Colouration, Camouflage and Mimicry in Animals

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Chapter 1

Animal Colouration

Animal colouration has been a topic of interest and research in biology for well over a century. Colours may be cryptic (functioning as an adaptation allowing the prevention of prey detection; aposematic (functioning as a warning of unprofitability) or may be the result of sexual selection. Colouration may also be function in mimicry of other organisms. The subject may be investigated in terms of both the chemical and physical basis of the colours (proximate cause) and the evolution of colouration (ultimate cause).

Camouflage is generally viewed as a result of natural selection, and involves an organism's colour blending in with its biotic (e.g. moss) or abiotic (e.g. sand) surroundings. Camouflage is often accompanied by behavioural adaptations that make the most of it, such as landing on areas of similar colour, and aligning the body correctly. It may involve costs as well as benefits, such as the cost of finding a suitable resting spot. Colour may change during the seasons, during an organism's life cycle, or even over very brief intervals, such as with the chameleon. Polymorphism may also occur, allowing individuals of the same species to have different camouflage, and making prey detection more difficult for predators. Organisms living in the same environment may come to have similar colouration through convergent evolution. Colours are an aspect of only one of the senses, and although the visual system is most important for humans, some animals cannot even see (such as those living in caves, underground, in the deep sea, or those active at night) and their colour may be of little or no adaptive value. These organisms rely primarily on other senses, such as olfaction and hearing, and even electroreception.

Concealment

Chapman's Zebras in Botswana

A camouflaged Jumping spider can easily capture prey.

The Goldenrod Crab Spider (*Misumena vatia*) has the capacity of changing colour by secreting a liquid yellow pigment into the outer cell layer of the body.

Cryptic colouration has evolved in many species that have been subjected to the pressures of predation and also in predatory species. Such colours help predators (aggressive resemblance or anticryptic colouring) and prey (protective resemblance or procryptic colouring). Protective resemblance is far commoner among animals than aggressive resemblance, in correspondence with the fact that predaceous forms are as a rule much larger and much less numerous than their prey. In the case of insectivorous vertebrates and their prey such differences exist in an exaggerated form. Cryptic colouring, whether used for defence or attack, may be either general or special. In general resemblance the animal, in consequence of its colouring, produces the same effect as its environment, but the conditions do not require any special adaptation of shape and outline. General resemblance is especially common among the animals inhabiting some uniformly coloured expanse of the Earth's surface, such as an ocean or a desert. In the former, animals of all shapes are frequently protected by their transparent blue colour; on the latter, equally diverse forms are defended by their sandy appearance. The effect of a uniform appearance may be produced by a combination of tints in startling contrast. Thus the black and white stripes of the zebra blend together at a little distance, and their proportion is such as exactly to match the pale tint which arid ground possesses when seen by moonlight (F Galton, *South Africa*, London, 1889).

Special resemblance is far commoner than general, and is the form which is usually met with on the diversified surface of the earth, on the shores, and in shallow water, as well as on the floating masses of algae on the surface of the ocean, such as the Sargasso Sea. In these environments the cryptic colouring of animals is usually aided by special modifications of shape, and by the instinct which leads them to assume particular attitudes. Complete stillness and the assumption of a certain attitude play an essential part in general resemblance on land; but in special resemblance the attitude is often highly specialized, and perhaps more important than any other element in the complex method by which concealment is effected. In special resemblance the combination of colouring, shape and attitude is such as to produce a more or less exact resemblance to some one of the objects in the environment, such as a leaf or twig, a patch of lichen, or flake of bark. In all cases the resemblance is to some object which is of no interest to the enemy or prey respectively. The animal is not hidden from view by becoming indistinguishable from its background, as in the cases of general resemblance, but it is mistaken for some well-known object.

In the past these effects were explained as a result of the direct influence of the environment upon the individual (GLL Georges-Louis Leclerc, Comte de Buffon), or by the inherited effects of effort and the use and disuse of parts (JEP Jean-Baptiste Lamarck), but natural selection, which can accumulate any and every variation which tends towards survival, has been the accepted explanation now for almost a century. A few of the chief types of methods by which concealment is effected may be briefly described. The colours of large numbers of vertebrate animals are darkest on the back, and become gradually lighter on the sides, passing into white on the belly. Abbott Handerson Thayer (*The Auk*, vol. xiii., 1896) has suggested that this gradation obliterates the appearance of solidity, which is due to shadow.

The colour-harmony, which is also essential to concealment, is produced because the back is of the same tint as the environment (e.g. earth) bathed in the cold blue-white of the sky, while the belly, being cold blue-white bathed in shadow and yellow earth reflections, produces the same effect. Thayer has made models (in the natural history museums at London, Oxford and Cambridge) which support his interpretation in a very convincing manner. This method of neutralizing shadow for the purpose of concealment by increased lightness of tint was first suggested by EB Poulton in the case of a larva (*Trans. Ent. Soc. Loud.*, 1887, p. 294) and a pupa (*Trans. Ent. Soc. Loud.*, 1888, pp. 596, 597), but he did not appreciate the great importance of the principle. In an analogous method an animal in front of a background of dark shadow may have part of its body obliterated by the existence of a dark tint, the remainder resembling, e.g., a part of a leaf (W Müller, *Zool. Jahr.* JW Spengel, Jena, 1886).

A camouflaged Orange Oak Leaf butterfly (centre)

This method of rendering invisible any part which would interfere with the resemblance is well known in mimicry. A common aid to concealment is the adoption by different individuals of two or more different appearances, each of which resembles some special object to which an enemy is indifferent. Thus the leaf-like butterflies (Kallima) present various types of colour and pattern on the under side of the wings, each of which closely resembles some well-known appearance presented by a dead leaf; and the common British yellow under-wing moth (Tryphaena pronuba) is similarly polymorphic on the upper side of its upper wings, which are exposed as it suddenly drops among dead leaves. Caterpillars and pupae are also commonly dimorphic, green and brown. Such differences as these extend the area which an enemy is compelled to search in order to make a living.

In many cases the cryptic colouring changes appropriately during the course of an individual life, either seasonally, as in the ptarmigan or Alpine Hare, or according as the individual enters a new environment in the course of its growth (such as larva, pupa, imago, etc.). In insects with more than one brood in the year, seasonal dimorphism is often seen, and the differences are sometimes appropriate to the altered condition of the environment as the seasons change. The causes of change in these and Arctic animals are insufficiently worked out: in both sets there are observations or experiments which indicate changes from within the organism, merely following the seasons and not caused by them, and other observations or experiments which prove that certain species are susceptible to the changing external influences. In certain species concealment is effected by the use of adventitious objects, which are employed as a covering. Examples of this allocryptic defence are found in the tubes of the caddis fly larvae (Trichoptera), or the objects made use of by crabs of the genera Hyas, Stenorhynchus, etc. Such animals are concealed in any environment. If sedentary, like the former example, they are covered up with local materials; if wandering, like the latter, they have the instinct to reclothe. Allocryptic methods may also be used for aggressive purposes, as the ant-lion larva, almost buried in sand, or the large frog Ceratophrys, which covers its back with earth when waiting for its prey. Another form of allocryptic defence is found in the use of the colour of the food in the digestive organs showing through the transparent body, and in certain cases the adventitious colour may be dissolved in the blood or secreted in superficial cells of the body: thus certain insects make use of the chlorophyll of their food (Poulton, *Proc. Roy. Soc.* liv. 417). The most perfect cryptic powers are possessed by those animals in which the individuals can change their colours into any tint which would be appropriate to a normal environment. This power is widely prevalent in fish, and also occurs in Amphibia and Reptilia (the chameleon affording a well-known example). Analogous powers exist in certain Crustacea and Cephalopoda. All these rapid changes of colour are due to changes in shape or position of superficial pigment cells controlled by the nervous system. That the latter is itself stimulated by light through the medium of the eye and optic nerve has been proved in many cases. Animals with a short life-history passed in a single environment, which, however, may be very different in the case of different individuals, may have a different form of variable cryptic colouring, namely, the power of adapting their colour once for all (many pupae), or once or twice (many larvae). In these cases the effect appears to be produced through the nervous system, although the stimulus of light probably acts on the skin and not through the eyes. Particoloured surfaces do not produce particoloured pupae, probably because the antagonistic stimuli neutralize each other in the central nervous system, which then disposes the superficial colours so that a neutral or intermediate effect is produced over the whole surface (Poulton, *Trans. Ent. Soc. Lond.*, 1892, p. 293).

Cryptic colouring may incidentally produce superficial resemblances between animals; thus desert forms concealed in the same way may gain a likeness to each other, and in the same way special resemblances, e.g. to lichen, bark, grasses, pine-needles, etc., may sometimes lead to a tolerably close similarity between the animals which are thus concealed. Such, likeness may be called syncryptic or common protective (or aggressive) resemblance, and it is to be distinguished from mimicry and common warning colours, in which the likeness is not incidental, but an end in itself. Syncryptic resemblances have much in common with those incidentally caused by functional adaptation, such as the mole-like forms produced in the burrowing Insectivora, Rodentia and Marsupialia. Such likeness may be called syntechnic resemblance, incidentally produced by dynamic similarity, just as syncryptic resemblance is produced by static similarity.

Warning and signalling (semantic colours)

A venomous coral snake.

Warning colouration is the exact opposite of camouflage, its function being to render the animal conspicuous to its enemies, so that it can be easily seen, well remembered, and avoided in future.

Warning colours are associated with some quality or weapon which renders the possessor unpleasant or dangerous, such as unpalatability, an evil odour, a sting, the poison-fang, etc. The object being to warn an enemy off, these colours are also called *aposematic*.

Recognition markings, on the other hand, are episematic, assisting the individuals of the same species to keep together when their safety depends upon numbers, or easily to follow each other to a place of safety, the young and inexperienced benefiting by the example of the older. Episematic characters are far less common than aposematic, and these than cryptic; although, as regards the latter comparison, the opposite impression is generally produced from the very fact that concealment is so successfully attained.

Warning or aposematic colours, together with the qualities they indicate, depend, as a rule, for their very existence upon the abundance of palatable food supplied by the animals with cryptic colouring (the *models*). Unpalatability, or even the possession of a sting, is not sufficient defence unless there is enough food of another kind to be obtained at the same time and place (Poulton, *Proc. Zool. Soc.*, 1887, p. 191). Hence insects with warning colours are not seen in temperate countries except at the time when insect life as a whole is most abundant; and in warmer countries, with well-marked wet and dry seasons, it will probably be found that warning colours are proportionately less developed in the latter.

In many species of African butterflies belonging to the genus *Junonia*, including the subgenus *Precis*, the wet-season broods are distinguished by the more or less conspicuous under sides of the wings, those of the dry season being highly cryptic. Warning colours are, like cryptic, assisted by special adaptations of the body-form, and especially by movements which assist to render the colour as conspicuous as possible. On this account animals with warning colours generally move or fly slowly, and it is the rule in butterflies that the warning patterns are similar on both upper and under sides of the wings.

Many animals, when attacked or disturbed, sham death (as it is commonly but wrongly described), falling motionless to the ground. In the case of well-concealed animals this instinct gives them a second chance of escape in the earth or among the leaves, etc., when they have been once detected; animals with warning colours are, on the other hand, enabled to assume a position in which their characters are displayed to the full (J. Portschinsky, Lepidopterorum Rossiae Biologia, St Petersburg, 1890, plate i. figs. 16, 17). In both cases a definite attitude is assumed, which is not that of death.

Other warning characters exist in addition to colouring: thus sound is made use of by the disturbed rattlesnake and the Indian Ec/jis, etc. Large birds, when attacked, often adopt a threatening attitude, accompanied by a terrifying sound. The cobra warns an intruder chiefly by attitude and the dilation of the flattened neck, the effect being heightened in some species by the spectacles. In such cases we often see the combination of cryptic and sematic methods, the animal being concealed until disturbed, when it instantly assumes an aposematic attitude. The advantage to the animal itself is clear: a poisonous snake gains nothing by killing an animal it cannot eat; while the poison does not cause immediate death, and the enemy would have time to injure or destroy the snake.

In the case of small unpalatable animals with warning colours the enemies would only first become aware of the unpleasant quality by tasting and often destroying their prey; but kin of the organism killed may gain by the experience thus conveyed, even though the individual might suffer. An insect-eating animal does not come into the world with knowledge: it has to learn by experience, and warning colours enable this education as to what to avoid to be gained by a small instead of a large waste of life. Furthermore, great tenacity of life is usually possessed by animals with warning colours. The tissues of aposematic insects generally possess great elasticity and power of resistance, so that large numbers of individuals can recover after very severe treatment.

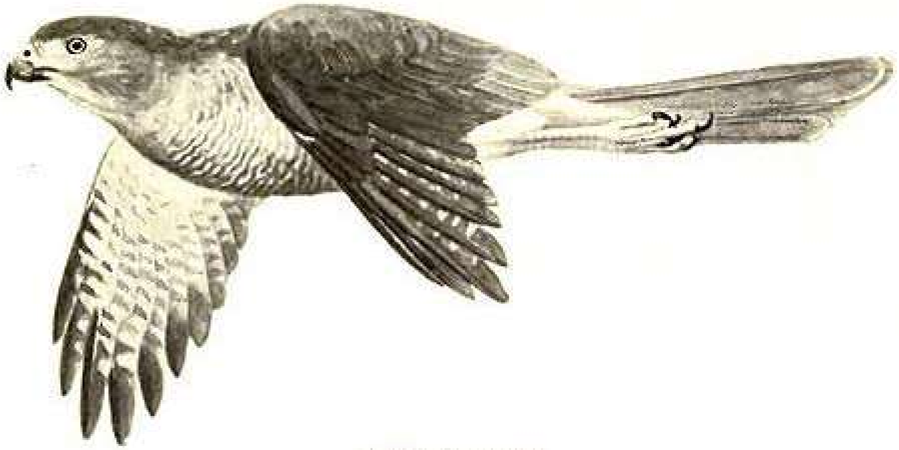
The brilliant warning colours of many caterpillars attracted the attention of Charles Darwin when he was thinking over his hypothesis of sexual selection, and he wrote to AR Wallace on the subject (C Darwin, *Life and Letters*, London, 1887, uI. 93). Wallace, in reply, suggested their interpretation as warning colours, a suggestion since verified by experiment (*Proc. Ent. Soc. Lond.*, 1867, p. lxxx; *Trans. Ent. Soc. Loud.*, 1869, pp. 21 and 27). Although animals with warning colours are probably but little attacked by the ordinary enemies of their class, they have special enemies which keep the numbers down to the average. Thus the cuckoo appears to be an insectivorous bird which will freely devour conspicuously coloured unpalatable larvae. The effect of the warning colours of caterpillars is often intensified by gregarious habits. Another aposematic use of colours and structures is to divert attention from the vital parts, and thus give the animal attacked an extra chance of escape. The large, conspicuous, easily torn wings of butterflies and moths act in this way, as is found by the abundance of individuals which may be captured with notches bitten symmetrically out of both wings when they were in contact. The eye-spots and tails so common on the hinder part of the hind wing, and the conspicuous apex so frequently seen on the fore wing, probably have this meaning. Their position corresponds to the parts which are most often found to be notched. In some cases (e.g. many Lycaenidae) the tail and eye-spot combine to suggest the appearance of a head with antennae at the posterior end of the butterfly, the deception being aided by movements of the hind wings. The flat-topped tussocks of hair on many caterpillars look like conspicuous fleshy projections of the body, and they are held prominently when the larva is attacked. If seized, the tussock comes out, and the enemy is greatly inconvenienced by the fine branched hairs. The tails of lizards, which easily break off, are to be similarly explained, the attention of the pursuer being probably still further diverted by the extremely active movements of the amputated member. Certain crabs similarly throw off their claws when attacked, and the claws continue to snap most actively. The tail of the dormouse, which easily comes off, and the extremely bushy tail of the squirrel, are probably of use in the same manner. Animals with warning colours often tend to resemble each other superficially.

This fact was first pointed out by Henry W. Bates in his paper on the theory of mimicry (*Trans. Linn. Soc.* vol. xxiii., 1862, p. 495). He showed that the conspicuous, presumably unpalatable, tropical American butterflies, belonging to very different groups, which are mimicked by others, also tend to resemble each other, the likeness being often remarkably exact. These resemblances were not explained by his theory of mimicry, and he could only suppose that they had been produced by the direct influence of a common environment. The problem was solved in 1879 by Fritz Müller, who suggested that life is saved by this resemblance between warning colours, inasmuch as the education of young inexperienced enemies is facilitated. Each species which falls into a group with common warning (synaposematic) colours contributes to save the lives of the other members. It is sufficiently obvious that the amount of learning and remembering, and consequently of injury and loss of life involved in the process, are reduced when many species in one place possess the same aposematic colouring, instead of each exhibiting a different danger-signal. These resemblances are often described as Mullerian mimicry, as distinguished from true or Batesian mimicry described in the next section. Similar synaposematic resemblances between the specially protected groups of butterflies were afterwards shown to exist in tropical Asia, the East Indian Islands and Polynesia by F Moore (*Proc. Zool. Soc.*, 1883, p. 201), and in Africa by EB Poulton (*Report Brit. Assoc.*, 1897, p. 688). R Meldola (*Ann. and Mag. Nat. Hist. X.*, 1882, p. 417) first pointed out and explained in the same manner the remarkable general uniformity of colour and pattern which runs through so many species of each of the distasteful groups of butterflies; while, still later, Poulton (*Proc. Zool. Soc.*, 1887, p. 191) similarly extended the interpretation to the synaposematic resemblances between animals of all kinds in the same country. Thus, for example, longitudinal or circular bands of the same strongly contrasted colours are found in species of many groups with distant affinities.

Certain animals, especially the Crustacea, make use of the special defence and warning colours of other animals. Thus the English hermit-crab, *Pagurus bernhardus*, commonly carries the sea-anemone, *Sagartia parasitica*, on its shell; while another English species, *Pagurus pridauxii*, inhabits a shell which is invariably clothed by the flattened anemone, *Adamsia palliata*.

The white patch near the tail which is frequently seen in the gregarious ungulates, and is often rendered conspicuous by adjacent black markings, probably assists the individuals in keeping together; and appearances with probably the same interpretation are found in many birds. The white upturned tail of the rabbit is probably of use in enabling the individuals to follow each other readily. The difference between a typical aposematic character appealing to enemies, and episematic intended for other individuals of the same species, is well seen when we compare such examples as (1) the huge banner-like white tail, conspicuously contrasted with the black or black and white body, by which the slow-moving skunk warns enemies of its power of emitting an intolerably offensive odour; (2) the small upturned white tail of the rabbit, only seen when it is likely to be of use and when the owner is moving, and, if pursued, very rapidly moving, towards safety.

Mimicry or pseudo-sematic colours



SHIKRA HAWK

The upper side of the tail is marked as in the Hawk-cuckoo

By permission of Messrs. Hutchinson & Co.

BRAIN-FEVER BIRD

The exact correspondence of this mimic with its model is notable even in black-and-white

By permission of Messrs. Hutchinson & Co.

Some hawk-cuckoos resemble sparrow-hawks.

The fact that animals with distant affinities may more or less closely resemble each other was observed long before the existing explanation was possible. Its recognition is implied in a number of insect names with the termination -formis, usually given to species of various orders which more or less closely resemble the stinging hymenoptera. The usefulness of the resemblance was suggested in Kirby and Spences *Introduction to Entomology*, London, 1817, ii. 223. H.W. Bates (*Trans. Linn. Soc.* vol. XXiII., 1862, p. 495) first proposed an explanation of mimicry based on the theory of natural selection. He supposed that every step in the formation and gradual improvement of the likeness occurred in consequence of its usefulness in the struggle for life. This was one of the first attempts to apply the theory of natural selection to a large class of phenomena up to that time well known but unexplained. Numerous examples of mimicry among tropical American butterflies were discussed by Bates in his paper; and in 1866 Wallace extended the hypothesis to the butterflies of the tropical East (*Trans. Linn, Soc.* vol. xxv., 1866, p. 19). The term mimicry is used in various senses. It is often extended, as indeed it was by Bates, to include all the superficial resemblances between animals and any part of their environment. Wallace, however, separated the cryptic resemblances already described, and the majority of naturalists have followed this convenient arrangement. In cryptic resemblance an animal resembles some object of no interest to its enemy (or prey), and in so doing is concealed; in mimicry an animal resembles some other animal which is specially disliked by its enemy, or some object which is specially attractive to its prey, and in so doing becomes conspicuous. Some naturalists have considered mimicry to include all superficial likenesses between animals, but such a classification would group together resemblances which have widely different uses.

The resemblance of a mollusc to the coral on which it lives, or an external parasite to the hair or skin of its host, would be procryptic; that between moths which resemble lichen, syncryptic; between distasteful insects, synaposematic; between the Insectivor mole and the Rodent mole-rat, syntechnic; the essential element in mimicry is that it is a false warning (pseud-aposematic) or false recognition (pseudepisematic) character.

Some have considered that mimicry indicates resemblance to a moving object; but apart from the non-mimetic likenesses between animals classified above, there are ordinary cryptic resemblances to drifting leaves, swaying bits of twig, etc., while truly mimetic resemblances are often specially adapted for the attitude of rest. Many use the term mimicry to include synaposematic as well as pseudo-sematic resemblances, calling the former Müllerian, the latter Batesian, mimicry. The objection to this grouping is that it takes little account of the deceptive element which is essential in mimicry. In synaposematic colouring the warning is genuine, in pseudaposematic it is a sham. The term mimicry has led to much misunderstanding from the fact that in ordinary speech it implies deliberate imitation. The production of mimicry in an individual animal has no more to do with consciousness or taking thought than any of the other processes of growth. Protective mimicry is here defined as an advantageous and superficial resemblance of one animal to another, which latter is specially defended so as to be disliked or feared by the majority of enemies of the groups to which both belong. Resemblance which appeals to the sense of sight, sometimes to that of hearing, and rarely to smell, but does not extend to deep-seated characters except when the superficial likeness is affected by them. Mutatis mutandis, this definition will apply to aggressive (pseudepisematic) resemblance. The conditions under which mimicry occurs have been stated by Wallace:

1. that the imitative species occur in the same area and occupy the same station as the imitated;
2. that the imitators are always the more defenceless;
3. that the imitators are always less numerous in individuals;

4. that the imitators differ from the bulk of their allies;
5. that the imitation, however minute, is external and visible only, never extending to internal characters or to such as do not affect the external appearance.

It is obvious that conditions 2 and 3 do not hold in the case of Müllerian mimicry. Mimicry has been explained, independently of natural selection, by the supposition that it is the common expression of the direct action of common causes, such as climate, food, etc.; also by the supposition of independent lines of evolution leading to the same result without any selective action in consequence of advantage in the struggle; also by the operation of sexual selection.

It is proposed, in conclusion, to give an account of the broad aspects of mimicry, and attempt a brief discussion of the theories of origin of each class of facts. It will be found that in many cases the argument here made use of applies equally to the origin of cryptic and sematic colours. The relationship between these classes has been explained: mimicry is, as Wallace has stated (Darwinism, London, 1889), merely an exceptional form of protective resemblance. Now, protective (cryptic) resemblance cannot be explained on any of the lines suggested above, except natural selection; even sexual selection fails, because cryptic resemblance is especially common in the immature stages of insect life. But it would be unreasonable to explain mimetic resemblance by one set of principles and cryptic by another and totally different set. Again, it may be plausible to explain the mimicry of one butterfly for another on one of the suggested lines, but the resemblance of a fly or moth to a wasp is by no means so easy, and here selection would be generally conceded; yet the appeal to antagonistic principles to explain such closely related cases would only be justified by much direct evidence. Furthermore, the mimetic resemblances between butterflies are not haphazard, but the models almost invariably belong only to certain sub-families, the Danainae and Acraeinae in all the warmer parts of the world, and, in tropical America, the Ithomiinae and Heliconiinae as well. These groups have the characteristics of aposematic species, and no theory but natural selection explains their invariable occurrence as models wherever they exist. It is impossible to suggest, except by natural selection, any explanation of the fact that mimetic resemblances are confined to changes which produce or strengthen a superficial likeness. Very deep-seated changes are generally involved, inasmuch as the appropriate instincts as to attitude, etc., are as important as colour and marking. The same conclusion is reached when we analyse the nature of mimetic resemblance and realize how complex it really is, being made up of colours, both pigmentary and structural, pattern, form, attitude and movement. A plausible interpretation of colour may be wildly improbable when applied to some other element, and there is no explanation except natural selection which can explain all these elements. The appeal to the direct action of local conditions in common often breaks down upon the slightest investigation, the difference in habits between mimic and model in the same locality causing the most complete divergence in their conditions of life. Thus many insects produced from burrowing larvae mimic those whose larvae live in the open. Mimetic resemblance is far commoner in the female than in the male, a fact readily explicable by selection, as suggested by Wallace, for the female is compelled to fly more slowly and to expose itself while laying eggs, and hence a resemblance to the slow-flying freely exposed models is especially advantageous. The facts that mimetic species occur in the same locality, fly at the same time of the year as their models, and are day-flying species even though they may belong to nocturnal groups, are also more or less difficult to explain except on the theory of natural selection, and so also is the fact that mimetic resemblance is produced in the most varied manner. A spider resembles its model, an ant, by a modification of its body-form into a superficial resemblance, and by holding one pair of legs to represent antennae; certain bugs (Hemiptera) and beetles have also gained a shape unusual in their respective groups, a shape which superficially resembles an ant; a Locustid (Myrmecophana) has the shape of an ant painted, as it were, on its body, all other parts resembling the background and invisible; a Membracid (Homoptera) is entirely unlike an ant, but is concealed by an ant-like shield. When we further realize that in this and other examples of mimicry the likeness is almost always detailed and remarkable, however it is attained, while the methods differ absolutely, we recognize that natural selection is the only possible explanation hitherto suggested. In the cases of aggressive mimicry an animal resembles some object which is attractive to its prey. Examples are found in the flower-like species of mantis, which attract the insects on which they feed. Such cases are generally described as possessing alluring colours, and are regarded as examples of aggressive (anticryptic) resemblance, but their logical position is here.

Male and female Goldie's Bird of Paradise

Darwin suggested the explanation of these appearances in his theory of sexual selection (*The Descent of Man*, London, 1874). The rivalry of the males for the possession of the females he believed to be decided by the preference of the latter for those individuals with especially bright colours, highly developed plumes, beautiful song, etc. Wallace did not accept the theory, but believed that natural selection, either directly or indirectly, accounts for all the facts. Probably the majority of naturalists follow Darwin in this respect. The subject is most difficult, and the interpretation of a great proportion of the examples in a high degree uncertain, so that a very brief account is here expedient. That selection of some kind has been operative is indicated by the diversity of the elements into which the effects can be analysed. The most complete set of observations on epigamic display was made by George W and Elizabeth G Peckham upon spiders of the family Attidae (Nat. Hist. Soc. of Wisconsin, vol. i., 1889). These observations afforded the authors conclusive evidence that the females pay close attention to the love-dances of the males, and also that they have not only the power, but the will, to exercise a choice among the suitors for their favour. Epigamic characters are often concealed except during courtship; they are found almost exclusively in species which are diurnal or semi-diurnal in their habits, and are excluded from those parts of the body which move too rapidly to be seen. They are very commonly directly associated with the nervous system; and in certain fish, and probably in other animals, an analogous heightening of effect accompanies nervous excitement other than sexual, such as that due to fighting or feeding. Although there is epigamic display in species with sexes alike, it is usually most marked in those with secondary sexual characters specially developed in the male. These are an exception to the rule in heredity, in that their appearance is normally restricted to a single sex, although in many of the higher animals they have been proved to be latent in the other, and may appear after the essential organs of sex have been removed or become functionless. This is also the case in the Aculeate Hymenoptera when the reproductive organs have been destroyed by the parasite Stylops. Wallace suggested that they are in part to be explained as recognition characters, in part as an indication of surplus vital activity in the male. More recent theories by the likes of W. D. Hamilton and Amotz Zahavi have also been proposed.

Chapter 2

Camouflage

A flounder blending in with the gravel on the sea floor.

A camouflaged sniper, an example of military camouflage

Camouflage is a method of crypsis (hiding). It allows an otherwise visible organism or object to remain unnoticed, by blending with its environment. Examples include a tiger's stripes, the battledress of a modern soldier and a butterfly camouflaging itself as a leaf. The theory of camouflage covers the various strategies which are used to achieve this effect.

In nature

Cryptic coloration is the most common form of camouflage, found to some extent in the majority of species. The simplest way is for an animal to be of a color similar to its surroundings. Examples include the "earth tones" of deer, squirrels, or moles (to match trees or dirt), or the combination of blue skin and white underbelly of sharks via countershading (which makes them difficult to detect from both above and below). More complex patterns can be seen in animals such as flounder, moths, and frogs, among many others.

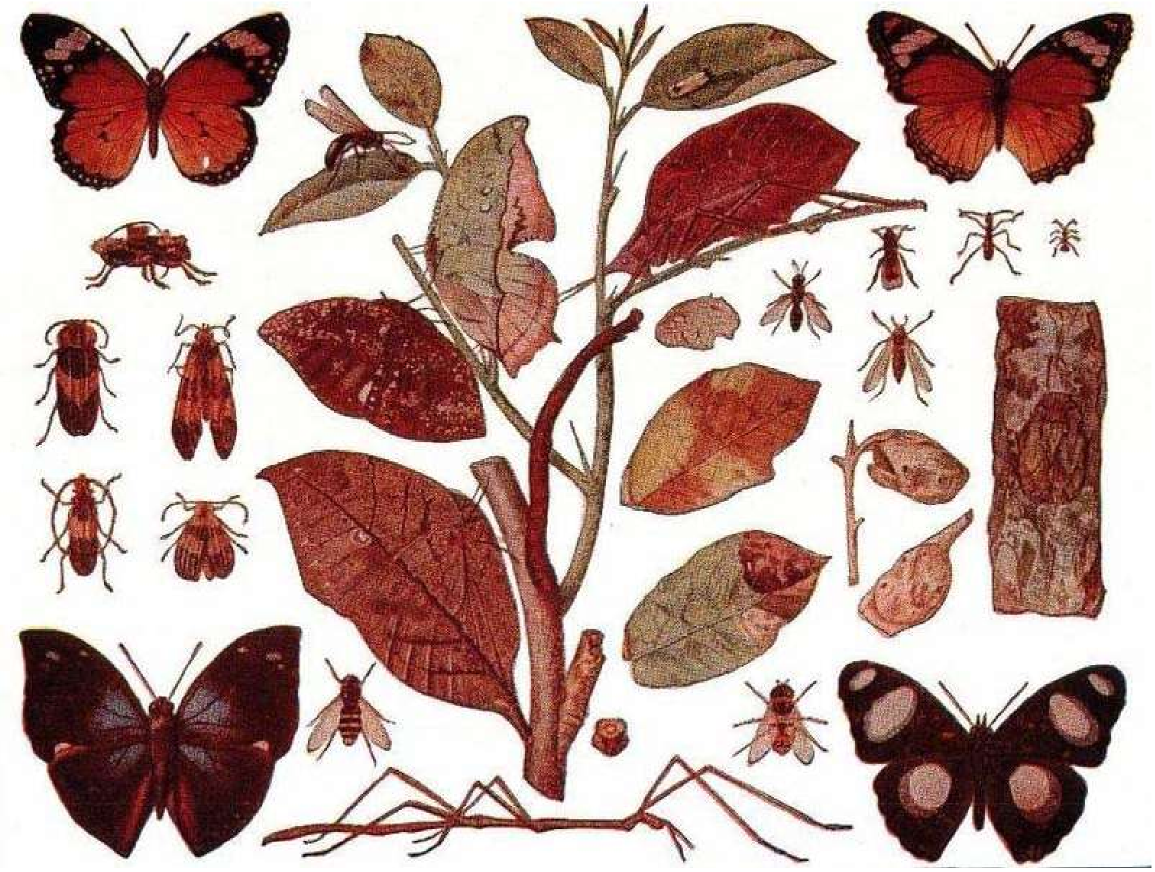
The type of camouflage a species will develop depends on several factors:

- The environment in which it lives. This is usually the most important factor.
- The physiology and behavior of an animal. Animals with fur need camouflage different from those with feathers or scales. Likewise, animals who live in groups use different camouflage techniques than those that are solitary.

- If the animal is preyed upon then the behavior or characteristics of its predator can influence how the camouflage develops. If the predator has achromatic vision, for example, then the animal will not need to match the color of its surroundings.

Animals produce colors in two ways:

- Biochromes: natural microscopic pigments that absorb certain wavelengths of light and reflect others, creating a visible color that is targeted towards its primary predator.
- Microscopic physical structures, which act like prisms to reflect and scatter light to produce a color that is different from the skin, such as the translucent fur of the Polar Bear, which actually has black skin.



Protective mimicry among insects

Cryptic coloration can change as well. This can be due to just a changing of the seasons, or it can be in response to more rapid environmental changes. For example, the Arctic fox has a white coat in winter, and a brown coat in summer. Mammals and birds require a new fur coat and new set of feathers respectively, but some animals, such as cuttlefish, have deeper-level pigment cells, called chromatophores, that they can control. Other animals such as certain fish species or the nudibranch can actually change their skin coloration by changing their diet. However, the most well-known creature that changes color, the chameleon, usually does not do so for camouflage purposes, but instead to express its mood.

Beyond colors, skin patterns are often helpful in cryptic coloration as well. The Cornsweet illusion describes visual perception as occurring through contrasts of outlines. One recognizes a dog, for example, not by its color as much as by its shape. Often what matters most for good cryptic coloration is to break up the outline of a creature's body. This can be seen in common domestic pets such as tabby cats, but striping overall in other animals such as tigers and zebras help them blend into their environment, the jungle and the grasslands respectively. The latter two provide an interesting example, as one's initial impression might be that their coloration does not match their surroundings at all, but tigers' prey are usually color blind to a certain extent such that they cannot tell the difference between orange and green, and zebras' main predators, lions, are color blind. In the case of zebras, the stripes also blend together so that a herd of zebras looks like one large mass, making it difficult for a lion to pick out any individual zebra. This same concept is used by many striped fish species as well. Among birds, the white "chinstraps" of Canada geese make a flock in tall grass appear more like sticks and less like birds' heads.

In nature, there is a strong evolutionary pressure for animals to blend into their environment or conceal their shape; for prey animals to avoid predators and for predators to be able to sneak up on prey. Natural camouflage is one method that animals use to meet these. There are a number of methods of doing so. One is for the animal to blend in with its surroundings, while another is for the animal to disguise itself as something uninteresting or something dangerous.

Hooded grasshopper

There is a permanent co-evolution of the sensory abilities of animals for whom it is beneficial to be able to detect the camouflaged animal, and the cryptic characteristics of the concealing species. Different aspects of crypsis and sensory abilities may be more or less pronounced in given predator-prey pairs of species.

Some cryptic animals also simulate natural movement, e.g., of a leaf in the wind. This is called procryptic behaviour or habit. Other animals attach or attract natural materials to their body for concealment. A few animals have chromatic response, changing color in changing environments, either seasonally (ermine, snowshoe hare) or far more rapidly with chromatophores in their integument (the cephalopod family). Some animals, notably in aquatic environments, also take steps to camouflage the odours they create that may attract predators. Some herd animals adopt a similar pattern to make it difficult to distinguish a single animal. Examples include stripes on zebras and the reflective scales on fish.

Gumleaf grasshopper, so named because of its mimicry of dead leaves

Hoplophrys oatesii crab hiding in a soft coral from East Timor.

An arctic hare's white colouration camouflages it in the snow

Camouflage allows predator to capture prey

The Egyptian Nightjar nests in the open sand with only its colouration to protect it

Scorpion fish resting beside a rope

A mackerel tabby cat blending with its (autumn) environment

Crab with red algae covering its body at Moss Beach, California

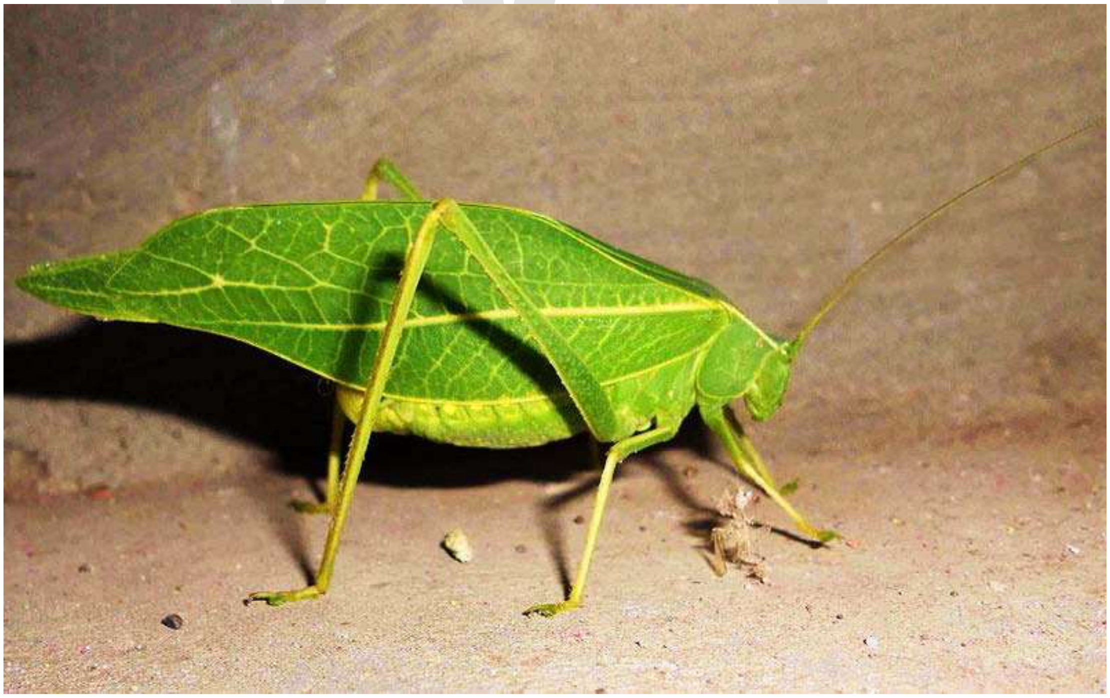
Countershaded Ibex are almost invisible in the Israeli desert.

A Bobcat blends with its winter surroundings, at Almaden Quicksilver County Park

Chameleon, Usambara mountains, Tanzania

Great male Leopard, made in Sabi Sands Private Game Reserve, South Africa

Tawny frogmouths in tree



Insect having mimicry of Green leaf

Zebras appear strikingly patterned to humans, but not to lions.

Chapter 3

Aposematism

The bright colours of this Granular Poison Frog serve as a warning to predators of its noxious taste.

Aposematism (from *apo*- away, and *sematic* sign/meaning), perhaps most commonly known in the context of **warning colouration**, describes a family of antipredator adaptations where a **warning signal** is associated with the unprofitability of a prey item to potential predators. It is one form of "advertising" signal, with many others existing such as the bright colours of flowers which lure pollinators. The warning signal may take the form of conspicuous colours, sounds, odours or other perceivable characteristics.

Aposematic signals are beneficial for both the predator and prey, who both avoid potential harm.

This tendency to become highly noticeable and distinct from harmless organisms is the antithesis of crypsis, or avoidance of detection. Aposematism has been such a successful adaptation that harmless organisms have repeatedly evolved to mimic aposematic species, a pattern known as Batesian mimicry. Another related pattern is Müllerian mimicry, where aposematic species come to resemble one another.

Defence mechanism

Flamboyant cuttlefish colours warning of toxicity

Aposematism is a secondary defence mechanism that warns potential predators of the existence of another primary defensive mechanism. The organism's primary means of defence may include:

Unpalatability
  such as from the bitter taste arising from some insects such as the ladybird or tiger moth, or the noxious odour produced by the skunk, or:
Other danger
  such as the poison glands of the poison dart frog, the sting of a velvet ant or neurotoxin in a black widow spider.

In these particular examples, the organism advertises its capabilities via either bright colouration in the case of the ladybird, frog and spider; or by conspicuous stripes in the case of the skunk. Various types of tiger moths advertise their unpalatability by either producing ultrasonic noises which warn bats to avoid them, or by warning postures which expose brightly-coloured body parts. Velvet ants have both bright colours *and* produce audible noises when grabbed (via stridulation), which serve to reinforce the warning.

Aposematic signals are primarily visual and involve bright and contrasting colours. They may be accompanied by one or more signals other than colour. These may be specific odours, sounds or behaviour. Together, the predator encounters a multi-modal signal which is more effectively detected.

Prevalence

The skunk is an example of mammalian aposematism.

Aposematism is widespread in invertebrates, particularly insects, but less so in vertebrates, being mostly confined to a smaller number of reptile, amphibian and fish species. Some plants, such as *Polygonum sagittatum*, a species of knotweed, are thought to employ aposematism to warn herbivores of chemical (such as unpalatability) or physical defences (such as prickled leaves or thorns). Sharply contrasting black-and-white skunks and zorillas are examples within mammals. Some brightly coloured birds with contrasting patterns may also be aposematic. An example is the Northern Flicker reportedly with bad-tasting, possibly toxic flesh.

Behaviour

The defence mechanism relies on the memory of the would-be predator; a bird that has once experienced a foul-tasting grasshopper will endeavour to avoid a repetition of the experience. One consequence of this is that aposematic species are often gregarious. Before the memory of a bad experience attenuates, the predator may have the experience reinforced through repetition, or else leave all the remaining and similarly coloured prey alone and safe. Aposematic organisms often move in a languid fashion as they have little need for speed and agility. Instead, their morphology is frequently tough and resistant to injury thereby allowing them to escape once the predator gets a bad taste or sting before the kill.

Origins of the theory

Gregarious nymphs of an aposematic milkweed bug, *Lygaeus kalmii*

Alfred Russel Wallace, in response to an 1866 letter from Charles Darwin, was the first to suggest that the conspicuous colour schemes of some insects might have evolved through natural selection as a warning to predators. Darwin had proposed that conspicuous colouring could be explained in many species by means of sexual selection practices, but had realised that this could not explain the bright colouring of some species of caterpillar since they were not sexually active. Wallace responded with the suggestion that as the contrasting coloured bands of a hornet warned of its defensive sting, so could the bright colours of the caterpillar warn of its unpalatability. He also pointed out that John Jenner Weir had observed that birds in his aviary would not attempt to catch or eat a certain common white moth, and that a white moth at dusk would be as conspicuous as a brightly coloured caterpillar during the day. After Darwin responded enthusiastically to the suggestion, Wallace made a request at a meeting of the Entomological Society of London for data that could be used to test the hypothesis. In response, John Jenner Weir conducted experiments with caterpillars and birds in his aviary for two years. The results he reported in 1869 provided the first experimental evidence for warning colouration in animals.

Mimicry

A venomous coral snake

The harmless red milk snake mimics the bright colours of the venomous coral snake

Aposematism is a sufficiently successful strategy that other organisms lacking the same primary defence means may come to mimic the conspicuous markings of their genuinely aposematic counterparts. For example, the Aegeria moth is a mimic of the yellow jacket wasp; it resembles the wasp, but is not capable of stinging. A predator who would thus avoid the wasp would similarly avoid the Aegeria.

This form of mimicry, where the mimic lacks the defensive capabilities of its 'model', is known as Batesian mimicry, after Henry Walter Bates, a British naturalist who studied Amazonian butterflies in the second half of the nineteenth century. Batesian mimicry finds greatest success when the ratio of *mimic* to *mimicked* is low; otherwise predators learn to recognise the imposters. Batesian mimics are known to adapt their mimicry to match the prevalence of aposematic organisms in their environment.

A second form of aposematism mimicry occurs when two organisms share the same anti-predation defence and mimic each other, to the benefit of both species. This form of mimicry is known as Müllerian mimicry, after Fritz Müller, a German naturalist who studied the phenomenon in the Amazon in the late nineteenth century. For example, a yellow jacket wasp and a honeybee are Müllerian mimics; their similar colouring teaches predators that a striped pattern is the pattern of a stinging insect. Therefore, a predator who has come into contact with either a wasp or a honeybee will likely avoid both in the future.

There are other forms of mimicry not related to aposematism, though these two forms are among the best known and most studied.

Chapter 4

Mimicry

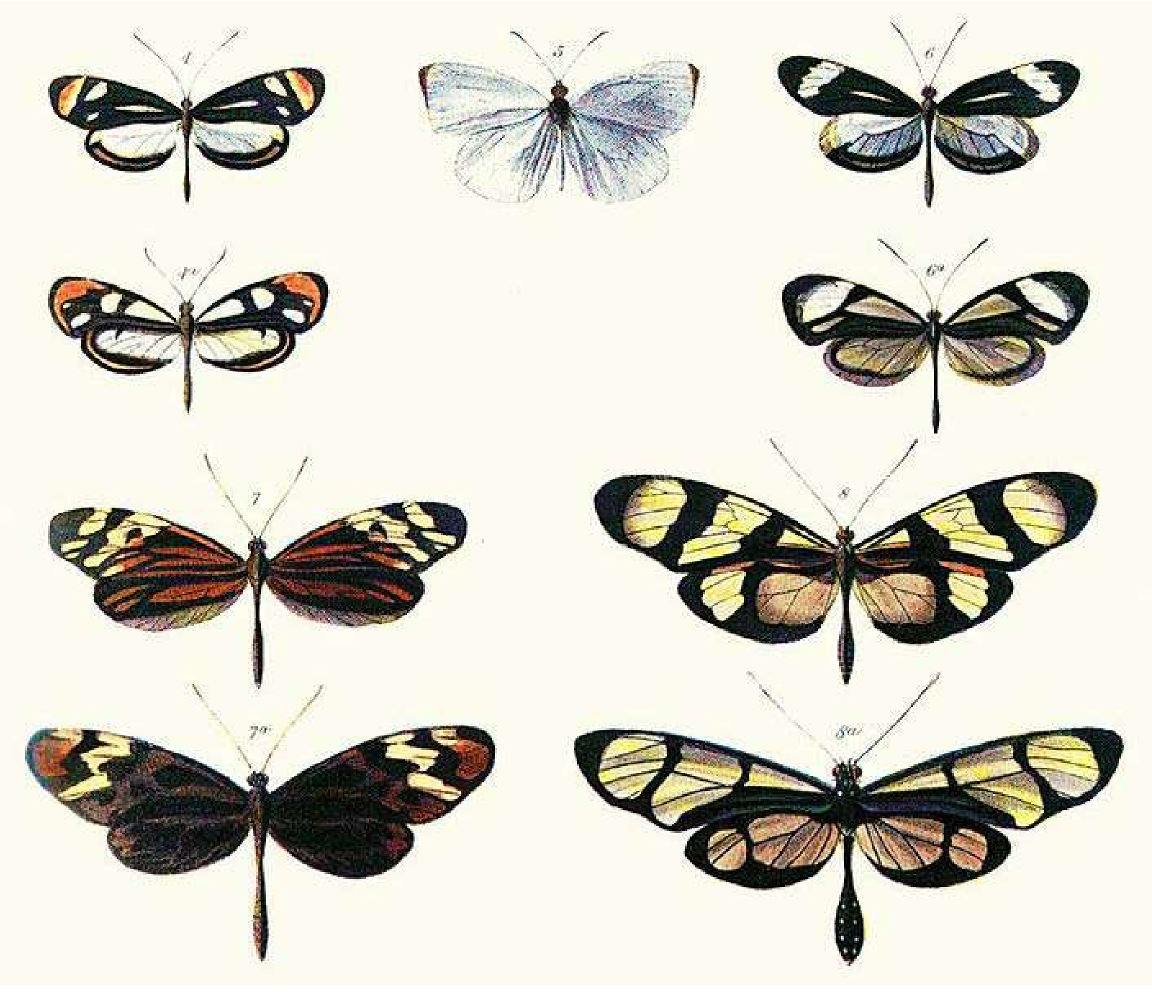


Plate from Henry Walter Bates (1862) illustrating Batesian mimicry between *Dismorphia* species (top row, third row) and various *Ithomiini* (Nymphalidae, second row, bottom row)

In evolutionary biology, **mimicry** is the similarity of one species to another which protects one or both. This similarity can be in appearance, behaviour, sound, scent and even location, with the mimics found in similar places to their models.

Mimicry occurs when a group of organisms, the *mimics*, evolve to share common perceived characteristics with another group, the *models*. The evolution is driven by the selective action of a *signal-receiver*, or *dupe*. For example, birds that use sight to identify palatable insects (the mimics), whilst avoiding the noxious models.

Collectively, this situation is known as a *mimicry complex*. The model is usually another species except in cases of automimicry. The signal-receiver is typically another intermediate organism like the common predator of two species, but may actually be the model itself, such as a moth resembling its spider predator. As an interaction, mimicry is in most cases advantageous to the mimic and harmful to the receiver, but may increase, reduce or have no effect on the fitness of the model depending on the situation. Models themselves are difficult to define in some cases, for example eye spots may not bear resemblance to any specific organism's eyes, and camouflage often cannot be attributed to a particular model.

A planthopper mimics a leaf (mimesis)

Camouflage, in which a species resembles its surroundings, is essentially a form of visual mimicry. In between camouflage and mimicry is **mimesis**, in which the mimic takes on the properties of a specific object or organism, but one to which the dupe is indifferent. The lack of a true distinction between the two phenomena can be seen in animals that resemble twigs, bark, leaves or flowers, in that they are often classified as camouflaged (a plant constitutes its "surroundings"), but are sometimes classified as mimics (a plant is also an organism).[p51] Crypsis is a broader concept which encompasses all forms of avoiding detection, such as mimicry, camouflage, hiding etc.

Though visual mimicry is most obvious to humans, other senses such as olfaction (smell) or hearing may be involved, and more than one type of signal may be employed. Mimicry may involve morphology, behavior, and other properties. In any case, the signal always functions to deceive the receiver by preventing it from correctly identifying the mimic. In evolutionary terms, this phenomenon is a form of co-evolution usually involving an evolutionary arms race.[p161] It should not be confused with convergent evolution, which occurs when species come to resemble one another *independently* by adapting to similar lifestyles.

Mimics may have different models for different life cycle stages, or they may be polymorphic, with different individuals imitating different models. Models themselves may have more than one mimic, though frequency dependent selection favors mimicry where models outnumber mimics. Models tend to be relatively closely related organisms, but mimicry of vastly different species is also known. Most known mimics are insects, though many other animal mimics including mammals are known. Plants and fungi may also be mimics, though less research has been carried out in this area.

Etymology

Use of the word mimicry dates back to 1637. It is derived from the Greek term *mimetikos*, "imitative," in turn from *mimetos*, the verbal adjective of *mimeisthai*, "to imitate." Originally used to describe people, it was only applied to other forms of life after 1851.

Classification

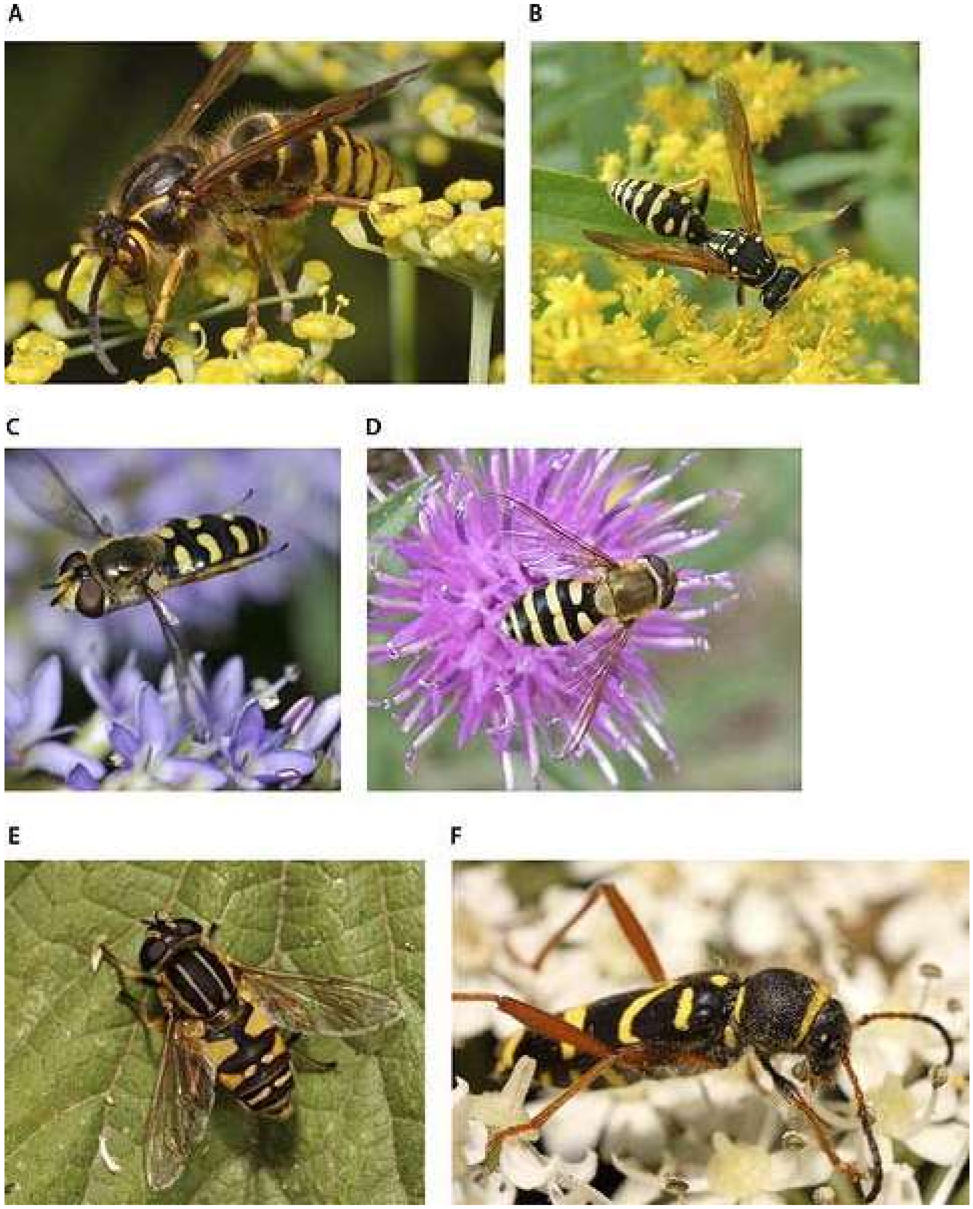
Many types of mimicry have been described. An overview of each follows, highlighting the similarities and differences between the various forms. Classification is often based on function with respect to the mimic (e.g. avoiding harm), though other parameters can also be used, and multidimensional classifications are required to understand the full picture. For this reason, some cases may belong to more than one class, e.g. automimicry and aggressive mimicry are not mutually exclusive, as one describes the species relationship between model and mimic, while the other describes the function for the mimic (obtaining food).

Defensive

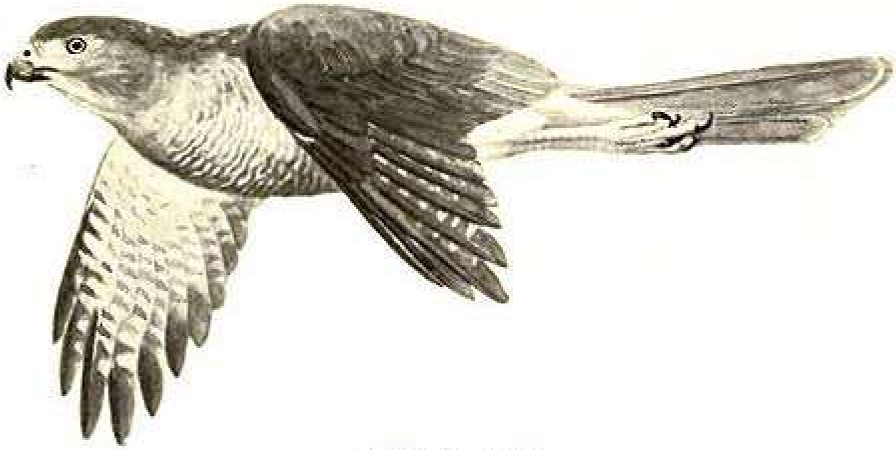
Macroxiphus sp katydid mimics an ant

Defensive or protective mimicry takes place when organisms are able to avoid an encounter that would be harmful to them by deceiving an enemy into treating them as something else. Four such cases are discussed here, the first three of which entail mimicry of an aposematic, harmful organism: Batesian mimicry, where a harmless mimic poses as harmful; Müllerian mimicry, where two harmful species share similar perceived characteristics; and Mertensian mimicry, where a deadly mimic resembles a less harmful but lesson-teaching model. Finally, Vavilovian mimicry, where weeds resemble crops, is discussed.

Batesian



Several species, including several hoverflies, mimic stinging species of wasp.



SHIKRA HAWK

The upper side of the tail is marked as in the Hawk-cuckoo

By permission of Messrs. Hutchinson & Co.

BRAIN-FEVER BIRD

The exact correspondence of this mimic with its model is notable even in black-and-white

By permission of Messrs. Hutchinson & Co.

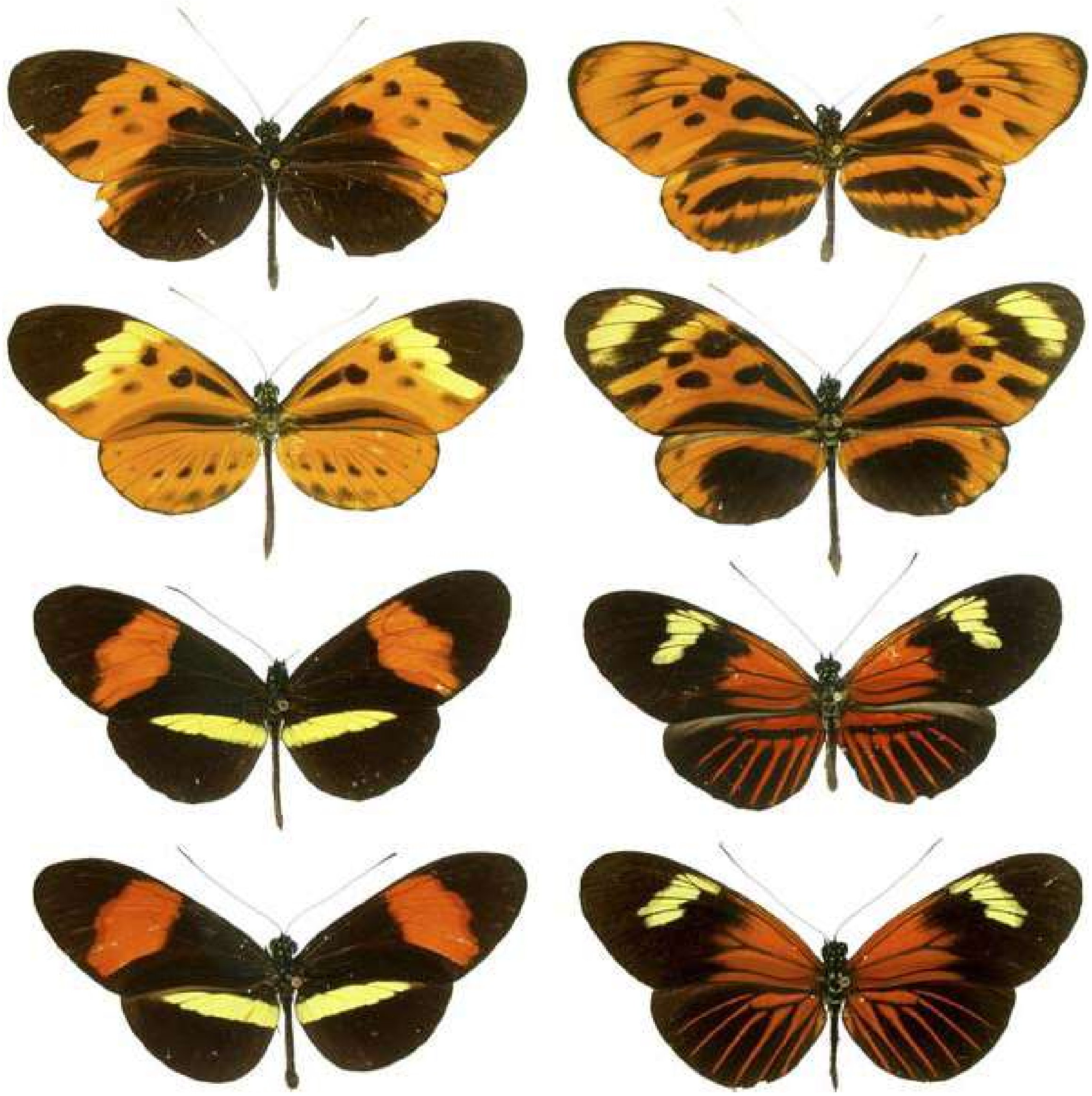
Some hawk-cuckoos resemble hawks like the Shikra.

In Batesian mimicry the mimic shares signals similar to the model, but does not have the attribute that makes it unprofitable to predators (e.g. unpalatability). In other words, a Batesian mimic is a sheep in wolf's clothing. It is named after Henry Walter Bates, an English naturalist whose work on butterflies in the Amazon rainforest (including *Naturalist on the River Amazons*) was pioneering in this field of study. Mimics are less likely to be found out when in low proportion to their model, a phenomenon known as negative frequency dependent selection which applies in most other forms of mimicry as well. This is not the case in Müllerian mimicry however, which is described next. Examples:

- Lepidoptera

  - The Ash Borer (*Podosesia syringae*), a moth of the Clearwing family (Sesiidae), is a Batesian mimic of the Common wasp because it resembles the wasp, but is not capable of stinging. A predator that has learned to avoid the wasp would similarly avoid the Ash Borer.
  - Plain Tiger (*Danaus chrysippus*) – an unpalatable model with a number of mimics.
  - Common Crow (*Euploea core*) – an unpalatable model with a number of mimics.
  - *Consul fabius* and *Eresia eunice* imitate unpalatable *Heliconius* butterflies such as *H. ismenius*.
  - Several palatable butterflies resemble different species from the highly noxious papilionine genus *Battus*.
  - Several palatable moths produce ultrasonic click calls to mimic the unpalatable tiger moths.
- The False Cobra (*Malpolon moilensis*) is a mildly venomous but harmless colubrid snake which mimics the characteristic "hood" of an Indian cobra's threat display. The Eastern Hognose Snake (*Heterodon platirhinos*) similarly mimics the threat display of venomous snakes.
- The milk snake resembles the deadly coral snake.
- Vespid wasps bear several harmless mimics including moths, beetles and hoverflies.
- Octopuses of the genus *Thaumoctopus* (the Mimic Octopus) are able to intentionally alter their body shape and color so that they resemble dangerous sea snakes or lionfish.

Müllerian



The Heliconius butterflies from the tropics of the Western Hemisphere are the classical model for Müllerian mimicry.

Müllerian mimicry describes a situation where two or more species have very similar warning or aposematic signals and both share genuine anti-predation attributes (e.g. being unpalatable). At first Bates could not explain why this should be so; if both were harmful why did one need to mimic another? The German naturalist Fritz Müller put forward the first explanation for this phenomenon: If two species were confused with one another by a common predator, individuals in both would be more likely to survive. This type of mimicry is unique in several respects. Firstly, both the mimic and the model benefit from the interaction, which could thus be classified as mutualism in this respect. The signal receiver is also advantaged by this system, despite being deceived regarding species identity, as it avoids potentially harmful encounters. The usually clear identity of mimic and model are also blurred. In cases where one species is scarce and another abundant, the rare species can be said to be the mimic. When both are present in similar numbers however it is more realistic to speak of each as *comimics* than of a distinct 'mimic' and 'model' species, as their warning signals tend to converge toward something intermediate between the two. Another theoretical problem comes up when one considers that the two species may exist on a continuum from the harmless to the highly noxious, raising the question of where Batesian mimicry ends and Müllerian convergence begins.

Examples:

- Lepidoptera
  - The Monarch Butterfly (*Danaus plexippus*) is a member of a Müllerian complex with the Viceroy butterfly (*Limenitis archippus*) in shared coloration patterns and display behavior. The Viceroy has subspecies with somewhat different coloration, each one very closely matching the local *Danaus* species. E.g., in Florida, the pairing is of the Viceroy and the Queen Butterfly, and in Mexico, the Viceroy resembles the Soldier Butterfly. Therefore, the Viceroy is a single species involved in three different Müllerian pairs. This example was long believed to be a case of Batesian mimicry, with the Viceroy being the mimic and the Monarch the model, but it was more recently determined that the Viceroy is actually the *more* unpalatable species, though there is considerable individual variation. While *L. archippus* is really bad-tasting, *Danaus* species tend to be toxic rather than just repugnant, due to their different food plants.
  - Unpalatable *Euploea* species look very similar.
  - The genus *Morpho* is palatable but are very strong fliers; birds – even species which are specialized for catching butterflies on the wing – find it very hard to catch them. The conspicuous blue coloration shared by most *Morpho* species seems to be a case of Müllerian mimicry.
  - The "orange complex" of species, including the heliconiines *Agraulis vanillae*, *Dryadula phaetusa*, and *Dryas iulia* which all taste bad.
  - Many different tiger moths make ultrasonic clicking calls to warn bats that they are unpalatable. Presumably a bat may learn to avoid *any* signalling moths, which would make this an example of Müllerian mimicry.
- Various bees and numerous vespid and sphecoid wasps: These animals are examples of Müllerian mimics because they have the aposematic yellow and black stripes (sometimes black and red, or black and white). Females of most of these species are potentially harmful to predators, fulfilling the second requirement of Müllerian mimicry. However, in essentially all such species, the males are harmless, and can thus be considered automimics of their conspecific females. There are also many genera in these groups where the females are not capable of stinging, and yet still possess aposematic coloration (e.g., the wasp genus *Cerceris*), so they are considered Batesian mimics.

Emsleyan/Mertensian

Texas Coral Snake, *Micrurus tener* (Top) and Mexican Milk Snake, *Lampropeltis triangulum annulata* (bottom).

Emsleyan or *Mertensian mimicry* describes unusual cases where deadly prey mimic a less dangerous species. It was first proposed by Emsley as a possible answer for the problem of Coral Snake mimicry in the New World. It was elaborated on by the German biologist Wolfgang Wickler in a chapter of *Mimicry in Plants and Animals*, who named it after the German herpetologist Robert Mertens. Sheppard points out that Hecht and Marien put forward a similar hypothesis ten years earlier.

This scenario is a little more difficult to understand, as in other types of mimicry it is usually the most harmful species that is the model. But if a predator dies, it cannot learn to recognize a warning signal, e.g. bright colors in a certain pattern. In other words, there is no advantage in being aposematic for an organism that is likely to kill any predator it succeeds in poisoning; such an animal would rather profit from being camouflaged, to avoid attacks altogether. If, however, there is some other species that is harmful but *not* deadly as well as aposematic, the predator may learn to recognize its particular warning colors and avoid such animals. A deadly species will then profit by mimicking the less dangerous aposematic organism, if this results in less attacks than camouflage would.

The exception here, ignoring any chance of animals learning by watching a conspecific die, is the possibility of not having to learn that it is harmful in the first place: instinctive genetic programming to be wary of certain signals. In this case, other organisms could benefit from this programming, and Batesian or Müllerian mimics of it could potentially evolve. In fact, it has been shown that some species do have an innate recognition of certain aposematic warnings. Hand-reared Turquoise-browed Motmots (*Eumomota superciliosa*), avian predators, instinctively avoid snakes with red and yellow rings. Other colors with the same pattern, and even red and yellow *stripes* with the same width as rings, were tolerated. However, models with red and yellow rings were feared, with the birds flying away and giving alarm calls in some cases. This provides one alternative explanation to Mertensian mimicry.

Examples:

- Some Milk Snake (*Lampropeltis triangulum*) subspecies (harmless), the moderately toxic False Coral Snakes (genus *Erythrolamprus*), and the deadly Coral Snakes all have a red background color with black and white/yellow rings. In this system, both the milk snakes and the deadly coral snakes are mimics, whereas the false coral snakes are the model.

Wasmannian

Wasmannian mimicry refers to cases where the mimic resembles a model along with which it lives (inquiline) in a nest or colony. Most of the models here are social insects such as ants, termites, bees and wasps.

Mimetic weeds

Rye is a secondary crop, originally being a mimetic weed of wheat.

Vavilovian mimicry describes weeds which come to share characteristics with a domesticated plant through artificial selection. It is named after Russian botanist and geneticist Nikolai Vavilov. Selection against the weed may occur either by manually killing the weed, or separating its seeds from those of the crop. The latter process, known as winnowing, can be done manually or by a machine.

Vavilovian mimicry presents an illustration of unintentional (or rather 'anti-intentional') selection by man. While some cases of artificial selection go in the direction desired, such as selective breeding, this case presents the opposite characteristics. Weeders do not want to select weeds that look increasingly like the cultivated plant, yet there is no other option. A similar problem in agriculture is pesticide. Vavilovian mimics may eventually be domesticated themselves, and Vavilov called these weeds-come-crops *secondary crops*.

It can be classified as defensive mimicry in that the weed mimics a protected species. This bears strong similarity to Batesian mimicry in that the weed does not share the properties that give the model its protection, and both the model and the dupe (in this case people) are harmed by its presence. There are some key differences, though; in Batesian mimicry the model and signal receiver are enemies (the predator would eat the protected species if could), whereas here the crop and its human growers are in a mutualistic relationship: the crop benefits from being dispersed and protected by people, despite being eaten by them. In fact, the crop's only 'protection' relevant here is its usefulness to humans. Secondly, the weed is not eaten, but simply destroyed. The only motivation for killing the weed is its effect on crop yields. Finally, this type of mimicry does not occur in ecosystems unaltered by humans.

One case is *Echinochloa oryzoides*, a species of grass which is found as a weed in rice (*Oryza sativa*) fields. The plant looks similar to rice and its seeds are often mixed in rice and difficult to separate. This close similarity was enhanced by the weeding process which is a selective force that increases the similarity of the weed in each subsequent generation.

Protective egg decoys

Unlike the above forms of mimicry, *Gilbertian mimicry* involves only two species. The potential host/prey drives away its parasite/predator by mimicking it, the reverse of host-parasite aggressive mimicry. It was coined by Pasteur as a term for such rare mimicry systems, and is named after the American ecologist Lawrence E. Gilbert.

This form of protective mimicry occurs in the genus *Passiflora*. The leaves of this plant contain toxins which deter herbivorous animals, however some *Heliconius* butterfly larvae have evolved enzymes which break down these toxins, allowing them to specialize on this genus. This has created further selection pressure on the host plants, which have evolved stipules that mimic mature *Heliconius* eggs near the point of hatching. These butterflies tend to avoid laying eggs near each existing ones, which helps avoid exploitative intraspecific competition between caterpillars—those that lay on vacant leaves provide their offspring with a greater chance of survival. Additionally, most *Heliconius* larvae are cannibalistic, meaning those leaves with older eggs will hatch first and eat the new arrivals. Thus, it seems such plants have evolved egg dummies due to these grazing herbivore enemies. The decoy eggs are also nectaries though, attracting predators of the caterpillars such as ants and wasps. The extent of their mimetic function is therefore slightly more difficult to assess.

The use of eggs is not essential to this system, only the species composition and protective function. Many other forms of mimicry also involve eggs, such as cuckoo eggs mimicking those of their host (the reverse of this situation), or plants seeds (often those with an elaiosome) being dispersed by ants, who treat them as they would their own eggs.

Protective mimicry within a species

Monarch caterpillars, shown feeding, vary in toxicity depending on their diet.

Browerian mimicry, named after Lincoln P. Brower and Jane Van Zandt Brower, is a form of *automimicry*; where the model belongs to the same species as the mimic. This is the analogue of Batesian mimicry within a single species, and occurs when there is a palatability spectrum within a population. One example is Monarch Butterflies (*Danaus plexippus*), which feed on milkweed species of varying toxicity. This species stores toxins from its host plant, which are maintained even in the adult (imago) form. As the levels of toxin will vary depending on diet during the larval stage, some individuals will be more toxic than others. The less palatable organisms will therefore be mimics of the more dangerous individuals, with their likeness already perfected. This need not be the case however; in sexually dimorphic species one sex may be more of a threat than the other, which could mimic the protected sex. Evidence for this possibility is provided by the behavior of a monkey from Gabon, which regularly ate male moths of the genus *Anaphe*, but promptly stopped after it tasted a noxious female.

Aggressive

Aggressive mimicry describes predators (or parasites) which share the same characteristics as a harmless species, allowing them to avoid detection by their prey (or host). The mimic may resemble the prey or host itself, or another organism which is either neutral or beneficial to the signal receiver. In this class of mimicry the model may be affected negatively, positively or not at all. Just as parasites can be treated as a form of predator, host-parasite mimicry is treated here as a subclass of aggressive mimicry.

The mimic may have a particular significance for duped prey. One such case is spiders, amongst which aggressive mimicry is quite common in both luring prey and stealthily approaching predators. One case is the Golden Orb Weaver (*Nephila clavipes*), which spins a conspicuous golden colored web in well-lit areas. Experiments show that bees are able to associate the webs with danger when the yellow pigment is not present, as occurs in less well-lit areas where the web is much harder to see. Other colors were also learned and avoided, but bees seemed least able to effectively associate yellow pigmented webs with danger. Yellow is the color of many nectar bearing flowers, however, so perhaps avoiding yellow is not worth while. Another form of mimicry is based not on color but pattern. Species such as *Argiope argentata* employ prominent patterns in the middle of their webs, such as zigzags. These may reflect ultraviolet light, and mimic the pattern seen in many flowers known as nectar guides. Spiders change their web day to day, which can be explained by bee's ability to remember web patterns. Bees are able to associate a certain pattern with a spatial location, meaning the spider must spin a new pattern regularly or suffer diminishing prey capture.

Another case is where males are lured towards what would seem to be a sexually receptive female; the model in this situation being the same species as the dupe. Beginning in the 1960s, James E. Lloyd's investigation of female fireflies of the genus *Photuris* revealed they emit the same light signals that females of the genus *Photinus* use as a mating signal. Further research showed male fireflies from several different genera are attracted to these "femmes fatales", and are subsequently captured and eaten. Female signals are based on that received from the male, each female having a repertoire of signals matching the delay and duration of the female of the corresponding species. This mimicry may have evolved from non-mating signals that have become modified for predation.

The Spotted Predatory Katydid (*Chlorobalius leucoviridis*) is an acoustic aggressive mimic of cicadas.

The listrosceline katydid *Chlorobalius leucoviridis* of inland Australia is capable of attracting male cicadas of the Tribe Cicadettini by imitating the species-specific reply clicks of sexually receptive female cicadas. This example of acoustic aggressive mimicry is similar to the *Photuris* firefly case in that the predator's mimicry is remarkably versatile – playback experiments show that *C. leucoviridis* is able to attract males of many cicada species, including Cicadettine cicadas from other continents, even though cicada mating signals are species-specific.

Some carnivorous plants may also be able to increase their rate of capture through mimicry.

Two Bluestreak cleaner wrasse cleaning a Potato grouper, *Epinephelus tukula*

Luring is not a necessary condition however, as the predator will still have a significant advantage by simply not being identified as such. They may resemble a mutualistic symbiont or a species of little relevance to the prey.

A case of the former situation is a species of cleaner fish and its mimic, though in this example the model is greatly disadvantaged by the presence of the mimic. Cleaner fish are the allies of many other species, which allow them to eat their parasites and dead skin. Some allow the cleaner to venture inside their body to hunt these parasites. However, one species of cleaner, the Bluestreak cleaner wrasse (*Labroides dimidiatus*), is the unknowing model of a mimetic species, the Sabre-toothed blenny (*Aspidontus taeniatus*). This wrasse, shown to the left cleaning a grouper of the genus *Epinephelus*, resides in coral reefs in the Indian and the Pacific Oceans, and is recognized by other fishes who then allow it to clean them. Its imposter, a species of blenny, lives in the Indian Ocean and not only looks like it in terms of size and coloration, but even mimics the cleaner's 'dance'. Having fooled its prey into letting its guard down, it then bites it, tearing off a piece of its fin before fleeing the scene. Fish grazed upon in this fashion soon learn to distinguish mimic from model, but because the similarity is close between the two they become much more cautious of the model as well, such that both are affected. Due to victim's ability to discriminate between foe and helper, the blennies have evolved close similarity, right down to the regional level.

Another interesting example that does not involve any luring is the Zone-tailed Hawk, which resembles the Turkey Vulture. It flies amongst the vultures, suddenly breaking from the formation and ambushing its prey. Here the hawk's presence is of no evident significance to the vultures, affecting them neither negatively or positively.

Parasites

Parasites can also be aggressive mimics, though the situation is somewhat different from those outlined above.

Some of the predators described have a feature that draws prey, and parasites can also mimic their host's natural prey, but are eaten themselves, a pathway into their host. *Leucochloridium*, a genus of flatworm, matures in the digestive system of songbirds, their eggs then passing out of the bird via the feces. They are then taken up by *Succinea*, a terrestrial snail. The eggs develop in this intermediate host, and then must find of a suitable bird to mature in. As the host birds do not eat snails, so the sporocyst has another strategy to reach its host's intestine. They are brightly colored and move in a pulsating fashion. A sporocyst-sac pulsates in the snail's eye stalks, coming to resemble an irresistible meal for a songbird. In this way, it can bridge the gap between hosts, allowing it to complete its life cycle. A nematode (*Myrmeconema neotropicum*) changes the colour of the abdomen of workers of the canopy ant *Cephalotes atratus* to make it appear like the ripe fruits of *Hyeronima alchorneoides*. It also changes the behaviour of the ant so that the gaster (rear part) is held raised. This presumably increases the chances of the ant being eaten by birds. The droppings of birds are collected by other ants and fed to their brood, thereby helping to spread the nematode.

In an unusual case, planidium larvae of some beetles of the genus *Meloe* will form a group and produce a pheromone that mimics the sex attractant of its host bee species; when the male bee arrives and attempts to mate with the mass of larvae, they climb onto his abdomen, and from there transfer to a female bee, and from there to the bee nest to parasitize the bee larvae.

Host-parasite mimicry is a two species system where a parasite mimics its own host. Cuckoos are a canonical example of brood parasitism, a form of kleptoparasitism where the mother has its offspring raised by another unwitting organism, cutting down the biological mother's parental investment in the process. The ability to lay eggs which mimic the host eggs is the key adaptation. The adaptation to different hosts is inherited through the female line in so-called gentes. Cases of *intraspecific* brood parasitism, where a female lays in conspecific's nest, as illustrated by the Goldeneye duck (*Bucephala clangula*), do not represent a case of mimicry.

Reproductive

Reproductive mimicry occurs when the actions of the dupe directly aid in the mimic's reproduction. This is common in plants, which may have deceptive flowers that do not provide the reward they would seem to. Other forms of mimicry have a reproductive component, such as Vavilovian mimicry involving seeds, and brood parasitism, which also involves aggressive mimicry.

Mimicry of flowers

Bakerian mimicry, named after Herbert G. Baker, is a form of automimicry where female flowers mimic male flowers of their own species, cheating pollinators out of a reward. This reproductive mimicry may not be readily apparent as members of the same species may still exhibit some degree of sexual dimorphism. It is common in many species of Caricaceae.

Like Bakerian mimicry, *Dodsonian mimicry* is a form of reproductive floral mimicry, but the model belongs to a different species than the mimic. The name refers to Calaway H. Dodson. By providing similar sensory signals as the model flower, it can lure its pollinators. Like Bakerian mimics, no nectar is provided. *Epidendrum ibaguense* of the family Orchidaceae resembles flowers of *Lantana camara* and *Asclepias curassavica*, and is pollinated by Monarch Butterflies and perhaps hummingbirds. Similar cases are seen in some other species of the same family. The mimetic species may still have pollinators of its own though, for example a lamellicorn beetle which usually pollinates correspondingly colored *Cistus* flowers is also known to aid in pollination of *Ophrys* species that are normally pollinated by bees.

Pseudocopulation

The Fly Orchid (*Ophrys insectifera*)

Pseudocopulation occurs when a flower mimics a female of a certain insect species, the males of which try to copulate with it. This is much like the aggressive mimicry in fireflies described above, but with a much more benign outcome for the pollinator. This form of mimicry has been called *Pouyannian mimicry*, after Pouyanne, who first described the phenomenon. It is most common in orchids which mimic females of the order Hymenoptera (generally bees and wasps), and may account for around 60% of pollinations. Depending on the morphology of the flower, a pollen sac called a pollinia is attached to the head or abdomen of the male. This is then transferred to the stigma of the next flower the male tries to inseminate, resulting in pollination. Visual mimicry is the most obvious sign of this deception for humans, but the visual aspect may be minor or non-existent. It is the senses of touch and olfaction that are most important.

Inter-sexual mimicry

Inter-sexual mimicry occurs when individuals of one sex in a species mimic members of the opposite sex. An example is the three male forms of the marine isopod, *Paracerceis sculpta*. Alpha males are the largest and guard a harem of females. Beta males mimic females and manage to enter the harem of females without being detected by the alpha males allowing them to mate. Gamma males are the smallest males and mimic juveniles. This also allows them to mate with the females without the alpha males detecting them. Some male Australian Giant Cuttlefish also mimic females, allowing them to mate undetected by other males.

Automimicry

Automimicry or *intraspecific mimicry* occurs within a single species, one case being where one part of an organism's body resembles another part. Examples include snakes in which the tail resembles the head and show behavior such as moving backwards to confuse predators and insects and fishes with eyespots on their hind ends to resemble the head. The term is also used when the mimic imitates other morphs within the same species. When males mimic females or *vice versa* this may be referred to as sexual mimicry.

Examples:

- Many insects have filamentous "tails" at the ends of their wings which are combined with patterns of markings on the wings themselves to create a "false head" which misdirects predators (e.g., hairstreak butterflies).
- Several pygmy owls bear "false eyes" on the back of their head to fool predators into believing the owl is alert to their presence.
- The yellow throated males of the Common Side-blotched Lizard use a 'sneaking' strategy in mating. They look and behave like unreceptive females. This strategy is effective against 'usurper' males with orange throats, but ineffective against blue throated 'guarder' males, which will chase them away.
- Female hyenas have pseudo-penises which make them look like males.

Other

Some forms of mimicry do not fit easily within the classification given above.

Owl butterflies (genus *Caligo*) bear eye-spots on the underside of their wings; if turned upside-down, their undersides resemble the face of an owl (such as the Short-eared Owl or the Tropical Screech Owl) for which in turn the butterfly predators – small lizards and birds – would be fooled. Thus it has been supposed that the eye-spots are a form of Batesian mimicry. However, the pose in which the butterfly resembles an owl's head is not normally adopted in life. Research suggests that eye-spots are not a form of mimicry and do not deter predators because they look like eyes. Rather the conspicuous contrast in the patterns on the wings deter predators.

Another case is floral mimicry induced by the discomycete fungus *Monilinia vaccinii-corymbosi*. In this unusual case, a fungal plant pathogen infects leaves of blueberries, causing them to secrete sugary substances including glucose and fructose, in effect mimicking the nectar of flowers. To the naked eye the leaves do not look like flowers, yet strangely they still attract pollinating insects like bees. As it turns out, the sweet secretions are not the only cues—the leaves also reflect ultraviolet, which is normally absorbed by the plant's leaves. Ultraviolet light is also employed by the host's flowers as a signal to insects, which have visual systems quite capable of picking up this low wavelength (300–400 nm) radiation. The fungus is then transferred to the ovaries of the flower where it produces mummified, inedible berries, which overwinter before infecting new plants. This case is unusual in that the fungus benefits from the deception, but it is the leaves which act as mimics, being harmed in the process. It bears similarity to host-parasite mimicry, but the host does not receive the signal. It also has a little in common with automimicry, but the plant does not benefit from the mimicry, and the action of the pathogen is required to produce it.

Evolution

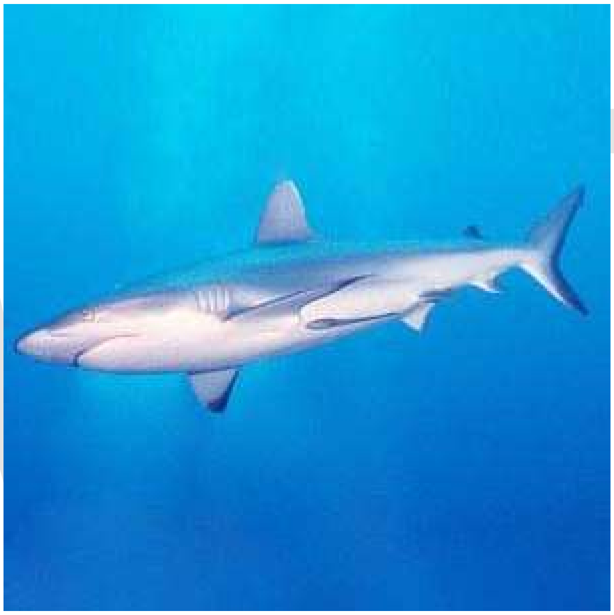
Ctenomorphodes chronus mimicking a eucalyptus twig

It is widely accepted that mimicry evolves as a positive adaptation; that is, the mimic gains fitness *via* convergent evolution which results in resemblance to another species. The lepidopterist (and sometime author) Vladimir Nabokov argued that much of insect mimicry, including the Viceroy/Monarch mimicry, resulted from the fact that coloration patterns in both species simply had a common structural basis, and thus the tendency for convergence by chance was high. However, this very example provides evidence to the contrary. The viceroy's color pattern is completely unlike any of the species to which it is closely related, and the viceroy itself has three color forms, each adapted to resemble a different species of *Danaus*. Also, many cases of mimicry (especially in large Batesian/Mũllerian complexes) involve insects from multiple orders that share virtually no structural similarities whatsoever; beetles, true bugs, moths, wasps, bees, and flies may all belong to a single mimetic complex, despite their biological differences.

The most widely accepted model used to explain the evolution of mimicry in butterflies is the two-step hypothesis. In this model the first step involves mutation in modifier genes that regulate a complex cluster of linked genes associated with large changes in morphology. The second step consists of selections on genes with smaller phenotypic effects and this leading to increasing closeness of resemblance. This model is supported by empirical evidence that suggests that there are only a few single point mutations that cause large phenotypic effects while there are numerous others that produce smaller effects. Some regulatory elements are now known to be involved in a supergene that is involved in the development of butterfly color patterns. Computational simulations of population genetics have also supported this idea.

Chapter 5

Countershading



Countershading employed by the grey reef shark.

Countershading, or **Thayer's Law**, is a form of camouflage. Countershading, in which an animal's pigmentation is darker dorsally, is often thought to have an adaptive effect of reducing conspicuous shadows cast on the ventral region of an animal's body. In essence the distribution of light on objects that are lit from above will cause unequal reflection of light on a solid body of uniform colour; such shadows could provide predators with visual cues to a prey's shape and projection. Countershading therefore reduces the ease of detection of prey by potential predators by counterbalancing the effects of shadowing.

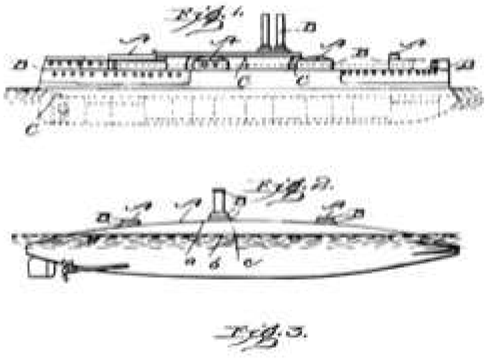
Examples

Countershading is observed in a large variety of animals, such as pronghorn antelope, White-tailed deer, squirrels, birds, and various lepidopteran larvae.

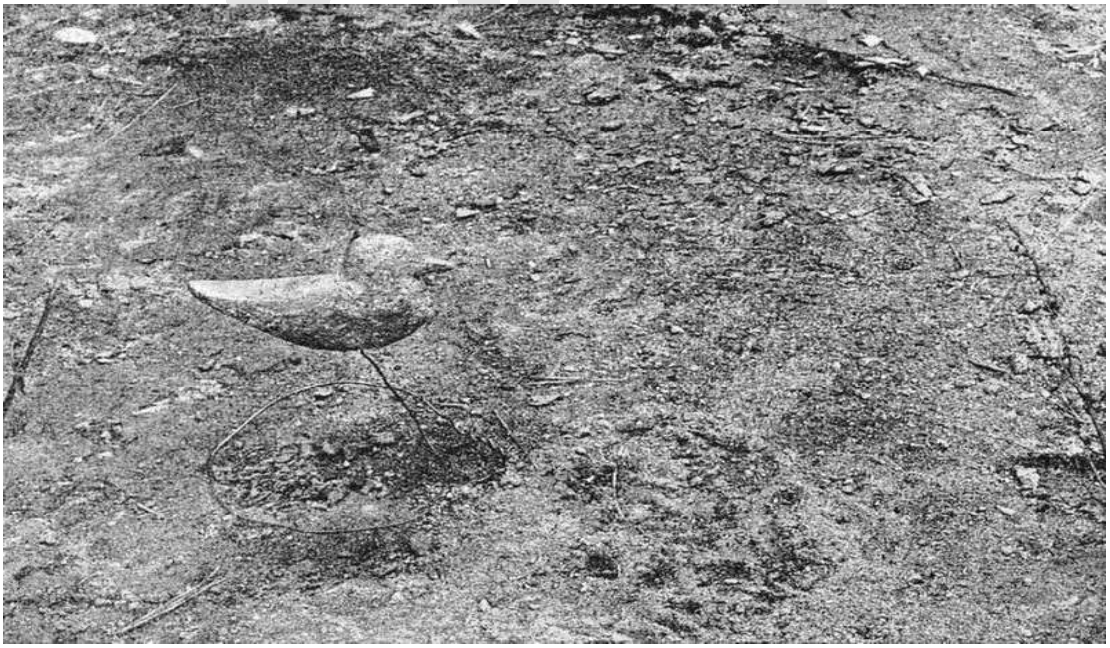
Alternatively, in many marine animals (including various species of fish such as marlins and sharks, penguins and cephalopods) this form of camouflage may work through background matching; when seen from the top, the darker dorsal area of the animal blends into the darkness of the water below, and when seen from below, the lighter ventral area blends into the sunlight from the surface.

Furthermore, countershading could also result from differential selection pressures on dorsal and ventral surfaces, from the need to protect against the damaging properties of UV light or abrasion.

History



The original drawings from Thayer's 1902 patent application



A photograph of a countershading study conducted by Thayer. The model on the left is camouflaged and visible whereas another on the right is countershaded and invisible

Abbott Handerson Thayer was one of the first to conduct extensive research on and to write about certain aspects of protective colouration in nature. In 1892, he wrote about the function of countershading in nature, in which he accounted for the white undersides of animals. For this reason countershading is sometimes called Thayer's Law.

Military camouflage sometimes uses the same principle; Thayer even obtained a patent in 1902 to paint warships using a countershaded scheme.

Anolis caroliensis showing blending camouflage and countershading

Salmon

Adelie penguins

Ringtailed lemur

Chapter 6

Bioluminescence

Flying and glowing firefly, a.k.a. *Photinus pyralis*

Female of *Lampyris noctiluca*, the Common Glowworm.

Bioluminescence is the production and emission of light by a living organism. Its name is a hybrid word, originating from the Greek *bios* for "living" and the Latin *lumen* "light". Bioluminescence is a naturally occurring form of chemiluminescence where energy is released by a chemical reaction in the form of light emission. Fireflies, anglerfish, and other creatures produce the chemicals luciferin (a pigment) and luciferase (an enzyme). The luciferin reacts with oxygen to create light. The luciferase acts as a catalyst to speed up the reaction, which is sometimes mediated by cofactors such as calcium ions or ATP. The chemical reaction can occur either inside or outside the cell. In bacteria, the expression of genes related to bioluminescence is controlled by an operon called the Lux operon.

Bioluminescence occurs in marine vertebrates and invertebrates, as well as microorganisms and terrestrial animals. Symbiotic organisms carried within larger organisms are also known to bioluminesce.

Characteristics

Bioluminescence is a form of luminescence, or "cold light" emission; less than 20% of the light generates thermal radiation. It should not be confused with fluorescence, phosphorescence or refraction of light.

Ninety percent of deep-sea marine life are estimated to produce bioluminescence in one form or another. Most marine light-emission belongs in the blue and green light spectrum, the wavelengths that can transmit through the seawater most easily. However, certain loose-jawed fishes emit red and infrared light and the genus *Tomopteris* emits yellow bioluminescence.

Non-marine bioluminescence is less widely distributed, but a larger variety in colours is seen. The two best-known forms of land bioluminescence are fireflies and glow worms. Other insects, insect larvae, annelids, arachnids and even species of fungi have been noted to possess bioluminescent abilities.

Some forms of bioluminescence are brighter (or only exist) at night, following a circadian rhythm.

Adaptations for bioluminescence

There are five main theories for bioluminescent traits:

Counterillumination camouflage

In some squid species bacterial bioluminescence is used for counterillumination so the animal matches the overhead environmental light seen from below. In these animals, photoreceptive vesicles have been found that control the contrast of this illumination to create optiminal matching. Usually these light organs are separate from the tissue containing the bioluminescent bacteria. However, in one species Euprymna scolopes these bacteria make up an integral component of the animal's light organ. Fireflies use their light mainly for attracting the opposite sex for mating.

Attraction

Firefly larva

Bioluminescence is used as a lure to attract prey by several deep sea fish such as the anglerfish. A dangling appendage that extends from the head of the fish attracts small animals to within striking distance of the fish. Some fish, however, use a non-bioluminescent lure.

The cookiecutter shark uses bioluminescence for camouflage, but a small patch on its underbelly remains dark and appears as a small fish to large predatory fish like tuna and mackerel swimming beneath it. When these fish try to consume the "small fish", they are bitten by the shark, which gouges out small circular "cookie cutter" shaped chunks of flesh from its hosts.

Dinoflagellates have an interesting twist on this mechanism. When a predator of plankton is sensed through motion in the water, the dinoflagellate luminesces. This in turn attracts even larger predators which will consume the would-be predator of the dinoflagellate.

The attraction of mates is another proposed mechanism of bioluminescent action. This is seen actively in fireflies, which use periodic flashing in their abdomens to attract mates in the mating season. In the marine environment this has only been well-documented in certain small crustaceans called ostracod. It has been suggested that pheromones may be used for long-distance communication, and bioluminescence used at close range to "home in" on the target.

Repulsion

Certain squid and small crustaceans use bioluminescent chemical mixtures or bioluminescent bacterial slurries in the same way as many squid use ink. A cloud of luminescence is expelled, confusing or repelling a potential predator while the squid or crustacean escapes to safety. Every species of firefly has larvae that glow to repel predators.

Communication

Communication between bacteria (quorum sensing) plays a role in the regulation of luminesence in many bacterial species. Using small extracellularly secreted molecules, they are able to adapt their behavior to only turn on genes for light production when they are at high cell densities.

Illumination

While most marine bioluminescence is green to blue, the Black Dragonfish produces a red glow. This adaptation allows the fish to see red-pigmented prey, which are normally invisible in the deep ocean environment where red light has been filtered out by the water column.

Biotechnology

Artistic rendering of bioluminescent Antarctic krill

Sepioteuthis lessoniana, one of many bioluminescent squid - 63 out of 100 genera of cuttlefish and squid contain species with the ability.

Bioluminescent organisms are a target for many areas of research. Luciferase systems are widely used in the field of genetic engineering as reporter genes. Luciferase systems have also been harnessed for biomedical research using bioluminescence imaging.

Vibrio symbiosis with numerous marine invertebrates and fish, namely the Hawaiian Bobtail Squid (*Euprymna scolopes*), are key experimental models for symbiosis, quorum sensing, and bioluminescence.

The structures of photophores, the light producing organs in bioluminescent organisms, are being investigated by industrial designers.

Proposed applications of engineered bioluminescence

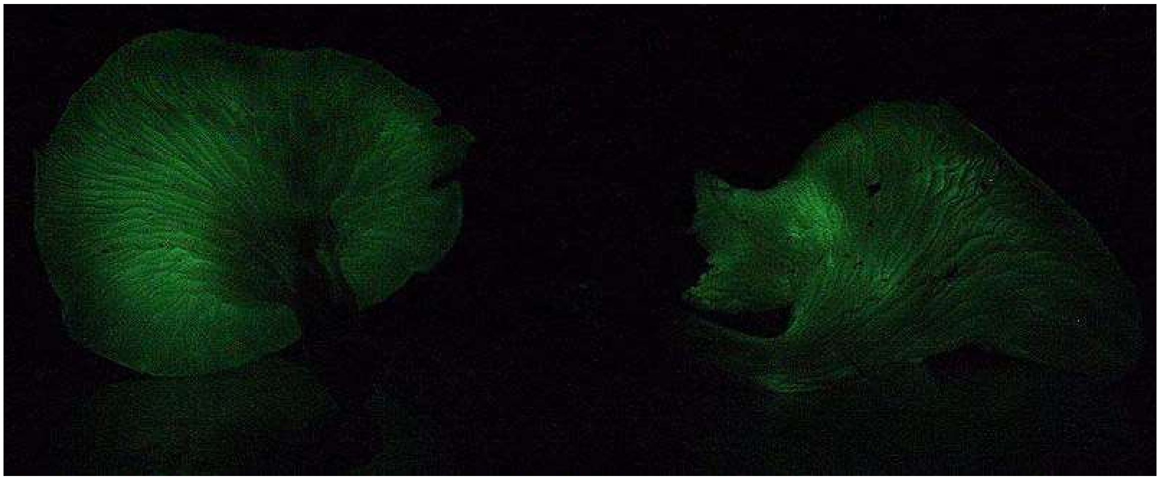
Some proposed applications of engineered bioluminescence include:

- Glowing trees to line highways to save government electricity bills
- Christmas trees that do not need lights, reducing danger from electrical fires
- Agricultural crops and domestic plants that luminesce when they need watering
- New methods for detecting bacterial contamination of meats and other foods
- Bio-identifiers for escaped convicts and mental patients
- Detecting bacterial species in suspicious corpses
- Novelty pets that bioluminesce (rabbits, mice, fish etc.)

Bioluminescent organisms

Omphalotus nidiformis

Example of a bioluminescent species of mushroom...



...glowing with the lights off.

Firefly (species unknown) with and without flash.

The fungus *Panellus stipticus* displaying bioluminescence.

All cells produce some form of bioluminescence within the electromagnetic spectrum, but most are neither visible nor noticeable to the naked eye. Every organism's bioluminescence is unique in wavelength, duration, timing and regularity of flashes. Below follows a list of organisms which have been observed to have visible bioluminescence.

Terrestrial organisms

Animals:

- certain arthropods
    - fireflies
    - click beetles
    - glow worms
        - railroad worms
    - certain mycetophilid flies
    - certain centipedes
    - certain millipedes
- a terrestrial mollusc (a tropical land snail)
    - *Quantula striata*
- annelids

Fungi:

- Mushrooms
    - Jack O'Lantern mushroom *(Omphalotus olearius)*
    - ghost fungus *(Omphalotus nidiformis)*
    - Honey mushroom
    - *Panellus stipticus*
    - several species of *Mycena*

Fish

- Anglerfish
- Cookie-cutter shark
- Flashlight fish
- Gulper eel
- Lanternfish
- Marine hatchetfish
- Midshipman fish
- Pineconefish
- Viperfish

Marine invertebrates

- many cnidarians
    - Sea pens
    - coral
    - *Aequorea victoria*, a jellyfish
- certain Ctenophores or "comb jellies"
- certain echinoderms (e.g. Ophiurida)
- certain crustaceans
    - ostracods
    - copepods
    - krill
- certain chaetognaths
- certain molluscs
    - certain clams, bivalves
    - certain nudibranchs, sea slugs
    - Octopus
        - Bolitaenidae
    - the order Teuthida
        - Colossal Squid
        - Mastigoteuthidae
        - Sepiolidae
        - Sparkling Enope Squid
        - Vampire squid

Blue ocean glow caused by myriad tiny organisms, such as Noctiluca.

Microorganisms

- Dinoflagellates
- Vibrionaceae (e.g. *Vibrio fischeri*, *Vibrio harveyi*, *Vibrio phosphoreum*)
- Members of the marine bacterial family Shewanellaceae, *Shewanella hanedai* and *Shewanella woodyi* have also been shown to be bioluminescent
- Fungi - A total of 71 species are bioluminescent including species of *Armillaria*, *Omphalotus*, *Mycena*, *Gerronema*, *Pleurotus*.

Chapter 7

Mimic Octopus

Mimic Octopus

Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda

Order:	Octopoda
Family:	Octopodidae
Subfamily:	Octopodinae
Genus:	***Thaumoctopus*** Norman & Hochberg, 2005
Species:	***T. mimicus***

Binomial name

Thaumoctopus mimicus
Norman & Hochberg, 2005

The **Mimic Octopus**, *Thaumoctopus mimicus*, is a species of octopus that has a strong ability to mimic other creatures. It grows up to 60 cm (2 feet) in length. Its normal colouring consists of brown and white stripes or spots.

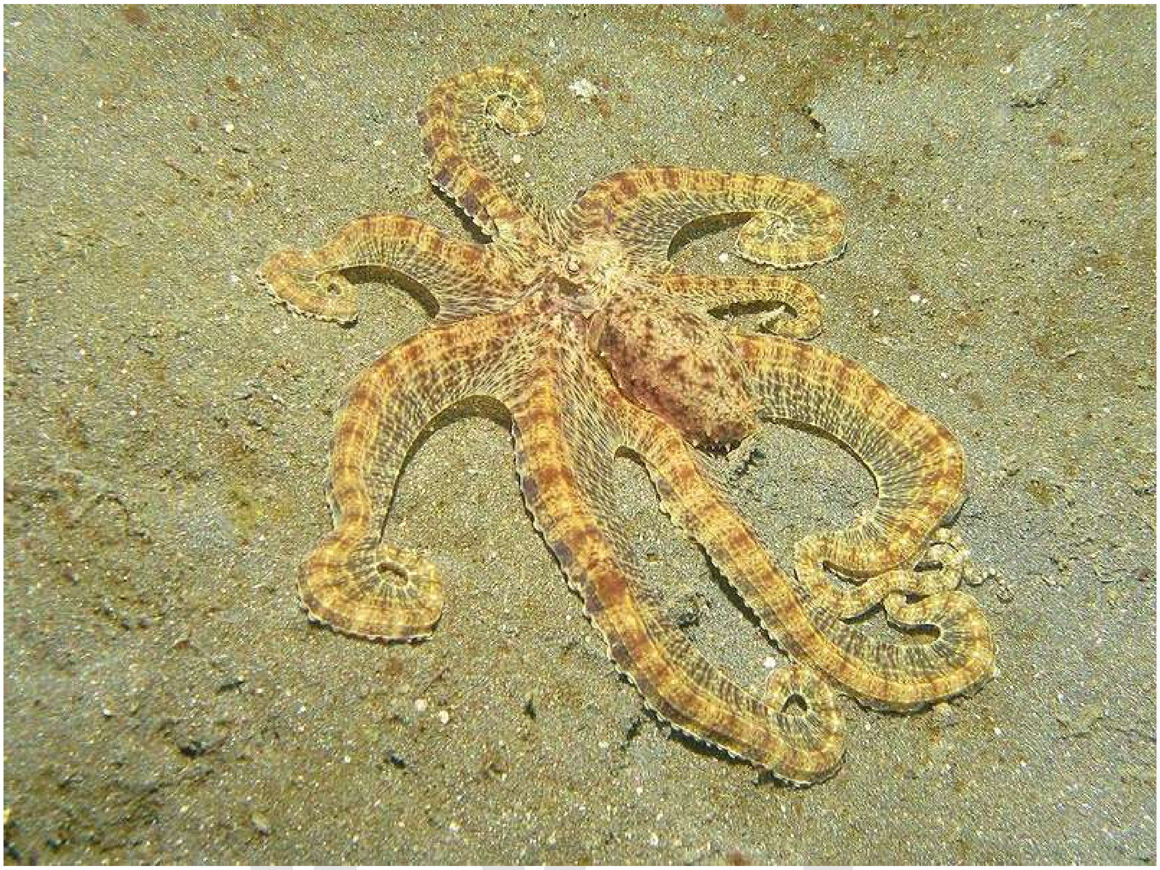
Living in the tropical seas of South East Asia, it was not discovered officially until 1998, off the coast of Sulawesi. The octopus mimics the physical likeness and movements of more than fifteen different species, including sea snakes, lionfish, flatfish, brittle stars, giant crabs, sea shells, stingrays, flounders, jellyfish, sea anemones, and mantis shrimp. It accomplishes this by contorting its body and arms, and changing colour.

Although all octopuses can change colour and texture, and many can blend with the sea floor, appearing as rocks, the mimic octopus is the first octopus species ever observed to impersonate other animals.

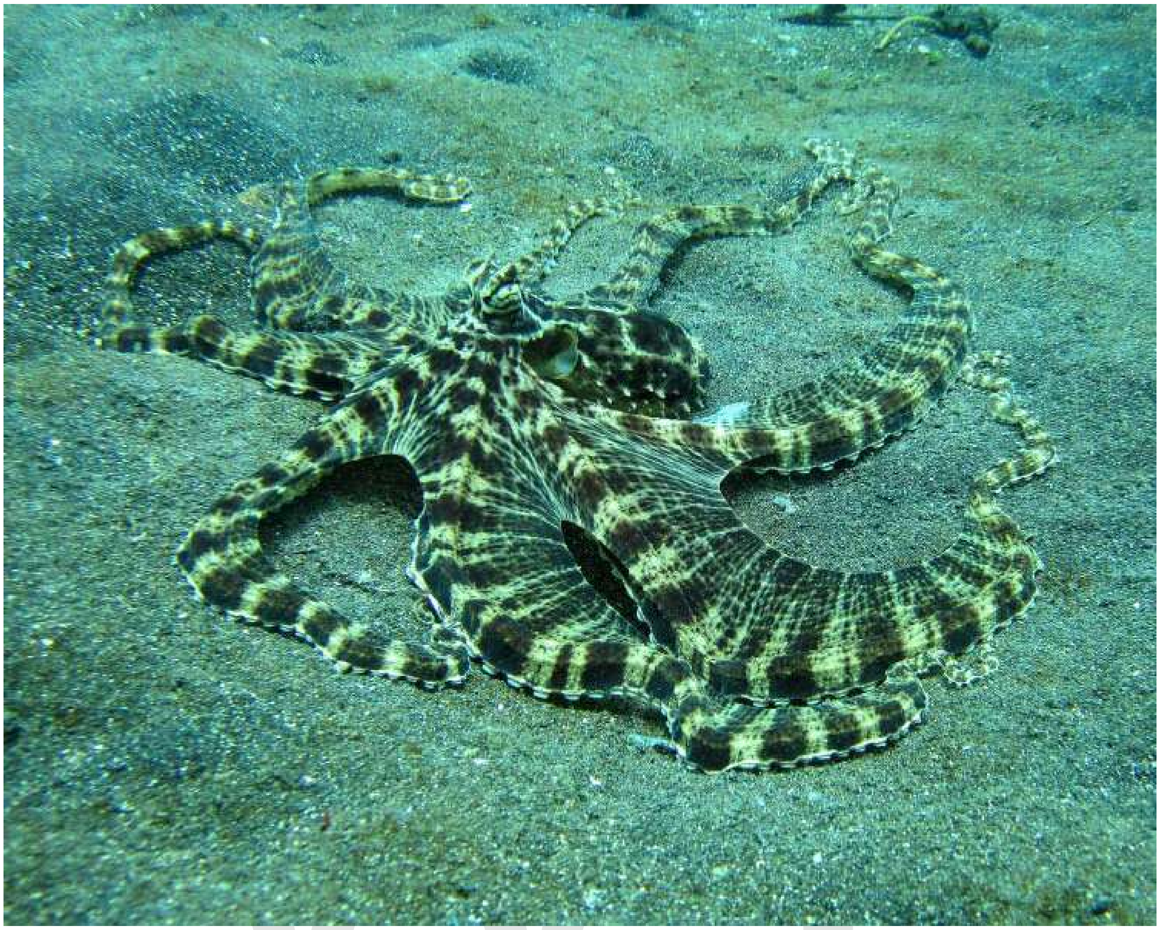
Based on observation, the mimic octopus may decide which animal to impersonate depending on local predators. For example, when the octopus was being attacked by damselfish, it was observed that the octopus appeared as a banded sea snake, a damselfish predator. The octopus impersonates the snake by turning black and yellow, burying six of its arms, and waving its other two arms in opposite directions.

The mimic octopus is often confused with *Wunderpus photogenicus*, another recently discovered species. The Wunderpus can be distinguished by the pattern of strong, fixed white markings on its body.

Habitat and behavior



Viewed from above



Mimic Octopus on a sandy seabed

Mimic octopuses have been known to live exclusively in nutrient-rich estuarine bays of Indonesia and Malaysia full of potential prey. They use a jet of water through their funnel to glide over the sand while searching for prey, typically small fish, crabs, and worms. Mimics are also prey themselves. Like other octopuses, their soft bodies are made of nutritious muscle, without spine or armor, and not obviously poisonous, making them desirable prey for such large deep water carnivores as barracuda and small sharks. Often unable to escape such predators, its mimicry of different "poisonous" creatures serves as its best defense. Mimicry also serves to allow it to prey upon animals that would ordinarily flee an octopus; it can imitate a crab as an apparent mate, only to devour its deceived "suitor".

This octopus mimics venomous sole, lion fish, sea snakes, sea anemones, and jellyfish. For example, the mimic is able to imitate a sole by pulling its arms in, flattening to a leaf-like shape, and increasing speed using a jet-like propulsion that resembles a sole. When spreading its legs and lingering on the ocean bottom, its arms trail behind to simulate the lion fish's fins. Raising all of its arms above its head with each arm bent in a curved zig-zag shape to resemble the lethal tentacles of a fish-eating sea anemone, it deters many fish. It imitates a large jellyfish by swimming to the surface and then slowly sinking with its arms spread evenly around its body.

Unlike the vast majority of octopuses, it regularly traverses tunnels and burrows in the sea floor to search for food and to conceal itself from predators. It can often be seen surveying its surroundings from one of these burrows, with only its eyes and head sticking out of the hole.

Feeding

Specimen from Lembeh Strait, North Sulawesi

The Mimic Octopus often feeds by covering an area of sand under a disc of webs while using the tips of its fine arms to flush small animals into its suckers. It can probe its arms deep into burrows or holes to search for prey which it can then pass to its mouth.

Chapter 8

Polychrotidae

Polychrotidae

Carolina Anole with dewlap extended

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Order:	Squamata
Suborder:	Iguania
Family:	**Polychrotidae**

Genera

- *Anisolepis*
- *Anolis*
- *Chamaeleolis*
- *Chamaelinorops*
- *Ctenonotus* - Eastern Antillean Anoles, Eastern Antillian Anoles
- *Dactyloa* - South American anoles
- *Enyalius*
- *Norops*
- *Phenacosaurus*
- *Polychrus*
- *Urostrophus*
- *Xiphosurus* - Hispaniolan giant

anole, Puerto Rican giant anole

Polychrotidae is a family of lizards commonly known as **anoles**. NCBI places the anole in subfamily **Polychrotinae** of the family Iguanidae. Four genera are common: *Anolis*, *Norops*, *Phenacosaurus*, and *Polychrus*.

Anole lizards are frequently and incorrectly called American chameleons or geckos, although they are not closely related to either of those groups. In fact, they are more closely related to iguanas. These misconceptions are likely due to their ability to alter their skin color and run up walls.

Characteristics and distribution

Anoles are small and common lizards that can be found throughout the southeastern United States, the Caribbean, and various other regions of the Western world. A large majority of them sport a green coloration, including the only species native to North America, the aptly named Green anole, although the green anole can change its color based on its mood and surroundings. Anoles are an exorbitantly diverse and plentiful group of lizards. There are currently about 372 known species. The Knight, Green, Bark Anole, and Cuban brown anoles can all be found in the United States, primarily in Florida, although the most prevalent of these species by far is the Cuban brown anole, which has pushed the native green (or "Carolina") anole population farther north.

Interestingly, when green anoles and brown anoles cohabit the same area, the brown anoles are primarily terrestrial or restrict themselves to the lower branches of bushes, while the green anoles stay higher. Brown anoles have also spread into East Texas. At a nursery in the Heights neighborhood of Houston, Texas, a stable population has established itself, hatchlings having been observed in the Spring of 2005.

All species of anole in the U.S. except the green anole were introduced through eggs nested in imported plants. It is notable that while nearly all anoles can change their color, the extent and variations of this ability differ widely throughout the individual anole species. For example, the green anole can change its color from a bright, leafy green to a dull brown color, while the Cuban brown can only change its shade of brown, along with the patterns on its back.

Anole out of hiding

Many anoles are between 8 and 18 cm (3–7 inches) in length. Some larger species, such as the Knight Anole, can surpass 12 inches (300 mm); some males of the Knight Anole species can even reach 20 inches (510 mm) in length.

Anoles' diets include live insects and other invertebrates, with crickets , spiders , and moths being some of the most commonly consumed prey. Anoles are opportunistic feeders, and may attempt to eat any attractive meal that is small enough. The primary foods for captive anoles are small feeder crickets that can be purchased at most pet stores.

Green Anole on railing

These subtropical lizards are semi arboreal. They usually inhabit regions around 3–6 m (10–20 feet) high. Shrubs, walls, fences, bushes, and short trees are common hiding places.

Most anoles are said to live between 4 and 8 years. Even anoles captured from the wild can live for several years if given acceptable living space and cared for properly—a healthy anole in captivity, being free from predators and natural disaster, may live well beyond seven years. Some anoles may even reach 14 years with careful and proper care.

Green anoles mating

Breeding occurs for several months beginning in late spring. Males employ head bobbing and dewlap extension in courtship. 1–2 small, soft shell eggs are laid among leaf litter. More clutches may be laid before mating season has ended.

Anole populations in each of the Martinique islands, despite remaining separate for an estimated six to eight million years, have not experienced significant evolution, and many mixed-island couples have successfully reproduced.

Anoles have many features that make them readily identifiable. They have a dewlap, made of erectile cartilage, that extends from the neck/throat area. Their toes are covered with structures that allow them to cling to many different surfaces. Also, their tails have the ability to break off at special segments in order to escape predators or fights. The tail itself continues to wriggle strongly for some minutes after detaching. This ability is known as autotomy. Anoles are also diurnal, which means that they are active during the daytime.

Some species of anoles exhibit sexual dimorphism, which allows one to discern between males and females fairly easily with the naked eye. In green anoles, the females are characterized by a pale dorsal stripe extending from neck to tail, generally smaller body, and a smaller head with a shorter snout. Female brown anoles share these characteristics, although their dorsal stripe is oftentimes wider with diamond-shaped or squiggly edges. This stripe may be present sometimes in males, especially young ones not yet fully grown, but it is always fainter with less defined edges. Some females have a small dewlap (pale and much smaller than those of the males); others not at all.

Territory

Anoles are very territorial. Although the lizards are small, their territories are usually quite big: around three square yards, females' usually smaller. Their territories often contain a basking area, a shady area, a high lookout, and always a place to hide from predators. They do not take kindly to other anoles in their territory. Often when an intruder is in the area, the anole raises its spine, fans its dewlap, and does "push-ups" accompanied by intermittent ultrasonic hisses. If this does not scare off the intruder, a fight proceeds in which the two anoles bite at each other's necks. If the anole loses (gives up) the intruder gains entrance, otherwise he leaves. Females rarely fight. Anoles have a wide range of territorial behavior from one head bob to a pressurized bite usually aimed for the snout or jaw of the lizard. When caught by a person they will tend to bite if agitated and require some effort to remove from skin. They very rarely draw blood or cause injury.

Relationship with humans

Female Green Anole on fake plant in captivity

Anoles function well as a native pest control as they will eat spiders, cockroaches, and other bugs and will run from humans whenever possible.

Chapter 9

Cephalopod

Cephalopods
Temporal range: Devonian – Recent
(Stem-groups from Cambrian)

Bigfin reef squid (*Sepioteuthis lessoniana*)

Scientific classification [e]

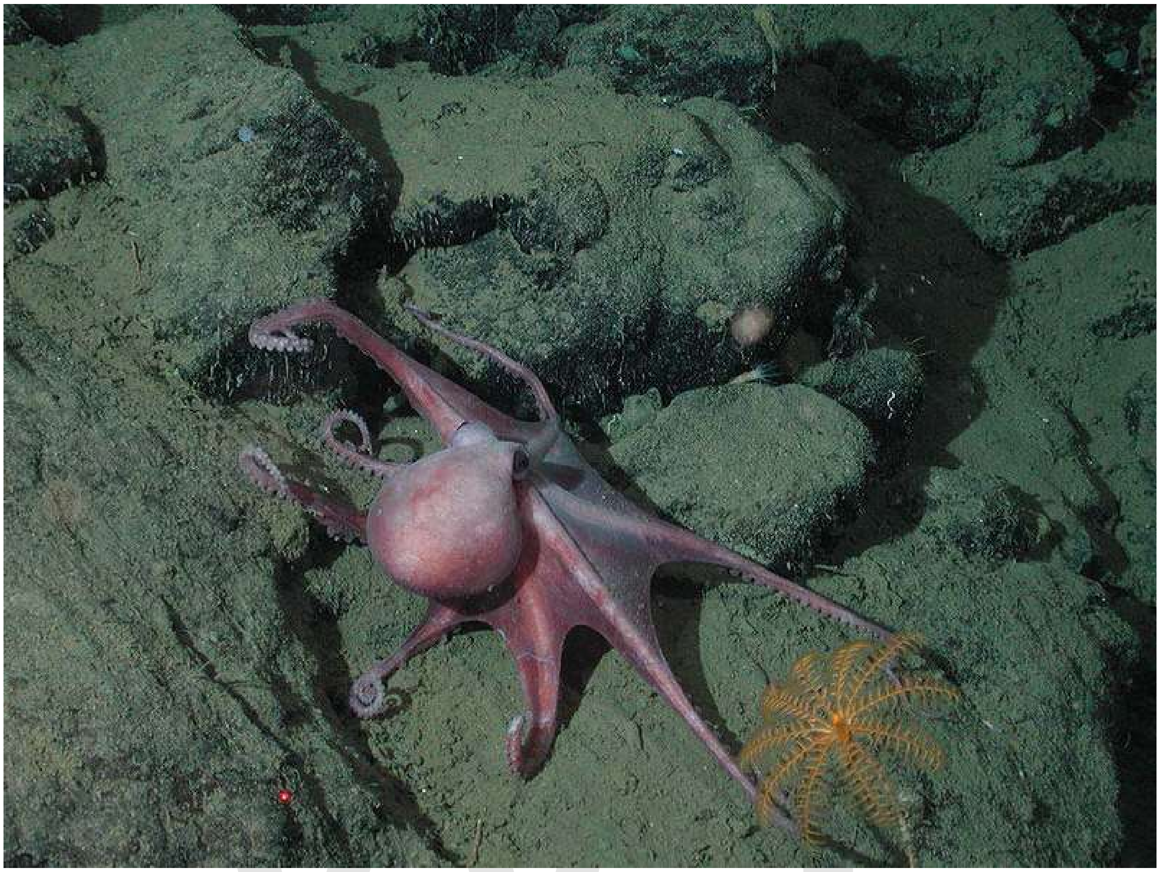
Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Cephalopoda** Cuvier, 1797

A **cephalopod** is any member of the molluscan class **Cephalopoda**. These exclusively marine animals are characterized by bilateral body symmetry, a prominent head, and a set of arms or tentacles (muscular hydrostats) modified from the primitive molluscan foot.

Fishermen sometimes call them **inkfish**, referring to their common ability to squirt ink. The study of cephalopods is a branch of malacology known as **teuthology**.

Cephalopods became dominant during the Ordovician period, represented by primitive nautiloids. The class now contains two, only distantly related, extant subclasses: Coleoidea, which includes octopuses, squid, and cuttlefish; and Nautiloidea, represented by *Nautilus* and *Allonautilus*. In the Coleoidea, the molluscan shell has been internalized or is absent, whereas in the Nautiloidea, the external shell remains. About 800 living species of cephalopods have been identified. Two important extinct taxa are the Ammonoidea (ammonites) and Belemnoidea (belemnites).

Distribution



Left: A pair of *Sepia officinalis* in shallow water
Right: *Benthoctopus* sp. on the Davidson Seamount at 2,422 m depth

There are around 800 extant species of cephalopod, although new species continue to be described. An estimated 11,000 extinct taxa have been described, although the soft-bodied nature of cephalopods means they are not easily fossilised.

Cephalopods are found in all the oceans of Earth. None of them can tolerate freshwater, but the brief squid, *Lolliguncula brevis*, found in Chesapeake Bay may be a notable exception in that it tolerates brackish water.

Cephalopods occupy most of the depth of the ocean, from the abyssal plane to the sea surface. Their diversity is greatest near the equator (~40 species retrieved in nets at 11°N by a diversity study) and decreases towards the poles (~5 species captured at 60°N).

Nervous system and behaviour

Left: An octopus opening a container with a screw cap
Right: Hawaiian bobtail squid, *Euprymna scolopes*, burying itself in the sand, leaving only the eyes exposed

Cephalopods are widely regarded as the most intelligent of the invertebrates, and have well developed senses and large brains (larger than those of gastropods). The nervous system of cephalopods is the most complex of the invertebrates, and their brain-to-body-mass ratio falls between that of warm- and cold-blooded vertebrates. The giant nerve fibers of the cephalopod mantle have been widely used as experimental material in neurophysiology for many years; their large diameter (due to lack of myelination) makes them relatively easy to study.

Cephalopods are social creatures; when isolated from their own kind, they will take to shoaling with fish.

Some cephalopods are able to fly distances up to 50 m. While the organisms are not particularly aerodynamic, they achieve these rather impressive ranges by use of jet-propulsion; water continues to be expelled from the funnel while the organism is in flight.

Senses

Cephalopods have advanced vision, can detect gravity with statocysts, and have a variety of chemical sense organs. Octopuses use their tentacles to explore their environment and can use them for depth perception.

The primitive nautilus eye functions similarly to a pinhole camera.

Vision

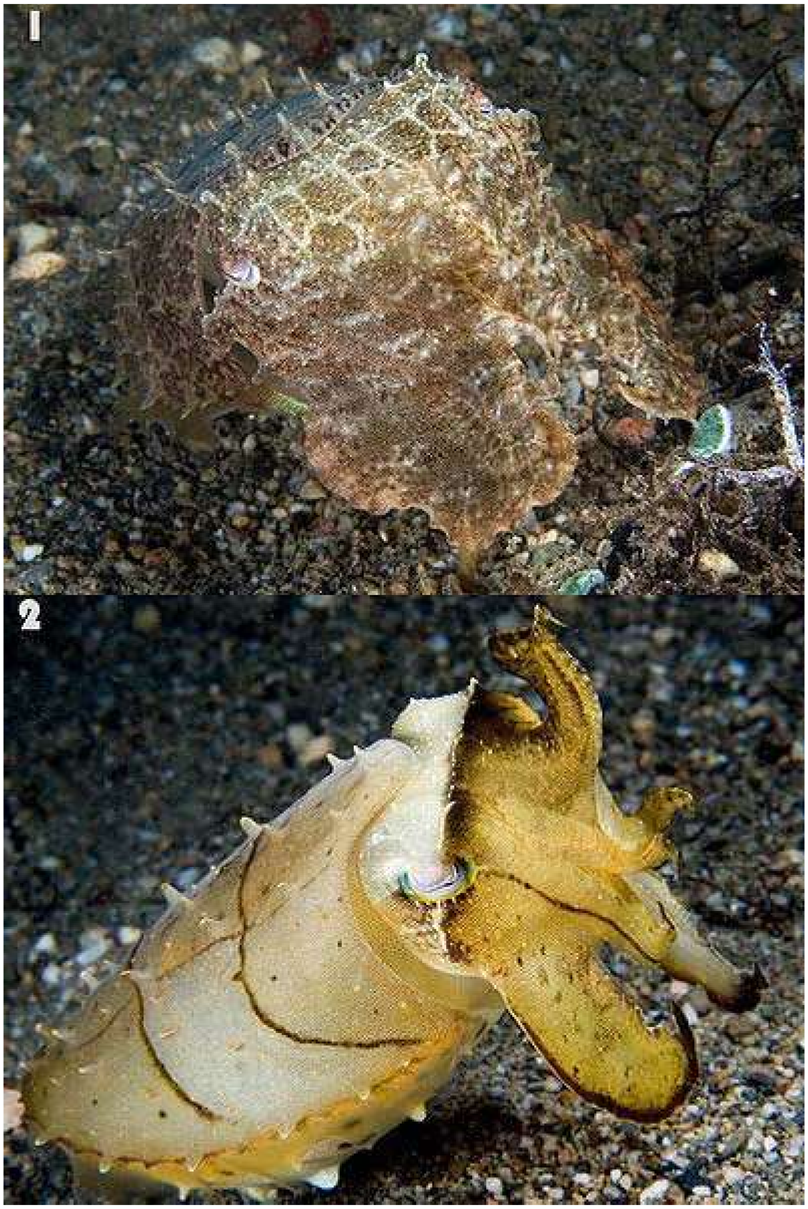
Most cephalopods rely on vision to detect predators and prey, and to communicate with one another. Consequently, cephalopod vision is acute: training experiments have shown that the common octopus can distinguish the brightness, size, shape, and horizontal or vertical orientation of objects. The morphological construction gives cephalopod eyes the same performance as sharks'; however, their construction differs, as cephalopods lack a cornea, and have an everted retina. Cephalopods' eyes are also sensitive to the plane of polarization of light. Surprisingly—given their ability to change color—all octopuses and most cephalopods are color blind. When camouflaging themselves, they use their chromatophores to change brightness and pattern according to the background they see, but their ability to match the specific color of a background may come from cells such as iridophores and leucophores that reflect light from the environment. They also produce visual pigments throughout their body, and may sense light levels directly from their body. Evidence of color vision has been found in the sparkling enope squid (*Watasenia scintillans*), which achieves color vision by the use of three distinct retinal molecules (A1, sensitive to red; A2, to purple, and A4, to yellow?) which bind to its opsin.

Unlike many other cephalopods, nautiluses do not have good vision; their eye structure is highly developed, but lacks a solid lens. They have a simple "pinhole" eye through which water can pass. Instead of vision, the animal is thought to use olfaction as the primary sense for foraging, as well as locating or identifying potential mates.

Hearing

Cephalopods can use their statocysts to detect sound.

Use of light



This broadclub cuttlefish (*Sepia latimanus*) can go from camouflage tans and browns (top) to yellow with dark highlights (bottom) in less than a second.

Most cephalopods possess chromatophores - that is, coloured pigments - which they can use in a startling array of fashions. As well as providing camouflage with their background, some cephalopods bioluminesce, shining light downwards to disguise their shadows from any predators that may lurk below. The bioluminescence is produced by bacterial symbionts; the host cephalopod is able to detect the light produced by these organisms. Bioluminescence may also be used to entice prey, and some species use colourful displays to impress mates, startle predators, or even communicate with one another. It is not certain whether bioluminescence is actually of epithelial origin or if it is a bacterial production.

Colouration

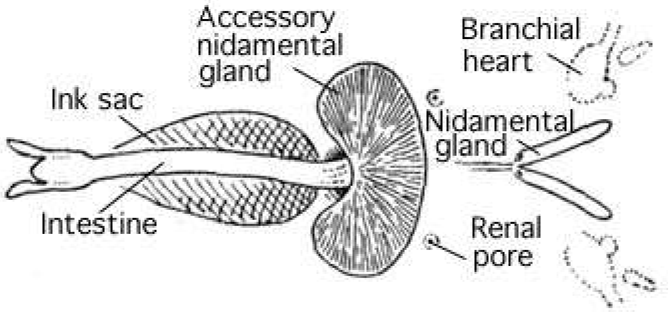
Colouration can be changed in milliseconds as they adapt to their environment, and the pigment cells are expandable by muscular contraction. Colouration is typically more pronounced in near-shore species than those living in the open ocean, whose functions tend to be restricted to camouflage by breaking their outline.

Evidence of original colouration has been detected in cephalopod fossils dating as far back as the Silurian; these orthoconic individuals bore concentric stripes, which are thought to have served as camouflage. Devonian cephalopods bear more complex colour patterns, whose function may be more complex.

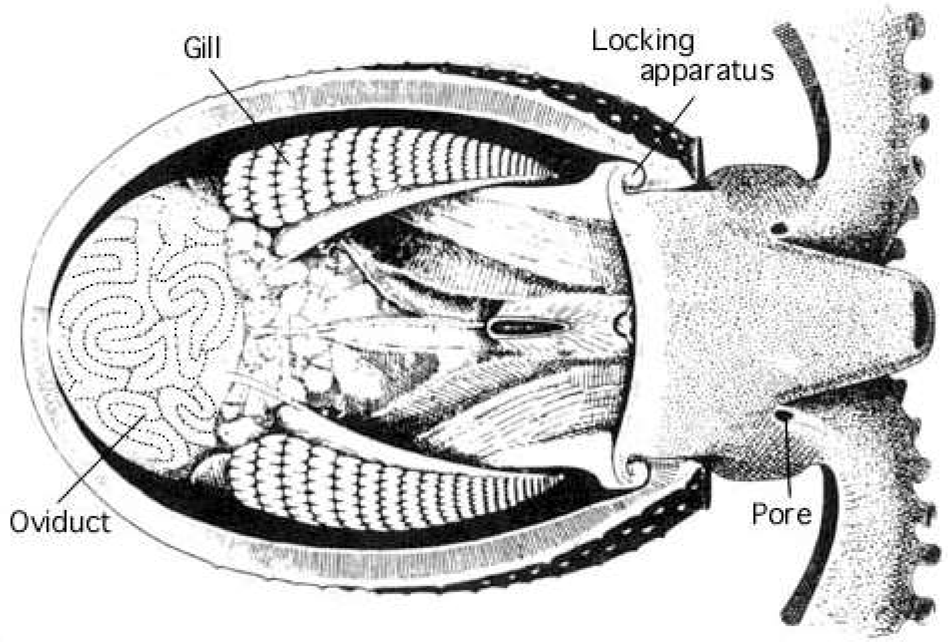
Ink

With the exception of the Nautilidae and the species of octopus belonging to the suborder Cirrina, all known cephalopods have an ink sac, which can be used to expel a cloud of dark ink to confuse predators. This sac is a muscular bag which originated as an extension of the hind gut. It lies beneath the gut and opens into the anus, into which its contents – almost pure melanin – can be squirted; its proximity to the base of the funnel means the ink can be distributed by ejected water as the cephalopod uses its jet propulsion. The ejected cloud of melanin is usually mixed, upon expulsion, with mucus, produced elsewhere in the mantle, and therefore forms a thick cloud, resulting in visual (and possibly chemosensory) impairment of the predator, like a smokescreen. However, a more sophisticated behaviour has been observed, in which the cephalopod releases a cloud, with a greater mucus content, that approximately resembles the cephalopod that released it (this decoy is referred to as a pseudomorph). This strategy often results in the predator attacking the pseudomorph, rather than its rapidly departing prey.

The inking behaviour of cephalopods has led to a common name of "inkfish", primarily used in fisheries science and the fishing industry, paralleling the terms white fish, oily fish, and shellfish.



Viscera of *Chtenopteryx sicula*



Viscera of *Ocythoe tuberculata*

Circulatory system

Cephalopods are the only mollusks with a closed circulatory system. Coleoids have two gill hearts (also known as branchial hearts) that move blood through the capillaries of the gills. A single systemic heart then pumps the oxygenated blood through the rest of the body.

Like most molluscs, cephalopods use hemocyanin, a copper-containing protein, rather than hemoglobin, to transport oxygen. As a result, their blood is colorless when deoxygenated and turns blue when exposed to air.

Respiration

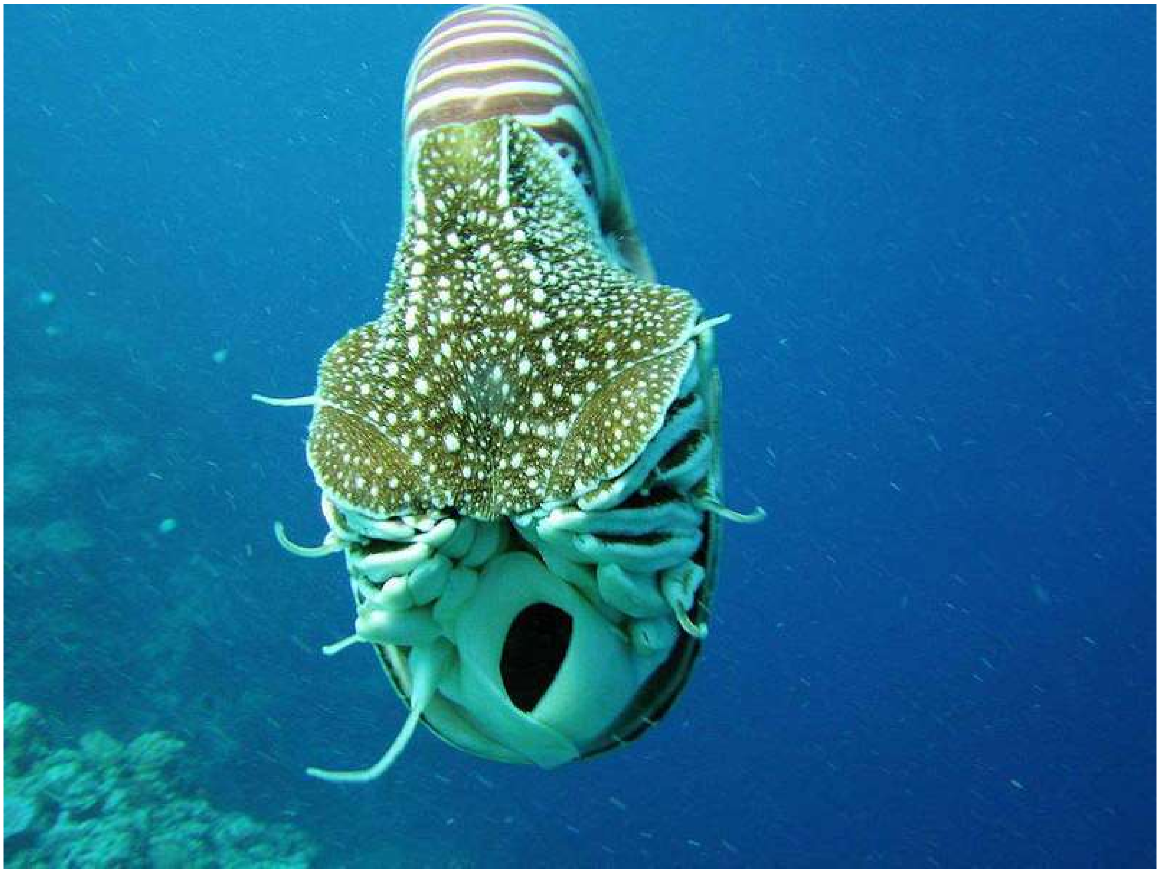
Cephalopods exchange gasses with the seawater by forcing water through their gills, which are attached to the roof of the organism. Water enters the mantle cavity on the outside of the gills, and the entrance of the mantle cavity closes. When the mantle contracts, water is forced through the gills, which lie between the mantle cavity and the funnel. The water's expulsion through the funnel can be used to power jet propulsion. The gills, which are much more efficient than those of other molluscs, are attached to the ventral surface of the mantle cavity. There is a trade-off with gill size regarding lifestyle. To achieve fast speeds, gills need to be small - water will be passed through them quickly when energy is needed, compensating for their small size. However, organisms which spend most of their time moving slowly along the bottom do not naturally pass much water through their cavity for locomotion; thus they have larger gills, along with complex systems to ensure that water is constantly washing through their gills, even when the organism is stationary. The water flow is controlled by contractions of the radial and circular mantle cavity muscles.

The gills of cephalopods are supported by a skeleton of robust fibrous proteins; the lack of mucopolysaccharides distinguishes this matrix from cartilage. The gills are also thought to be involved in excretion, with NH_4^+ being swapped with K^+ from the seawater.

Locomotion and buoyancy

Octopuses swim headfirst, with arms trailing behind

While all cephalopods can move by jet propulsion, this is a very energy-consuming way to travel compared to the tail propulsion used by fish. The relative efficiency of jet propulsion decreases further as animal size increases; paralarvae are far more efficient than juvenile and adult individuals. Since the Paleozoic era, as competition with fish produced an environment where efficient motion was crucial to survival, jet propulsion has taken a back role, with fins and tentacles used to maintain a steady velocity. Whilst jet propulsion is never the sole mode of locomotion, the stop-start motion provided by the jets continues to be useful for providing bursts of high speed - not least when capturing prey or avoiding predators. Indeed, it makes cephalopods the fastest marine invertebrates, and they can out-accelerate most fish. The jet is supplemented with fin motion; in the squid, the fins flap each time that a jet is released, amplifying the thrust; they are then extended between jets (presumably to avoid sinking). Oxygenated water is taken into the mantle cavity to the gills and through muscular contraction of this cavity, the spent water is expelled through the hyponome, created by a fold in the mantle. The size difference between the posterior and anterior ends of this organ control the speed of the jet the organism can produce. The velocity of the organism can be accurately predicted for a given mass and morhpology of animal. Motion of the cephalopods is usually backward as water is forced out anteriorly through the hyponome, but direction can be controlled somewhat by pointing it in different directions. Some cephalopods accompany this expulsion of water with a gunshot-like popping noise, thought to function to frighten away potential predators.



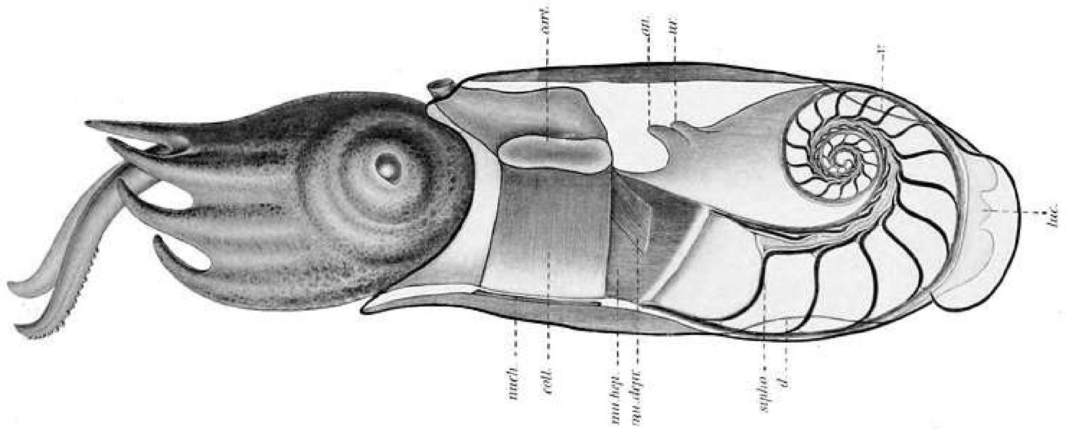
Nautilus belauensis seen from the front, showing the opening of the hyponome

Early cephalopods are thought to have produced jets by drawing their body into their shells, as *Nautilus* does today. *Nautilus* is also capable of creating a jet by undulations of its funnel; this slower flow of water is more suited to the extraction of oxygen from the water. The jet velocity in *Nautilus* is much slower than in coleoids, but less musculature and energy is involved in its production. Jet thrust in cephalopods is controlled primarily by the maximum diameter of the funnel orifice (or, perhaps, the average diameter of the funnel) and the diameter of the mantle cavity. Changes in the size of the orifice are used most at intermediate velocities. The absolute velocity achieved is limited by the cephalopod's requirement to inhale water for expulsion; this intake limits the maximum velocity to eight body-lengths per second, a speed which most cephalopods can attain after two funnel-blows. Water refills the cavity by entering not only through the orifices, but also though the funnel. To accommodate the rapid changes in water intake and expulsion, the orifices are highly flexible and can change their size by a factor of twenty; the funnel radius, conversely, changes only by a factor of around 1.5.

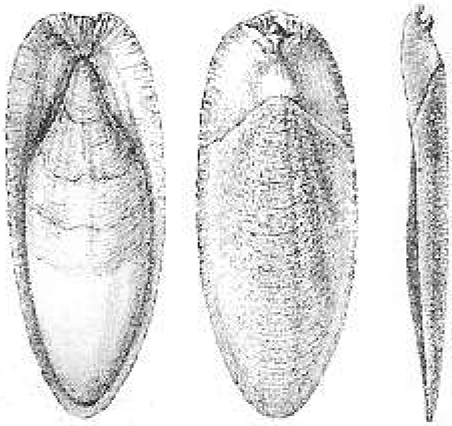
Some octopus species are also able to walk along the sea bed. Squids and cuttlefish can move short distances in any direction by rippling of a flap of muscle around the mantle.

While most cephalopods float (i.e. are neutrally buoyant or nearly so; in fact most cephalopods are about 2-3% denser than seawater), they achieve this in different ways. Some, such as *Nautilus*, allow gas to diffuse into the gap between the mantle and the shell; others allow purer water to ooze from their kidneys, forcing out denser salt water from the body cavity; others, like some fish, accumulate oils in the liver; and some octopuses have a gelatinous body with lighter chlorine ions replacing sulfate in the body chemistry.

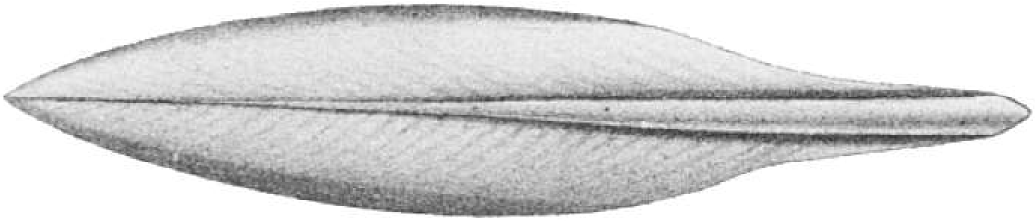
Shell



Cross section of *Spirula spirula*, showing the position of the shell inside the mantle



Cuttlebone of *Sepia officinalis*



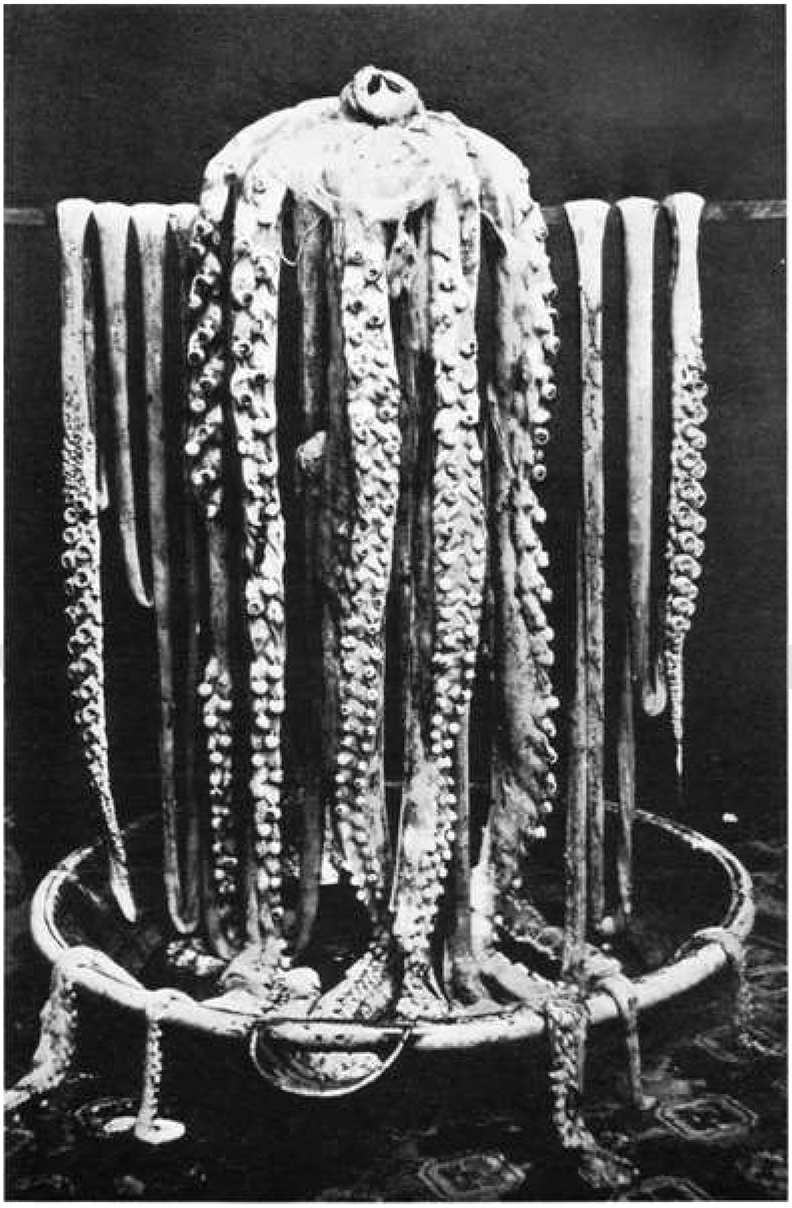
Gladius of *Sepioteuthis lessoniana*

Nautiluses are the only extant cephalopods with an external shell. However, all molluscan shells are formed from the ectoderm (outer layer of the embryo); in cuttlefish (*Sepia* spp.), for example, an invagination of the ectoderm forms during the embryonic period, resulting in a shell that is internal in the adult. The same is true of the chitinous gladius of squid and octopus. Cirrate octopuses have cartilaginous fin supports, which are sometimes referred to as a "shell vestige" or "gladius". The Incirrina have no vestige of an internal shell, and some squid also lack a gladius. Interestingly, the shelled coleoids do not form a clade or even a paraphyletic group. The *Spirula* shell begins as an organic structure, and is then very rapidly mineralized. Shells that are "lost" may be lost by resorption of the calcium carbonate component.

Females of the octopus genus *Argonauta* secrete a specialised paper-thin eggcase in which they reside, and this is popularly regarded as a "shell", although it is not attached to the body of the animal.

The largest group of shelled cephalopods, the ammonites, are extinct, but their shells are very common as fossils.

The deposition of carbonate, leading to a mineralized shell, appears to be related to the acidity of the organic shell matrix; shell-forming cephalopods have an acidic matrix, whereas the gladius of squid has a basic matrix.



Left: A giant squid found in Logy Bay, Newfoundland, in 1873. The two long feeding tentacles are visible on the extreme left and right.
Right: Detail of the tentacular club of *Abraliopsis morisi*

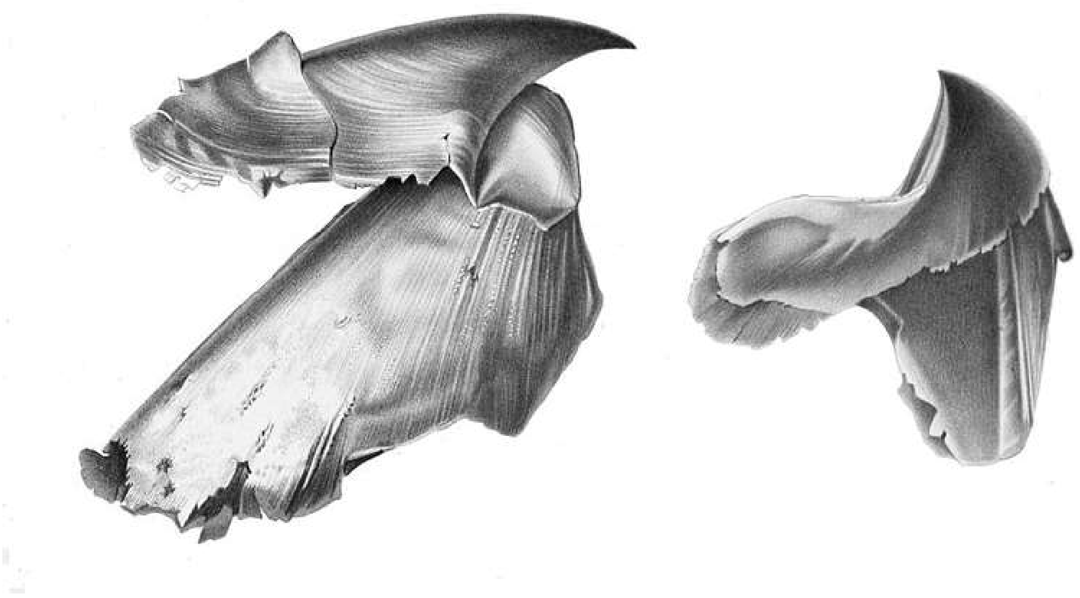
Head appendages

Cuttlefish and squid have five pairs of muscular appendages surrounding their mouths. The longer two, termed tentacles, are actively involved in capturing prey; they can lengthen rapidly (in as little as 15 milliseconds). In giant squid they may reach a length of 8 metres. They may terminate by broadening into a sucker-coated club.The shorter four pairs are termed arms, and are involved in holding and manipulating the captured organism. They too have suckers, on the side closest to the mouth; these help to hold onto the prey.

The tentacle consists of a thick central nerve cord (which must be thick to allow each sucker to be controlled independently) surrounded by circular and radial muscles. Because the volume of the tentacle remains constant, contracting the circular muscles decreases the radius and permits the rapid increase in length. Typically a 70% lengthening is achieved by decreasing the width by 23%.

The size of the tentacle is related to the size of the buccal cavity; larger, stronger tentacles can hold prey as small bites are taken from it; with more numerous, smaller tentacles, prey is swallowed whole, so the mouth cavity must be larger.

Feeding



The two-part beak of the giant squid, *Architeuthis* sp.

All living cephalopods have a two-part beak; most have a radula, although it is reduced in most octopus and absent altogether in *Spirula*. They feed by capturing prey with their tentacles, drawing it in to their mouth and taking bites from it. They have a mixture of toxic digestive juices, some of which are manufactured by symbiotic algae, which they eject from their salivary glands onto their captured prey held in their mouth. These juices separate the flesh of their prey from the bone or shell. The salivary gland has a small tooth at its end which can be poked into an organism to digest it from within.

The digestive gland itself is rather short. It has four elements, with food passing through the crop, stomach and caecum before entering the intestine. Most digestion, as well as the absorption of nutrients, occurs in the digestive gland, sometimes called the liver. Nutrients and waste materials are exchanged between the gut and the digestive gland through a pair of connections linking the gland to the junction of the stomach and caecum. Cells in the digestive gland directly release pigmented excretory chemicals into the lumen of the gut, which are then bound with mucus passed through the anus as long dark strings, ejected with the aid of exhaled water from the funnel.

Radula

Amphioctopus marginatus eating a crab

The cephalopod radula consists of multiple symmetrical rows of up to nine teeth – thirteen in fossil classes. The organ is reduced or even vestigial in certain octopus species and is absent in *Spirula*. The teeth may be homodont (i.e. similar in form across a row), heterodont (otherwise), or ctenodont (comb-like). Their height, width and number of cusps is variable between species. The pattern of teeth repeats, but each row may not be identical to the last; in the octopus, for instance, the sequence repeats every five rows.

Cephalopod radulae are known from fossil deposits dating back to the Ordovician. They are usually preserved within the cephalopod's body chamber, commonly in conjunction with the mandibles; but this need not always be the case; many radulae are preserved in a range of settings in the Mason Creek. Radulae are usually difficult to detect, even when they are preserved in fossils, as the rock must weather and crack in exactly the right fashion to expose them; for instance, radulae have only been found in nine of the 43 ammonite genera, and they are rarer still in non-ammonoid forms: only three pre-Mesozoic species possess one.

Excretory system

Most cephalopods possess a single pair of large nephridia. Filtered nitrogenous waste is produced in the pericardial cavity of the branchial hearts, each of which is connected to a nephridium by a narrow canal. The canal delivers the excreta to a bladder-like renal sac, and also resorbs excess water from the filtrate. Several outgrowths of the lateral vena cava project into the renal sac, continuously inflating and deflating as the branchial hearts beat. This action helps to pump the secreted waste into the sacs, to be released into the mantle cavity through a pore.

Nautilus, unusually, possesses four nephridia, none of which are connected to the pericardial cavities.

Ammonium

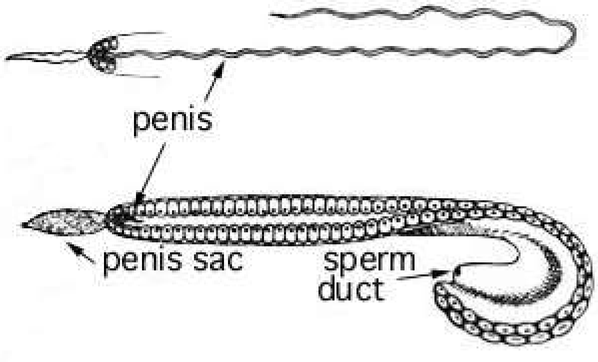
The handling of ammonia is thought to be important in shell formation in terrestrial molluscs, and in other nonmolluscan lineages.

Because protein (i.e. flesh) is a major constituent of the cephalopod diet, large amounts of ammonium are produced as waste. The main organs involved with the release of this excess ammonium are the gills.

The rate of this release is the lowest in the shelled cephalopods *Nautilus* and *Sepia*, probably as a result of their use of nitrogen to fill their shells with gas to produce buoyancy. Other cephalopods use ammonium in a similar way, storing the ions (as ammonium chloride) themselves to reduce their overall density and thus become more buoyant.

Reproduction and life cycle

Female *Argonauta argo* with eggcase and eggs



Detail of the hectocotylus of *Ocythoe tuberculata*

A dissected male specimen of *Onykia ingens*, showing a non-erect penis (the white tubular structure located below most of the other organs)

A specimen of the same species exhibiting elongation of the penis to 67 cm in length

With a few exceptions, Coleoidea live short lives with rapid growth. Most of the energy extracted from their food is used for growing. The penis in most male Coleoidea is a long and muscular end of the gonoduct used to transfer spermatophores to a modified arm called a hectocotylus. That, in turn, is used to transfer the spermatophores to the female. In species where the hectocotylus is missing, the penis is long and able to extend beyond the mantle cavity and transfers the spermatophores directly to the female. Deep water squid have the greatest known penis length relative to body size of all mobile animals, second in the entire animal kingdom only to certain sessile barnacles. Penis elongation in *Onykia ingens* may result in a penis that is as long as the mantle, head and arms combined.

Most cephalopods tend towards a semelparous reproduction strategy; they lay many small eggs in one batch and die afterwards. The Nautiloidea, on the other hand, stick to iteroparity; they produce a few large eggs in each batch and live for a long time.

External sexual characteristics are lacking in cephalopods, so cephalopods use colour communication. A courting male will approach a likely looking opposite number flashing his brightest colours, often in rippling displays. If the other cephalopod is female and receptive, her skin will change colour to become pale, and mating will occur. If the other cephalopod remains brightly coloured, it is taken as a warning.

The male has a sperm-carrying arm, known as the hectocotylous arm, with which to impregnate the female. In many cephalopods, mating occurs head to head and the male may simply transfer sperm to the female. Others may detach the sperm-carrying arm and leave it attached to the female. In the paper nautilus, this arm remains active and wriggling for some time, prompting the zoologists who discovered it to conclude it was some sort of worm-like parasite. It was duly given a genus name *Hectocotylus*, which held for some time until the mistake was discovered.

Nidamental glands are involved in the secretion of egg cases or the gelatinous substance comprising egg masses. The eggs may be brooded: female paper nautilus construct a shelter for the young, while Gonatiid squid carry a larva-laden membrane from the hooks on their arms. Other cephalopods deposit their young under rocks and aerate them with their tentacles hatching. Often, though, the eggs are left to their own devices; many squid lay sausage-like bunches of eggs in crevices or occasionally on the sea floor. Cuttlefish lay their eggs separately in cases and attach them to coral or algal fronds. Fossilised egg clutches show that ammonites also laid clutches of eggs.

Cephalopods are occasionally long-lived, especially in the deep water or polar forms, but most of the group live fast and die young, maturing rapidly to their adult size. Some may gain as much as 12% of their body mass each day. Most live for one to two years, reproducing and then dying shortly thereafter.

To free up resources for reproduction, many squid are known to resorb the muscle tissue of their mantle and tentacles, breaking down the tissue and using the energy contained therein to produce more gametes.

Egg cases laid by a female squid

Embryology

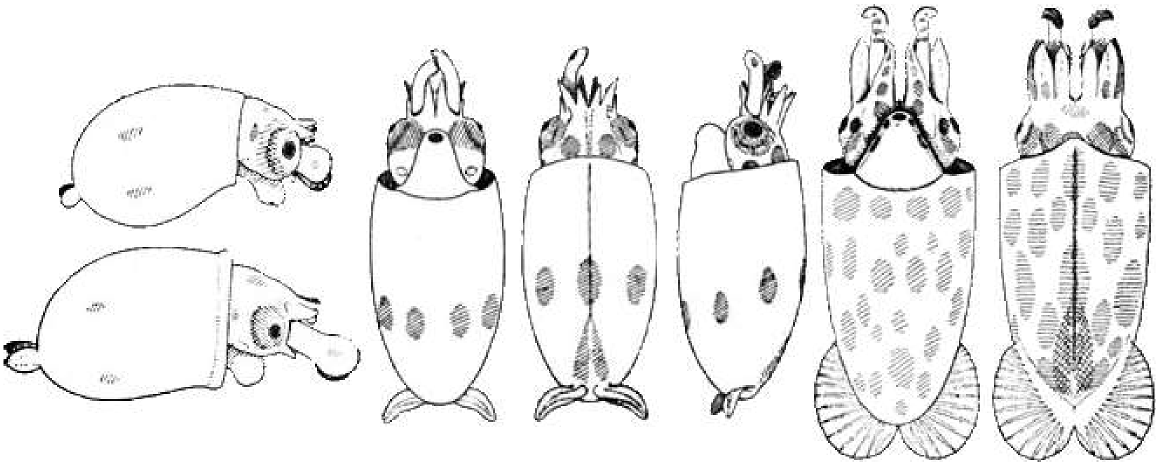
Unlike most other molluscs, cephalopods do not have a distinct larval stage. The fertilised ovum initially divides to produce a disc of germinal cells at one pole, with the yolk remaining at the opposite pole. The germinal disc grows to envelop and eventually absorb the yolk, forming the embryo. The tentacles and arms first appear at the hind part of the body, where the foot would be in other molluscs, and only later migrate towards the head.

The funnel of cephalopods develops on the top of their head, whereas the mouth develops on the opposite surface. The early embryological stages are reminiscent of ancestral gastropods and extant Monoplacophora.

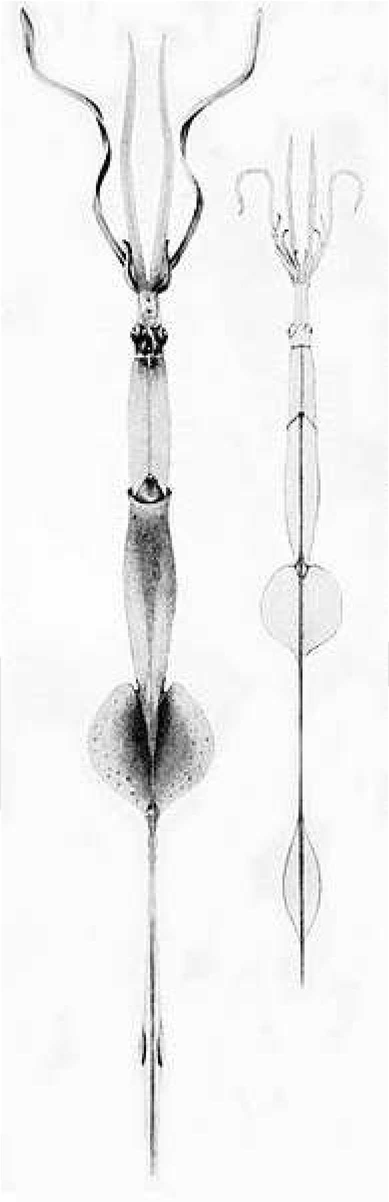
The shells develop from the ectoderm as an organic framework which is subsequently mineralised. In *Sepia*, which has an internal shell, the ectoderm forms an invagination whose pore is sealed off before this organic framework is deposited.

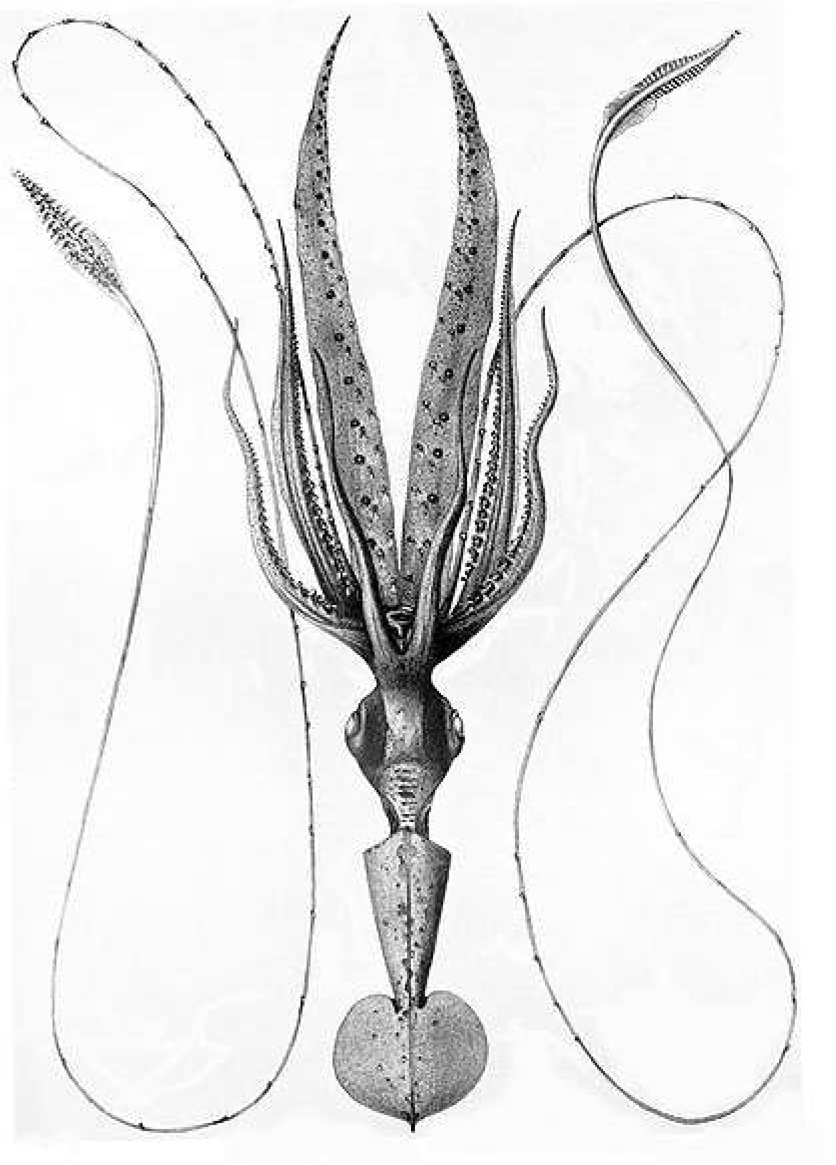
The gene *engrailed* is expressed first in the arms, funnel and optic vesicles, and is only later present in the tentacles and eyelids. It is expressed in embryonic stages 17–19 in all arm buds, and subsequently in the future-tentacles in stages 24–5, suggesting that it may serve a role in the differential development of tentacles. Sequential expression of Hox genes is also observed in cephalopod arms.

Development



Chtenopteryx sicula paralarvae. **Left:** Two very young paralarvae. The circular tentacular clubs bear approximately 20 irregularly arranged suckers. Two chromatophores are present on each side of the mantle. **Centre:** Ventral, dorsal and side views of a more advanced paralarva. An equatorial circulet of seven large yellow-brown chromatophores is present on the mantle. Posteriorly the expanded vanes of the gladius are visible in the dorsal view. **Right:** Ventral and dorsal views of a very advanced paralarva.





Left: Immature specimens of *Chiroteuthis veranyi*. In this paralarval form, known as the doratopsis stage, the pen is longer than the mantle and 'neck' combined

Right: A mature *Chiroteuthis veranyi*. This species has some of the longest tentacles in proportion to its size of any known cephalopod.

Cephalopod eggs span a large range of sizes, from 1 to 30 mm in diameter. The length of time before hatching is highly variable; smaller eggs in warmer waters are the fastest to hatch, and newborns can emerge after as little as a few days. Larger eggs in colder waters can develop for over a year before hatching.

The process from spawning to hatching follows a similar trajectory in all species, the main variable being the amount of yolk available to the young and when it is absorbed by the embryo.

Young do not pass through a larval stage, strictly speaking. They quickly learn how to hunt, using encounters with prey to refine their strategies.

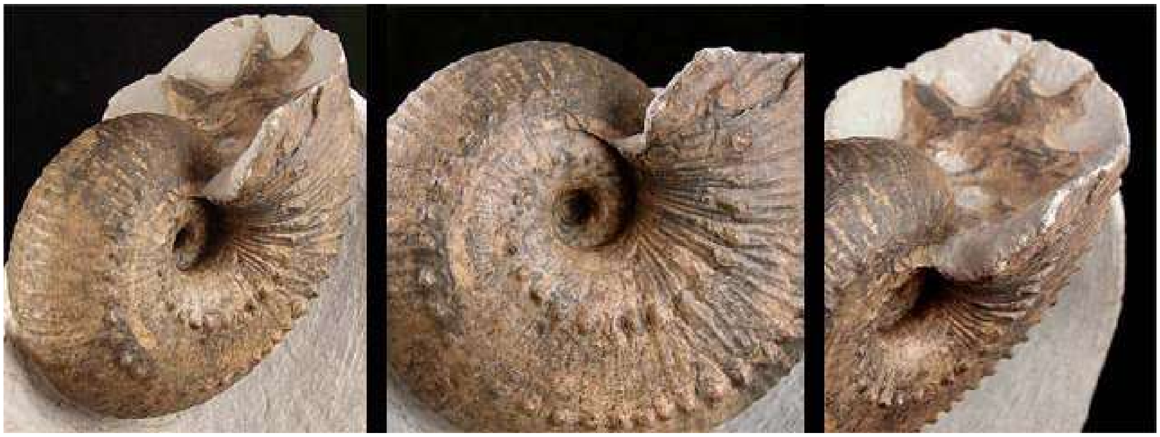
Growth in juveniles is usually allometric, whilst adult growth is isometric.

Evolution

The traditional view of cephalopod evolution holds that they evolved in the Late Cambrian from a monoplacophoran-like ancestor with a curved, tapering shell, which was closely related to the gastropods (snails). The similarity of the early shelled cephalopod *Plectronoceras* to some gastropods was used in support of this view. The development of a siphuncle would have allowed the shells of these early forms to become gas-filled (thus buoyant) in order to support them and keep the shells upright while the animal crawled along the floor, and separated the true cephalopods from putative ancestors such as *Knightoconus*, which lacked a siphuncle. Neutral or positive buoyancy (i.e. the ability to float) would have come later, followed by swimming in the Plectronocerida and eventually jet propulsion in more derived cephalopods.

However, some morphological evidence is difficult to reconcile with this view, and the redescription of *Nectocaris pteryx*, which did not have a shell and appeared to possess jet propulsion in the manner of "derived" cephalopods, complicated the question of the order in which cephalopod features developed – provided *Nectocaris* is a cephalopod at all.

Early cephalopods were likely predators near the top of the food chain. They underwent pulses of diversification during the Ordovician period to become diverse and dominant in the Paleozoic and Mesozoic seas. In the Early Palaeozoic, their range was far more restricted than today; they were mainly constrained to sublittoral regions of shallow shelves of the low latitudes, and usually occur in association with thrombolites. A more pelagic habit was gradually adopted as the Ordovician progressed. Deep-water cephalopods, whilst rare, have been found in the Lower Ordovician - but only in high-latitude waters. The mid Ordovician saw the first cephalopods with septa strong enough to cope with the pressures associated with deeper water, and could inhabit depths greater than 100–200 m. The direction of shell coiling would prove to be crucial to the future success of the lineages; endogastric coiling would only permit large size to be attained with a straight shell, whereas exogastric coiling - initially rather rare - permitted the spirals familiar from the fossil record to develop, with their corresponding large size and diversity. (Endogastric mean the shell is curved so as the ventral or lower side is longitudinally concave (belly in); exogastric means the shell is curve so as the ventral side is longitudinally convex (belly out) allowing the funnel to be pointed backwards beneath the shell.)



An ammonitic ammonoid with the body chamber missing, showing the septal surface (especially at right) with its undulating lobes and saddles

The ancestors of coleoids (including most modern cephalopods) and the ancestors of the modern nautilus, had diverged by the Floian Age of the Early Ordovician Period, over 470 million years ago. The Bactritida, an Silurian–Triassic group of orthocones, are widely held to be paraphyletic to the coleoids and ammonoids – that is, the latter groups arose from within the Bactritida. An increase in the diversity of the coleoids and ammonoids is observed around the start of the Devonian period, and corresponds with a profound increase in fish diversity. This could represent the origin of the two derived groups.

Unlike most modern cephalopods, most ancient varieties had protective shells. These shells at first were conical but later developed into curved nautiloid shapes seen in modern nautilus species. Competitive pressure from fish is thought to have forced the shelled forms into deeper water, which provided an evolutionary pressure towards shell loss and gave rise to the modern coleoids, a change which led to greater metabolic costs associated with the loss of buoyancy, but which allowed them to recolonise shallow waters. However, some of the straight-shelled nautiloids evolved into belemnites, out of which some evolved into squid and cuttlefish. The loss of the shell may also have resulted from evolutionary pressure to increase manoeuvrability, resulting in a more fish-like habit.

Phylogeny

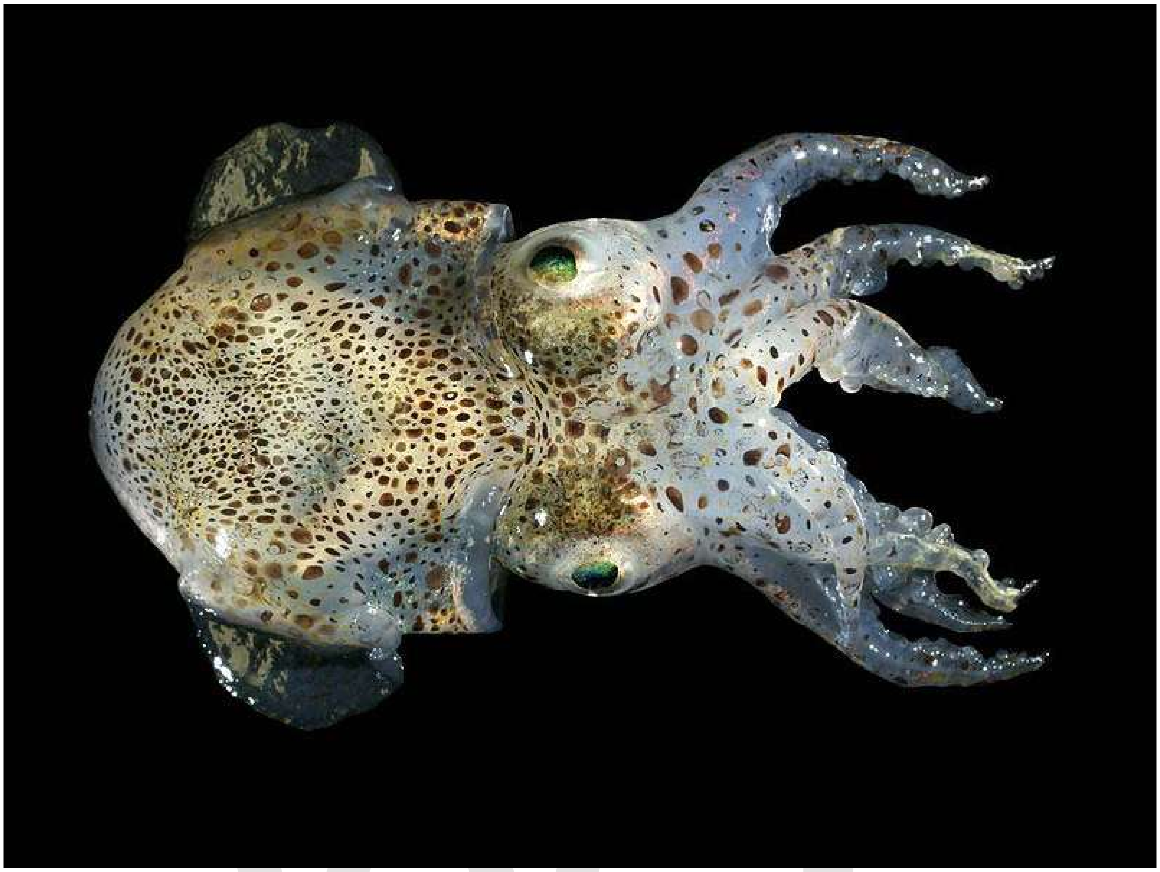
The internal phylogeny of the cephalopods is difficult to constrain; many molecular techniques have been adopted, but the results produced are conflicting. *Nautilus* tends to be considered an outgroup, with *Vampyroteuthis* forming an outgroup to other squid; however in one analysis the nautiloids, octopus and teuthids plot as a polytomy. Some molecular phylogenies do not recover the mineralized coleoids (*Spirula*, *Sepia*, and *Metasepia*) as a clade; however, others do recover this more parsimonious-seeming clade, with *Spirula* as a sister group to *Sepia* and *Metasepia* in a clade that had probably diverged before the end of the Triassic.

Molecular estimates for clade divergence vary. One 'statistically robust' estimate has *Nautilus* diverging from *Octopus* at 415 ± 24 million years ago.

Taxonomy

Chambered Nautilus (*Nautilus pompilius*)

Common Cuttlefish (*Sepia officinalis*)



Atlantic Bobtail (*Sepiola atlantica*)

European Squid (*Loligo vulgaris*)

Common Octopus (*Octopus vulgaris*)

The classification presented here, for recent cephalopods, follows largely from Current Classification of Recent Cephalopoda (May 2001), for fossil cephalopods takes from Arkell et al. 1957, Teichert and Moore 1964, Teichert 1988, and others. The three subclasses are traditional, corresponding to the three orders of cephalopods recognized by Bather.

Class Cephalopoda († indicates extinct groups)

- Subclass Nautiloidea: Fundamental ectocochliate cephalopods that provided the source for the Ammonoidea and Coleoidea.
    - Order † Plectronocerida: the ancestral cephalopods from the Cambrian Period
    - Order † Ellesmerocerida (500 to 470 Ma)
    - Order † Endocerida (485 to 430 Ma)
    - Order † Actinocerida (480 to 312 Ma)
    - Order † Discosorida (482 to 392 Ma)
    - Order † Pseudorthocerida (432 to 272 Ma)
    - Order † Tarphycerida (485 to 386 Ma)
    - Order † Oncocerida (478.5 to 324 Ma)
    - Order Nautilida (extant; 410.5 to 0 Ma)
    - Order † Orthocerida (482.5 to 211.5 Ma)
    - Order † Ascocerida (478 to 412 Ma)
    - Order † Bactritida (418.1 to 260.5 Ma)

- Subclass † Ammonoidea: Ammonites (479 to 65 Ma)
    - Order † Goniatitida (388.5 to 252 Ma)
    - Order † Ceratitida (254 to 200 Ma)
    - Order † Ammonitida (215 to 66 Ma)
- Subclass Coleoidea (410.0 Ma-Rec)
    - Cohort † Belemnoidea: Belemnites and kin
        - Genus † *Jeletzkya*
        - Order † Aulacocerida (265 to 183 Ma)
        - Order † Phragmoteuthida (189.6 to 183 Ma)
        - Order † Hematitida (339.4 to 318.1 Ma)
        - Order † Belemnitida (339.4 to 65.5 Ma)
        - Genus † *Belemnoteuthis* (189.6 to 183 Ma)
    - Cohort Neocoleoidea
        - Superorder Decapodiformes (also known as Decabrachia or Decembranchiata)
            - ?Order † Boletzkyida
            - Order Spirulida: Ram's Horn Squid
            - Order Sepiida: cuttlefish
            - Order Sepiolida: pygmy, bobtail and bottletail squid
            - Order Teuthida: squid
        - Superorder Octopodiformes (also known as Vampyropoda)
            - Family † Trachyteuthididae
            - Order Vampyromorphida: Vampire Squid
            - Order Octopoda: octopus

Other classifications differ, primarily in how the various decapod orders are related, and whether they should be orders or families.

Suprafamilial classification of the Treatise

This is the older classification that combines those found in parts K and L of the Treatise on Invertebrate Paleontology, which forms the basis for and is retained in large part by classifications that have come later.

Nautiloids in general, (Teichert and Moore 1964) Sequence as given.

> Subclass † Endoceratoidea. Not used by Flower, e.g. Flower and Kummel 1950, interjocerids included in the Endocerida.
> Order † Endocerida
> Order † Intejocerida
> Subclass † Actinoceratoidea Not used by Flower, ibid
> Order † Actinocerida
> Subclass † Nautiloidea Nautiloidea in the restricted sense.
> Order † Ellesmerocerida Plectronocerida subsequently split off as separate order.
> Order † Orthocerida Includes orthocerids and pseudorthocerids
> Order † Ascocerida

Order † Oncocerida
Order † Discosorida
Order † Tarphycerida
Order † Barrandeocerida A polyphyletic group now included in the Tarphycerida
Order Nautilida
Subclass † Bactritoidea
Order † Bactritida

Paleozoic Ammonoidea (Miller, Furnish, and Schindewolf, 1957)

Suborder † Anarcestina
Suborder † Clymeniina
Suborder † Goniatitina
Suborder † Prolecanitina

Mesozoic Ammonoidea (Arkel et al., 1957)

Suborder † Ceratitina
Suborder † Phylloceratina
Suborder † Lytoceratina
Suborder † Ammonitina

Subsequent revisions include the establishment of three Upper Cambrian orders, the Plectronocerida, Protactinocerida and Yanhecerida; separation of the pseudorthocerids as the Pseudorthocerida, and elevating orthoceritoids as the Subclass Orthoceratoidea.

Shevyrev classification

Shevyrev (2005) suggested a division into eight subclasses, mostly comprising the more diverse and numerous fossil forms, although this classification has been criticized as arbitrary.

Various species of ammonites

Holotype of *Ostenoteuthis siroi* from family Ostenoteuthidae.

A fossilised belemnite

Class Cephalopoda

- Subclass † Ellesmeroceratoidea
    - Order † Plectronocerida (501 to 490 Ma)
    - Order † Protactinocerida

    - Order † Yanhecerida
    - Order † Ellesmerocerida (500 to 470 Ma)
- Subclass † Endoceratoidea (485 to 430 Ma)
    - Order † Endocerida (485 to 430 Ma)
    - Order † Intejocerida (485 to 480 Ma)
- Subclass † Actinoceratoidea
    - Order † Actinocerida (480 to 312 Ma)
- Subclass Nautiloidea (490.0 Ma- Rec)
    - Order † Basslerocerida (490 to 480 Ma)
    - Order † Tarphycerida (485 to 386 Ma)
    - Order † Lituitida (485 to 480 Ma)
    - Order † Discosorida (482 to 392 Ma)
    - Order † Oncocerida (478.5 to 324 Ma)
    - Order Nautilida (410.5 Ma-Rec)
- Subclass † Orthoceratoidea (482.5 to 211.5 Ma)
    - Order † Orthocerida (482.5 to 211.5 Ma)
    - Order † Ascocerida (478 to 412 Ma)
    - Order † Dissidocerida (479 to 457.5 Ma)
    - Order † Bajkalocerida
- Subclass † Bactritoidea (422 to 252 Ma)
- Subclass † Ammonoidea (410 to 66 Ma)
- Subclass Coleoidea (410.0 Ma-rec)

Cladistic classification

Pyritized fossil of *Vampyronassa rhodanica*, a vampyromorphid from the Lower Callovian (164.7 million years ago)

Another recent system divides all cephalopods into two clades. One includes nautilus and most fossil nautiloids. The other clade (Neocephalopoda or Angusteradulata) is closer to modern coleoids, and includes belemnoids, ammonoids, and many orthocerid families. There are also stem group cephalopods of the traditional Ellesmerocerida that belong to neither clade.

Monophyly of coeloids

The coeloids have been thought to possibly represent a polyphyletic group, although this has not been supported by the rising body of molecular data.

Post-mortem decay

After death, if undisturbed, cephalopods decay relatively quickly. Their muscle softens within a couple of days, and may swell; egg sacs can swell so much that they rip through the mantle. Subsequently, the organs shrink again; at this point the organism may start to break up into fragments. The eyes retain their size while the head shrinks around them. The gills may remain swollen at this point. After around a week, the carcass collapses in on itself and begins to disintegrate. The ink sac solidifies around this point. After a fortnight little is left but a blob with eyes, arms and ink sac visible. After a couple of months, these are only recognisable as flattened dark stains - although in some cases the eye lenses can remain intact for up to a year.

Chapter 10

Acanthuridae

Acanthuridae

Sohal surgeonfish, *Acanthurus sohal*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Order:	Perciformes
Suborder:	Acanthuroidei
Family:	**Acanthuridae**

Genera

Acanthurus
Ctenochaetus
Naso (unicornfishes)
Paracanthurus
Prionurus
Zebrasoma

Acanthuridae ("thorn tail") is the family of **surgeonfishes**, **tangs**, and **unicornfishes**. The family includes about 80 species in six genera, all of which are marine fish living in tropical seas, usually around coral reefs. Many of the species are brightly colored and popular for aquaria.

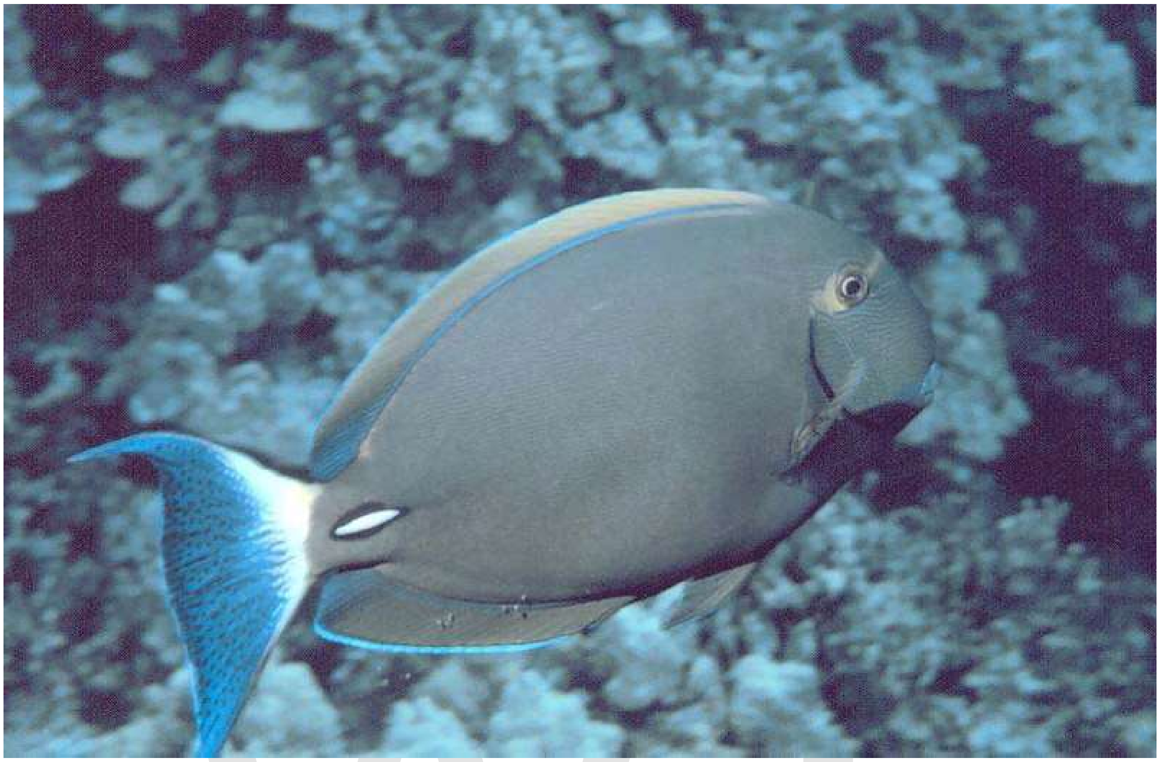
The distinctive characteristic of the family is the spines, one or more on either side of the tail, which are dangerously sharp. The dorsal, anal and caudal fins are large, extending for most of the length of the body. The small mouths have a single row of teeth used for grazing on algae.

Surgeonfishes sometimes feed as solitary individuals, but they also often travel and feed in schools. It has been suggested that feeding in schools is a mechanism for overwhelming the highly aggressive defense responses of small territorial damselfishes that vigorously guard small patches of algae on coral reefs.

Most species are relatively small and have a maximum length of 15–40 cm (6–16 in), but some members of the genus *Acanthurus*, some members of the genus *Prionurus*, and most members of the genus *Naso* can grow larger, with the whitemargin unicornfish (*N. annulatus*), the largest species in the family, reaching a length of up to a metre (3,3 ft). These fishes can grow quickly in aquariums so it is advisable to check the average growth size and suitability before adding to a marine aquarium.

Species

Achilles tang, *Acanthurus achilles*



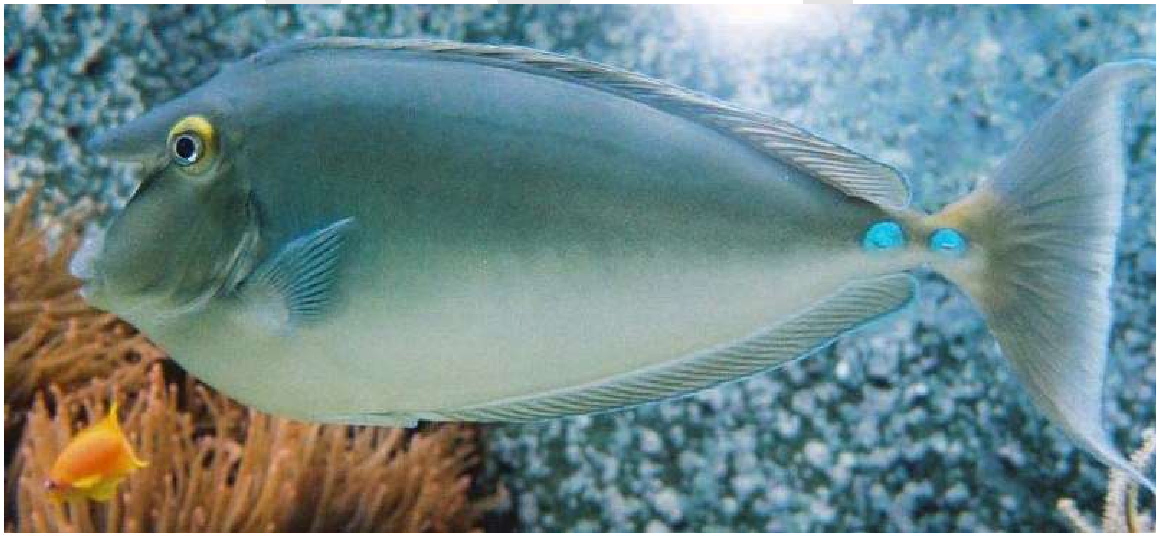
Eyestripe surgeonfish, *Acanthurus dussumieri*

Powderblue surgeonfish, *Acanthurus leucosternon*

Doubleband surgeonfish, *Acanthurus tennenti*

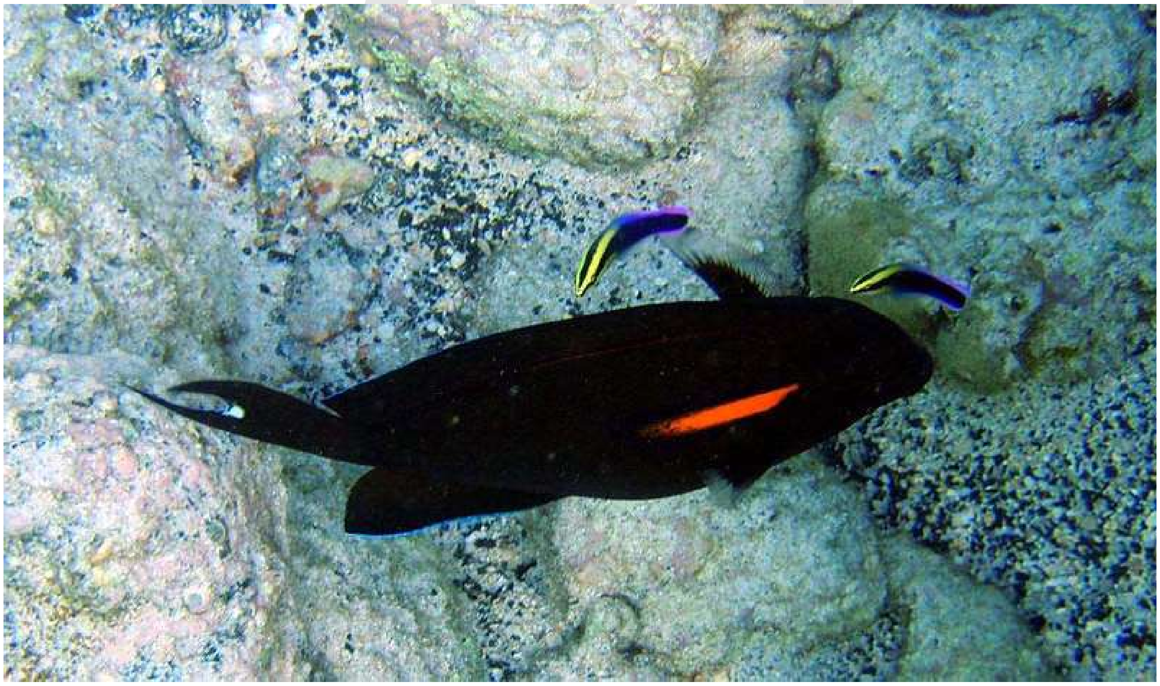
Kole Tang, *Ctenochaetus strigosus*

Elongate unicornfish, *Naso lopezi*



Bluespine unicornfish, *Naso unicornis*

Red Sea sailfin tang, *Zebrasoma desjardinii*



Orangespot surgeonfish, *Acanthurus olivaceus*, is being cleaned by two Hawaiian cleaner wrasse, *Labroides phthirophagus*

Regal Tang, *Paracanthurus hepatus* in an aquarium

- Genus *Acanthurus*
    - Achilles tang, *Acanthurus achilles* Shaw, 1803.
    - Whitefin surgeonfish, *Acanthurus albipectoralis* Allen & Ayling, 1987.
    - Orange-socket surgeonfish, *Acanthurus auranticavus* Randall, 1956.
    - Ocean surgeon, *Acanthurus bahianus* Castelnau, 1855.
    - Black-spot surgeonfish, *Acanthurus bariene* Lesson, 1831.
    - Ringtail surgeonfish, *Acanthurus blochii* Valenciennes, 1835.
    - Doctorfish tang, *Acanthurus chirurgus* (Bloch, 1787).
    - Chronixis surgeonfish, *Acanthurus chronixis* Randall, 1960.
    - Atlantic Blue tang surgeonfish, *Acanthurus coeruleus* Bloch & Schneider, 1801.
    - Eyestripe surgeonfish, *Acanthurus dussumieri* Valenciennes, 1835.
    - Fowler's surgeonfish, *Acanthurus fowleri* de Beaufort, 1951.
    - Black surgeonfish, *Acanthurus gahhm* (Forsskål, 1775).
    - Finelined surgeonfish, *Acanthurus grammoptilus* Richardson, 1843.
    - Whitespotted surgeonfish, *Acanthurus guttatus* Forster, 1801.
    - Japan surgeonfish, *Acanthurus japonicus* (Schmidt, 1931).
    - Palelipped surgeonfish, *Acanthurus leucocheilus* Herre, 1927.
    - Whitebar surgeonfish, *Acanthurus leucopareius* (Jenkins, 1903).
    - Powderblue surgeonfish, *Acanthurus leucosternon* Bennett, 1833.
    - Lined surgeonfish, *Acanthurus lineatus* (Linnaeus, 1758).

    - White-freckled surgeonfish, *Acanthurus maculiceps]* (Ahl, 1923).
    - Elongate surgeonfish, *Acanthurus mata* (Cuvier, 1829).
    - Monrovia doctorfish, *Acanthurus monroviae* Steindachner, 1876.
    - Whitecheek surgeonfish, *Acanthurus nigricans* (Linnaeus, 1758).
    - Epaulette surgeonfish, *Acanthurus nigricauda* Duncker & Mohr, 1929.
    - Brown surgeonfish, *Acanthurus nigrofuscus* (Forsskål, 1775).
    - Bluelined surgeonfish, *Acanthurus nigroris* Valenciennes, 1835.
    - Bluelined surgeon, *Acanthurus nubilus* (Fowler & Bean, 1929).
    - Orangespot surgeonfish, *Acanthurus olivaceus* Bloch & Schneider, 1801.
    - Black-barred surgeonfish, *Acanthurus polyzona* (Bleeker, 1868).
    - Chocolate surgeonfish, *Acanthurus pyroferus* Kittlitz, 1834.
    - Gulf surgeonfish, *Acanthurus randalli* Briggs & Caldwell, 1957.
    - *Acanthurus reversus* Randall & Earle, 1999.
    - Sohal surgeonfish, *Acanthurus sohal* (Forsskål, 1775).
    - Doubleband surgeonfish, *Acanthurus tennentii* Günther, 1861.
    - Thompson's surgeonfish, *Acanthurus thompsoni* (Fowler, 1923).
    - Convict surgeonfish, *Acanthurus triostegus* (Linnaeus, 1758).
    - Indian Ocean mimic surgeonfish, *Acanthurus tristis* Randall, 1993.
    - Yellowfin surgeonfish, *Acanthurus xanthopterus* Valenciennes, 1835.
- Genus *Ctenochaetus*
    - Twospot surgeonfish, *Ctenochaetus binotatus* Randall, 1955.
    - *Ctenochaetus cyanocheilus* Randall & Clements, 2001.
    - *Ctenochaetus flavicauda* Fowler, 1938.
    - *Ctenochaetus hawaiiensis*
    - Striped-fin surgeonfish, *Ctenochaetus marginatus* (Valenciennes, 1835).
    - Striated surgeonfish, *Ctenochaetus striatus* (Quoy & Gaimard, 1825).
    - Kole Tang, *Ctenochaetus strigosus* (Bennett, 1828).
    - Tomini surgeonfish, *Ctenochaetus tominiensis* Randall, 1955.
    - *Ctenochaetus truncatus* Randall & Clements, 2001.
- Genus *Naso*
    - Whitemargin unicornfish, *Naso annulatus* (Quoy & Gaimard, 1825).
    - Humpback unicornfish, *Naso brachycentron* (Valenciennes, 1835).
    - Spotted unicornfish, *Naso brevirostris* (Cuvier, 1829).
    - *Naso caeruleacauda* Randall, 1994.
    - Gray unicornfish, *Naso caesius* Randall & Bell, 1992.
    - Elegant unicornfish, *Naso elegans* (Rüppell, 1829).
    - Horseface unicornfish, *Naso fageni* Morrow, 1954.
    - Sleek unicornfish, *Naso hexacanthus* (Bleeker, 1855).
    - Orangespine unicornfish, *Naso lituratus* (Forster, 1801).
    - Elongate unicornfish, *Naso lopezi* Herre, 1927.
    - *Naso maculatus* Randall & Struhsaker, 1981.
    - Squarenose unicornfish, *Naso mcdadei* Johnson, 2002.
    - Slender unicorn, *Naso minor* (Smith, 1966).
    - *Naso reticulatus* Randall, 2001.
    - Oneknife unicornfish, *Naso thynnoides* (Cuvier, 1829).
    - Bulbnose unicornfish, *Naso tonganus* (Valenciennes, 1835).

    - Humpnose unicornfish, *Naso tuberosus* Lacépède, 1801.
    - Bluespine unicornfish, *Naso unicornis* (Forsskål, 1775).
    - Bignose unicornfish, *Naso vlamingii* (Valenciennes, 1835).
- Genus *Paracanthurus*
    - Palette surgeonfish, *Paracanthurus hepatus* (Linnaeus, 1766).
- Genus *Prionurus*
    - Biafra doctorfish, *Prionurus biafraensis* (Blache & Rossignol, 1961).
    - *Prionurus chrysurus* Randall, 2001.
    - Razor surgeonfish, *Prionurus laticlavius* (Valenciennes, 1846).
    - Yellowspotted sawtail, *Prionurus maculatus* (Randall & Struhsaker, 1981).
    - Sixplate sawtail, *Prionurus microlepidotus* Lacépède, 1804.
    - Yellowtail surgeonfish, *Prionurus punctatus* Gill, 1862.
    - Scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835.
- Genus *Zebrasoma*
    - Red Sea sailfin tang, *Zebrasoma desjardinii* (Bennett, 1836).
    - Yellow tang, *Zebrasoma flavescens* (Bennett, 1828).
    - Spotted tang, *Zebrasoma gemmatum* (Valenciennes, 1835).
    - Longnose surgeonfish, *Zebrasoma rostratum* (Günther, 1875).
    - Twotone tang, *Zebrasoma scopas* (Cuvier, 1829).
    - Sailfin tang, *Zebrasoma veliferum* (Bloch, 1795).
    - Purple tang, *Zebrasoma xanthurum* (Blyth, 1852).
    - *Zebrasoma xanthurus*

Etymology and taxonomic history

The name of the family is derived from the Greek words *akantha* and *oura*, which loosely translate to "thorn" and "tail", respectively. This refers to the distinguishing characteristic of the family, the "scalpel" found each member's caudal peduncle.

In the early 1900s, the family was called **Hepatidae**.

In the aquarium

Tangs are very sensitive to disease in the home aquarium. However if the tang is fed enough algae and the aquarium is properly maintained disease should not be a problem. It is usually necessary to quarantine the animals for a period before introducing them to the aquarium.

Adults range from 15–40 cm (6-15 in.) in length and most grow quickly even in aquariums. When considering a tang for an aquarium it is important to consider the size to which these fish can grow. Larger species such as the popular **Pacific Blue tang surgeonfish** (of *Finding Nemo* fame), Naso or **lipstick tang**, clown and sohal tangs can grow to 40 cm (15 in.) and require swimming room and hiding places.

Many also suggest adding aggressive tangs to the aquarium last as they are territorial and may fight and possibly kill other fish.

Tangs primarily graze on macroalgae, such as caulerpa and gracilias, although they have been observed in an aquarium setting to eat meat-based fish foods. A popular technique for aquarists, is to grow macroalgae in a sump or refugium. This technique not only is economically beneficial, but serves to promote enhanced water quality through nitrate absorption. The growth of the algae can then be controlled by feeding it to the tang.

Chapter 11

Chameleon

Chameleon	
	
Common Chameleon, *Chamaeleo chamaeleon*	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Order:	Squamata
Suborder:	Lacertilia
Infraorder:	Iguania
Family:	**Chamaeleonidae**

Subfamilies and Genera

- Chamaeleoninae
    - *Bradypodion*
    - *Calumma*
    - *Chamaeleo*
    - *Furcifer*
    - *Kinyongia*
    - *Nadzikambia*
- Brookesiinae
    - *Brookesia*
    - *Rieppeleon*
    - *Rhampholeon*

Chameleons (family Chamaeleonidae) are a distinctive and highly specialized clade of lizards. They are distinguished by their parrot-like zygodactylous feet, their separately mobile and stereoscopic eyes, their very long, highly modified, and rapidly extrudable tongues, their swaying gait, the possession by many of a prehensile tail, crests or horns on their distinctively shaped heads, and the ability of some to change color. Uniquely adapted for climbing and visual hunting, the approximately 160 species of chameleon range from Africa, Madagascar, Spain and Portugal, across south Asia, to Sri Lanka, have been introduced to Hawaii, California and Florida, and are found in warm habitats that vary from rain forest to desert conditions.

Etymology

The English word *chameleon* (also *chamaeleon*) derives from Latin *chamaeleō*, a borrowing of the Ancient Greek χαμαιλέων (*khamailéōn*), a compound of χαμαί (*khamaí*) "on the ground" and λέων (*léōn*) "lion". The Greek word is a calque translating the Akkadian *nēš qaqqari*, "ground lion".

Evolution

The oldest known chameleon fossil is that of *Chamaeleo caroliquarti*, found in Europe and dated to about 26 mya. However the chameleons are probably far older than that, perhaps sharing a common ancestor with iguanids and agamids more than 100 mya (agamids being more closely related). Fossil evidence has also been found in Africa and Asia, and suggests that chameleons were once more widespread than they are today. They may have their origins in Madagascar, which today is home to nearly half of all the 150 or more known species in this family, and later dispersed to other areas. Monophyly of the family is supported by several studies.

Description

Cape Dwarf Chameleon, Tokai, South Africa

Chameleons vary greatly in size and body structure, with maximum total length varying from 3.3 cm (1.3 in.) in *Brookesia minima* (one of the world's smallest reptiles) to 68.5 cm (27 in.) in the male *Furcifer oustaleti*. Many have head or facial ornamentation, such as nasal protrusions, or horn-like projections in the case of *Chamaeleo jacksonii*, or large crests on top of their head, like *Chamaeleo calyptratus*. Many species are sexually dimorphic, and males are typically much more ornamented than the female chameleons. Chameleons are often sold at pet stores and are not rare to have as household pets. Below is a table of common pet chameleons:

Species' Scientific Name	Species' Common Name	Typical Total Length (Male)	Typical Total Length (Female)	Color	Typical Lifespan (Years)
Chamaeleo calyptratus	Veiled Chameleon	14"-24"	10-13"	Green & Light Colors	≈5
Chamaeleo jacksonii	Jackson's Chameleon	9"-13"	10"-13"	Green & Light Colors	≈5-10

Furcifer pardalis	Panther Chameleon	15"-21"	9"-13"	Darker Colors	≈5 (2-3 for birthing females)
Rhampholeon brevicaudatus	Bearded Pygmy Chameleon	2"-3"	2"-3"	Brown, Beige, Green	≈3-5
Rhampholeon spectrum	Spectral Pygmy Chameleon	3"-4"	2"-4"	Tan & Gray	Unknown
Rhampholeon temporalis	Pygmy Chameleon	2.5"-4"	2"-3.5"	Gray & Brown	Unknown

Chameleon species have in common their foot structure, eyes, tongues and a lack of ears.

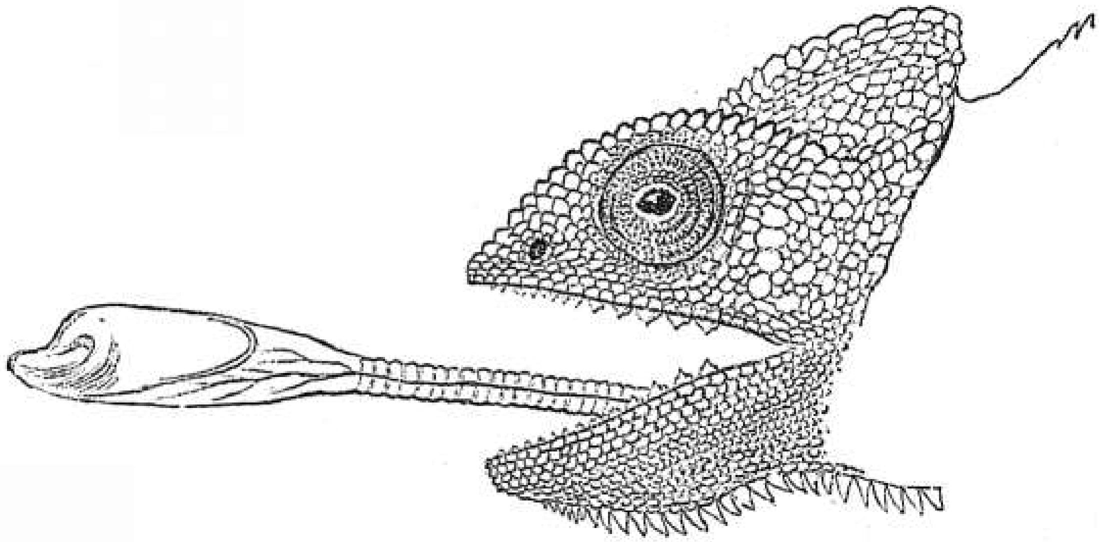
Oustalet's Chameleon, Ambalavao, Madagascar

Chameleons are didactyl: on each foot the five toes are fused into a group of two and a group of three, giving the foot a tongs-like appearance. These specialized feet allow chameleons to grip tightly to narrow branches. Each toe is equipped with a sharp claw to gain traction on surfaces such as bark when climbing. The claws make it easy to see how many toes are fused into each part of the foot — two toes on the outside of each front foot and three on the inside.

Their eyes are the most distinctive among the reptiles. The upper and lower eyelids are joined, with only a pinhole large enough for the pupil to see through. They can rotate and focus separately to observe two different objects simultaneously, this lets their eyes move independently from each other. It in effect gives them a full 360-degree arc of vision around their body. When prey is located, both eyes can be focused in the same direction, giving sharp stereoscopic vision and depth perception. They have very good eyesight for reptiles, letting them see small insects from a long (5–10 m) distance.

They lack a vomeronasal organ. Also, like snakes, they do not have an outer or a middle ear. This suggests that chameleons might be deaf, although snakes can sense vibration using a bone called the quadrate. Furthermore, some or maybe all chameleons, can communicate via vibrations that travel through solid substrates such as branches.

Chameleons have very long tongues (sometimes longer than their own body length) which they are capable of rapidly extending out of the mouth.



Head of *Chamæleon calcaratus*, **with projected tongue.**

Tongue structure

The tongue extends out faster than human eyes can follow, at around 26 body lengths per second. The tongue hits the prey in about 30 thousandths of a second. The tongue of the chameleon is a complex arrangement of bone, muscle and sinew. At the base of the tongue there is a bone and this is shot forward giving the tongue the initial momentum it needs to reach the prey quickly. At the tip of the elastic tongue there is a muscular, club-like structure covered in thick mucus that forms a suction cup. Once the tip sticks to a prey item, it is drawn quickly back into the mouth, where the chameleon's strong jaws crush it and it is consumed. Ultraviolet light is part of the visible spectrum for chameleons. Chameleons exposed to ultraviolet light show increased social behavior and activity levels, are more inclined to bask and feed and are also more likely to reproduce as it has a positive effect on the pineal gland.

Distribution and habitat

The tiny, usually brown-colored *Brookesia* chameleons are mainly terrestrial

Chameleons are primarily found in the mainland of sub-Saharan Africa and on the island of Madagascar, although a few species are also found in northern Africa, southern Europe, the Middle East, southern India, Sri Lanka and several smaller islands in the western Indian Ocean. There are introduced, feral populations of veiled and Jackson's chameleons in Hawaii and isolated pockets of feral Jackson's chameleons have been reported in California and Florida.

Chameleons inhabit all kinds of tropical and mountain rain forests, savannas and sometimes deserts and steppes. The "typical" chameleons from the subfamily Chamaeleoninae are arboreal and usually found in trees or bushes, although a few (notably the Namaqua Chameleon) are partially or largely terrestrial. Most species from the subfamily Brookesiinae, which includes the genera *Brookesia*, *Rieppeleon* and *Rhampholeon*, live low in vegetation or on the ground among leaf litter.

Reproduction

West Usambara Two-Horned Chameleon (*Kinyongia multituberculata*) in the Usambara mountains, Tanzania.

Chameleons are mostly oviparous, some being ovoviviparous.

The oviparous species lay eggs after a 3–6 week gestation period. The female will climb down to the ground and begin digging a hole, anywhere from 10–30 cm (4–12 in.) deep depending on the species. The female turns herself around at the bottom of the hole and deposits her eggs. Once finished, the female buries lina and leaves the nesting site. Clutch sizes vary greatly with species. Small *Brookesia* species may only lay 2–4 eggs, while large Veiled Chameleons (*Chamaeleo calyptratus*) have been known to lay clutches of 80–100 eggs. Clutch sizes can also vary greatly among the same species. Eggs generally hatch after 4–12 months, again depending on species. The eggs of Parson's Chameleon (*Calumma parsonii*), a species which is rare in captivity, are believed to take upwards of 24 months to hatch.

The ovoviviparous species, such as the Jackson's Chameleon (*Chamaeleo jacksonii*) have a 5–6 month gestation period. The newborn are in a transparent membrane and they are still sleeping, once they touch the ground or branch, they will wake up and attempt to crawl out of the membrane. The female can have 8–31 live young at once.

Feeding behavior

Chameleons generally eat locusts, mantis, crickets, grasshopper and other insects, but larger chameleons have been known to eat small birds and other lizards. A few species, such as Jackson's Chameleon (*C. jacksonii*) and the Veiled Chameleon (*C. calyptratus*) will consume small amounts of plant matter. Chameleons prefer running water to still water.

Chameleons require lots of vitamins and minerals. To ensure sufficient nutrients, zoo-keepers "gut-load" insects before feeding them to chameleons, by rearing them on a diet of potatoes, fish flakes (tropical), dry puppy food, dark leafy greens, etc. and dusting them with vitamin and mineral powders.

Change of color

Camouflage of a Common Chameleon in its natural environment (vicinity of Oueslatia, Tunisia)

This Common Chameleon (*Chamaeleo chamaeleon*) turned black

Some chameleon species are able to change their skin colors. Different chameleon species are able to change different colors which can include pink, blue, red, orange, green, black, brown, light blue, yellow, turquoise and purple.

The primary purpose of color change has been found to be due to social signalling, as opposed to camouflage, although both social signalling color change, and color change for purposes of camouflage do occur in most chameleons, to some extent. Color change is also used as an expression of the physiological condition of the lizard, and as a social indicator to other chameleons. Research suggests that social signaling was the primary driving force behind the evolution of color change, and that camouflage evolved as a secondary concern. Chameleons tend to show darker colors when angered, or attempting to scare or intimidate others, and males show lighter, multi-colored patterns when courting females.

Some varieties of chameleon - such as the Smith's dwarf chameleon - use their color-changing ability to blend in with their surroundings, as an effective form of camouflage.

The desert dwelling Namaqua Chameleon also uses color change as an aid to thermoregulation, becoming black in the cooler morning to absorb heat more efficiently, then a lighter grey colour to reflect light during the heat of the day - or showing both colours at the same time, neatly separated left from right by the spine.

Chameleons have specialized cells, collectively called chromatophores, that lie in layers under their transparent outer skin. The cells in the upper layer, called xanthophores and erythrophores, contain yellow and red pigments respectively. Below these is another layer of cells called iridophores or guanophores, and they contain the colorless crystalline substance guanine. These are particularly strong reflectors of the blue part of incident light. If the upper layer of chromatophores appears mainly yellow, the reflected light becomes green (blue plus yellow). A layer of dark melanin contained in melanophores is situated even deeper under the reflective iridophores. The melanophores determine the 'lightness' of the reflected light. These specialized cells are full of pigment granules, which are located in their cytoplasm. Dispersion of the pigment granules in the cell grants the intensity of appropriate color. If the pigment is equally distributed in the cell, the whole cell has the intensive color, which depends on the type of chromatophore cell. If the pigment is located only in the centre of the cell, cell appears to be transparent. All these pigment cells can rapidly relocate their pigments, thereby influencing the color of the chameleon.

Chamaeleo melleri

Parasites

A number of monoxenous coccidia are known to infect these species including species of the genera *Choleoeimeria*, *Eimeria* and *Isospora*.

Recognised parasites include:

- *Choleoeimeria bohemii* - Meller's chameleon (*Chamaeleo melleri*)
- *Choleoeimeria brookesiae* - spiny leaf chameleon (*Brookesia decaryi*)
- *Choleoeimeria glawi* - panther chameleon (*Furcifer pardalis*)
- *Choleoeimeria hirbayah* - veiled chameleon (*Chamaeleo calyptratus*)
- *Choleoeimeria largeni* - graceful chameleon (*Chamaeleo gracilis*)
- *Choleoeimeria tilburyi* - Jackson's chameleon (*Chamaeleo jacksonii*)

- *Eimeria hajeki* - pygmy chameleon (*Rampholeon temporalis*)
- *Eimeria vencesi* - panther chameleon (*Furcifer pardalis*)
- *Eimeria worthi* - Oustalet's chameleon (*Furcifer oustaleti*)

- *Isospora brygooi* - panther chameleon (*Furcifer pardalis*)
- *Isospora jaracimrmani* - veiled chameleon (*Chamaeleo calyptratus*)

Chapter 12

Cuttlefish

Cuttlefish

Sepia latimanus, East Timor

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Superorder:	Decapodiformes
Order:	**Sepiida** Zittel, 1895

Suborders and Families

- †Vasseuriina
    - †Vasseuriidae
    - †Belosepiellidae
- Sepiina
    - †Belosaepiidae
    - Sepiadariidae
    - Sepiidae

Cuttlefish are marine animals of the order **Sepiida**. They belong to the class Cephalopoda (which also includes squid, octopuses, and nautiluses). Despite their name, cuttlefish are not fish but molluscs. Recent studies indicate that cuttlefish are among the most intelligent invertebrates. Cuttlefish also have one of the largest brain-to-body size ratios of all invertebrates.

The origin of the word cuttlefish can be found in the old English term *cudele*, which derived in the 15th century from the Norwegian *koddi* (cushion, testicle) and the Middle German *kudel* (pouch), a good description of the cephalopod's shape. The Greco-Roman world valued the cephalopod as a source of the unique brown pigment that the creature releases from its siphon when it is alarmed. The word for it in Greek and Latin, *sepia* (later *seppia* in Italian), is used to refer to a brown pigment in English.

Cuttlefish have an internal shell (the cuttlebone), large W-shaped pupils, and eight arms and two tentacles furnished with denticulated suckers, with which they secure their prey. They generally range in size from 15 cm (5.9 in) to 25 cm (9.8 in), with the largest species, *Sepia apama*, reaching 50 cm (20 in) in mantle length and over 10.5 kg (23 lb) in weight.

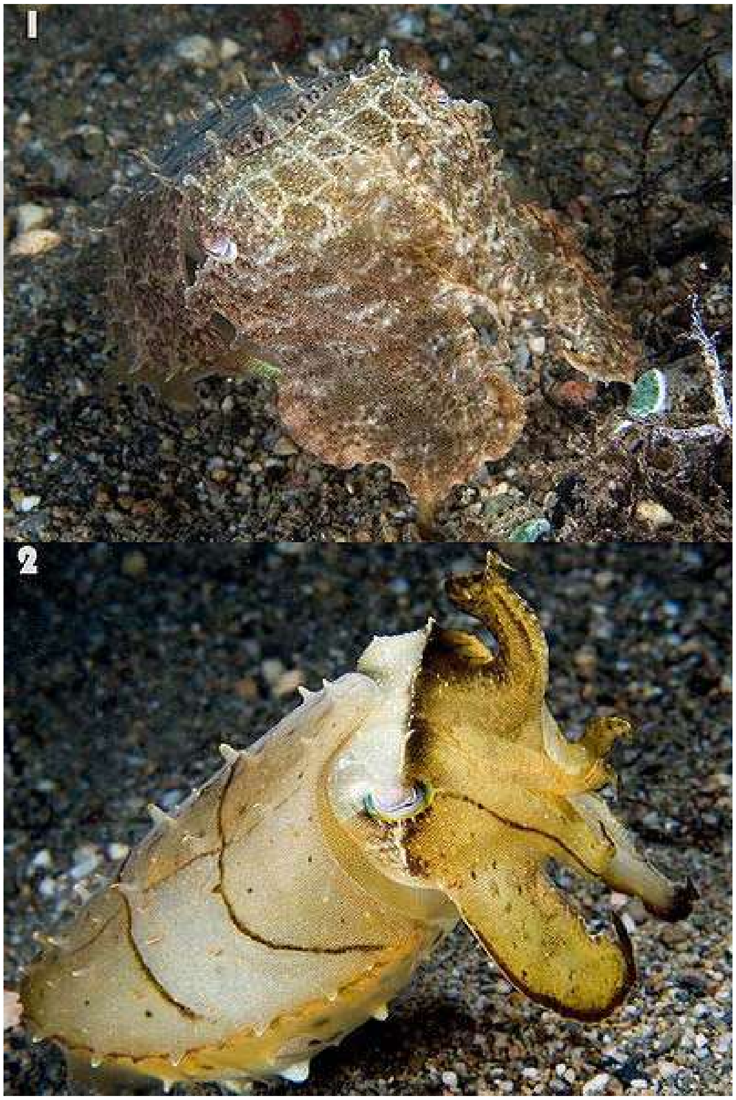
Cuttlefish eat small molluscs, crabs, shrimp, fish, octopuses, worms, and other cuttlefish. Their predators include dolphins, sharks, fish, seals and other cuttlefish. Their life expectancy is about one to two years.

Cuttlefish in its natural habitat

Physiology

Cuttlebone

Cuttlefish possess an internal structure called the cuttlebone, which is porous and is made of aragonite. This provides the cuttlefish with buoyancy. Buoyancy can be regulated by changing the gas-to-liquid ratio in the chambered cuttlebone via the ventral siphuncle. Each species has a distinct shape, size, and pattern of ridges or texture on the cuttlebone. The cuttlebone is unique to cuttlefish, one of the features that distinguishes them from their squid relatives. Jewelers and silversmiths traditionally use cuttlebones as moulds for casting small objects but they are probably better known as the tough material given to parakeets and other caged birds as a source of dietary calcium.



This Broadclub Cuttlefish (*Sepia latimanus*) can go from camouflage tans and browns (top) to yellow with dark highlights (bottom) in less than a second.

Skin

An infant cuttlefish protects itself with camouflage

Cuttlefish are sometimes referred to as the chameleon of the sea because of their remarkable ability to rapidly alter their skin color at will. Cuttlefish change color and light polarity to communicate to other cuttlefish and to camouflage themselves from predators.

This color-changing function is produced by groups of red, yellow, brown, and black pigmented chromatophores above a layer of reflective iridophores and leucophores, with up to 200 of these specialized pigment cells per square millimeter, which corresponds to about 359 DPI. The pigmented chromatophores have a sac of pigment and a large membrane that is folded when retracted. There are 6-20 small muscle cells on the sides which can contract to squash the elastic sac into a disc against the skin. Yellow chromatophores (xanthophores) are closest to the surface of the skin, red and orange are below (erythrophores), and brown or black are just above the iridophore layer (melanophores). The iridophores reflect blue and green light. Iridophores are plates of chitin or protein, which can reflect the environment around a cuttlefish. They are responsible for the metallic blues, greens, golds, and silvers often seen on cuttlefish. All of these cells can be used in combinations. For example, orange is produced by red and yellow chromatophores, while purple can be created by a red chromatophore and an iridophore. The cuttlefish can also use an iridophore and a yellow chromatophore to produce a brighter green. As well as being able to influence the color of light as it reflects off their skin, cuttlefish can also affect the light's polarization, which can be used to signal to other marine animals, many of which can also sense polarization.

Eyes

Close up of a cuttlefish eye

Cuttlefish eyes are among the most developed in the animal kingdom. The organogenesis of cephalopod eyes differs fundamentally from that of vertebrates like humans. Superficial similarities between cephalopod and vertebrate eyes are thought to be examples of convergent evolution. The cuttlefish pupil is a smoothly-curving W shape. Although they cannot see color, they can perceive the polarization of light, which enhances their perception of contrast. They have two spots of concentrated sensor cells on their retina (known as foveae), one to look more forward, and one to look more backward. The lenses, instead of being reshaped as they are in humans, are pulled around by reshaping the entire eye to change focus. Unlike the vertebrate eye, there is no blind spot as the optic nerve is positioned behind the retina.

Scientists have speculated that cuttlefish's eyes are fully developed before birth and start observing their surroundings while still in the egg. One team of French researchers has additionally suggested that cuttlefish prefer to hunt the prey they saw before hatching.

Circulation

The blood of a cuttlefish is an unusual shade of green-blue because it uses the copper-containing protein hemocyanin to carry oxygen instead of the red iron-containing protein hemoglobin that is found in vertebrates' blood. The blood is pumped by three separate hearts: two branchial hearts pump blood to the cuttlefish's pair of gills (one heart for each), and the third pumps blood around the rest of the body. Cuttlefish blood must flow more rapidly than most other animals because hemocyanin carries substantially less oxygen than hemoglobin.

Ink

Cuttlefish have ink, like squid and octopuses, which they use to help evade predators.

Toxicity

Like octopuses and some squid, all cuttlefish have bacterially-produced neurotoxins in their saliva.

Pfeffer's Flamboyant Cuttlefish from Sipadan, Malaysia

The muscles of Pfeffer's Flamboyant Cuttlefish contain a highly toxic compound that is yet to be identified. Mark Norman with Museum Victoria in Victoria, Australia, has shown the toxin to be as lethal as that of a fellow cephalopod, the blue-ringed octopus.

Ecology

Diet

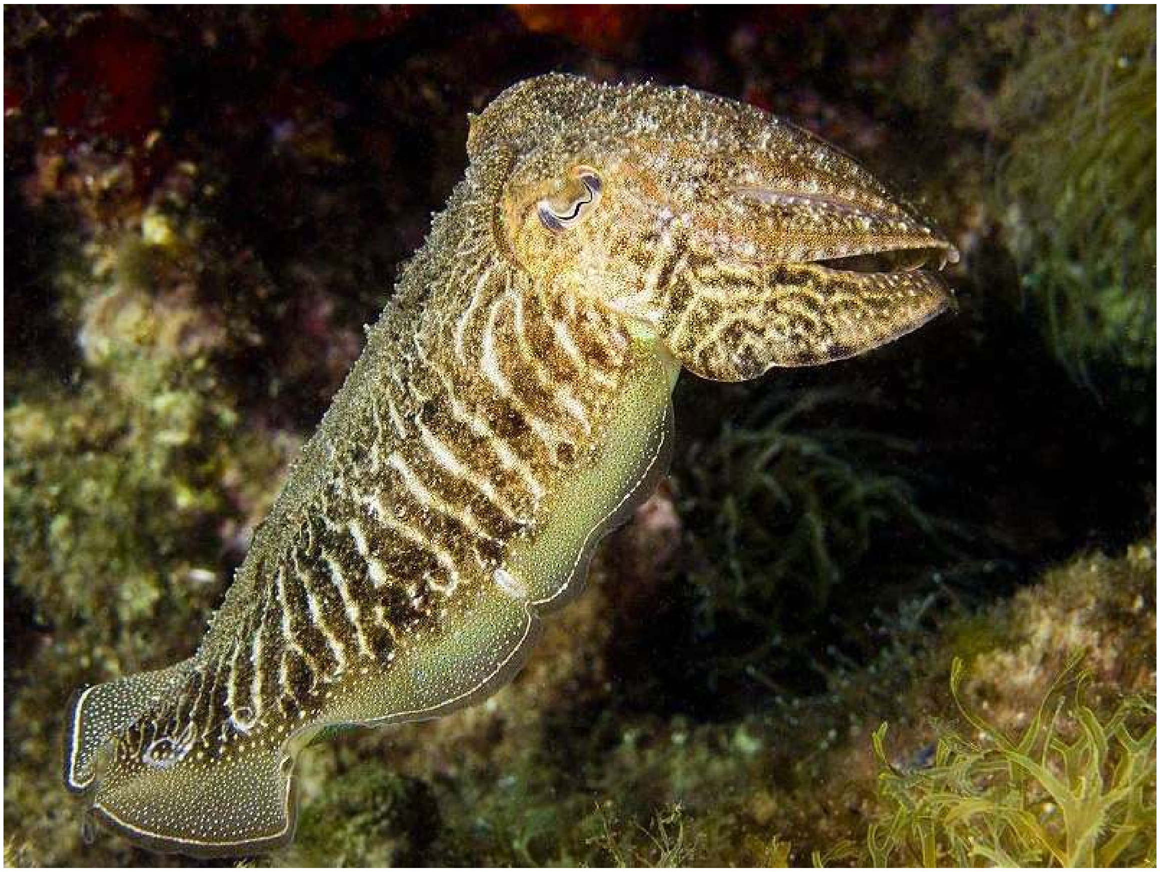
The preferred diet of the cuttlefish is crabs and fish. They feed on small shrimp shortly after hatching.

The cuttlefish uses its camouflage to hunt and sneak up on its prey. When it gets close enough, it opens its eight arms and shoots out two long feeding tentacles. On the end of each is a pad covered in suckers that grabs and pulls prey toward its beak.

Range and habitat

Family Sepiidae, which contains all cuttlefish, inhabit tropical/temperate ocean waters. They are mostly shallow-water animals although they are known to go to depths of about 600 metres (2,000 ft). They have an unusual biogeographic pattern: totally absent from the Americas, but present along the coasts of east and south Asia, western Europe, the Mediterranean, as well as all coasts of Africa and Australia. By the time the family evolved, ostensibly in the Old World, the north Atlantic possibly had become too cold and deep for these warm water species to cross.

Taxonomy



Sepia officinalis from Turkish waters

There are over 120 species of cuttlefish currently recognised, grouped into 5 genera. Sepiadariidae contains seven species and 2 genera; all the rest are in Sepiidae.

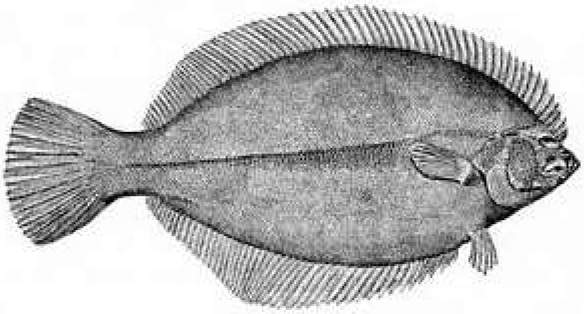
- CLASS CEPHALOPODA
    - Subclass Nautiloidea: nautilus
    - Subclass Coleoidea: squid, octopus, cuttlefish
        - Superorder Octopodiformes
        - Superorder Decapodiformes
            - ?Order †Boletzkyida
            - Order Spirulida: Ram's Horn Squid
            - Order **Sepiida**: cuttlefish
                - Suborder †Vasseuriina
                    - Family †Vasseuriidae
                    - Family †Belosepiellidae
                - Suborder Sepiina
                    - Family †Belosaepiidae

    - Family Sepiadariidae
    - Family Sepiidae
  - Order Sepiolida: bobtail squid
  - Order Teuthida: squid

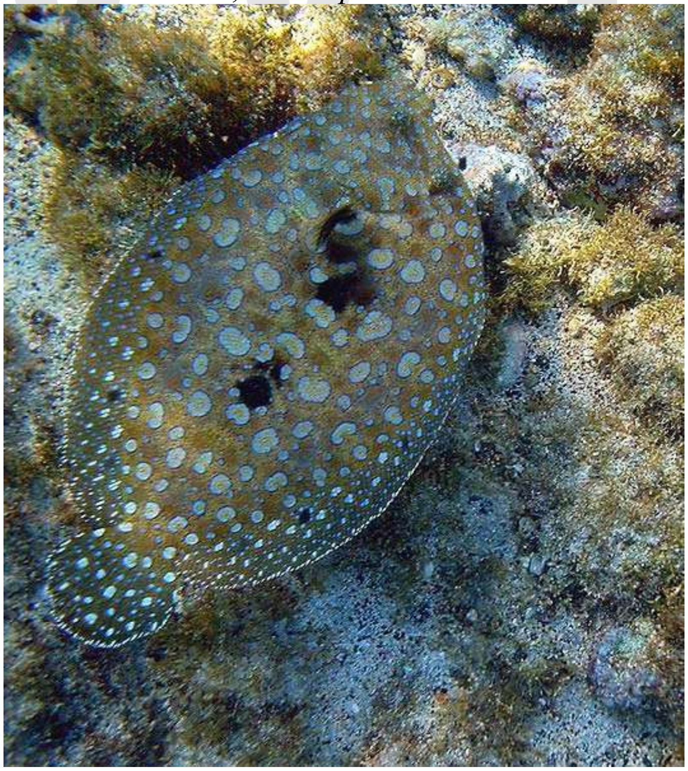
Chapter 13

Flounder and Four-Spotted flounder

Flounder



Winter flounder, *Pseudopleuronectes americanus*



Flowery flounder, *Bothus mancus*, Bahía de la Chiva, at Hawaii

The **flounder** is an ocean-dwelling flatfish species that is found in coastal lagoons and estuaries of the Northern Atlantic and Pacific Oceans.

Taxonomy

There are a number of geographical and taxonomical species to which flounder belong.

- Western Atlantic
    - Summer flounder (also known as *fluke*) - *Paralichthys dentatus*
    - Southern flounder - *Paralichthys lethostigma*
    - Winter flounder - *Pseudopleuronectes americanus*

- European waters
    - European flounder - *Platichthys flesus*

- Off the coast of Japan
    - Olive flounder - *Paralichthys olivaceus*

Eye migration

In its life cycle, an adult flounder has two eyes situated on one side of its head, where at hatching one eye is located on each side of its brain. One eye migrates to the other side of the body as a process of metamorphosis as it grows from larval to juvenile stage. As an adult, a flounder changes its habits and camouflages itself by lying on the bottom of the ocean floor as protection against predators. As a result, the eyes are then on the side which faces up. The side to which the eyes migrate is dependent on the species type.

Habitat

Flounder ambush their prey, feeding at soft muddy areas of the sea bottom, near bridge piles, docks and coral reefs, and have been also found at the bottom of the Mariana trench, the deepest known ocean canyon. Swiss scientist Jacques Piccard and US Navy Lt. Don Walsh reached a depth of 10,916 meters (35,814 ft) and were surprised to discover sole or flounder about 30 cm long.

A flounder's diet consists mainly of fish spawn, crustaceans, polychaetes and small fish. Flounder typically grow to a length of 12.5–37.5 centimetres (4.9–14.8 in), and as large as 60 centimeters (23.6 in). Their width is about half their length.

Threats

A flounder blending into its environment

World stocks of large predatory fish and large ground fish such as sole and flounder were estimated in 2003 to be only about 10% of pre-industrial levels, largely due to overfishing. Most overfishing is due to the extensive activities of the fishing industry. Current estimates suggest that approximately 30 million flounder (excluding sole) are alive in the world today. In the Gulf of Mexico, along the coast of Texas, research indicates the flounder population could be as low as 15 million due to heavy overfishing and industrial pollution.

According to Seafood Watch, Atlantic flounder and sole are currently on the list of seafood that sustainability-minded consumers should avoid.

Four-Spotted flounder

Four-Spotted Flounder

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Order:	Pleuronectiformes
Family:	Paralichthyidae
Genus:	*Paralichthys*
Species:	***P. oblongus***

Binomial name

Paralichthys oblongus
(Jordan & Evermann, 1896)

The **Four-Spotted Flounder**, *Paralichthys oblongus* (Jordan and Evermann, 1896), also called American Four-Spotted Flounder or simply Four-Spot, is a flatfish and member of the left-eyed flounder family Paralichthyidae.

Description

As with most members of the left-eye flounders they can change the color and pattern of their dark side to match the surrounding bottom, and are also capable of rapidly burrowing into muddy or sandy bottoms. The back, which may vary in overall color from light brown to dark gray, is marked with four large and quite conspicuous black "eye-like" spots edged with a much lighter color, two of them situated at each margin of the body. The teeth are sharp and well developed. The underside is pale pinkish, almost translucent in certain areas. Data collected from fishing trawlers suggests adults average about 10 to 12 inches long with 16 inches likely being the maximum size. Adults are predatory and mostly piscivorous, preying on any small fish such as sand lance and Atlantic silverside, as well as squid.

Habitat

A range in the western Atlantic from the Gulf of Maine, and perhaps as far north as Nova Scotia, south to Florida, preferring water depths of at least 12 fathoms and as far out as to the continental shelf. Little is documented of the breeding and seasonal migratory habits of this fish.

Commercial fishing, angling, and food quality

The Four-spotted flounder is most often taken commercially by fishing trawlers. Due to its small size and lack of abundance inshore it is not prized or even well known by recreational anglers who may often mistake this flounder for its relative the Summer Flounder *Paralichthys dentatus*, as it shares a similar offshore range, appearance, and feeding habits. In addition to the obvious four spots and more translucent underside, the Four-Spot can also be identified from the Summer Flounder by its slightly more elongated shape and proportionately larger eyes. The meat is white and considered to have a very mild taste like that of the Summer flounder and Southern flounder *Paralichthys lethostigma*.

Chapter 14

Frog

Frogs
Temporal range: Triassic–present

Australian Green Tree Frog (*Litoria caerulea*)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Subclass:	Lissamphibia
Order:	**Anura** Merrem, 1820

Suborders

Archaeobatrachia
Mesobatrachia
Neobatrachia

Native distribution of frogs (in black)

Frogs are amphibians in the order Anura (meaning "tail-less", from Greek *an-,* without + *oura*, tail), formerly referred to as *Salientia* (Latin *salere* (*salio*), "to jump"). Most frogs are characterized by a short body, webbed digits (fingers or toes), protruding eyes and the absence of a tail. Frogs are widely known as exceptional jumpers, and many of the anatomical characteristics of frogs, particularly their long, powerful legs, are adaptations to improve jumping performance. Due to their permeable skin, frogs are often semi-aquatic or inhabit humid areas, but move easily on land. They typically lay their eggs in puddles, ponds or lakes, and their larvae, called tadpoles, have gills and develop in water. Adult frogs follow a carnivorous diet, mostly of arthropods, annelids and gastropods. Frogs are most noticeable by their call, which can be widely heard during the night or day, mainly in their mating season.

The distribution of frogs ranges from tropic to subarctic regions, but most species are found in tropical rainforests. Consisting of more than 5,000 species described, they are among the most diverse groups of vertebrates. However, populations of certain frog species are declining significantly.

A popular distinction is often made between frogs and toads on the basis of their appearance, but this has no taxonomic basis. (Members of the anuran family Bufonidae are called true toads, but many species from other families are also called toads.) In addition to their ecological importance, frogs have many cultural roles, such as in literature, symbolism and religion, and they are also valued as food and as pets.

Etymology and terminology

The name frog derives from Old English *frogga*, (compare Old Norse *frauki*, German *Frosch*, older Dutch spelling *kikvorsch*), cognate with Sanskrit *plava* (frog), probably deriving from Proto-Indo-European *praw* = "to jump".

A distinction is often made between frogs and toads on the basis of their appearance, caused by the convergent adaptation among so-called toads to dry environments; however, this distinction has no taxonomic basis. The only family exclusively given the common name "toad" is Bufonidae, but many species from other families are also called "toads," and the species within the toad genus *Atelopus* are referred to as "harlequin frogs".

Taxonomy

The order *Anura* contains 4,810 species in 33 families, of which the Leptodactylidae (1100 spp.), Hylidae (800 spp.) and Ranidae (750 spp.) are the richest in species. About 88% of amphibian species are frogs.

European Fire-bellied Toad (*Bombina bombina*)

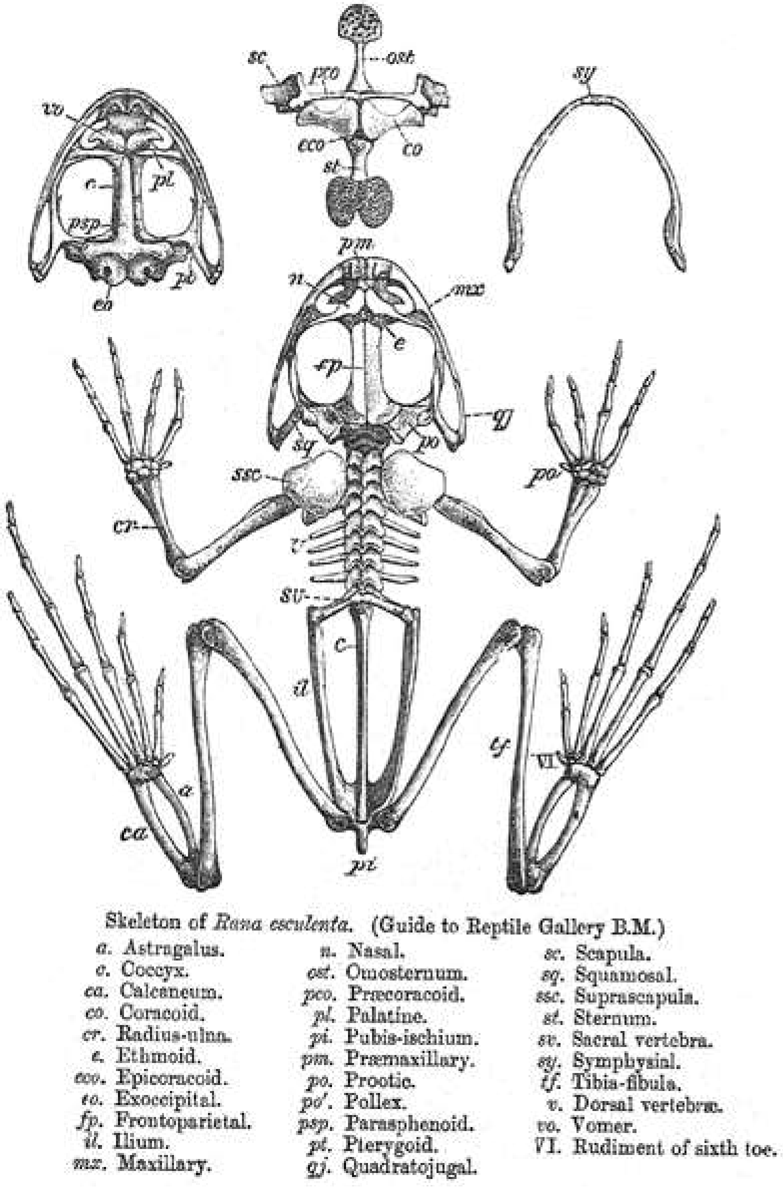
Young American bullfrog found in a stream in New Jersey

The use of the common names "frog" and "toad" has no taxonomic justification. From a taxonomic perspective, all members of the order Anura are frogs, but only members of the family Bufonidae are considered "true toads". The use of the term "frog" in common names usually refers to species that are aquatic or semi-aquatic with smooth and/or moist skins, and the term "toad" generally refers to species that tend to be terrestrial with dry, warty skin. An exception is the fire-bellied toad (*Bombina bombina*): while its skin is slightly warty, it prefers a watery habitat.

Frogs and toads are broadly classified into three suborders: Archaeobatrachia, which includes four families of primitive frogs; Mesobatrachia, which includes five families of more evolutionary intermediate frogs; and Neobatrachia, by far the largest group, which contains the remaining 24 families of "modern" frogs, including most common species throughout the world. Neobatrachia is further divided into the Hyloidea and Ranoidea. This classification is based on such morphological features as the number of vertebrae, the structure of the pectoral girdle, and the morphology of tadpoles. While this classification is largely accepted, relationships among families of frogs are still debated. Future studies of molecular genetics should soon provide further insights to the evolutionary relationships among anuran families.

Some species of anurans hybridise readily. For instance, the Edible Frog (*Rana esculenta*) is a hybrid of the Pool Frog (*R. lessonae*) and the Marsh Frog (*R. ridibunda*). *Bombina bombina* and *Bombina variegata* similarly form hybrids, although these are less fertile, giving rise to a hybrid zone.

Morphology and physiology



Skeleton of *Rana*

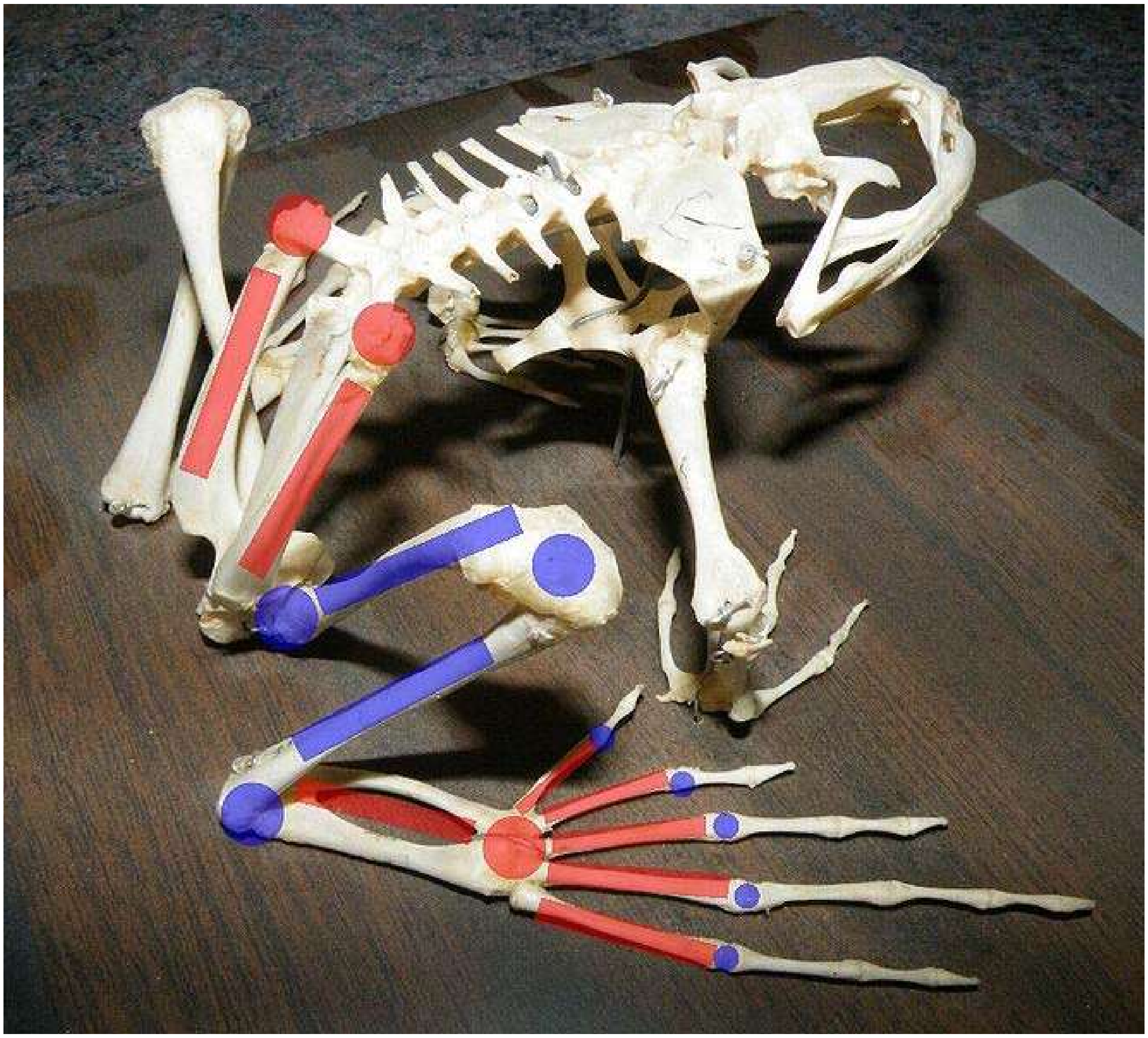
The morphology of frogs is unique among amphibians. Compared with the other two groups of amphibians, (salamanders and caecilians), frogs are unusual because they lack tails as adults and their legs are more suited to jumping than walking. The physiology of frogs is generally like that of other amphibians (and differs from other terrestrial vertebrates) because oxygen can pass through their highly permeable skin. This unique feature allows frogs to "breathe" largely through their skin. Because the oxygen is dissolved in an aqueous film on the skin and passes from there to the blood, the skin must remain moist at all times; this makes frogs susceptible to many toxins in the environment, some of which can similarly dissolve in the layer of water and be passed into their bloodstream. This may be the cause of the decline in frog populations.

Many characteristics are not shared by all of the approximately 5,250 described frog species. However, some general characteristics distinguish them from other amphibians. Frogs are usually well suited to jumping, with long hind legs and elongated ankle bones. They have a short vertebral column, with no more than ten free vertebrae, followed by a fused tailbone (urostyle or coccyx), typically resulting in a tailless phenotype.

Frogs range in size from 10 mm (0.39 in) (*Brachycephalus didactylus* of Brazil and *Eleutherodactylus iberia* of Cuba) to 300 mm (12 in) (goliath frog, *Conraua goliath*, of Cameroon). The skin hangs loosely on the body because of the lack of loose connective tissue. Skin texture varies: it can be smooth, warty or folded. Frogs have three eyelid membranes: one is transparent to protect the eyes underwater, and two vary from translucent to opaque. Frogs have a tympanum on each side of the head, which is involved in hearing and, in some species, is covered by skin. Most frogs have teeth, specifically pedicellate teeth in which the crow is separated from the root by fibrous tissue. Most only have teeth on the edge of the upper jaw (*maxillary teeth*) as well as *vomerine teeth* on the roof of their mouth. They do not have any teeth on their lower jaw, so they usually swallow their food whole. The teeth are mainly used to hold the prey and keep it in place till they can get a good grip on it and swallow their meal, assisted by retracting their eyes into their head. True toads lack any teeth at all, and some species (Pyxicephalus) which prey on relatively large organisms (including mice and other frogs) have cone shaped projections of bone, called odontoid processes, at the front of the lower jaw which function like teeth.

Feet and legs

Tyler's Tree Frog (*Litoria tyleri*) illustrates large toe pads and webbed feet



A bullfrog skeleton, showing elongate limb bones and extra joints. Red marks indicate bones which have been substantially elongated in frogs and joints which have become mobile. Blue indicates joints and bones which have not been modified or only somewhat elongated.

The structure of the feet and legs varies greatly among frog species, depending in part on whether they live primarily on the ground, in water, in trees, or in burrows. Frogs must be able to move quickly through their environment to catch prey and escape predators, and numerous adaptations help them do so.

Many frogs, especially those that live in water, have webbed toes. The degree to which the toes are webbed is directly proportional to the amount of time the species lives in the water. For example, the completely aquatic African dwarf frog (*Hymenochirus sp.*) has fully webbed toes, whereas the toes of White's tree frog (*Litoria caerulea*), an arboreal species, are only a half or a quarter webbed.

Arboreal frogs have "toe pads" to help grip vertical surfaces. These pads, located on the ends of the toes, do not work by suction. Rather, the surface of the pad consists of interlocking cells, with a small gap between adjacent cells. When the frog applies pressure to the toe pads, the interlocking cells grip irregularities on the substrate. The small gaps between the cells drain away all but a thin layer of moisture on the pad, and maintain a grip through capillarity. This allows the frog to grip smooth surfaces, and does not function when the pads are excessively wet.

In many arboreal frogs, a small "intercalary structure" in each toe increases the surface area touching the substrate. Furthermore, since hopping through trees can be dangerous, many arboreal frogs have hip joints that allow both hopping and walking. Some frogs that live high in trees even possess an elaborate degree of webbing between their toes, as do aquatic frogs. In these arboreal frogs, the webs allow the frogs to "parachute" or control their glide from one position in the canopy to another.

Ground-dwelling frogs generally lack the adaptations of aquatic and arboreal frogs. Most have smaller toe pads, if any, and little webbing. Some burrowing frogs have a toe extension—a metatarsal tubercle—that helps them to burrow. The hind legs of ground dwellers are more muscular than those of aqueous and tree-dwelling frogs.

Sometimes during the tadpole stage, one of the animal's rear leg stubs is eaten by a dragonfly nymph. In some of these cases, the full leg grows anyway, and in other cases, it does not, although the frog may still live out its normal lifespan with only three legs. Other times, a parasitic flatworm called *Riberoria trematodes* digs into the rear of a tadpole, where it rearranges the limb bud cells, which sometimes causes the frog to have extra legs.

Jumping

Rainforest Rocket Frog jumping

Frogs are generally recognized as exceptional jumpers, and the best jumper of all vertebrates. The Australian rocket frog, *Litoria nasuta*, can leap over 50 times its body length (5.5 cm), resulting in jumps of over 2 meters. The acceleration of the jump may be up to twice gravity. There are tremendous differences between species in jumping capability, but within a species, jump distance increases with increasing size, but relative jumping distance (body-lengths jumped) decreases.

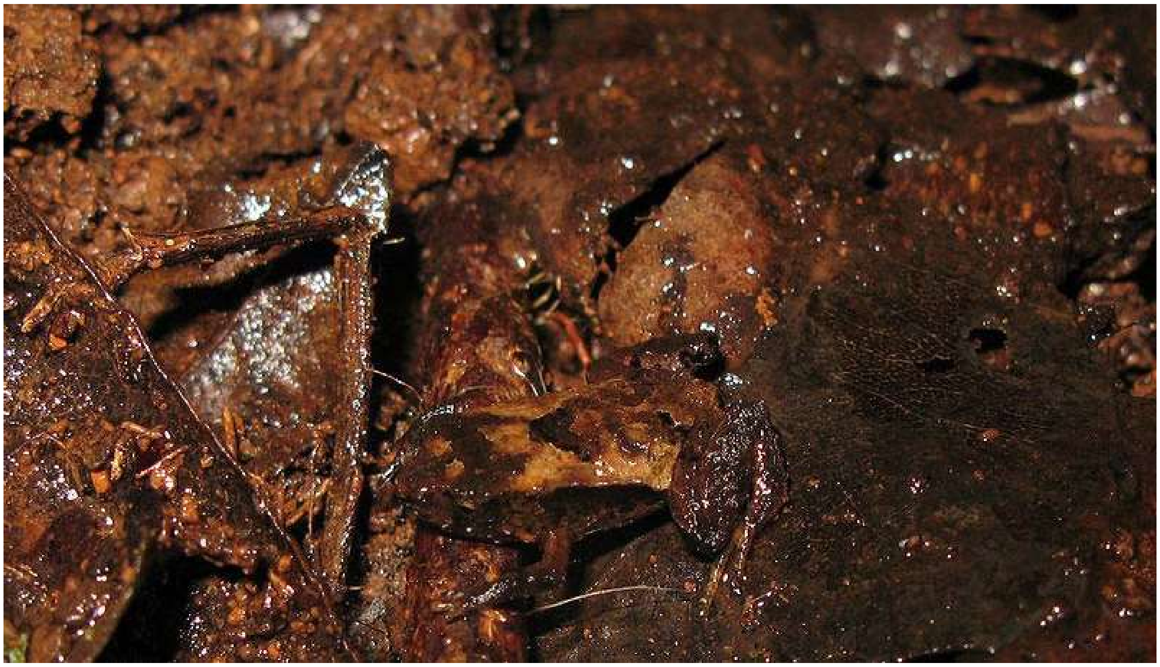
While frog species can use a variety of locomotor modes (running, walking, gliding, swimming, and climbing), more are either proficient at jumping or descended from ancestors who were, with much of the musculo-skeletal morphology modified for this purpose. The tibia, fibula and tarsals have been fused into a single, strong bone, as have the radius and ulna in the forelimbs (which must absorb the impact of landing). The metatarsals have become elongated to add to the leg length and allow the frog to push against the ground for longer during a jump. The illium has elongated and formed a mobile joint with the sacrum which, in specialist jumpers such as Ranids or Hylids, functions as an additional limb joint to further power the leaps. This elongation of the limbs results in the frog being able to apply force to the ground for longer during a jump, which in turn results in a longer, faster jump.

The muscular system has been similarly modified. The hind limbs of the ancestor of frogs presumably contained pairs of muscles which would act in opposition (one muscle to flex the knee, a different muscle to extend it), as is seen in most other limbed animals.

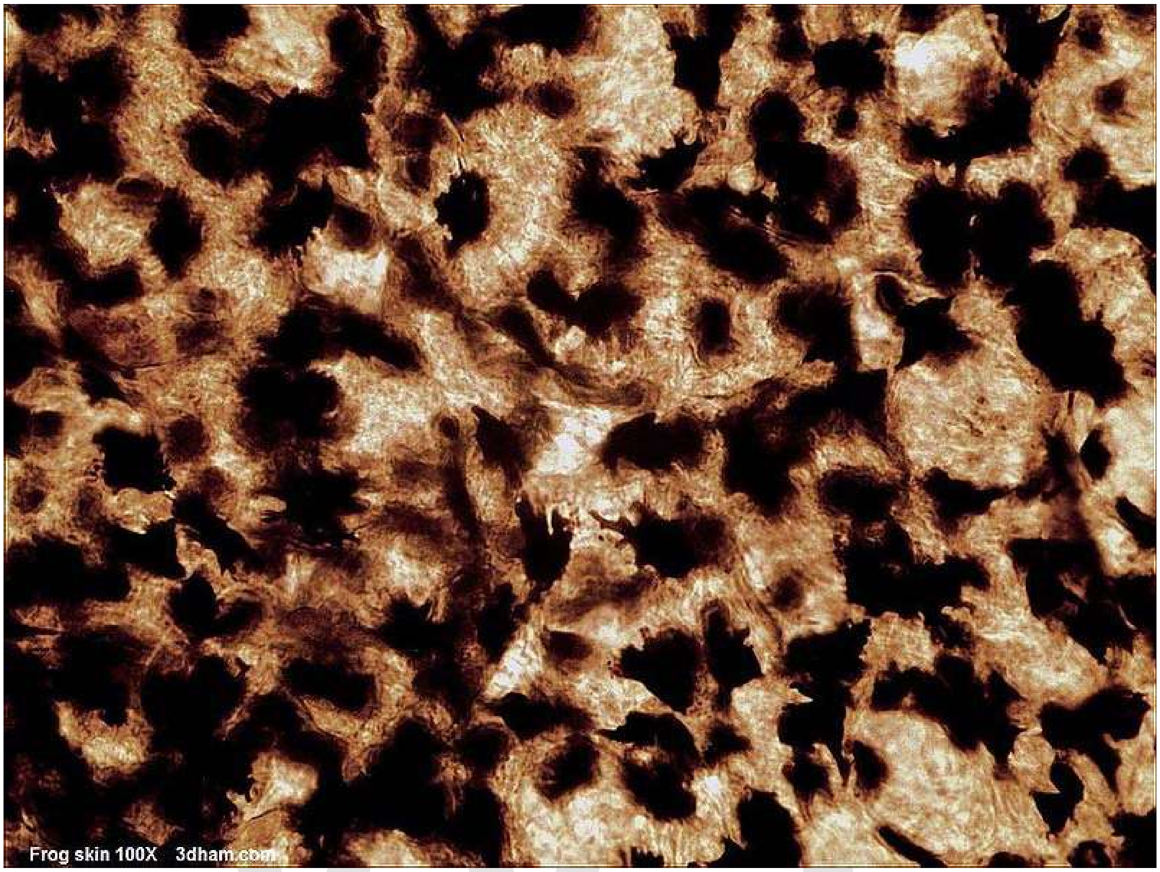
However, in modern frogs, almost all muscles have been modified to contribute to the action of jumping, with only a few small muscles remaining to bring the limb back to the starting position and maintain posture. The muscles have also been greatly enlarged, with the muscles involved in jumping accounting for over 17% of the total mass of the frog.

In some extremely capable jumpers, such as the cuban tree frog, the peak power exerted during a jump can exceed what muscle is capable of producing. Currently, it is hypothesized that frogs are storing muscular energy by stretching their tendons like springs, then triggering the release all at once, allowing the frog to increase the energy of its jump beyond the limits of muscle-powered acceleration. A similar mechanism has already been documented in locusts and grasshoppers.

Skin



Pouched Frog (*Assa darlingtoni*) camouflaged against leaf litter.



Microscopic view of frog skin

Many frogs are able to absorb water and oxygen directly through the skin, especially around the pelvic area. However, the permeability of a frog's skin can also result in water loss. Some tree frogs reduce water loss with a waterproof layer of skin. Others have adapted behaviours to conserve water, including engaging in nocturnal activity and resting in a water-conserving position. This position involves the frog lying with its toes and fingers tucked under its body and chin, respectively, with no gap between the body and substrate. Some frog species will also rest in large groups, touching the skin of the neighbouring frog. This reduces the amount of skin exposed to the air or a dry surface, and thus reduces water loss. These adaptations only reduce water loss enough for a predominantly arboreal existence, and are not suitable for arid conditions.

Camouflage is a common defensive mechanism in frogs. Most camouflaged frogs are nocturnal, which adds to their ability to hide. Nocturnal frogs usually find the ideal camouflaged position during the day to sleep. Some frogs have the ability to change colour, but this is usually restricted to shades of one or two colours. For example, White's tree frog varies in shades of green and brown. Features such as warts and skin folds are usually found on ground-dwelling frogs, where a smooth skin would not disguise them effectively. Arboreal frogs usually have smooth skin, enabling them to disguise themselves as leaves.

Certain frogs change colour between night and day, as light and moisture stimulate the pigment cells and cause them to expand or contract.

Poison

Many frogs contain mild toxins that make them unpalatable to potential predators. For example, all toads have large poison glands—the parotoid glands—located behind the eyes, on the top of the head. Some frogs, such as some poison dart frogs, are especially toxic. The chemical makeup of toxins in frogs varies from irritants to hallucinogens, convulsants, nerve poisons, and vasoconstrictors. Many predators of frogs have adapted to tolerate high levels of these poisons. Others, including humans, may be severely affected.

Oophaga pumilio, a poison dart frog, contains numerous alkaloids which deter predators

Some frogs obtain poisons from the ants and other arthropods they eat; others, such as the Australian Corroboree Frogs (*Pseudophryne corroboree* and *Pseudophryne pengilleyi*), can manufacture an alkaloid not derived from their diet. Some native people of South America extract poison from the poison dart frogs and apply it to their darts for hunting, although few species are toxic enough to be used for this purpose. It was previously a misconception the poison was placed on arrows rather than darts. The common name of these frogs was thus changed from "poison arrow frog" to "poison dart frog" in the early 1980s. Poisonous frogs tend to advertise their toxicity with bright colours, an adaptive strategy known as aposematism. There are at least two non-poisonous species of frogs in tropical America (*Eleutherodactylus gaigei* and *Lithodytes lineatus*) that mimic the colouration of dart poison frogs' coloration for self-protection (Batesian mimicry).

Because frog toxins are extraordinarily diverse, they have raised the interest of biochemists as a "natural pharmacy". The alkaloid epibatidine, a painkiller 200 times more potent than morphine, is found in some species of poison dart frogs. Other chemicals isolated from the skin of frogs may offer resistance to HIV infection. Arrow and dart poisons are under active investigation for their potential as therapeutic drugs.

The skin secretions of some toads, such as the Colorado River toad and cane toad, contain bufotoxins, some of which, such as bufotenin, are psychoactive, and have therefore been used as recreational drugs. Typically, the skin secretions are dried and smoked. Skin licking is especially dangerous, and appears to constitute an urban myth.

Respiration and circulation

The skin of a frog is permeable to oxygen and carbon dioxide, as well as to water. There are a number of blood vessels near the surface of the skin. When a frog is underwater, oxygen is transmitted through the skin directly into the bloodstream. On land, adult frogs use their lungs to breathe. Their lungs are similar to those of humans, but the chest muscles are not involved in respiration, and there are no ribs or diaphragm to support breathing. Frogs breathe by taking air in through the nostrils (which often have valves which close when the frog is submerged), causing the throat to puff out, then compressing the floor of the mouth, which forces the air into the lungs. In August 2007 an aquatic frog named *Barbourula kalimantanensis* was discovered in a remote part of Indonesia. The Bornean Flat-headed Frog (*B. kalimantanensis*) is the first species of frog known to science without lungs.

Frogs are known for their three-chambered heart, which they share with all tetrapods except birds, crocodilians and mammals. In the three-chambered heart, oxygenated blood from the lungs and de-oxygenated blood from the respiring tissues enter by separate atria, and are directed via a spiral valve to the appropriate vessel—aorta for oxygenated blood and pulmonary artery for deoxygenated blood. This special structure is essential to keeping the mixing of the two types of blood to a minimum, which enables frogs to have higher metabolic rates, and to be more active than otherwise.

Some species of frog have remarkable adaptations that allow them to survive in oxygen deficient water. The lake titicaca frog (*Telmatobius culeus*) is one such species and to survive in the poorly oxygenated waters of Lake Titicaca it has incredibly wrinkly skin that increases its surface area to enhance gas exchange. This frog will also do 'push-ups' on the lake bed to increase the flow of water around its body.

Digestion and excretion

The frog's digestive system begins with the mouth. Frogs have teeth along their upper jaw called the maxillary teeth, which are used to grind food before swallowing. These teeth are very weak, and cannot be used to catch or harm agile prey. Instead, the frog uses its sticky tongue to catch food (such as flies or other insects). The food then moves through the esophagus into the stomach. The food then proceeds to the small intestine (duodenum and ileum) where most digestion occurs. Frogs carry pancreatic juice from the pancreas, and bile (produced by the liver) through the gallbladder from the liver to the small intestine, where the fluids digest the food and extract the nutrients. When the food passes into the large intestine, the water is reabsorbed and wastes are routed to the cloaca. All wastes exit the body through the cloaca and the cloacal vent.

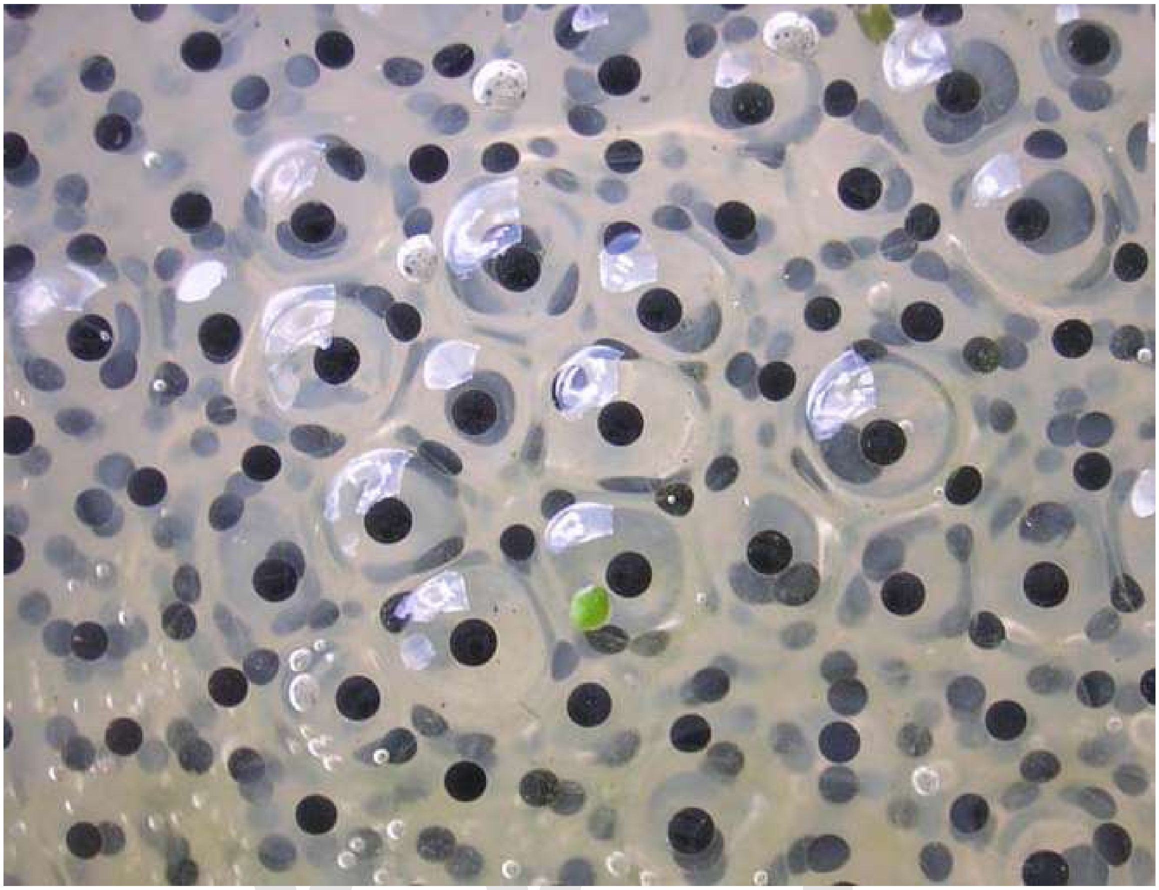
Nervous system

The frog has a highly developed nervous system which consists of a brain, spinal cord and nerves. Many parts of the frog's brain correspond with those of humans. The medulla oblongata regulates respiration, digestion, and other automatic functions. Muscular coordination and posture are controlled by the cerebellum. The relative size of the cerebrum of a frog is much smaller than that of a human. Frogs have ten cranial nerves (nerves which pass information from the outside directly to the brain) and ten pairs of spinal nerves (nerves which pass information from extremities to the brain through the spinal cord). By contrast, all amniotes (mammals, birds and reptiles) have twelve cranial nerves. Frogs do not have external ears; the eardrums (tympanic membranes) are directly exposed. As in all animals, the ear contains semicircular canals which help control balance and orientation. Due to their short cochlea, frogs use electrical tuning to expand their range of audible frequencies.

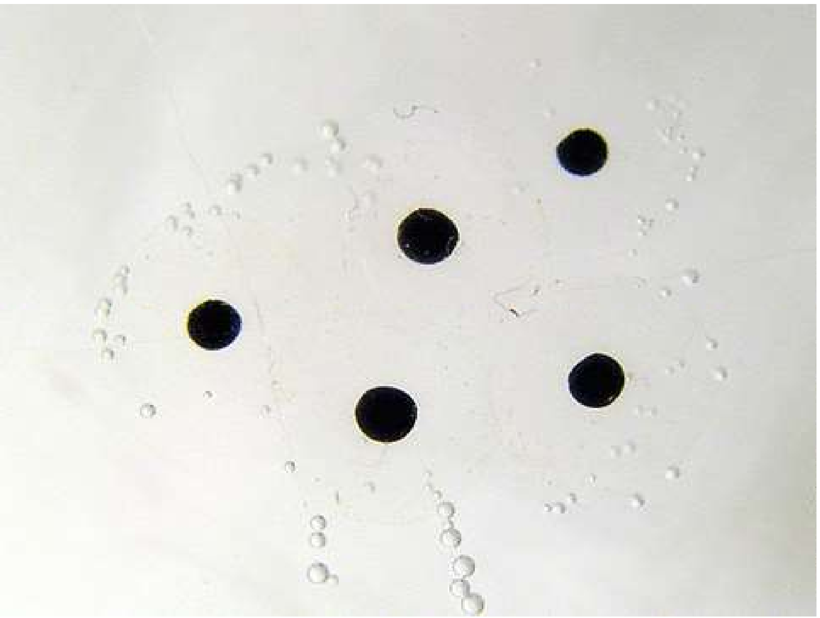
Natural history

The life cycle of frogs, like that of other amphibians, consists of four main stages: egg, tadpole, metamorphosis and adult. The reliance of frogs on an aquatic environment for the egg and tadpole stages gives rise to a variety of breeding behaviours that include the well-known mating calls used by the males of most species to attract females to the bodies of water that they have chosen for breeding. Some frogs also look after their eggs—and in some cases even the tadpoles—for some time after laying.

Life cycle



Frogspawn



Frogspawn development

Tadpole of Haswell's Froglet (*Paracrinia haswelli*

The life cycle of a frog starts with an egg. A female generally lays gelatinous egg masses containing thousands of eggs, in water. Each anuran species lays eggs in a distinctive, identifiable manner. An example are the long strings of eggs laid by the common American toad. The eggs are highly vulnerable to predation, so frogs have evolved many techniques to ensure the survival of the next generation. In colder areas the embryo is black to absorb more heat from the sun, which speeds up the development. Most commonly, this involves synchronous reproduction. Many individuals will breed at the same time, overwhelming the actions of predators; the majority of the offspring will still die due to predation, but there is a greater chance some will survive. Another way in which some species avoid the predators and pathogens eggs are exposed to in ponds is to lay eggs on leaves above the pond, with a gelatinous coating designed to retain moisture. In these species the tadpoles drop into the water upon hatching. The eggs of some species laid out of water can detect vibrations of nearby predatory wasps or snakes, and will hatch early to avoid being eaten. Some species, such as the Cane Toad (*Bufo marinus*), lay poisonous eggs to minimise predation. While the length of the egg stage depends on the species and environmental conditions, aquatic eggs generally hatch within one week. Other species go through their whole larval phase inside the eggs or the mother, or they have direct development. Unlike salamanders and newts, frogs and toads never become sexually mature while still in their larval stage.

Eggs hatch and continue life as tadpoles (occasionally known as polliwogs), which typically have oval bodies and long, vertically flattened tails. At least one species (Nannophrys ceylonensis) has tadpoles that are semi-terrestrial and live among wet rocks, but as a general rule, free living larvae are fully aquatic. They lack eyelids and have a cartilaginous skeleton, a lateral line system, gills for respiration (external gills at first, internal gills later) and tails with dorsal and ventral folds of skin for swimming. From pretty early onward they develop a gill pouch that covers the gills and the front legs and also the lungs are developed in an early stage as an accessory breathing organ. Some species which go through the metamorphosis inside the egg and hatch to small frogs never develop gills, instead there are specialised areas of skin that takes care of the respiration. Tadpoles also lack true teeth, but the jaws in most species usually have two elongate, parallel rows of small keratinized structures called keradonts in the upper jaw while the lower jaw has three rows of keradonts, surrounded by a horny beak, but the number of rows can be lower or absent, or much higher. Tadpoles are typically herbivorous, feeding mostly on algae, including diatoms filtered from the water through the gills. Some species are carnivorous at the tadpole stage, eating insects, smaller tadpoles, and fish. Cannibalism has been observed among tadpoles. Early developers who gain legs may be eaten by the others, so the late bloomers survive longer. This has been observed in England in the species *Rana temporaria* (common frog).

Tadpoles are highly vulnerable to predation by fish, newts, predatory diving beetles and birds such as kingfishers. Poisonous tadpoles are present in many species, such as Cane Toads. The tadpole stage may be as short as a week, or tadpoles may overwinter and metamorphose the following year in some species, such as the midwife toad (*Alytes obstetricans*) and the common spadefoot (*Pelobates fuscus*). In the Pipidae, with the exception for Hymenochirus, the tadpoles have paired anterior barbels which make them resemble small catfish.

With the exception of the base of the tail, where a few vertebral structures develop to give rise to the urostyle later in life, the tail lacks the completely solid, segmental, skeletal elements of cartilage or bony tissue that are so typical for other vertebrates, although it does contain a notochord

At the end of the tadpole stage, frogs undergo metamorphosis, in which they undergo a transition into the adult form. This metamorphosis last typically only 24 hours and consists of:

Larva of the common frog *Rana temporaria* a day before metamorphisis

Common frog - Metamorphosis stage. Notice the deformed jaws, large eyes and the remains of the gill pouch.

Young frog with tail remains after metamorphosis

Adult leopard frog

- The disappearance of the gill pouch, making the front legs visible.
- The transformation of the jaws into the big jaws of predatory frogs (most tadpoles are scraping of algae or are filter feeders)
- The transformation of the digestive system: the long spiral gut of the larva is being replaced by the typical short gut of a predator.
- An adaptation of the nervous system for stereoscopic vision, locomotion and feeding
- A quick growth and movement of the eyes to higher up the skull and the formation of eyelids.
- Formation of skin glands, thickening of the skin and loss of the lateral line system
- An eardrum is developed to lock the middle ear.

The disappearance of the tail is somewhat later (occurs at higher thyroxin levels) and after the tail has been resorbed the animals are ready to leave the water. The material of the tail is being used for a quick growth of the legs. The disappearing of the larval structures is a regulated process called apoptosis.

Incident of frog cannibalism

After metamorphosis, young adults may leave the water and disperse into terrestrial habitats, or continue to live in the aquatic habitat as adults. Almost all species of frogs are carnivorous as adults, eating invertebrates such as arthropods, annelids and gastropods. A few of the larger species may eat prey such as small mammals, fish and smaller frogs. Some frogs use their sticky tongues to catch fast-moving prey, while others capture their prey and force it into their mouths with their hands. However, there are a very few species of frogs that primarily eat plants. Adult frogs are themselves preyed upon by birds, large fish, snakes, otters, foxes, badgers, coatis, and other animals. Frogs are also eaten by people.

Frogs and toads can live for many years; though little is known about their life span in the wild, captive frogs and toads are recorded living up to 40 years.

Frogs from temperate climates hibernate through the winter, and 4 species are known to freeze during this time, most notably Rana sylvatica.

Reproduction of frogs

Once adult frogs reach maturity, they will assemble at a water source such as a pond or stream to breed. Many frogs return to the bodies of water where they were born, often resulting in annual migrations involving thousands of frogs. In continental Europe, a large proportion of migrating frogs used to die on roads, before special fences and tunnels were built for them.

Male and female Common toad (*Bufo bufo*) in amplexus

A Male and Female common toad in amplexus. The black strands are eggs released into open water minutes after birth.

Once at the breeding ground, male frogs call to attract a mate, collectively becoming a chorus of frogs. The call is unique to the species, and will attract females of that species. Some species have satellite males who do not call, but intercept females that are approaching a calling male.

The male and female frogs then undergo amplexus. This involves the male mounting the female and gripping her (sometimes with special nuptial pads) tightly. Fertilization is external: the egg and sperm meet outside of the body. The female releases her eggs, which the male frog covers with a sperm solution. The eggs then swell and develop a protective coating. The eggs are typically brown or black, with a clear, gelatin-like covering.

Most temperate species of frogs reproduce between late autumn and early spring. In the UK, most common frog populations produce frogspawn in February, although there is wide variation in timing. Water temperatures at this time of year are relatively low, typically between four and 10 degrees Celsius. Reproducing in these conditions helps the developing tadpoles because dissolved oxygen concentrations in the water are highest at cold temperatures. More importantly, reproducing early in the season ensures that appropriate food is available to the developing frogs at the right time.

Parental care

Colour plate from Ernst Haeckel's 1904 *Kunstformen der Natur*, depicting frog species that include two examples of parental care.

Although care of offspring is poorly understood in frogs, it is estimated that up to 20% of amphibian species may care for their young in one way or another, and there is a great diversity of parental behaviours. Some species of poison dart frog lay eggs on the forest floor and protect them, guarding the eggs from predation and keeping them moist. The frog will urinate on them if they become too dry. After hatching, a parent (the sex depends upon the species) will move them, on its back, to a water-holding bromeliad.

The parent then feeds them by laying unfertilized eggs in the bromeliad until the young have metamorphosed. Other frogs carry the eggs and tadpoles on their hind legs or back (e.g. the midwife toads, *Alytes spp.*). Some frogs even protect their offspring inside their own bodies. The male Australian Pouched Frog (*Assa darlingtoni*) has pouches along its side in which the tadpoles reside until metamorphosis. The female Gastric-brooding Frogs (genus *Rheobatrachus*) from Australia, now probably extinct, swallows its tadpoles, which then develop in the stomach. To do this, the Gastric-brooding Frog must stop secreting stomach acid and suppress peristalsis (contractions of the stomach). Darwin's Frog (*Rhinoderma darwinii*) from Chile puts the tadpoles in its vocal sac for development. Some species of frog will leave a 'babysitter' to watch over the frogspawn until it hatches.

The evolution of parental care in frogs is driven primarily by the size of the water body in which they breed. There is an inverse relationship between the level of parental care in a frog species and the degree of parental care they exhibit—frogs that breed in smaller water bodies tend to have more complex parental care behaviors. Water body size shows this strong relationship with parental care because it encompasses several important variables that interact to select for parental care: predation, desiccation, competition, and resource limitation. Because predation of eggs and larvae is high in large water bodies, a number of frog species evolved terrestrial oviposition. Once eggs are deposited on land, the desiccating terrestrial environment demands uniparental care in the form of egg hydration to ensure egg survival. The subsequent need to transport hatched tadpoles to a water source requires an even more intense form of uniparental care. In small water bodies where predators are mostly absent, such as phytotelmata (water-filled leaf axils or small woody cavities), inter-tadpole competition becomes the variable that constrains tadpole survival. Certain frogs species avoid this competition by evolving the use of smaller phytotelmata as tadpole deposition sites. However, while these smaller tadpole rearing sites are free of competition, they also lack nutrients. Because they do not have sufficient nutrients to support a tadpole without parental provisioning behavior, frog species that transitioned from the use of larger to smaller phytotelmata have evolved trophic (unfertilized) egg laying. In this complex form of biparental care, the female provides her offspring with nutritive eggs. While each of these variables select for different behaviors, they correlate with the size of a species' tadpole-rearing site and influence the degree of parental care displayed by a species.

Call

A male *Dendropsophus microcephalus* displaying its vocal sac during its call.

Some frog calls are so loud, they can be heard up to a mile away. The call of a frog is unique to its species. Frogs call by passing air through the larynx in the throat. In most calling frogs, the sound is amplified by one or more vocal sacs, membranes of skin under the throat or on the corner of the mouth that distend during the amplification of the call. The field of neuroethology studies the neurocircuitry that underlies frog audition.

Some frogs lack vocal sacs, such as those from the genera *Heleioporus* and *Neobatrachus*, but these species can still produce a loud call. Their buccal cavity is enlarged and dome-shaped, acting as a resonance chamber that amplifies their call. Species of frog without vocal sacs and that do not have a loud call tend to inhabit areas close to flowing water. The noise of flowing water overpowers any call, so they must communicate by other means.

The main reason for calling is to allow males to attract a mate. Males call either individually or in a group called a chorus. Females of many frog species, for example *Polypedates leucomystax*, produce calls reciprocal to the males', which act as the catalyst for the enhancement of reproductive activity in a breeding colony. A male frog emits a release call when mounted by another male. Tropical species also have a rain call that they make on the basis of humidity cues prior to a rain shower. Many species also have a territorial call that is used to chase away other males. All of these calls are emitted with the mouth of the frog closed.

A distress call, emitted by some frogs when they are in danger, is produced with the mouth open, resulting in a higher-pitched call. The effectiveness of the call is unknown; however, it is suspected the call intrigues the predator until another animal is attracted, distracting them enough for its escape.

Many species of frog have deep calls, or croaks. The English onomatopoeic spelling is "ribbit". The croak of the American bullfrog (*Rana catesbiana*) is sometimes spelt "jug o' rum". Other examples are Ancient Greek *brekekekex koax koax* for probably *Rana ridibunda*, and the description in Rigveda 7:103.6 *gómāyur éko ajámāyur ékaḥ* = "one has a voice like a cow's, one has a voice like a goat's".

Distribution and conservation status

The Red-eyed Tree Frog (*Litoria chloris*) is a species of tree frog native to eastern Australia.

The habitat of frogs extends almost worldwide, but they do not occur in Antarctica and are not present on many oceanic islands. The greatest diversity of frogs occurs in the tropical areas of the world, where water is readily available, suiting frogs' requirements due to their skin. Some frogs inhabit arid areas such as deserts, where water may not be easily accessible, and rely on specific adaptations to survive. The Australian genus *Cyclorana* and the American genus *Pternohyla* will bury themselves underground, create a water-impervious cocoon and hibernate during dry periods. Once it rains, they emerge, find a temporary pond and breed. Egg and tadpole development is very fast in comparison to most other frogs so that breeding is complete before the pond dries up. Some frog species are adapted to a cold environment; for instance the wood frog, whose habitat extends north of the Arctic Circle, buries itself in the ground during winter when much of its body freezes.

Golden toad (*Bufo periglenes*) – last seen in 1989

Frog populations have declined dramatically since the 1950s: more than one third of species are believed to be threatened with extinction and more than 120 species are suspected to be extinct since the 1980s. Among these species are the golden toad of Costa Rica and the Gastric-brooding frogs of Australia. Habitat loss is a significant cause of frog population decline, as are pollutants, climate change, the introduction of non-indigenous predators/competitors, and emerging infectious diseases including chytridiomycosis. Many environmental scientists believe that amphibians, including frogs, are excellent biological indicators of broader ecosystem health because of their intermediate position in food webs, permeable skins, and typically biphasic life (aquatic larvae and terrestrial adults). It appears that it is the species with both aquatic eggs and aquatic larvae that are most affected by the decline, while those with direct development are the most resistant.

A Canadian study conducted in 2006, suggested heavy traffic near frog habitats as a large threat to frog populations. In a few cases, captive breeding programs have been attempted to alleviate the pressure on frog populations, and these have proved successful. In 2007, it was reported the application of certain probiotic bacteria could protect amphibians from chytridiomycosis. One current project, The Panama Amphibian Rescue and Conservation Project, has subsequently been developed in order to rescue species at risk of chytridiomycosis in eastern Panama, and to develop field applications of this probiotic cure.

Zoos and aquariums around the world named 2008 the Year of the Frog, to draw attention to the conservation issues.

Evolution

A fossilized frog from the Czech Republic, possibly *Palaeobatrachus gigas*

Until the discovery of the Early Permian *Gerobatrachus hottoni* in 2008, a stem-batrachian with many salamander-like characteristics, the earliest known proto-frog was *Triadobatrachus massinoti*, from the 250 million year old early Triassic of Madagascar.

The skull is frog-like, being broad with large eye sockets, but the fossil has features diverging from modern amphibia. These include a different ilium, a longer body with more vertebrae, and separate vertebrae in its tail (whereas in modern frogs, the tail vertebrae are fused, and known as the *urostyle* or *coccyx*). The tibia and fibula bones are unfused and separate, making it probable *Triadobatrachus* was not an efficient leaper.

Another fossil frog, *Prosalirus bitis*, was discovered in 1995. The remains were recovered from Arizona's Kayenta Formation, which dates back to the Early Jurassic epoch, somewhat younger than *Triadobatrachus*. Like *Triadobatrachus*, *Prosalirus* did not have greatly enlarged legs, but had the typical three-pronged pelvic structure. Unlike *Triadobatrachus*, *Prosalirus* had already lost nearly all of its tail and was well adapted for jumping.

The earliest known "true frog" is *Vieraella herbsti*, from the early Jurassic (188–213 million years ago). It is known only from the dorsal and ventral impressions of a single animal and was estimated to be 33 mm (1.3 in) from snout to vent. *Notobatrachus degiustoi* from the middle Jurassic is slightly younger, about 155–170 million years old. It is likely the evolution of modern *Anura* was completed by the Jurassic period. The main evolutionary changes involved the shortening of the body and the loss of the tail.

The earliest full fossil record of a modern frog is of sanyanlichan, which lived 125 million years ago and had all modern frog features, but bore 9 presacral vertebrae instead of the 8 of modern frogs.

Frog fossils have been found on all continents except Antarctica, but biogeographic evidence suggests they inhabited Antarctica when it was warmer.

Uses in agriculture and research

Frogs are raised commercially for several purposes. Frogs are used as a food source; frog legs are a delicacy in China, France, the Philippines, the north of Greece and in many parts of the American South, especially Louisiana. Dead frogs are sometimes used for dissections in high school and university anatomy classes, often after being injected with coloured plastics to enhance the contrast between the organs. This practice has declined in recent years with the increasing concerns about animal welfare.

Frogs have served as important model organisms throughout the history of science. Eighteenth-century biologist Luigi Galvani discovered the link between electricity and the nervous system through studying frogs. The African clawed frog or platanna (*Xenopus laevis*) was first widely used in laboratories in pregnancy assays in the first half of the 20th century. When human chorionic gonadotropin, a hormone found in substantial quantities in the urine of pregnant women, is injected into a female *X. laevis*, it induces them to lay eggs. In 1952, Robert Briggs and Thomas J. King cloned a frog by somatic cell nuclear transfer, the same technique later used to create Dolly the Sheep, their experiment was the first time successful nuclear transplantation had been accomplished in metazoans.

Frogs are used in cloning research and other branches of embryology because frogs are among the closest living relatives of man to lack egg shells characteristic of most other vertebrates, and therefore facilitate observations of early development. Although alternative pregnancy assays have been developed, biologists continue to use *Xenopus* as a model organism in developmental biology because it is easy to raise in captivity and has a large and easily manipulatable embryo. Recently, *X. laevis* is increasingly being displaced by its smaller relative *X. tropicalis*, which reaches its reproductive age in five months rather than one to two years (as in *X. laevis*), facilitating faster studies across generations. The genome sequence of *X. tropicalis* will probably be completed by 2015 at the latest.

Cultural beliefs

Moche Frog 200 A.D. Larco Museum Collection Lima, Peru

Frogs feature prominently in folklore, fairy tales and popular culture. They tend to be portrayed as benign, ugly, clumsy, but with hidden talents. Examples include Michigan J. Frog, *The Frog Prince*, and Kermit the Frog. Michigan J. Frog, featured in the Warner Brothers cartoon *One Froggy Evening*, only performs his singing and dancing routine for his owner. Once another person looks at him, he will return to a frog-like pose. "The Frog Prince" is a fairy tale of a frog who turns into a handsome prince once kissed. Kermit the Frog, on the other hand, is a conscientious and disciplined character of *The Muppet Show* and *Sesame Street*; while openly friendly and greatly talented, he is often portrayed as cringing at the fanciful behavior of more flamboyant characters.

The Moche people of ancient Peru worshipped animals and often depicted frogs in their art. In Panama local legend promised luck to anyone who spotted a golden frog in the wild and some believed that when Panamanian Golden Frogs died, they would turn into a gold talisman, known as a huaca. Today, despite being extinct in the wild, Panamanian Golden Frogs remain an important cultural symbol and can be found on decorative cloth molas made by the Kuna Indians, on T-shirts, as inlaid design on a new overpass in Panama City and even on lottery tickets.

Chapter 15

Seahorse

Seahorses
Temporal range: 23–0 Ma
Lower Miocene to Present

Hippocampus sp.

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Subclass:	Neopterygii
Infraclass:	Teleostei
Order:	Syngnathiformes
Family:	Syngnathidae
Subfamily:	Hippocampinae
Genus:	***Hippocampus*** Rafinesque, 1810

Seahorses compose the fish genus ***Hippocampus*** within the family Syngnathidae, in order Syngnathiformes. Syngnathidae also includes the pipefishes. "Hippocampus" comes from the Ancient Greek *hippos* meaning "horse" and *kampos* meaning “sea monster”.

There are nearly 50 species of seahorse. They are mainly found in shallow tropical and temperate waters throughout the world. They prefer to live in sheltered areas such as seagrass beds, coral reefs, or mangroves. Colonies have been found in European waters such as the Thames Estuary. From North America down to South America there are approximately four species, ranging from the very small (dwarf seahorses are only about 2.5 cm (1 in)) to much larger specimens off the Pacific Coast of Central America (the foot-long *H. ingens*). *H. erectus* are larger seahorses that range from Nova Scotia to around Uruguay. Three species live in the Mediterranean Sea: *H. hippocampus* (long snout), *H. brevirostris* (short snout) and *H. fuscus* (immigrated from the Red Sea). These fish form territories, with males staying in about 1 square meter (11 sq ft) of their habitat while females range about one hundred times that area. They bob around in sea grass meadows, mangrove stands, and coral reefs where they adopt murky brown and gray patterns to camouflage themselves among the sea grass. During social moments or in unusual surroundings, seahorses turn bright colors.

Description

Spiny seahorse *Hippocampus hystrix* from East Timor holding on to soft coral with its prehensile tail

Seahorses are named for their equine profile. Although they are bony fish, they do not have scales, but rather a thin skin stretched over a series of bony plates arranged in rings throughout their body. Each species has a distinct number of rings. Seahorses swim upright, another characteristic that is not shared by their close pipefish relatives, which swim horizontally. Seahorses have a coronet on their head, which is distinct to each individual, much like a human fingerprint. They swim very poorly by using a dorsal fin, which they rapidly flutter and pectoral fins, located behind their eyes, which they use to steer. Seahorses have no caudal fin. Since they are poor swimmers, they are most likely to be found resting, with their prehensile tails wound around a stationary object. They have long snouts, which they use to suck up food, and eyes that can move independently of each other, much like a chameleon. Seahorses eat small shrimp, tiny fish, crustaceans and plankton.

Evolution and fossil record

Anatomical evidence, supported by molecular, physical, and genetic evidence, demonstrates that seahorses are highly modified pipefish. The fossil record of seahorses, however, is very sparse. The best known and best studied fossils are specimens of *H. guttulatus* (though literature more commonly refers to them under the synonym of *H. ramulosus*), from the Marecchia River Formation of Rimini Province, Italy, dating back to the Lower Pliocene, about 3 million years ago. The earliest known seahorse fossils are of two pipefish-like species, *H. sarmaticus* and *H. slovenicus* from the coprolitic horizon of Tunjice Hills, a middle Miocene lagerstätte in Slovenia dating back about 13 million years. Molecular dating finds that pipefish and seahorses separated during the Late Oligocene. This has led to speculation that seahorses evolved in response to large areas of shallow-water, newly created as the result of tectonic events. The shallow water allowed the expansion of seagrass habitats that selected for the camouflage offered by the seahorses' upright posture. These tectonic changes occurred in the Western Pacific Ocean suggesting an origin there with molecular data suggesting two later and separate invasions of the Atlantic Ocean.

Reproduction

Pregnant seahorse, New York Aquarium

The male seahorse is equipped with a brood pouch on the ventral, or front-facing, side. When mating, the female seahorse deposits up to 1,500 eggs in the male's pouch. The male carries the eggs for anywhere from 9 to 45 days until they emerge, expelling fully-developed, miniature seahorses in the water. Once the seahorse babies are released into the water, the male's role is done and he offers no further care.

Courtship

Before breeding, seahorses court for several days. Scientists believe the courtship behavior synchronizes the animals' movements so that the male can receive the eggs when the female is ready to deposit them. During this time they may change color, swim side by side holding tails or grip the same strand of sea grass with their tails and wheel around in unison in what is known as a “pre-dawn dance". They eventually engage in a “true courtship dance" lasting about 8 hours, during which the male pumps water through the egg pouch on his trunk which expands and opens to display its emptiness. When the female’s eggs reach maturity, she and her mate let go of any anchors and snout-to-snout, drift upward out of the seagrass, often spiraling as they rise. The female inserts her ovipositor into the male’s brood pouch and deposits dozens to thousands of eggs. As the female releases her eggs, her body slims while his swells. Both animals then sink back into the seagrass and she swims away.

Gestation

West Australian seahorse, *H. subelongatus*

The male releases his sperm directly into seawater where it fertilizes the eggs, which are then embedded in the pouch wall and become surrounded by a spongy tissue. The male supplies the eggs with prolactin, the same hormone responsible for milk production in pregnant mammals. The pouch provides oxygen as well as a controlled environment incubator. The eggs then hatch in the pouch where the salinity of the water is regulated; this prepares the newborns for life in the sea. Throughout gestation, which in most species requires two to four weeks, his mate visits him daily for “morning greetings”. They interact for about 6 minutes, reminiscent of courtship. The female then swims away until the next morning, and the male returns to vacuuming up food through his snout.

Research published in 2007 indicates the male releases sperm into the surrounding sea water during fertilization, and not directly into the pouch as previously thought.

Birth

White's seahorse, *H. whitei*

The number of young released by the male seahorse averages 100–200 for most species, but may be as low as 5 for the smaller species, or as high as 1,500. When the fry are ready to be born, the male expels them with muscular contractions. He typically gives birth at night and is ready for the next batch of eggs by morning when his mate returns. Like almost all other fish species, seahorses do not nurture their young after birth. Infants are susceptible to predators or ocean currents which wash them away from feeding grounds or into temperatures too extreme for their delicate bodies. Fewer than 0.5% of infants survive to adulthood, explaining why litters are so large. These survival rates are actually fairly high compared to other fish, because of their protected gestation, making the process worth the great cost to the father. The eggs of most other fish are abandoned immediately after fertilization.

Questions surrounding reproductive roles

Reproduction is energetically costly to the male. This brings into question why the sexual role reversal even takes place. In an environment where one partner incurs more energy costs than the other, Bateman's principle suggests that the lesser contributor takes the role of the aggressor. Male seahorses are more aggressive and sometimes “fight” for female attention. According to Amanda Vincent of Project Seahorse, only males tail-wrestle and snap their heads at each other. This discovery prompted further study of energy costs. To estimate the female’s direct contribution, researcher Heather D. Masonjones, associate professor of biology at the University of Tampa, chemically analyzed the energy stored in each egg. To measure the burden on the male, Masonjones measured its oxygen consumption. By the end of incubation, the male consumed almost 33% more oxygen than before mating. The study concluded that the female's energy expenditure while generating eggs is twice that of males during incubation confirming the standard hypothesis.

Why the male seahorse (and other members of Syngnathidae) carries the offspring through gestation is unknown, though some researchers believe it allows for shorter birthing intervals, in turn resulting in more offspring. Given an unlimited number of ready and willing partners, males have the potential to produce 17 percent more offspring than females in a breeding season. Also, females have “time-outs” from the reproductive cycle that are 1.2 times longer than those of males. This seems to be based on mate choice, rather than physiology. When the female’s eggs are ready, she must lay them in a few hours or eject them into the water column. Making eggs is a huge cost to her physically, since they amount to about a third of her body weight. To protect against losing a clutch, the female demands a long courtship. The daily greetings help to cement the bond between the pair.

Monogamy

One common misconception about seahorses is that they mate for life. Many species of seahorses form pair bonds that last through at least the breeding season. Some species show a higher level of mate fidelity than others. However, many species readily switch mates when the opportunity arises. *H. abdominalis* and *H. breviceps* have been shown to breed in groups, showing no continuous mate preference. Many more species mating habits have not been studied, so it is unknown how many species are actually monogamous, or how long those bonds actually last.

Although monogamy within fish is not common, it does appear to exist for some. In this case, the mate guarding hypothesis may be an explanation. This hypothesis states “males remain with a single female because of ecological factors that make male parental care and protection of offspring especially advantageous." Because the rates of survival for newborn seahorses are so low, incubation is essential. Though not proven, males could have taken on this role because of the lengthy period the females require to produce their eggs. If males incubate while females prepare the next clutch (amounting to 1/3 of body weight), they can reduce the interval between clutches.

Feeding habits

Seahorses feed on small crustaceans floating in the water or crawling on the bottom. With excellent camouflage and a lot of patience, seahorses ambush prey that float within striking range. Mysid shrimp and other small crustaceans are favorites, but some seahorses have been observed eating other kinds of invertebrates and even larval fish.

In aquaria

Seahorses (*Hippocampus erectus*) at the New England Aquarium, USA.

While many aquarium hobbyists keep seahorses as pets, seahorses collected from the wild tend to fare poorly in home aquaria. Many eat only live foods such as brine shrimp and are prone to stress, which damages their immune systems and makes them susceptible to disease.

In recent years, however, captive breeding has become more popular. Such seahorses survive better in captivity, and are less likely to carry diseases. They eat frozen mysidacea (crustaceans) that are readily available from aquarium stores, and do not experience the stress of moving out of the wild. Although captive-bred seahorses are more expensive, they take no toll on wild populations.

Seahorses should be kept in an aquarium to themselves, or with compatible tank-mates. Seahorses are slow feeders, and fast, aggressive feeders will leave them without food.

Seahorses can co-exist with many species of shrimp and other bottom-feeding creatures. Gobies also make good tank-mates. Keepers are generally advised to avoid eels, tangs, triggerfish, squid, octopus, and sea anemones.

Animals sold as "freshwater seahorses" are usually the closely related pipefish, of which a few species live in the lower reaches of rivers. The supposed true "freshwater seahorse" called *H. aimei* was not a real species, but a name sometimes used for Barbour's and Hedgehog seahorses. The latter is a species that can be found in brackish waters, but not actually a freshwater fish.

Use in Chinese medicine

Medicinal seahorse.

Seahorses, silkie, and cordyceps after being used to make a broth

Seahorse and scorpion skewers as street food in China

Seahorse populations are thought to have been endangered in recent years by overfishing and habitat destruction. The seahorse is used in traditional Chinese herbology, and as many as 20 million seahorses may be caught each year and sold for this purpose. Medicinal seahorses are not readily bred in captivity as they are susceptible to disease and it is believed that they have different medicinal properties from aquarium seahorses. Seahorses are also used as medicines by the Indonesians, the Central Filipinos, and many other ethnic groups around the world.

Import and export of seahorses has been controlled under CITES since May 15, 2004. However, Indonesia, Japan, Norway, and South Korea have chosen to opt out of the trade rules set by CITES.

The problem may be exacerbated by the growth of pills and capsules as the preferred method of ingesting medication as they are cheaper and more available than traditional, individually tailored prescriptions of raw medicinals but the contents are harder to track. Seahorses once had to be of a certain size and quality before they were accepted by TCM practitioners and consumers. But declining availability of the preferred large, pale and smooth seahorses has been offset by the shift towards prepackaged medicines, which make it possible for TCM merchants to sell previously unused juvenile, spiny and dark-coloured animals. Today almost a third of the seahorses sold in China are prepackaged. This adds to the pressure on the species.

Taxonomy

Common seahorse, *Hippocampus kuda*

- Genus *Hippocampus*
    - Big-belly seahorse, *H. abdominalis* Lesson, 1827 (New Zealand and south and east Australia)
    - Winged seahorse, *H. alatus* Kuiter, 2001
    - West African seahorse, *H. algiricus* Kaup, 1856
    - Narrow-bellied seahorse, *H. angustus* Günther, 1870

  - Barbour's seahorse, *H. barbouri* Jordan & Richardson, 1908
  - Pygmy seahorse, *H. bargibanti* Whitley, 1970 West Pacific area (Indonesia, Philippines, Papua New Guinea, Solomon Islands, etc.)
  - False-eyed seahorse, *H. biocellatus* Kuiter, 2001
  - Réunion seahorse, *H. borboniensis* Duméril, 1870
  - Short-head seahorse or knobby seahorse, *H. breviceps* Peters, 1869 (south and east Australia)
  - Giraffe seahorse, *H. camelopardalis* Bianconi, 1854
  - Knysna seahorse, *H. capensis* Boulenger, 1900
  - *H. colemani* Kuiter, 2003
  - Tiger tail seahorse, *H. comes* Cantor, 1850
  - Crowned seahorse, *H. coronatus* Temminck & Schlegel, 1850
  - Denise's pygmy seahorse, *H. denise* Lourie & Randall, 2003
  - Lined seahorse, *H. erectus* Perry, 1810 (east coast of the Americas, between Nova Scotia and Uruguay)
  - Fisher's seahorse, *H. fisheri* Jordan & Evermann, 1903
  - Sea pony, *H. fuscus* Rüppell, 1838 (Indian Ocean)
  - Big-head seahorse, *H. grandiceps* Kuiter, 2001
  - Long-snouted seahorse, *H. guttulatus* Cuvier, 1829
  - Eastern spiny seahorse, *H. hendriki* Kuiter, 2001
  - Short-snouted seahorse, *H. hippocampus* (Linnaeus, 1758) (Mediterranean Sea and Atlantic Ocean)
  - Thorny seahorse, *H. histrix* Kaup, 1856 (Indian Ocean, Persian Gulf, Red Sea, and the Far East)
  - Pacific seahorse, *H. ingens* Girard, 1858 (Pacific coast of North, Central and South America)
  - Jayakar's seahorse, *H. jayakari* Boulenger, 1900
  - Collared seahorse, *H. jugumus* Kuiter, 2001
  - Great seahorse, *H. kelloggi* Jordan & Snyder, 1901
  - Common seahorse, *H. kuda* Bleeker, 1852
  - Lichtenstein's seahorse, *H. lichtensteinii* Kaup, 1856
  - Bullneck seahorse, *H. minotaur* Gomon, 1997
  - Japanese seahorse, *H. mohnikei* Bleeker, 1854
  - Monte Bello seahorse, *H. montebelloensis* Kuiter, 2001
  - Northern spiny seahorse, *H. multispinus* Kuiter, 2001
  - *H. pontohi* Lourie and Kuiter, 2008
  - High-crown seahorse, *H. procerus* Kuiter, 2001
  - Queensland seahorse, *H. queenslandicus* Horne, 2001
  - Longsnout seahorse, *H. reidi* Ginsburg, 1933 (Caribbean coral reefs)
  - Satomi's pygmy seahorse, *H. satomiae* Lourie and Kuiter, 2008
  - Half-spined seahorse, *H. semispinosus* Kuiter, 2001
  - *H. severnsi* Lourie and Kuiter, 2008
  - Shiho's seahorse, *H. sindonis* Jordan & Snyder, 1901
  - Hedgehog seahorse, *H. spinosissimus* Weber, 1913
  - West Australian seahorse, *H. subelongatus* Castelnau, 1873
  - Longnose seahorse, *H. trimaculatus* Leach, 1814

- White's seahorse, *H. whitei* Bleeker, 1855 (east Australia)
- Zebra seahorse, *H. zebra* Whitley, 1964
- Dwarf seahorse, *H. zosterae* Jordan & Gilbert, 1882 (Gulf of Mexico and the Caribbean)

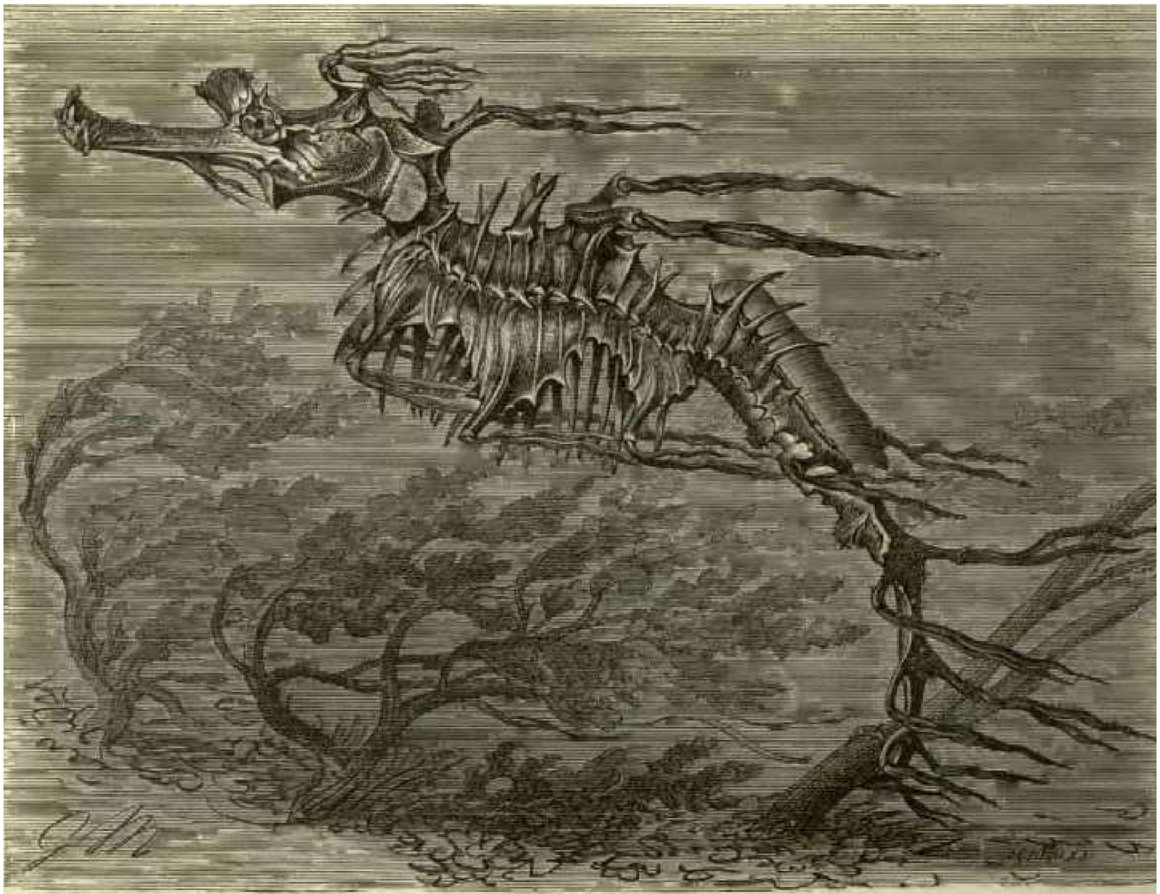
Pygmy seahorses

Hippocampus satomiae attached to a coral

Pygmy Seahorses are less than 15 millimeters (0.6 in) tall and 17 millimeters (0.7 in) wide members of the genus. Previously the term was applied exclusively to the species *H. bargibanti* but since 1997, discoveries have made this term obsolete. The species *H. minotaur*, *H. denise*, *H. colemani*, *H. pontohi*, *H. severnsi* and *H. satomiae* have been described. Other species that are believed to be unclassified have also been reported in books, dive magazines and on the Internet. They can be distinguished from other species of seahorse by their 12 trunk rings, low number of tail rings (26–29), the location in which young are brooded in the trunk region of males and their extremely small size. Molecular analysis (of ribosomal RNA) of 32 *Hippocampus* species found that *H. bargibanti* belongs in a separate clade from other members of the genus and therefore that the species diverged from the other species in the "ancient" past.

Most pygmy seahorses are well camouflaged and live in close association with other organisms including colonial hydrozoans (*Lytocarpus* and *Antennellopsis*), coralline algae (*Halimeda*) sea fans (*Muricella*, *Annella*, *Acanthogorgia*). This combined with their small size accounts for why most species have only been noticed in recent years.

Heraldry



FUCUS-LIKE SEA-HORSE ($\frac{2}{3}$ nat. size).

'Fucus like seahorse' from Lydekker's *The Royal Natural History*

A sculpture of a heraldic seahorse that adorned an 18th or 19th century French naval vessel

In heraldry, a seahorse is depicted as a creature with the foreparts of a horse and the hindparts of a fish.

Threats & Future

Most seahorse species are data deficient. This means there is not enough information to make a proper assessment about their risk of extinction. Because seahorse population is unknown, there is a greater risk of losing more seahorses because of the lack of information about how many are dying each year, how many are being born, how many are used for souvenirs, etc. Seahorse habitats are in great danger though. Coral reefs and seagrass beds are deteriorating, meaning seahorses have fewer places to live. Also as stated above, seahorses are used to Chinese Medicine and as souvenirs, which definitely cuts their population down significantly each year.

Chapter 16

Misumena Vatia

Goldenrod Crab Spider	
	
Goldenrod crab spider capturing a wasp	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Arachnida
Order:	Araneae
Family:	Thomisidae
Genus:	*Misumena*
Species:	***M. vatia***
Binomial name	
Misumena vatia (Clerck, 1757)	
Synonyms	
Araneus vatius *Aranea calycina* *Aranea 4-lineata* *Aranea kleinii* *Aranea osbekii* *Aranea hasselquistii* *Aranea uddmanni*	

Aranea scorpiformis
Aranea virginea
Aranea citrea
Aranea citrina
Aranea sulphereoglobosa
Aranea sulphurea
Aranea quinquepuncata
Aranea albonigricans
Aranea calicina
Aranea cretata
Misumena citrea
Thomisus citreus
Thomisus calycinus
Thomisus dauci
Thomisus pratensis
Thomisus spinipes
Thomisus scorpiformis
Thomisus quadrilineatus
Thomisus viridis
Thomisus phrygiatus
Thomisus devius
Thomisus fartus
Thomisus vatius
Pachyptile devia
Thomisus cucurbitinus
Misumena oblonga
Misumena calycina
Misumena occidentalis
Misumenops vatia

Misumena vatia is a species of crab spider with holarctic distribution. In North America, where it is the largest and best-known flower spider, it is called the **goldenrod crab spider** or **flower (crab) spider**, because it is commonly found hunting in goldenrod sprays in the autumn.

Young male, imitating a flower

Young males in the early summer may be quite small and easily overlooked, but females can grow up to 10 mm (excluding legs); males reach 5 mm at most.

These spiders may be yellow or white, depending on the flower in which they are hunting. Especially younger females, which may hunt on a variety of flowers such as daisies and sunflowers, may change color "at will". Older females require large amounts of relatively large prey to produce the best possible clutch of eggs. They are therefore, in North America, most commonly found in goldenrod (*Solidago sp.*), a bright yellow flower which attracts large numbers of insects, especially in autumn. It is often very hard even for a searching human to recognize one of these spiders on a yellow flower.

Reproduction

The much smaller males scamper from flower to flower in search of females and are often seen missing one or more of their legs. This may be due either to near misses by predators such as birds or to fighting with other males.

When a male finds a female, he climbs over her head over her opisthosoma onto her underside, where he inserts his pedipalps to inseminate her.

The young reach a size of about 5mm by autumn and spend the winter on the ground. They molt for the last time in May of the next year.

Color change

These spiders change color by secreting a liquid yellow pigment into the outer cell layer of the body. On a white base, this pigment is transported into lower layers, so that inner glands, filled with white guanine, become visible. If the spider dwells longer on a white plant, the yellow pigment is often excreted. It will then take the spider much longer to change to yellow, because it will have to produce the yellow pigment first. The color change is induced by visual feedback; spiders with painted eyes were found to have lost this ability.

The color change from white to yellow takes between 10 and 25 days, the reverse about six days. The yellow pigments have been identified as kynurenine and 3-hydroxykynurenine

male *M. vatia*

Female *Misumena vatia*, on Achillea millefolium flowers

Misumena vatia