Animal Colouration

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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.

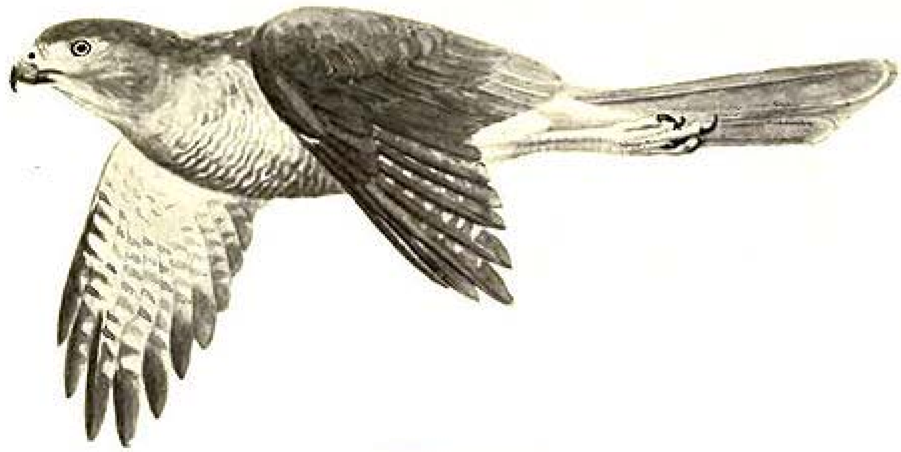
The brilliant warning colours of many caterpillars attracted the attention of Charles Darwin when he was thinking over his hypothesis of sexual selection, and he wrote to AR Wallace on the subject (C Darwin, *Life and Letters*, London, 1887, uI. 93). Wallace, in reply, suggested their interpretation 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.

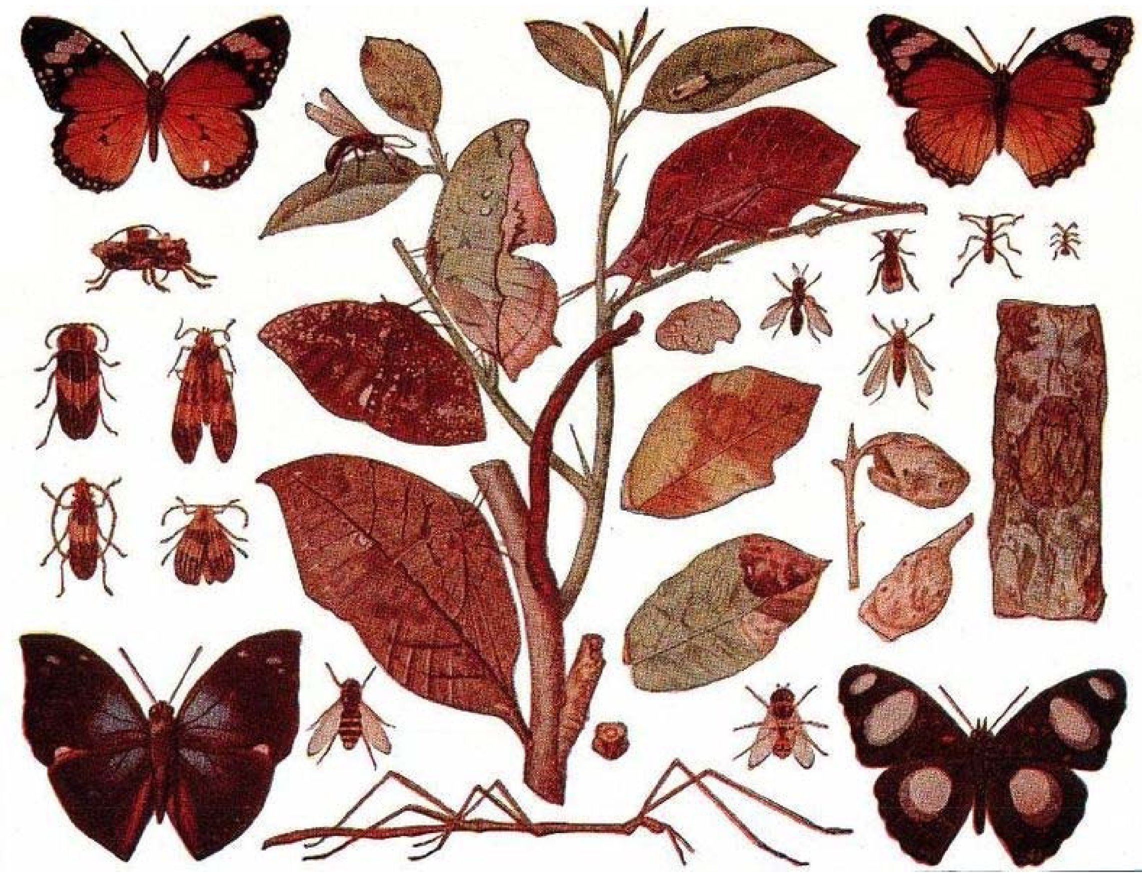
The type of camouflage a species will develop depends on several factors:

- 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

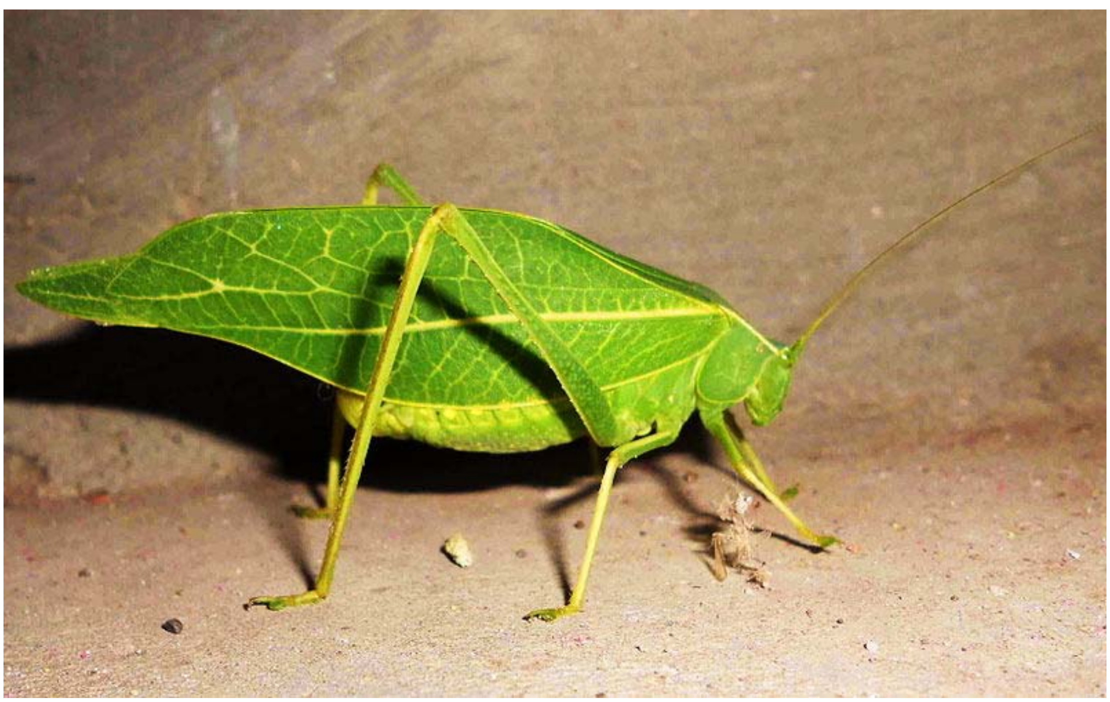
Countershaded Ibex are almost invisible in the Israeli desert.

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

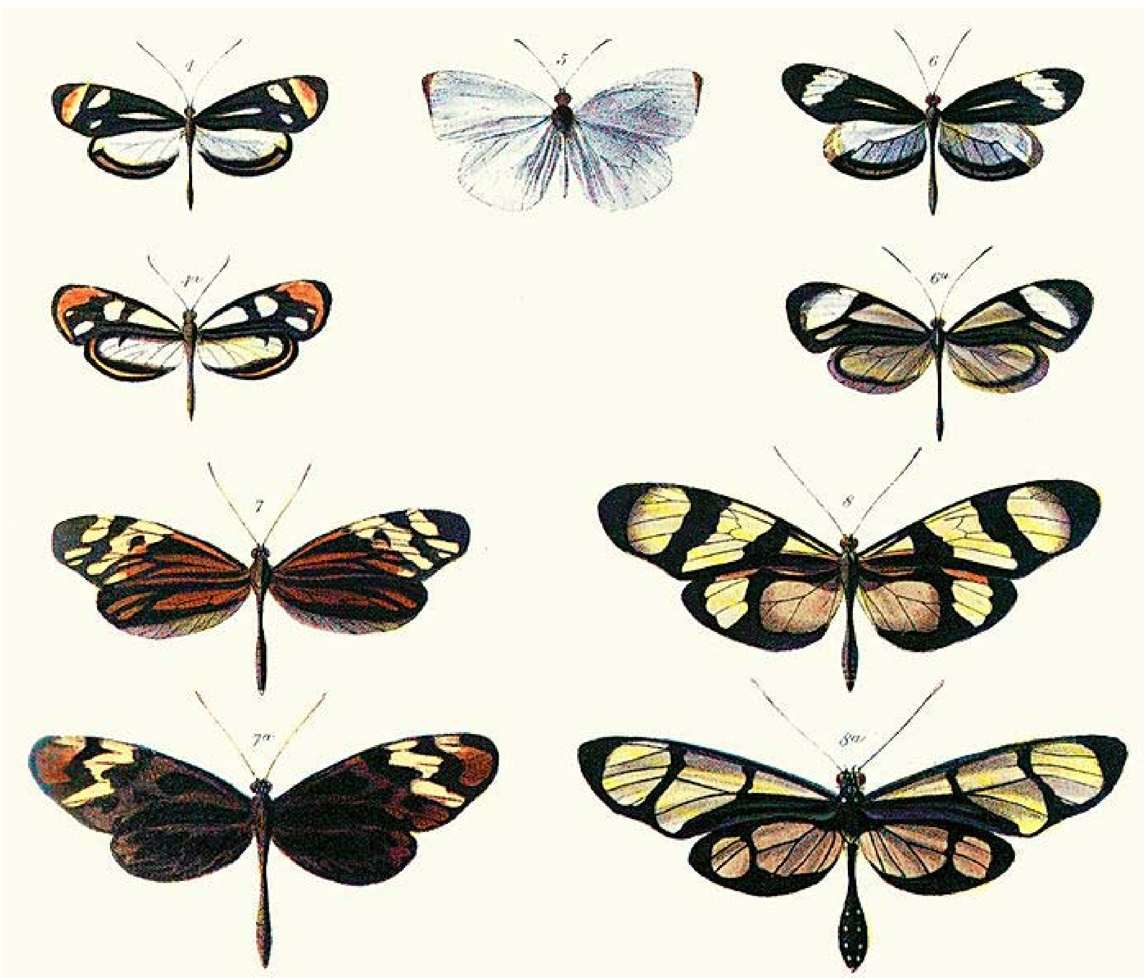


Plate from Henry Walter Bates (1862) illustrating Batesian mimicry between *Dismorphia* species (top row, third row) and various *Ithomiini* (Nymphalidae, second row, bottom row)

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.

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.

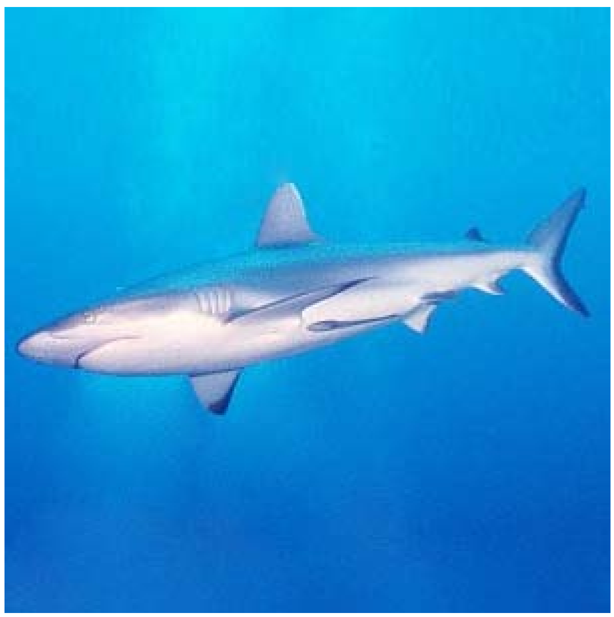
Ctenomorphodes chronus mimicking a eucalyptus twig

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.

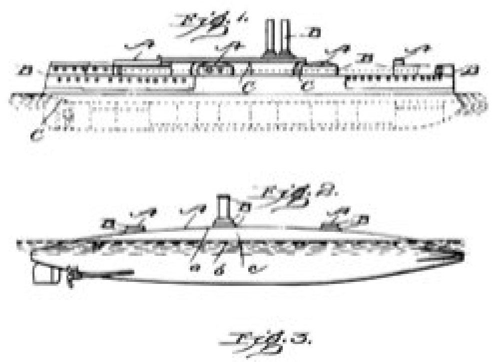
Examples

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

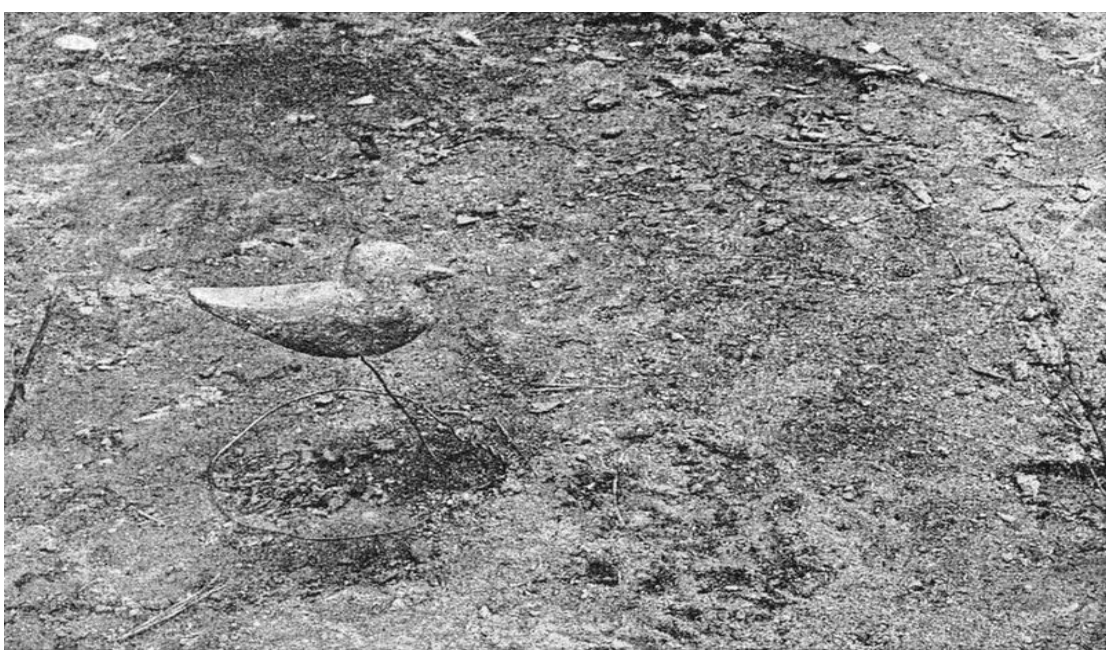
Alternatively, in many marine animals (including various species of fish such as marlins and sharks, penguins and cephalopods) this form of camouflage may work through background matching; when seen from the top, the darker dorsal area of the animal blends into the darkness of the water below, and when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

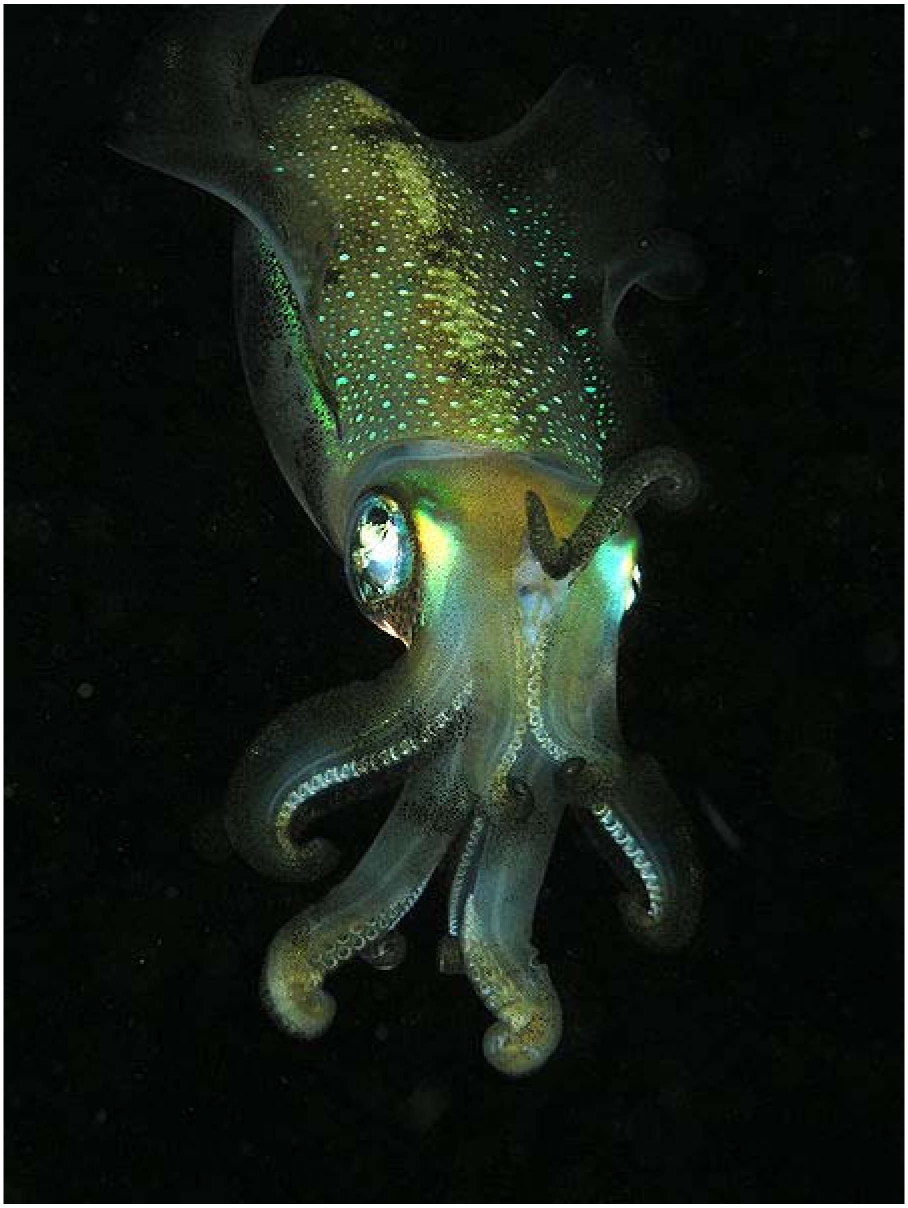
Communication between bacteria (quorum sensing) plays a role in the regulation of luminesence in many bacterial species. Using small extracellularly secreted molecules, they are able to adapt their behavior to only turn on genes for light production when they are at high cell densities.

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

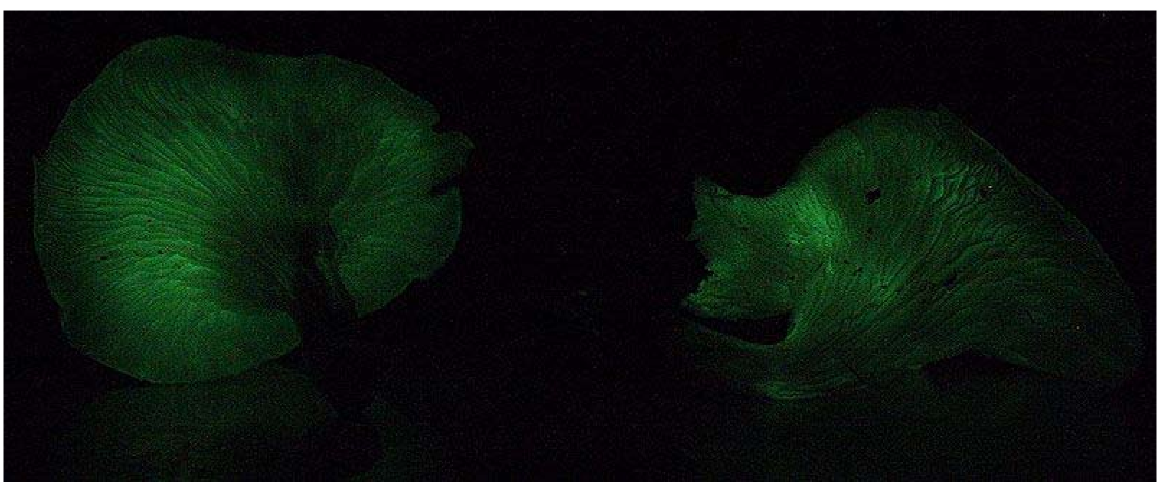
Some proposed applications of engineered bioluminescence include:

- 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.

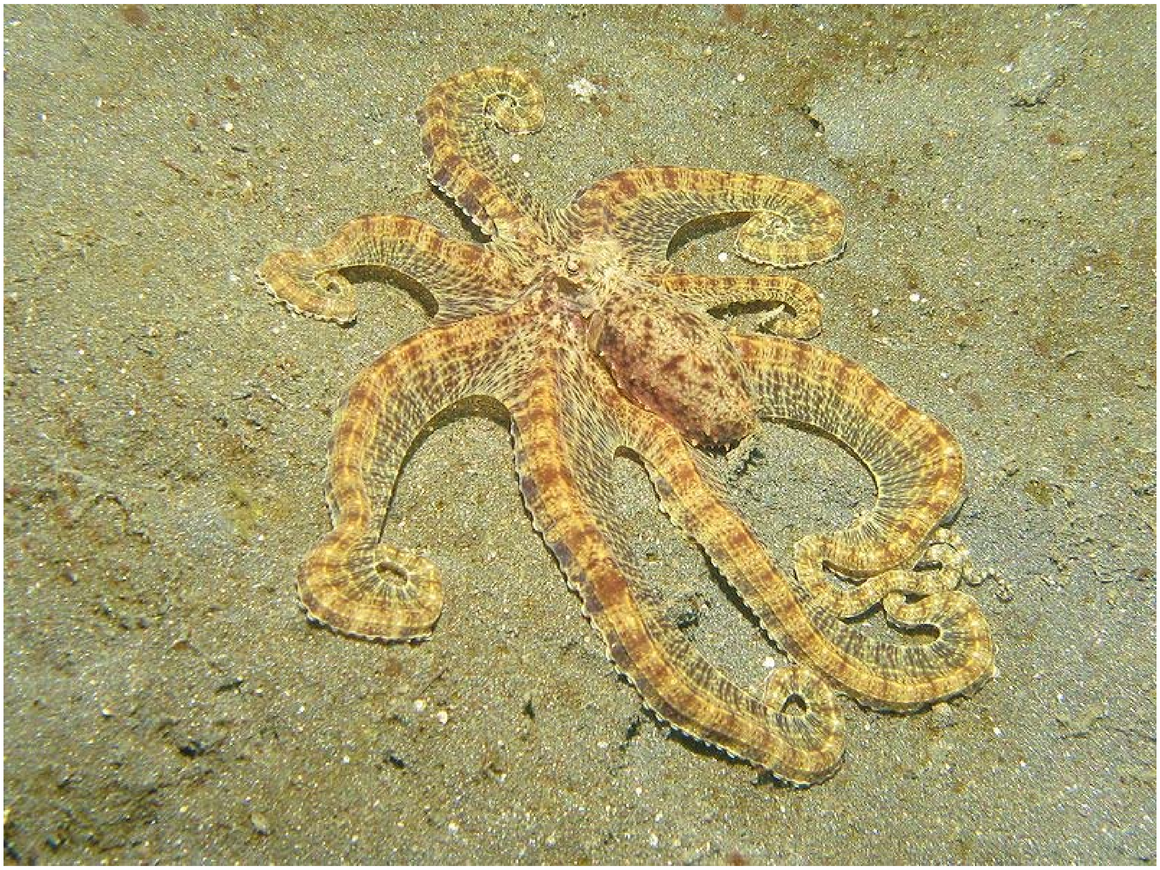
Living in the tropical seas of South East Asia, it was not discovered officially until 1998, off the coast of Sulawesi. The octopus mimics the physical likeness and movements of more than fifteen different species, including sea snakes, lionfish, flatfish, brittle stars, giant crabs, sea shells, stingrays, 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.

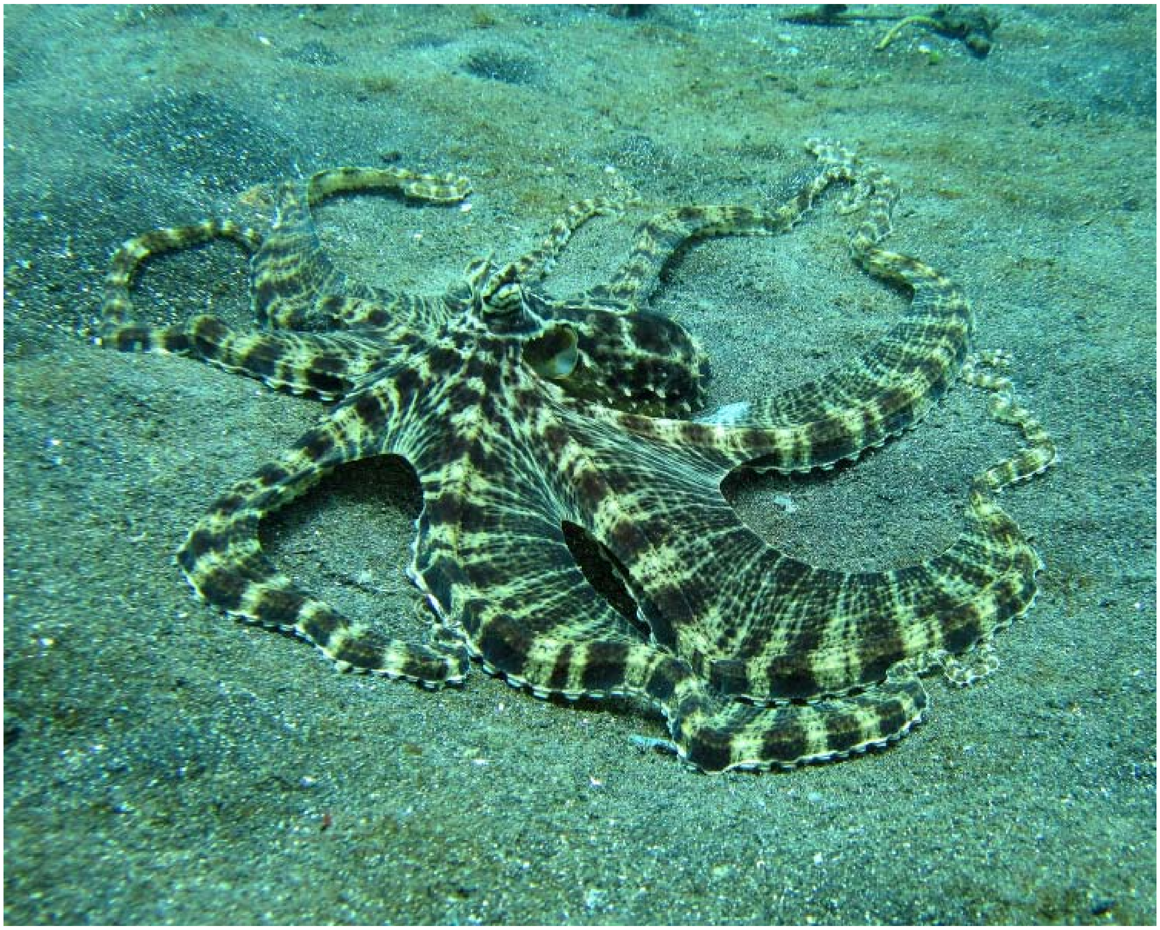
Based on observation, the mimic octopus may decide which animal to impersonate depending on local predators. For example, when the octopus was being attacked by damselfish, it was observed that the octopus appeared as a banded sea snake, a damselfish predator. The octopus impersonates the snake by turning 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

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 the Latin *chamaeleo* which is borrowed from the Ancient Greek *χαμαιλέων* (*khamaileon*), a compound of*χαμαί* (khamai) "on the earth, on the ground" + *λέων* (*leon*) "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. A monophyletic 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.

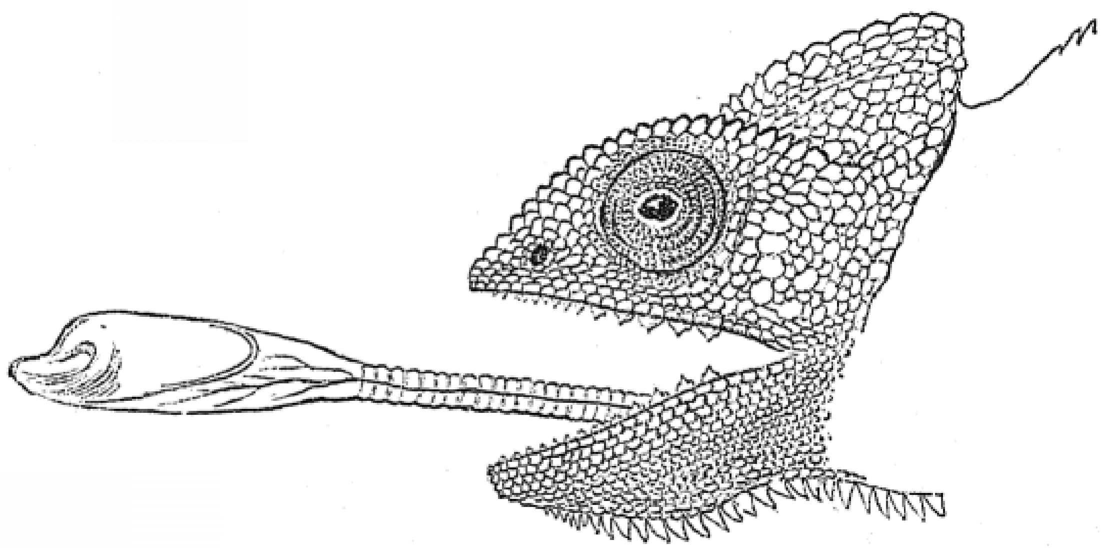
Oustalet's Chameleon, Ambalavao, Madagascar

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 independentely 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 amphiboluri* - bearded dragons (*Pogona vitticeps*)
- *Isospora brygooi* - panther chameleon (*Furcifer pardalis*)
- *Isospora jaracimrmani* - veiled chameleon (*Chamaeleo calyptratus*)

Chapter- 9

Cuttlefish

Cuttlefish	
	
Sepia latimanus, East Timor	
Scientific classification	
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.

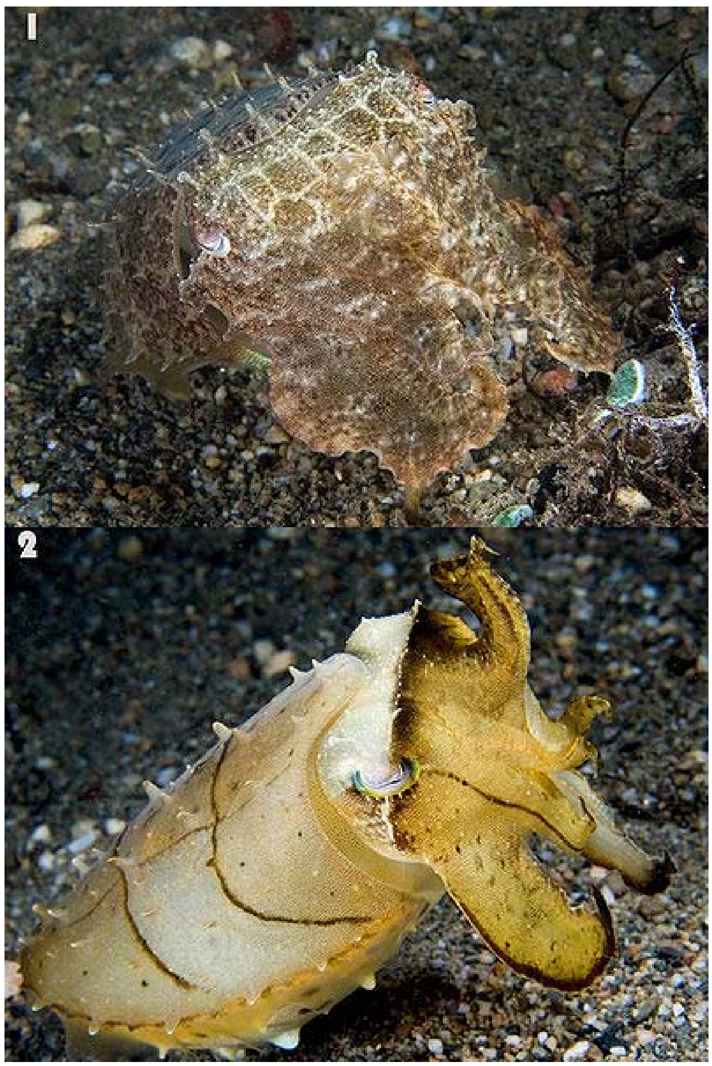
Cuttlefish have an internal shell (the cuttlebone), large W-shaped pupils, and eight arms and two tentacles furnished with denticulated suckers, with which they secure their prey. They generally range in size from 15 cm (5.9 in) to 25 cm (9.8 in), with the largest species, *Sepia apama*, reaching 50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

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 backwards. 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 haemoglobin 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 haemoglobin.

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

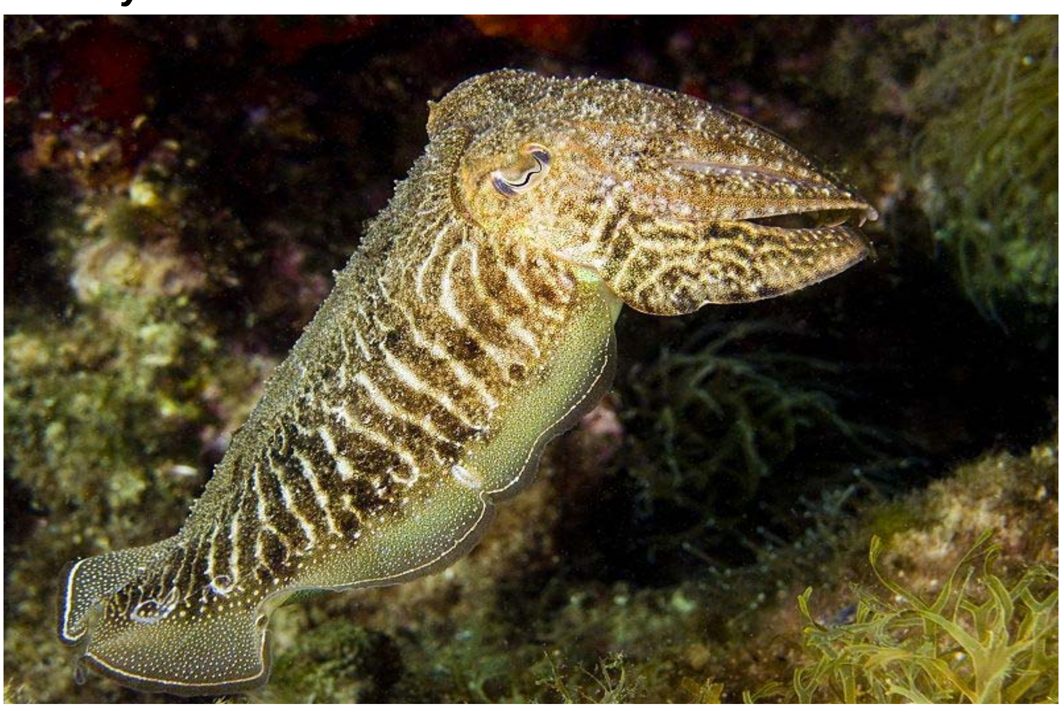
The preferred diet of the cuttlefish is crabs and fish.

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