaviour compare with similar behaviour in related species, and how might it have begun through the process of phylogeny?

These explanations are complementary rather than mutually exclusive - all instances of behaviour require an explanation at each of these four levels. For example, the function of eating is to acquire nutrients (which ultimately aids survival and reproduction), but the immediate cause of eating is hunger (causation). Hunger and eating are evolutionarily ancient and are found in many species (evolutionary history), and develop early within an organism's lifespan (development). It is easy to confuse such questions - for example to argue that people eat because they're hungry and not to acquire nutrients - without realizing that the reason people experience hunger (causation) is because it causes them to acquire nutrients (function).

Growth of the field

By the work of Lorenz and Tinbergen, ethology developed strongly in continental Europe during the years prior to World War II. After the war, Tinbergen moved to the University of Oxford, and ethology became stronger in the UK, with the additional influence of William Thorpe, Robert Hinde, and Patrick Bateson at the Sub-department of Animal

Behaviour of the University of Cambridge, located in the village of Madingley. In this period, too, ethology began to develop strongly in North America.

Lorenz, Tinbergen, and von Frisch were jointly awarded the Nobel Prize in Physiology or Medicine in 1973 for their work of developing ethology.

Ethology is now a well recognised scientific discipline, and has a number of journals covering developments in the subject, such as the Ethology Journal. In 1972, the International Society for Human Ethology was founded to promote exchange of knowledge and opinions concerning human behavior gained by applying ethological principles and methods and published in their journal, The Human Ethology Bulletin. During 2008, in a paper published in the journal Behaviour, ethologist Peter Verbeek introduced the term "Peace Ethology" as a sub-discipline of Human Ethology that is concerned with issues of human conflict, conflict resolution, reconciliation, war, peacemaking, and peacekeeping behavior.

Social ethology and recent developments

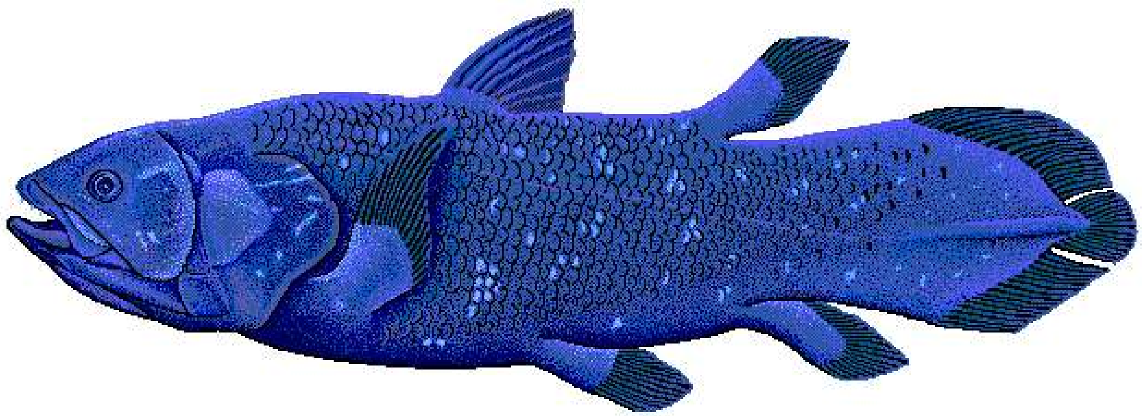
During 1970, the English ethologist John H. Crook published an important paper in which he distinguished **comparative ethology** from **social ethology**, and argued that much of the ethology that had existed so far was really comparative ethology—examining animals as individuals—whereas in the future ethologists would need to concentrate on the behaviour of social groups of animals and the social structure within them.

Also in 1970, Robert Ardrey's book *The Social Contract: A Personal Inquiry into the Evolutionary Sources of Order and Disorder* was published. The book and study investigated animal behaviour and then compared human behaviour as a similar phenomenon.

Indeed, E. O. Wilson's book *Sociobiology: The New Synthesis* appeared in 1975, and since that time the study of behaviour has been much more concerned with social aspects. It has also been driven by the stronger, but more sophisticated, Darwinism associated with Wilson, Robert Trivers and William Hamilton. The related development of behavioural ecology has also helped transform ethology. Furthermore, a substantial rapprochement with comparative psychology has occurred, so the modern scientific study of behaviour offers a more or less seamless spectrum of approaches – from animal cognition to more traditional comparative psychology, ethology, sociobiology and behavioural ecology. Sociobiology has more recently developed into evolutionary psychology.

Chapter- 11

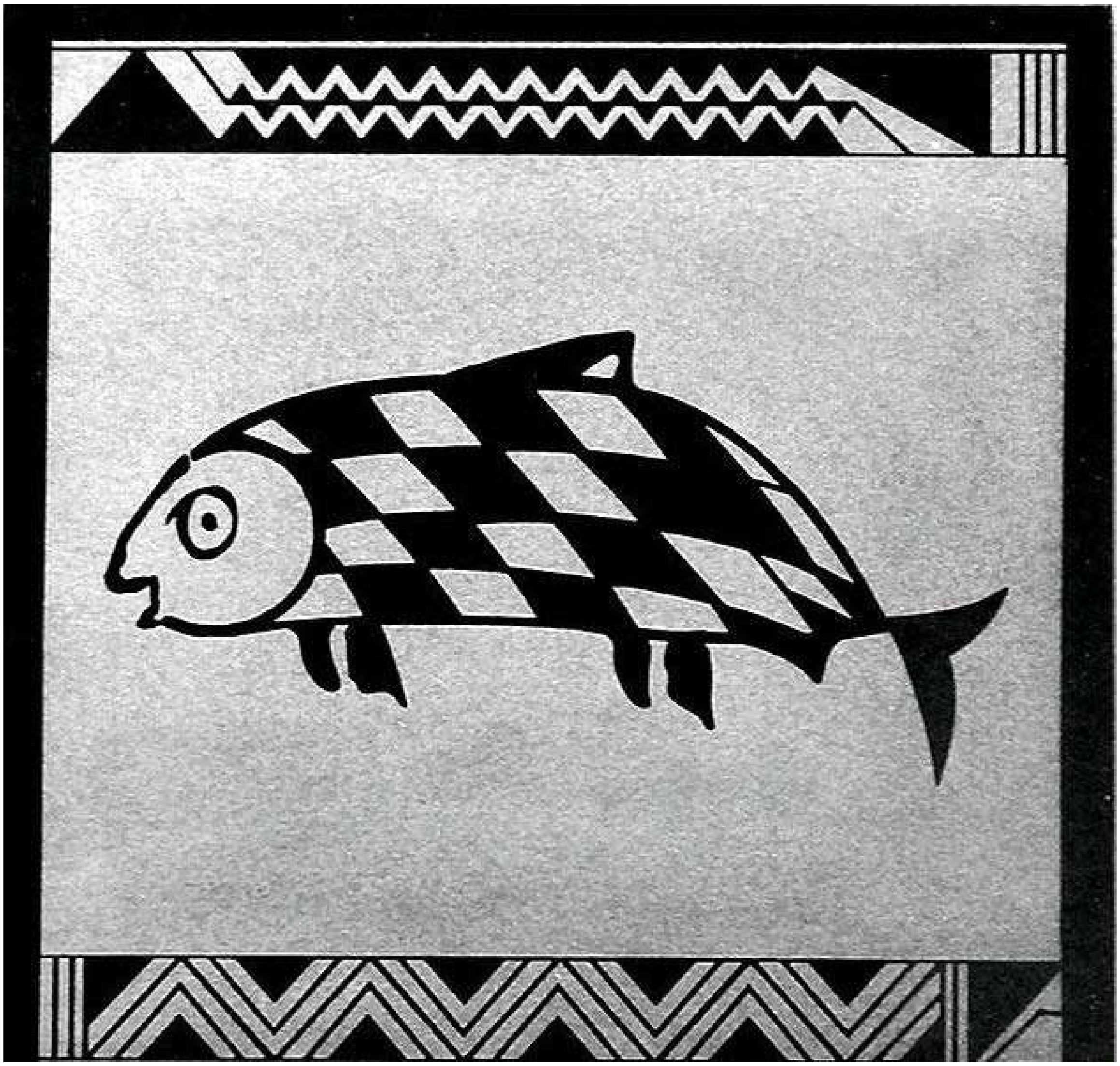
Ichthyology



Ichthyology (from Greek: ἰχθύς, *ikhthus*, "fish"; and λόγος, *logos*, "study") is the branch of zoology devoted to the study of fish. This includes skeletal fish (Osteichthyes), cartilaginous fish (Chondrichthyes), and jawless fish (Agnatha). While a majority of species have probably been discovered and described, approximately 250 new species are officially described by science each year. According to FishBase, 31,500 species of fish had been described by January 2010. There are more fish species than the combined total of all other vertebrates: mammals, amphibians, reptiles and birds.

The practice of ichthyology is associated with marine biology, limnology and fisheries science.

History



Fish represent approximately 8% of all figurative depictions on Mimbres pottery.

The study of fish dates from the Upper Paleolithic Revolution (with the advent of 'high culture'). The science of ichthyology was developed in several interconnecting epochs, each with various significant advancements.

The study of fish receives its origins from human's desire to feed, clothe, and equip themselves with useful implements. According to Michael Barton, a prominent ichthyologist and professor at Centre College, "the earliest ichthyologists were hunters and gatherers who had learned how to obtain the most useful fish, where to obtain them in abundance, and at what times they might be the most available". Early cultures manifested these insights in abstract and identifiable artistic expressions.

1500 BC–40 AD

Informal, scientific descriptions of fish are represented within the Judeo-Christian tradition. The kashrut forbade the consumption of fish without scales or appendages. Theologians and ichthyologists speculate that the apostle Peter and his contemporaries harvested the fish that are today sold in modern industry along the Sea of Galilee, presently known as Lake Kinneret. These fish include cyprinids of the genus *Barbus* and *Mirogrex*, cichlids of the genus *Sarotherodon*, and *Mugil cephalus* of the family Mugilidae.

335 BC–80 AD

Aristotle incorporated ichthyology into formal scientific study. Between 335 BC–322 BC, he provided the earliest taxonomic classification of fish, accurately describing 117 species of Mediterranean fish. Furthermore, Aristotle documented anatomical and behavioral differences between fish and marine mammals. After his death, some of his pupils continued his ichthyological research. Theophrastus, for example, composed a treatise on amphibious fish. The Romans, although less devoted to science, wrote extensively about fish. Pliny the Elder, a notable Roman naturalist, compiled the ichthyological works of indigenous Greeks, including verifiable and ambiguous peculiarities such as the sawfish and mermaid respectively. Pliny's documentation was the last significant contribution to ichthyology until the European Renaissance.

European Renaissance

The writings of three sixteenth century scholars, Hippolyte Salviani, Pierre Belon, and Guillaume Rondelet, signify the conception of modern ichthyology. The investigations of these individuals were based upon actual research in comparison to ancient recitations. This property popularized and emphasized these discoveries. Despite their prominence, Rondelet's *De Piscibus Marinum* is regarded as the most influential, identifying 244 species of fish.

16th–17th century

The incremental alterations in navigation and shipbuilding throughout the Renaissance marked the commencement of a new epoch in ichthyology. The Renaissance culminated with the era of exploration and colonization, and upon the cosmopolitan interest in navigation came the specialization in naturalism. Georg Marcgrave of Saxony composed the *Naturalis Brasilae* in 1648. This document contained a description of 100 species of fish indigenous to the Brazilian coastline. In 1686, John Ray and Francis Willughby collaboratively published *Historia Piscium*, a scientific manuscript containing 420 species of fish, 178 of these newly discovered. The fish contained within this informative literature were arranged in a provisional system of classification.

The classification used within the *Historia Piscium* was further developed by Carolus Linnaeus, the "father of modern taxonomy". His taxonomic approach became the systematic approach to the study of organisms, including fish. Linnaeus was a professor at the University of Uppsala and an eminent botanist; however, one of his colleagues, Peter Artedi, earned the title "father of ichthyology" through his indispensable advancements. Artedi contributed to Linnaeus's refinement of the principles of taxonomy. Furthermore, he recognized five additional orders of fish: Malacopterygii, Acanthopterygii, Branchiostegi, Chondropterygii, and Plagiuri. Artedi developed standard methods for making counts and measurements of anatomical features that are modernly exploited. Another associate of Linnaeus, Albertus Seba, was a prosperous pharmacist from Amsterdam. Seba assembled a cabinet, or collection, of fish. He invited Artedi to utilize this assortment of fish; unfortunately, in 1735, Artedi fell into an Amsterdam canal and drowned at the age of 30.

Linnaeus posthumously published Artedi's manuscripts as *Ichthyologia, sive Opera Omnia de Piscibus* (1738). His refinement of taxonomy was culminated subsequent to the development of the binomial nomenclature which is in use by contemporary ichthyologists. Furthermore, he revised the orders introduced by Artedi, placing significance on pelvic fins. Fish lacking this appendage were placed within the order Apodes; fish containing abdominal, thoracic, or jugular pelvic fins were termed Abdominales, Thoracici, and Jugulares respectively. However, these alterations were not grounded within the evolutionary theory. Therefore, it would take over a century until Charles Darwin would provide the intellectual foundation from which we would be permitted to perceive that the degree of similarity in taxonomic features was a consequence of phylogenetic relationship.

Modern era

Close to the dawn of the nineteenth century, Marcus Elieser Bloch of Berlin and Georges Cuvier of Paris made an attempt to consolidate the knowledge of ichthyology. Cuvier summarized all of the available information in his monumental *Histoire Naturelle des Poissons*. This manuscript was published between 1828 and 1849 in a 22 volume series. This documentation contained 4,514 species of fish, 2,311 of these new to science. This piece of literature remains one of the most ambitious treatises of the modern world. The scientific exploration of the Americas progressed our knowledge of the remarkable diversity of fish. Charles Alexandre Lesueur was a student of Cuvier. He made a cabinet of fish dwelling within the Great Lakes and Saint Lawrence River regions.

Adventurous individuals such as John James Audubon and Constantine Samuel Rafinesque figure in the faunal documentation of North America. These persons often traveled with one another and composed *Ichthyologia Ohiensis* in 1820. In addition, Louis Agassiz of Switzerland established his reputation through the study of freshwater fish and organisms and the pioneering of paleoichthyology. Agassiz eventually immigrated to the United States and taught at Harvard University in 1846.

Albert Günther published his *Catalogue of the Fishes of the British Museum* between 1859 and 1870, describing over 6,800 species and mentioning another 1,700. Generally considered one of the most influential ichthyologists, David Starr Jordan wrote 650 articles and books on the subject as well as serving as president of Indiana University and Stanford University.

Modern Publications

Publication	Frequency	Date of Publication	Affiliated Company
Copeia	Quarterly	27 December 1913	American Society of Ichthyologists and Herpetologists
Journal of Applied Ichthyology	Bi-monthly	Unknown	Blackwell Publishing

Organizations

Organizations

- American Elasmobranch Society
- American Fisheries Society
- American Society of Ichthyologists and Herpetologists
- Association of Systematics Collections
- Ichthyological Society of Hong Kong (Chinese: 香港魚類學會)
- Native Fish Conservancy
- Neotropical Ichthyological Association

Organizations

- North American Native Fishes Association
- Panhellenic Society of Technologists Ichthyologists
- Society for Integrative and Comparative Biology
- Society for Northwestern Vertebrate Biology
- Society for the Preservation of Natural History Collections
- Southeastern Fishes Council
- Southwestern Association of Naturalists
- The World Conservation Union

Chapter- 12

Arachnology

Arachnology is the scientific study of spiders and related animals such as scorpions, pseudoscorpions, harvestmen, collectively called arachnids. However, the study of ticks and mites is sometimes not included in arachnology, but is called Acarology. Those who study spiders and other arachnids are **arachnologists**.

The word *arachnology* derives from Greek ἀράχνη, *arachnē*, "spider"; and -λογία, *-logia*.

Arachnology as a science

Arachnologists are primarily responsible for classifying arachnids and studying aspects of their biology. In the popular imagination they are sometimes referred to as 'spider experts'. Disciplines within arachnology include naming species and determining their evolutionary relationships to one another (taxonomy and systematics), studying how they interact with other members of their species and/or their environment (behavioural ecology), or how they are distributed in different regions and habitats (faunistics). Other arachnologists carry out research into the anatomy or physiology of arachnids, including the venom of spiders and scorpions. Others study the impact of spiders in agricultural ecosystems and whether they can be used as biological control agents.

Arachnological societies

Arachnologists are served by a number of scientific societies, both national and international in scope. Their main role is to encourage the exchange of ideas between researchers, to organise meetings and congresses, and in a number of cases to publish academic journals. Some are also involved in outreach programs, like the *European spider of the year*, which raise awareness of these animals among the general public.

- American Arachnological Society (AAS)
- Arachnological Society of Japan
- Arachnologische Gesellschaft e.V.(AraGes)
- Australasian Arachnological Society (AAS)
- Belgische Arachnologische Vereniging/Société Arachnologique de Belgique (AraBel)
- British Arachnological Society (BAS)
- Czech Arachnological Society
- European Society of Arachnology (ESA)
- International Society of Arachnology (ISA)
- Grupo Ibérico de Aracnología-Sociedad Entomológica Aragonesa (GIA)
- Turkish Arachnological Society

Arachnological journals

Scientific journals devoted to the study of arachnids include:

- *Acta Arachnologica* — produced by the Japanese society

- *Acta Arachnologica Sinica*
- *Arachnologischen Mitteilungen* — produced by the AraGes
- *Bulletin of the British Arachnological Society* — produced by the BAS
- *Journal of Arachnology* — produced by the AAS
- *Revista Ibérica de Aracnología* — produced by the GIA
- *Revue Arachnologique*
- *Turkish Journal of Arachnology* — produced by the Turkish Society

Popular arachnology

In the 1970s, arachnids - particularly tarantulas - started to become popular as exotic pets. Many tarantulas thus become more widely known by their common names such as the Mexican redknee tarantula (*Brachypelma smithi*).

Various societies now focus on the husbandry, care, study and captive breeding of tarantulas, and other arachnids. They also typically produce journals or newsletters with articles and advice on these subjects. Examples would be:

- American Tarantula Society (ATS)
- British Tarantula Society (BTS)
- Deutsche Arachnologische Gesellschaft e.V.

Chapter- 13

Cetology

A researcher fires a biopsy dart at an orca. The dart will remove a small piece of the whale's skin and bounce harmlessly off the animal.

Cetology (from Greek κῆτος, *kētos*, "whale"; and -λογία, *-logia*) is the branch of marine mammal science that studies the approximately eighty species of whales, dolphins, and porpoise in the scientific order Cetacea.

Cetologists, or those who practice cetology, seek to understand and explain cetacean evolution, distribution, morphology, behavior, community dynamics, and other topics.

History

Observations about Cetacea have been recorded since at least classical times. Ancient Greek fishermen created an artificial notch on the dorsal fin of dolphins entangled in nets so that they could tell them apart years later.

Approximately 2,300 years ago, Aristotle carefully took notes on cetaceans while traveling on boats with fishermen in the Aegean Sea. In his book *Historia animalium* (History of animals), Aristotle was careful enough to distinguish between the baleen whales and toothed whales, a taxonomical separation still used today. He also described the Sperm Whale and the common dolphin, stating that they can live for at least twenty-five or thirty years. His achievement was remarkable for its time, because even today it is very difficult to estimate the life-span of advanced marine animals.

After Aristotle's death, much of the knowledge he had gained about cetaceans was lost, only to be re-discovered during the Renaissance.

Many of the medieval texts on cetaceans comes mainly from Scandinavia and Iceland, most come about around the mid-13th century.

One of the better known is *Speculum Regale*. In this text is described various species that lived around the island of Iceland. It mentions "orcs" that had dog-like teeth and would demonstrate the same kind of aggression towards other cetaceans as wild dogs would do to other terrestrial animals. The text even illustrated the hunting technique of Orcs, which are now called Orcas.

The *Speculum Regale* describes other cetaceans, including the Sperm Whale and Narwhal. Many times they were seen as terrible monsters, such as killers of men, and destroyers of ships. They even bore them odd names such as "Pig Whale", "Horse Whale", and "Red Whale".

But not all creatures described were said to be fierce. Some were seen to be good, such as whales that drove shoals of herring towards the shore. This was seen as very helpful to fisherman.

Many of the early studies were based on dead specimens and myth. The little information that was gathered was usual length, and a rough outer body anatomy. Because these animals live in water their entire lives, early scientists did not have the technology to go study these animals further. It was not until the 16th century that things would begin to change. That cetaceans would be proved to be mammals rather than fish.

Aristotle, as said above, argued they were mammals. But Pliny the Elder stated that they were fish, and it was followed by many naturalists. However, Pierre Belon (1517–1575) and G. Rondelet (1507–1566) persisted on convincing they were mammals. They argued that the animals had lungs and a uterus, just like mammals. Not until 1758, when Swedish botanist Carolus Linnaeus (1707–1778) published the tenth edition of *Systema Naturae*, were they seen as mammals.

Only decades later, French zoologist and paleontologist Baron Georges Cuvier (1769–1832) described the animals as mammals without any hind legs. Skeletons were assembled and displayed in the first natural history museums, and on a closer look and comparisons with other extinct animal fossils led zoologists to conclude that cetaceans came from a family of ancient land mammals.

Between the 9th-20th century, much of our information on cetaceans came from whalers. Whalers were the most knowledgeable about the animals, but their information was regarding migration routes and outer anatomy, and only little information of behavior.

During the 1960s, people began studying the animals intensively, often in dedicated research institutes such as the Tethys Research Institute in Milan. This came from both concern about wild populations and also the capture of larger animals such as the Orca, and gaining popularity of dolphin shows in marine parks.

Studying cetaceans

Humpback Whales often have distinct markings that enable scientists to identify individuals.

Studying cetaceans presents numerous challenges. Cetaceans only spend 10% of their time on the surface, and all they do at the surface is breathe. There is very little behavior seen at the surface.

It is also impossible to find any signs that an animal has been in an area. Cetaceans do not leave tracks that can be followed, nor do they leave dung that can tell important information about their diet. Many times Cetology consists of waiting and paying close attention.

Cetologists use equipment including hydrophones to listen to calls of communicating animals, binoculars and other optical devices for scanning the horizon, cameras, notes, and a few other devices and tools.

An alternative method of studying cetaceans is through examination of dead carcasses that wash up on the shore. If properly collected and stored, these carcasses can provide important information that is difficult to obtain in field studies.

Identifying individuals

In recent decades, methods of identifying individual cetaceans have enabled accurate population counts and insights into the lifecycles and social structures of various species.

One such successful system is photo-identification. This system was popularized by Michael Bigg, a pioneer in modern orca (killer whale) research. During the mid 1970s, Bigg and Graeme Ellis photographed local orcas in the British Columbian seas. After examining the photos, they realized they could recognize certain individual whales by looking at the shape and condition of the dorsal fin, and also the shape of the saddle patch. These are as unique as a human fingerprint; no one animal's looks exactly like another's. After they could recognize certain individuals, they found that the animals travel in stable groups called pods. Researchers use photo identification to identify specific individuals and pods.

The photographic system has also worked well in humpback whale studies. Researchers use the color of the pectoral fins and color of the fluke to identify individuals. Scars from orca attacks found on the flukes of humpbacks are also used in identification.

Chapter- 14

Neuroethology

Echolocation in bats is one model system in neuroethology

Neuroethology (from Greek *νεῦρον* - *neuron* "nerve" and *ἦθος* - *ethos* "habit or custom") is the evolutionary and comparative approach to the study of animal behavior and its underlying mechanistic control by the nervous system. This interdisciplinary branch of neuroscience endeavors to understand how the central nervous system translates biologically relevant stimuli into natural behavior". For example, many bats are capable of echolocation which is used for prey capture and navigation. Their ultrasonic calls and auditory systems are highly specialized for this function. The auditory system of bats is often cited as an example for how acoustic properties of sounds can be converted into a sensory map of behaviorally relevant features of sounds . Neuroethologists hope to uncover general principles of the nervous system from the study of animals with exaggerated or specialized behaviors.

As its name implies, neuroethology is a multidisciplinary field composed of neurobiology (the study of the nervous system) and ethology (the study of behavior in natural conditions). A central theme of the field of neuroethology, delineating it from other branches of neuroscience, is this focus on natural behavior. Natural behaviors may be thought of as those behaviors generated through means of natural selection (i.e. finding mates, navigation, locomotion, predator avoidance) rather than behaviors in disease states, or behavioral tasks that are particular to the laboratory.

Philosophy

Neuroethology is an integrative approach to solving problems in animal behavior, drawing upon several disciplines. Often, neuroethologists choose to study animals that are "specialists" in a particular type of behavior the researcher wishes to study (i.e. honeybees and their social behavior, bat echolocation, owl sound localization). The idea that an ideal animal exists for studying specific behaviors is based on Krogh's principle. The neuroethological approach stems from the idea that animals' nervous systems have evolved to address problems of sensing and acting in certain environmental niches. Central to the dogma of neuroethology, therefore, is the idea that nervous systems are best understood in the context of the problems they have evolved to solve.

The scope of neuroethological inquiry might be summarized by Jörg-Peter Ewert, a pioneer of neuroethology, when he considers the types of questions central to neuroethology in his 1980 introductory text to the field:

1. How are stimuli detected by an organism?
2. How are environmental stimuli in the external world represented in the nervous system?
3. How is information about a stimulus acquired, stored and recalled by the nervous system?
4. How is a behavioral pattern encoded by neural networks?
5. How is behavior coordinated and controlled by the nervous system?
6. How can the ontogenetic development of behavior be related to neural mechanisms?

Often central to addressing questions in neuroethology are comparative methodologies, drawing upon knowledge about related organisms' nervous systems, anatomies, life histories, behaviors and environmental niches. While it is not unusual for many types of neurobiology experiments to give rise to behavioral questions, many neuroethologists often begin their research programs by observing a species' behavior in its natural environment. Other approaches to understanding nervous systems include the systems identification approach, popular in engineering. The idea is to stimulate the system using a non-natural stimulus with certain properties. The system's response to the stimulus may be used to analyze the operation of the system. Such an approach is useful for linear systems, but the nervous system is notoriously nonlinear, and neuroethologists argue that such an approach is limited. This argument is supported by experiments in the auditory system. These experiments show that neural responses to complex sounds, like social calls, can not be predicted by the knowledge gained from studying the responses due to pure tones (one of the non-natural stimuli favored by auditory neurophysiologists). This is because of the non-linearity of the system.

Modern neuroethology is largely influenced by the research techniques used. Neural approaches are necessarily very diverse, as is evident through the variety of questions asked, measuring techniques used, relationships explored, and model systems employed. Techniques utilized since 1984 include the use of intracellular dyes, which make maps of identified neurons possible, and the use of brain slices, which bring vertebrate brains into better observation through intracellular electrodes (Hoyle 1984). Currently, other fields toward which neuroethology may be headed include computational neuroscience, molecular genetics, neuroendocrinology. The existing field of neural modeling may also expand into neuroethological terrain, due to its practical uses in robotics. In all this, neuroethologists must use the right level of simplicity to effectively guide research towards accomplishing the goals of neuroethology.

Critics of neuroethology might consider it a branch of neuroscience concerned with 'animal trivia'. Though neuroethological subjects tend not to be traditional neurobiological model systems (i.e. *Drosophila*, *C. elegans*, or *Danio rerio*), neuroethological approaches emphasizing comparative methods have uncovered many concepts central to neuroscience as a whole, such as lateral inhibition, coincidence detection, and sensory maps. The discipline of neuroethology has also discovered and explained the only vertebrate behavior for which the entire neural circuit has been described: the electric fish jamming avoidance response. Beyond its conceptual contributions, neuroethology makes indirect contributions to advancing human health. By understanding simpler nervous systems, many clinicians have used concepts uncovered by neuroethology and other branches of neuroscience to develop treatments for devastating human diseases.

Historical origins

The field of neuroethology owes part of its existence to the establishment of ethology as a unique discipline within the discipline of Zoology. Although animal behavior had been studied since the time of Aristotle (384-342 BC), it was not until the early twentieth century that ethology finally became distinguished from natural science (a strictly descriptive field) and ecology. The main catalysts behind this new distinction were the research and writings of Konrad Lorenz and Niko Tinbergen.

Konrad Lorenz was born in Austria in 1903, and is widely known for his contribution of the theory of fixed action patterns (FAPs): endogenous, instinctive behaviors involving a complex sequence of movements that are triggered ("released") by a certain kind of stimulus. This sequence always proceeds to completion, even if the original stimulus is removed. It is also species-specific and performed by nearly all members. Lorenz constructed his famous "hydraulic model" to help illustrate this concept, as well as the concept of action specific energy, or drives.

Niko Tinbergen was born in the Netherlands in 1907 and worked closely with Lorenz in the development of the FAP theory; their studies focused on the egg retrieval response of nesting geese. Tinbergen performed extensive research on the releasing mechanisms of particular FAPs, and used the bill-pecking behavior of baby herring gulls as his model system. This led to the concept of the supernormal stimulus. Tinbergen is also well known for his four questions that he believed ethologists should be asking about any given animal behavior; among these is that of the mechanism of the behavior, on a physiological, neural and molecular level, and this question can be thought of in many regards as the keystone question in neuroethology. Tinbergen also emphasized the need for ethologists and neurophysiologists to work together in their studies, a unity that has become a reality in the field of neuroethology.

Unlike behaviorism, which studied animals' reactions to non-natural stimuli in artificial, laboratory conditions, ethology sought to categorize and analyze the natural behaviors of animals in a field setting. Similarly, neuroethology asks questions about the neural bases of *naturally occurring* behaviors, and seeks to mimic the natural context as much as possible in the laboratory.

Although the development of ethology as a distinct discipline was crucial to the advent of neuroethology, equally important was the development of a more comprehensive understanding of Neuroscience. Contributors to this new understanding were the Spanish Neuroanatomist, Ramon y Cajal, and physiologists Charles Sherrington, Edgar Adrian, Alan Hodgkin, and Andrew Huxley. Charles Sherrington, who was born in Great Britain in 1857, is famous for his work on the nerve synapse as the site of transmission of nerve impulses, and for his work on reflexes in the spinal cord. His research also led him to hypothesize that every muscular activation is coupled to an inhibition of the opposing muscle. He was awarded a Nobel Prize for his work in 1932 along with Lord Edgar Adria who made the first physiological recordings of neural activity from single nerve fibers.

Alan Hodgkin and Andrew Huxley (born 1914 and 1917, respectively, in Great Britain), are known for their collaborative effort to understand the production of action potentials in giant squid neurons. The pair also proposed the existence of ion channels to facilitate action potential initiation, and were awarded the Nobel Prize in 1963 for their efforts.

As a result of this pioneering research, many scientists then sought to connect the physiological aspects of the nervous and sensory systems to specific behaviors. These scientists – Karl von Frisch, Erich von Holst, and Theodore Bullock – are frequently referred to as the “fathers” of neuroethology. Neuroethology did not really come into its own, though, until the 1970s and 1980s, when new, sophisticated experimental methods allowed researchers such as Mark Konishi, Walter Heiligenberg, Jörg-Peter Ewert, and others to study the neural circuits underlying verifiable behavior.

Modern neuroethology

The International Society for Neuroethology (ISN) represents the present discipline of neuroethology, which was founded on the occasion of the NATO-Advanced Study Institute "Advances in Vertebrate Neuroethology" (August 13-24, 1981) organized by J.-P. Ewert, D.J. Ingle and R.R. Capranica, held at the University of Kassel in Hofgeismar, Germany (cf. report Trends in Neurosci. 5:141-143,1982). The first president of ISN was Theodore H. Bullock. The ISN has met every three years since its first meeting in Tokyo in 1986.

Its membership draws from many research programs around the world; many of its members are students and faculty members from medical schools and neurobiology departments from various universities. Modern advances in neurophysiology techniques have enabled more exacting approaches in an ever-increasing number of animal systems, as size limitations are being dramatically overcome. Survey of the most recent (2007) congress of the ISN meeting symposia topics gives some idea of the field’s breadth:

- Comparative aspects of spatial memory (rodents, birds, humans, bats)
- Influences of higher processing centers in active sensing (primates, owls, electric fish, rodents, frogs)
- Animal signaling plasticity over many time scales (electric fish, frogs, birds)
- Song production and learning in passerine birds
- Primate sociality
- Optimal function of sensory systems (flies, moths, frogs, fish)
- Neuronal complexity in behavior (insects, computational)
- Contributions of genes to behavior (Drosophila, honeybees, zebrafish)
- Eye and head movement (crustaceans, humans, robots)
- Hormonal actions in brain and behavior (rodents, primates, fish, frogs, and birds)
- Cognition in insects (honeybee)

Application to technology

Neuroethology can help create advancements in technology through an advanced understanding of animal behavior. Model systems were generalized from the study of simple and related animals to humans. For example the neuronal cortical space map discovered in bats, a specialized champion of hearing and navigating, elucidated the concept of a computational space map. In addition, the discovery of the space map in the barn owl led to the first neuronal example of the Jeffress model. This understanding is translatable to understanding spatial localization in humans, a mammalian relative of the bat. Today, knowledge learned from neuroethology are being applied in new technologies. For example, Randall Beer and his colleagues used algorithms learned from insect walking behavior to create robots designed to walk on uneven surfaces (Beer et al.). . Neuroethology and technology contribute to one another bidirectionally.

Neuroethologists seek to understand the neural basis of a behavior as it would occur in an animal's natural environment but the techniques for neurophysiological analysis are lab-based, and cannot be performed in the field setting. This dichotomy between field and lab studies poses a challenge for neuroethology. From the neurophysiology perspective, experiments must be designed for controls and objective rigor, which contrasts with the ethology perspective—that the experiment be applicable to the animal's natural condition, which is uncontrolled, or subject to the dynamics of the environment. An early example of this is when Walter Rudolf Hess developed focal brain stimulation technique to examine a cat's brain controls of vegetative functions in addition to other behaviors. Even though this was a breakthrough in technological abilities and technique, it was not used by many neuroethologists originally because it compromised a cat's natural state, and, therefore, in their minds, devalued the experiments' relevance to real situations.

When intellectual obstacles like this were overcome, it led to a golden age of neuroethology, by focusing on simple and robust forms of behavior, and by applying modern neurobiological methods to explore the entire chain of sensory and neural mechanisms underlying these behaviors (Zupanc 2004). New technology allows neuroethologists to attach electrodes to even very sensitive parts of an animal such as its brain while it interacts with its environment. The founders of neuroethology ushered this understanding and incorporated technology and creative experimental design. Since then even indirect technological advancements such as battery-powered and waterproofed instruments have allowed neuroethologists to mimic natural conditions in the lab while they study behaviors objectively. In addition, the electronics required for amplifying neural signals and for transmitting them over a certain distance have enabled neuroscientists to record from behaving animals performing activities in naturalistic environments. Emerging technologies can complement neuroethology, augmenting the feasibility of this valuable perspective of natural neurophysiology.

Another challenge, and perhaps part of the beauty of neuroethology, is experimental design. The value of neuroethological criteria speak to the reliability of these experiments, because these discoveries represent behavior in the environments in which they evolved. Neuroethologists foresee future advancements through using new technologies and techniques, such as computational neuroscience, neuroendocrinology, and molecular genetics that mimic natural environments.

Case studies

Jamming avoidance response

In 1963, two scientists, Akira Watanabe and Kimihisa Takeda, discovered the behavior of the jamming avoidance response in the knifefish *Eigenmannia* sp. In collaboration with T.H. Bullock and colleagues, the behavior was further developed. Finally, the work of W. Heiligenberg expanded it into a full neuroethology study by examining the series of neural connections that led to the behavior. *Eigenmannia* is a weakly electric fish that can self-generate electric discharges through electrocytes in its tail. Furthermore, it has the ability to electrolocate by analyzing the perturbations in its electric field. However when the frequency of a neighboring fish's current is very close (less than 20 Hz difference) to that of its own, the fish will avoid having their signals interfere through a behavior known as Jamming Avoidance Response. If the neighbor's frequency is higher than the fish's discharge frequency, the fish will lower its frequency, and vice versa. The sign of the frequency difference is determined by analyzing the "beat" pattern of the incoming interference which consists of the combination of the two fish's discharge patterns.

Neuroethologists performed several experiments under *Eigenmannia*'s natural conditions to study how it determined the sign of the frequency difference. They manipulated the fish's discharge by injecting it with curare which prevented its natural electric organ from discharging. Then, an electrode was placed in its mouth and another was placed at the tip of its tail. Likewise, the neighboring fish's electric field was mimicked using another set of electrodes. This experiment allowed neuroethologists to manipulate different discharge frequencies and observe the fish's behavior. From the results, they were able to conclude that the electric field frequency, rather than an internal frequency measure, was used as a reference. This experiment is significant in that not only does it reveal a crucial neural mechanism underlying the behavior but also demonstrates the value neuroethologists place on studying animals in their natural habitats.

Feature analysis in toad vision

The recognition of prey and predators in the toad was first studied in depth by Jörg-Peter Ewert. He began by observing the natural prey-catching behavior of the common toad (*Bufo bufo*) and concluded that the animal followed a sequence that consisted of stalking, binocular fixation, snapping, swallowing and mouth-wiping. However, initially, the toad's actions were dependent on specific features of the sensory stimulus: whether it demonstrated worm or anti-worm configurations. It was observed that the worm configuration, which signaled prey, was initiated by movement along the object's long axis, whereas anti-worm configuration, which signaled predator, was due to movement along the short axis (Zupanc 2004).

Ewert and coworkers adopted a variety of methods to study the predator versus prey behavior response. They conducted recording experiments where they inserted electrodes into the brain, while the toad was presented with worm or anti-worm stimuli. This technique was repeated at different levels of the visual system and also allowed feature detectors to be identified. In focus was the discovery of prey-selective neurons in the optic tectum, whose axons could be traced towards the snapping pattern generating cells in the hypoglossal nucleus. The discharge patterns of prey-selective tectal neurons in response to prey objects – in freely moving toads – „predicted" prey-catching reactions such as snapping. Another approach, called stimulation experiment, was carried out in freely moving toads. Focal electrical stimuli were applied to different regions of the brain, and the toad's response was observed. When the thalamic-pretectal region was stimulated, the toad exhibited escape responses, but when the tectum was stimulated in an area close to prey-selective neurons, the toad engaged in prey catching behavior (Carew 2000). Furthermore, neuroanatomical experiments were carried out where the toad's thalamic-pretectal/tectal connection was lesioned and the resulting deficit noted: the prey-selective properties were abolished both in the responses of prey-selective neurons and in the prey catching behavior. These and other experiments suggest that prey selectivity results from pretecto-tectal influences.

Ewert and coworkers showed in toads that there are stimulus-response mediating pathways that translate perception (of visual sign stimuli) into action (adequate behavioral responses). In addition there are modulatory loops that initiate, modify or specify this mediation (Ewert 2004). Regarding the latter, for example, the telencephalic caudal ventral striatum is involved in a loop gating the stimulus-response mediation in a manner of directed attention. The telencephalic ventral medial pallium („primordium hippocampi"), however, is involved in loops that either modify prey-selection due to associative learning or specify prey-selection due to non-associative learning, respectively.