

2.1 A Succession of Molecular Events Leads to the Formation of a Bird

Most living organisms start from a single fertilized cell which, following a series of divisions, gives rise to an embryo that later gets transformed into a juvenile and finally becomes an adult. This is a much more dramatic and orchestrated event than we tend to think.

We are not dealing with a steady accumulation of cell upon cell, building a great pile, like pebbles assembled in a pyramid, but are confronted with a process that involves many levels of molecular intervention and cell interaction. In addition, a permanent formation of new cells is accompanied by an equally violent cell destruction. During the shaping of an embryo whole tissues are eliminated and others change their address rapidly (Gilbert 2000).

The source of information, that initially starts the orchestration of these embryonic events is the well known DNA (deoxyribonucleic acid). This macromolecule lies embedded in the chromosome's proteins. It is common knowledge that DNA contains a genetic code written in its four bases. Remarkable is that DNA by itself cannot deliver this information to any other molecule. It is only when specific proteins bind to its bases that it starts replicating its genetic information building new copies on demand. Its original message may become also transcribed into RNA (ribonucleic acid). This macromolecule has a variety of functions in the cell, the most important being its involvement as a messenger of the genetic code in the subsequent synthesis of proteins.

These last molecules function both as building blocks of cellular structures as well as directors of cell functions. The atomic configuration that the proteins present to other molecules is critical in deciding the reactions that shape the body of the embryo and all the successive transformations that finally lead to the adult stage (Abzhanov et al. 2006).

The journey, between DNA and the final structure or function, is a long one. This transfer of messages from level to level, along a treacherous pass, could easily go wrong and never produce a bird or a human (Fig. 2.1).

Surprisingly – but it could hardly be otherwise – there is a system of check points, repair processes and guiding mechanisms that, at every step, ensure that the order furnished by the initial DNA message is maintained to the very end – the organism's body pattern. Obviously, all these types of canalizing mechanisms are also carried out by molecules. What is new is that many of them are small ones. MicroRNAs have a length of 21–22 nucleotides, yet are able to regulate gene expression shaping the road map of the emerging embryo (Carrington and Ambros 2003). Other small molecules, such as hormones, perform critical functions in securing the pathways and molecular cascades that lead to the modification of organs and of behaviour (Shen et al. 1995).

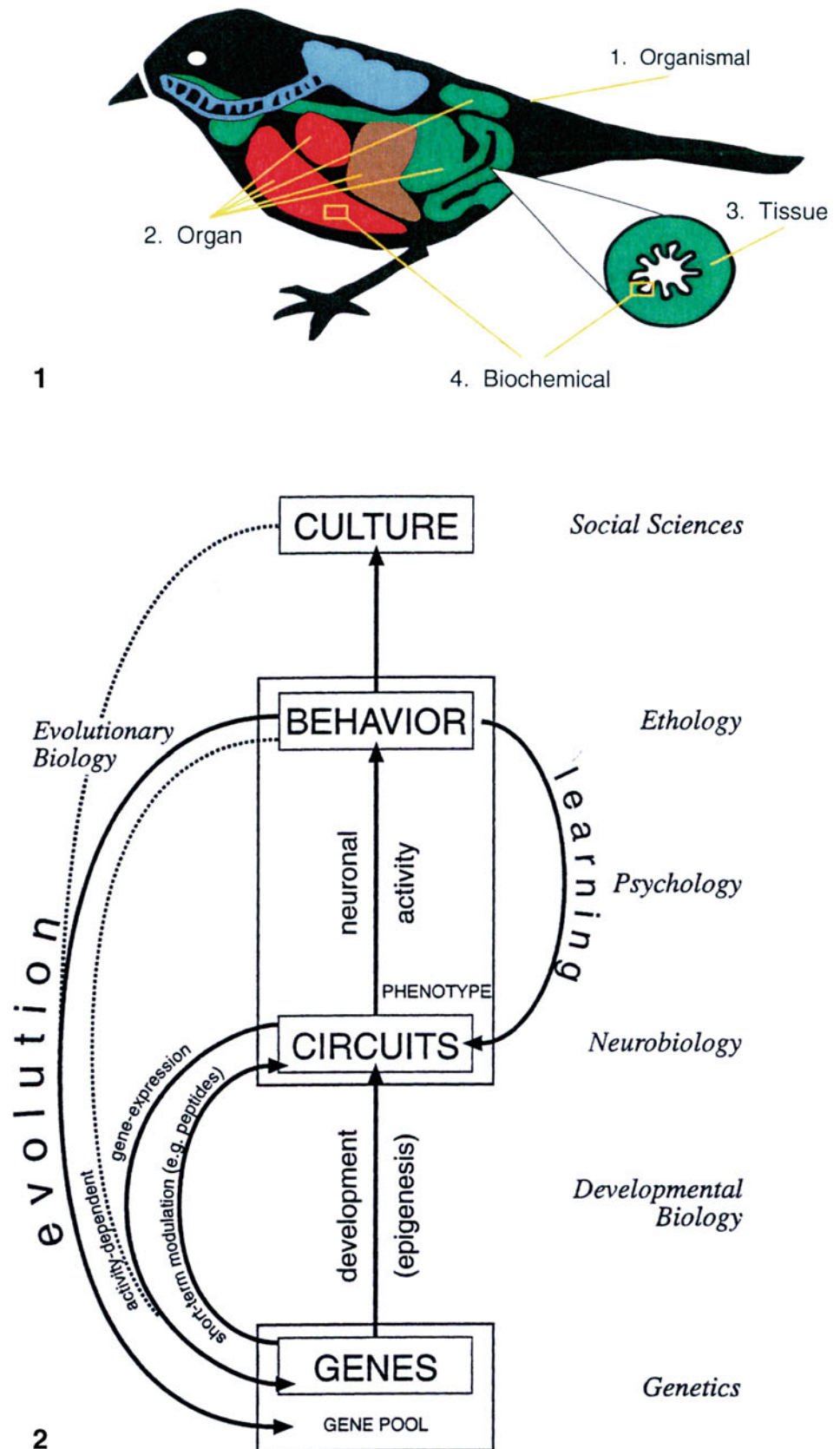
When we contemplate a bird we only see the final product of an enormous succession of molecular interactions, so well intertwined and so rigidly directed, that only a bird, and not an amorphous heap of cells, is produced every time a fertilized egg starts on its hazardous journey.

2.2 Permanence of Characters in Inheritance and Development

Several levels must be considered in the analysis of any biological pattern.

The adult structure is seen to be transmitted to the progeny with an impressive regularity. It is this order that allows to collect a group of animals under the designation of a species. If there were to be no order in inheritance there could be no permanence of characters and as such no species, genus, family, order, class or phylum could have been conceived. It was the discovery of regularity in the transmission of characters that ended the confusion that reigned in this discipline and made genetics to emerge as an independent science. The year was 1900. Until then every plant or animal trait was considered to be carried to the progeny at random. It was the rediscovery of Mendel's rules of

Fig. 2.1 (1) A bird, like any other living organism, consists of four levels of organization: (1) Organismal, (2) Organ, (3) Tissue and (4) Biochemical. The structures and functions of these four levels result from the action of molecular processes having their origin in the DNA sequences of the chromosomes. The molecular pathways can now be mapped all the way from the gene to the feather colour or song behaviour. (2) **The primary role of genes in development, behaviour and evolution, leading to different levels of structural and functional organization as well as cognition.** The **genotype** is the genetic constitution of an organism, as distinguished from its physical appearance which is called its **phenotype**. **Epigenetics** deals with the mechanisms by which genes bring about their phenotypic effects. The action of genes changes during the whole organism's development due to internal as well as external causes. Genes are dependent on the action of other genes and the intervention of the environment



inheritance, by three independent laboratories, that uncovered that the transmission was not accidental.

On the other hand it took nearly 100 years to establish, on a genetic basis, that an equally rigid order took place during the development of the embryo. In this process many laboratories were involved and different types of experiments complemented one another revealing an orchestrated process, from fertilization to birth, in which many different types of molecules intervene at well defined times (Gehring et al. 2009). Although paradoxal, the permanence and order are accompanied by dynamism and variation, but both are also under control.

2.3 No Animal is Structurally or Physiologically Static – Programmed Cell Death

The person whom you meet today is not the same tomorrow. Every human starts as a single cell, the fertilized egg, but ends up being a compilation of 100 trillion cells (Venter 2002). Specific groups of this cell assembly are programmed to die every 24 h. In humans the astronomical figure of ten billion cells die, in each adult, each day and are replaced by other cells with similar functions. In the blood, the skin, the intestines and the uterus thousands of cells are being substituted all the time (Elmore 2007). What is to be noted is that they are produced with the same function and in the same organ, in such enormous numbers. No confusion is allowed, the cells cannot escape the established program.

Caenorhabditis elegans is a small nematode. Its body, in an adult hermaphrodite, contains exactly 959 somatic cells. In the adult male there are 1,031 plus a variable number of germ cells. Such a low number, and a nearly transparent body, makes it an animal of choice to study embryonic development. This unique combination has permitted to follow the origin and fate of every cell. During embryogenesis 671 cells are generated in the hermaphrodite, of these 113 (in the male 111) undergo programmed cell death and the remainder differentiate or become blast cells (Sulston et al. 1983). In this worm two genes, *ced-3* and *ced-4*, were found to be essential for programmed cell death (Adams and Cory 1998). As pointed out by several embryologists there is little room for randomness.

Among the molecules that are responsible for this program are ceramides. These are bioactive lipids that play important roles as second messengers in animals. This family of signal molecules can profoundly affect cell fate. Ceramides are known to participate in programmed cell death from humans to plants (Liang et al. 2003).

2.4 The Origin of Feathers is a Source of Controversy – They Evolved in Dinosaurs Before Birds Appeared

Feathers belong to a class of evolutionary events that appear suddenly as novelties which have no clear antecedents. Feathers do not occur in ancestral animals and have no related structures in contemporary relatives. As Prum and Brush (2003) point out the generally accepted interpretation of evolution “does not give much guidance for understanding the emergence of entirely new structures, including digits, limbs, eyes and feathers”. They also stress that the assumption that feathers were derived from reptilian scales or emerged as a result of flight were false leads that need to be abandoned. They add that *Archaeopteryx* does not give any clues as to how feathers evolved because the feathers of this fossil bird are nearly identical to those of present day birds.

Recently, various groups of paleontologists have collected a series of dinosaur fossils in China which revealed that these reptiles were feathered and that their feathers were more primitive than those of *Archaeopteryx* and of living birds. They came to the conclusion that they originated and had different forms already in carnivorous dinosaurs before the origin of flight and the appearance of birds (Chen et al. 1998; Xu et al. 1999; Zhang and Zhou 2000; Ji et al. 1998; Norell et al. 2002).

2.5 “Fingers Evolved to Play the Piano” – The Idea of Purpose in Biological Thought

Prum and Brush (2003) put it clearly: “Proposing that feathers evolved for flight now appears to be like hypothesizing that fingers evolved to play the piano”. The idea of purpose in natural processes has its roots in the scholastic doctrines of the Middle Ages. The French philosopher Voltaire, whom we need to thank for destroying many of the myths that circulated as late as the 1700s, dismissed this type of thinking with a simple statement: “God gave us the nose to wear glasses”.

We are usually not aware that several of the concepts that we use in science are rooted in ancient and unfounded assumptions that have been discarded long ago.

2.6 The Biological Pattern of Birds is Written on their Feathers

Every event in animal development and pattern formation seems so evident that it tends to be taken for granted. What seems most natural appears, on further study, to be the result

of an underlying organization that from the beginning was difficult to discern.

When one contemplates a bird, about 90% of what one sees is feathers. In the Tundra Swan they are 25,216. The number of feathers per bird is estimated to be between 20,000 and 80,000 depending on the species (Yu et al. 2004). Only the beak and the legs are usually free of them.

In some cases feathers grow on the base of bills and along the legs of certain species. Crested seriema (*Cariama cristata*) displays a panoply of head feathers located on the margin of the beak. Verreaux's Eagle (*Aquila verreauxii*) and the Ornate hawk-eagle (*Spizaetus ornatus*) have their legs covered with feathers.

The feathers are actually the bearers of the patterns displayed by the main part of the body, the skin being seldom seen.

2.7 Feather Growth and Replacement are Highly Ordered

The feathers, which are formed as extensions of the skin, are produced, modified and shed (actually dying) at regular intervals during the organism's development. Ornithologists have studied this event with the utmost care in many families. Unexpectedly the cycle of feather growth and replacement turned out to be highly ordered: in time, position and function.

Chicks of Hawks and Eagles (Accipitridae) are initially covered by a first down, which is soon followed by a second down and later by the full adult plumage. Hence, the feathers are generated at three different times.

The feathers of the wing are divided into primaries and secondaries according to their location on this organ. Wing moult generally begins with the inner primaries and proceeds outwards, whereas the secondaries moult inwards starting from the outermost feather. In Woodswallows (Artamidae) the adults have a complete postbreeding moult, in which the primaries are moulted outwards and the secondaries inwards. The same sequence is repeated in the Plovers (Charadriidae) which start by moulting the primaries outwards and the secondaries inwards. Other families may have a less regular replacement but one that still follows defined sequences. In some Kingfishers the primary moult is descendant starting with the innermost primary *P1*, in other species it is also descendant but starts at *P1* and *P7*. Other groups have an ascendant and descendant sequence from *P7* and descendant from *P1*. Yet, in every case a specific feather is the starting point.

The whole body is involved in this dynamic process. The moult of the tail is centripetal in herons starting from the outer rectrices (tail feathers) and working its way inwards. The wild turkeys go through five different moults from natal and juvenile to adult plumage. In juveniles tail feathers are

replaced centrifugally (in bilateral symmetry from the inside out) but in adults the tail moults centripetally (from the outside in). The terms centripetal and centrifugal were introduced by bird specialists when confronted with the symmetry of this organ dynamics. The direction of tail replacement may be even reversed but still follows a pattern that is clearly recognized.

2.8 The Regeneration of Feathers Occurs Periodically Being Dependent on Day Length and Hormone Activity

Another type of control is evident in the regeneration of feathers. The annual cycle of various species of birds disclosed that the formation of new feathers is related to the amount of daylight being present during the year.

In the Mallard (*Anas platyrhynchos*) there is a postnuptial moult in males and females after the summer solstice. This is followed by a prenuptial moult in males, but in the females this change of feathers takes place after the winter solstice (Fig. 2.2) (Bluhm 1988; Lind et al. 2010). There is a certain amount of variation but this type of cycle is common to many species of waterfowl.

The moulting is also influenced by hormones. Annual peaks of thyroxine levels coincide with postnuptial moult. Administration of thyroxine induces moult in domestic ducks, whereas androgens inhibit it (Bluhm 1988). This means that the replacement of feathers is controlled by hormones.

2.9 Hormones Control the Size, Shape and Colour of Feathers

The females and males of many avian species differ in their plumage. An example is the hen and the rooster. The tail feathers of the male are long and curved, those of the hen are shorter and form a fan. These feather patterns can be easily modified by sex hormones.

The sex hormones of vertebrates are steroids, derived from cholesterol, formed in the gonads of both sexes. The two most important are the estrogens and androgens. Estrogens predominate in the female and androgens in the male. These steroids are responsible for the development of the sexual apparatus and of secondary sex characteristics that involve many body features.

In birds inhabiting the temperate zone the progressive increase in day length – as spring approaches – induces growth of the gonads. The testicular weight in some species increasing up to 500 times. This is accompanied by a large rise in the levels of sex hormones which are also known to promote the differentiation of sex-related morphological features such as plumage form and colour (Eckert and Randall 1978).

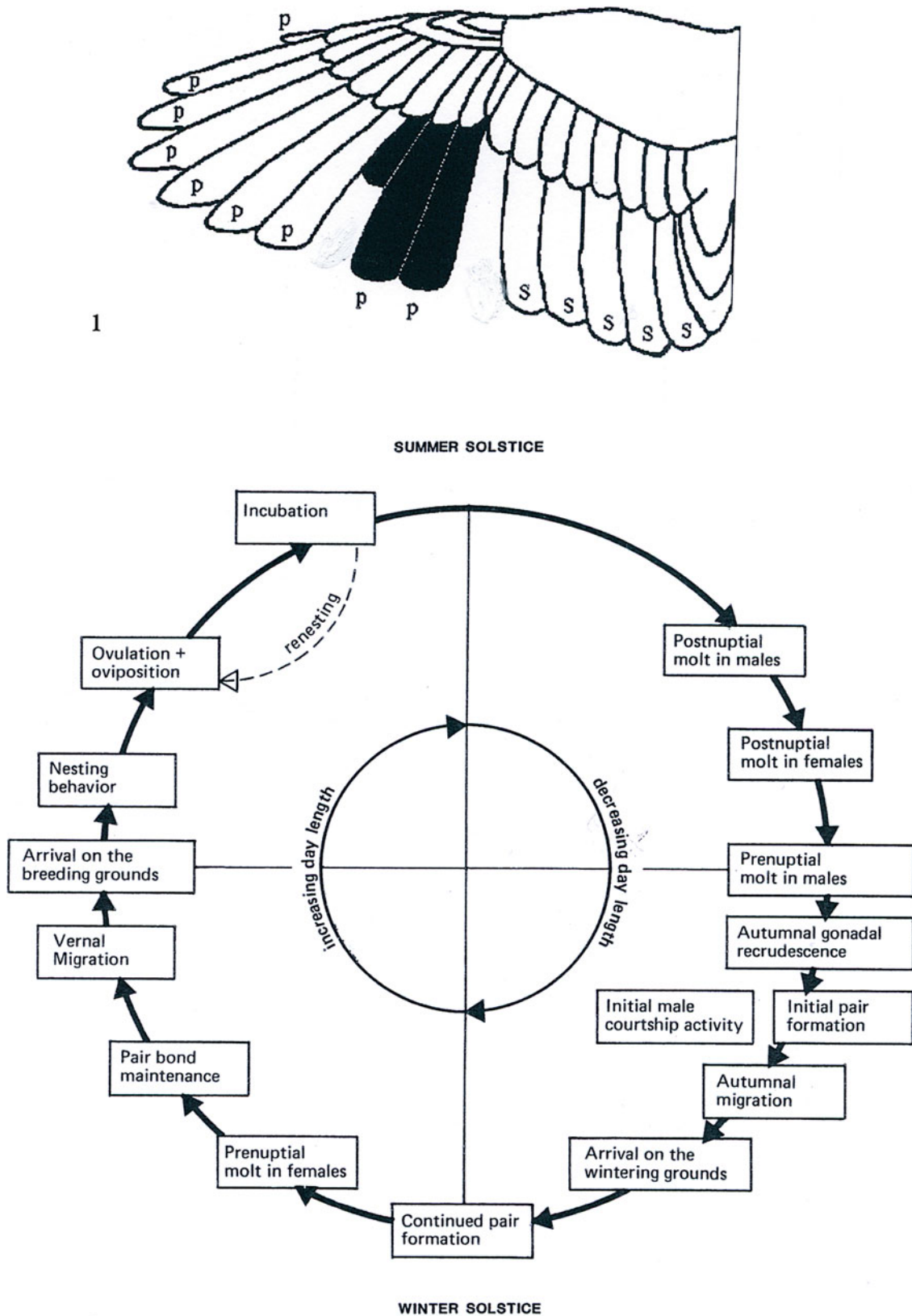


Fig. 2.2 (1) A passerine wing in moult (*p* primary; *s* secondary feathers). Primaries and secondaries are collectively called remiges. Dark feathers are new feathers (fully-grown or in growth). (2) Summary of the major components of the moulting cycle of the Mallard

(*Anas platyrhynchos*). Most individuals attempt to breed as yearlings. Prenuptial moult in males and postnuptial moult in males as well as prenuptial moult in females and postnuptial moult in females occur at specific times related to day length

The steroids bind to feather follicles exerting their effects directly by binding to receptor proteins on the cells. Hens from which the ovary has been removed become like males. Similarly the feathers of castrated males turn into a feminized appearance. Roosters can also be transformed into having a female feathering morphology by mutations in genes located outside the sex chromosomes (Yu et al. 2004).

2.10 Two Genes are Responsible for Feather Development

Hair, nails, scales, as well as feathers, are skin organs that result from the controlled proliferation of cells in the outer skin layer. All four structures consist mainly of the protein keratin. In feathers: 90% is the protein beta keratin, 1% lipids, 8% water and the remaining fraction is composed mainly of the pigment melanin.

Two genes are involved in the embryonic development of vertebrate limbs. *Sonic hedgehog* produces a protein that induces cell proliferation and *bone morphogenetic protein 2* regulates cell proliferation and promotes cell differentiation. These two genes also determine the growth of feathers, their differentiation and the time at which they are formed and discarded.

A feather starts in the bird embryo when the epidermis thickens over a condensation of cells in the underlying dermis. The next step is the formation of a feather germ that results in the building of a follicle from which the feather emerges. The two genes are turned on and off producing the separate structures called rachis, barbs and barbules (Pough et al. 2005).

2.11 Proteins and Other Molecules Decide Hierarchical Order in Feather Branching

The latest techniques in molecular biology have been used to study feather development. The way branching arises in morphogenesis leading to ramified structures has been investigated in lungs and kidneys but the corresponding process in feathers is unique due to its nonrandomness and hierarchy of structural organization.

Avian sarcoma retrovirus was used to deliver genes to flight feather follicles in chickens during regeneration. Feather branching is due to the antagonistic balance between *noggin* and *bone morphogenetic protein 4*. This protein promotes rachis formation and barb fusion whereas *noggin* has the contrary effect of barb branching. The gene *sonic hedgehog* is part of this event inducing cell death which results in the formation of spaces between the barbs (Yu et al. 2002) (Fig. 2.3).

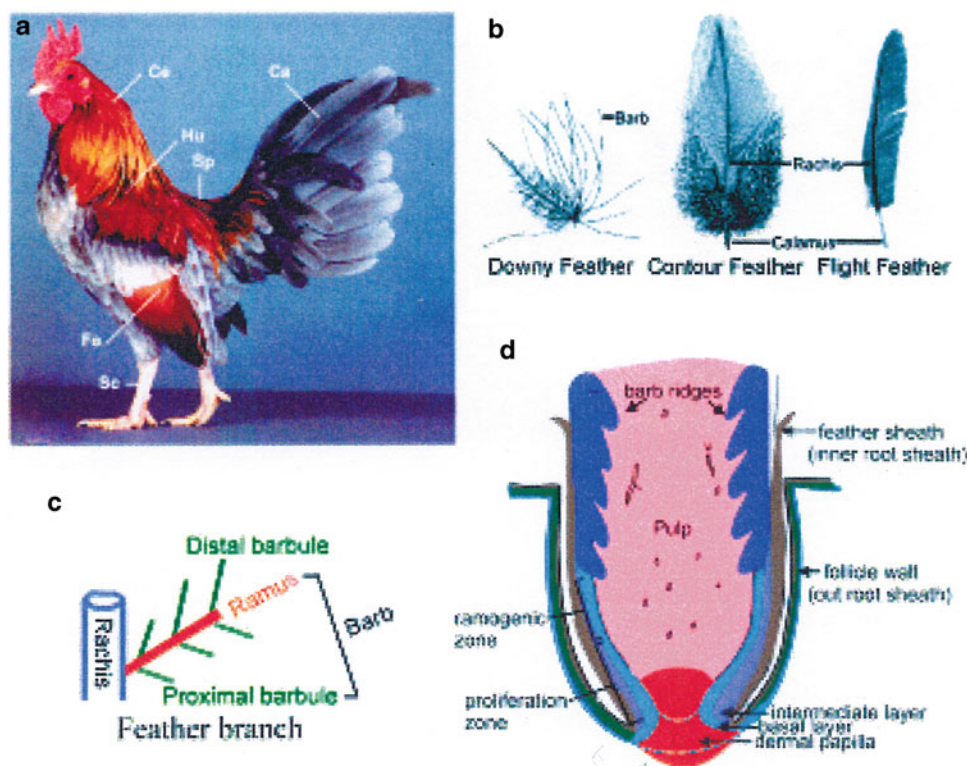


Fig. 2.3 The basics of feathers. (a) A rooster with plumage showing the different feather tracts on different parts of the body. *Ca* caudal tract, *Ce* cervical tract, *Fe* femoral tract, *Hu* humerus tract, *Sc* scale region, *Sp* spinal tract. (b) Major types of feathers: radially symmetric

downy feather, bilaterally symmetric contour feather, and bilaterally asymmetric flight feather (remiges). Schematic diagrams to show (c) the three basic levels of feather branches, and (d) the major zones of cellular activities of a sectioned developing feather follicle

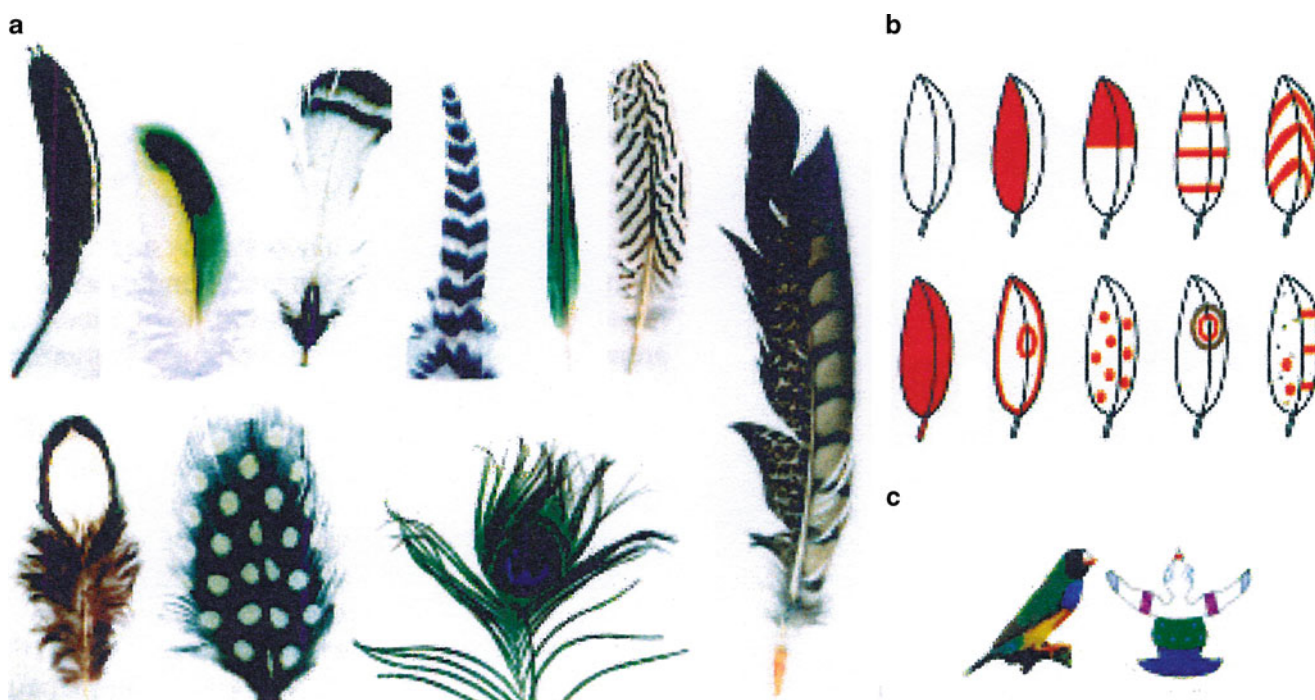


Fig. 2.4 Pigment patterns of feathers. (a) Representative pigment patterns within a feather. Feathers are from chicken, zebra finch and peacock. (b) From these, some basic patterns such as bars, chevrons,

circles and dots are derived. Note that pigments in the *left* and *right* vane are under different control. (c) Pigment patterns extend to the body level in symmetrical fashion

Feathers go through a cycle of death and rebirth that is usually called moulting. Flight feathers can regenerate repetitively and rapidly after plucking. Following this event replication competent avian sarcoma retrovirus was injected into chick flight feather follicles using an improved procedure. This virus carried dominant negative genes. When the feather regenerated the expression of these genes revealed that the *bone morphogenetic protein 2* and *4* caused the formation of a giant rachis and barb fusions. On the other hand the antagonist *noggin* split off the rachis and caused excessive branching of barb ridges. In situ hybridization and immunostaining led to the recognition of molecular expression patterns in different cell types. *Bone morphogenetic proteins 2* and *4* appeared in the barbule plate when these cells started to form. In another study using chick and duck embryos the interactions between *sonic hedgehog* and *bone morphogenetic protein 2* reinforced the evidence associating these genes with feather development (Yu et al. 2004) (Figs. 2.4 and 2.5).

2.12 Chemistry and Physics of Colours

Colour belongs mainly to the domain of chemistry and physics but it may also depend on the microscopic arrangement of structural components. Feathers with their many bright colours cover the whole rainbow and beyond.

The principal yellow pigments in tit passerines are: lutein, zeaxanthin and cryptoxanthin. The first is obtained from the ingested caterpillars, the intensity of the yellow colour being directly related to the abundance of these insect larvae. The red pigment, zooerythrine, is a lipochrome dependent for its effect on diet (Fig. 2.6). The belly of Trogons becomes reddish when it consumes carotenoids. Carotenes are orange pigments found in plants. But the red, yellow and green colours of many Woodpeckers are also due to carotenoid pigments.

Other pigments such as astaxanthin and doradexanthin are responsible for red. Lutein, zeaxanthin and cryptoxanthin stand for yellow but also for green colours. Picrofulvins are responsible for the yellow colour in some species. The chemical formulae of these pigments as well as their chemical interdependence are well established (Stradi et al. 2001; Rutz et al. 2010).

Colour may have a physical origin such as in iridescence which results from the variation of reflectance spectra at different viewing angles. This is evident in the breast of pigeons and the dark parts of the plumage of Woodpeckers. Iridescence is a phenomenon caused by regular microstructures in the feathers connected with the distribution of molecules in thin layers. A drop of oil falling on a water surface builds a molecular film in which light emits the colours of the rainbow. Hence these colours do not spring from any pigment but are a pure physical event. In birds iridescence is

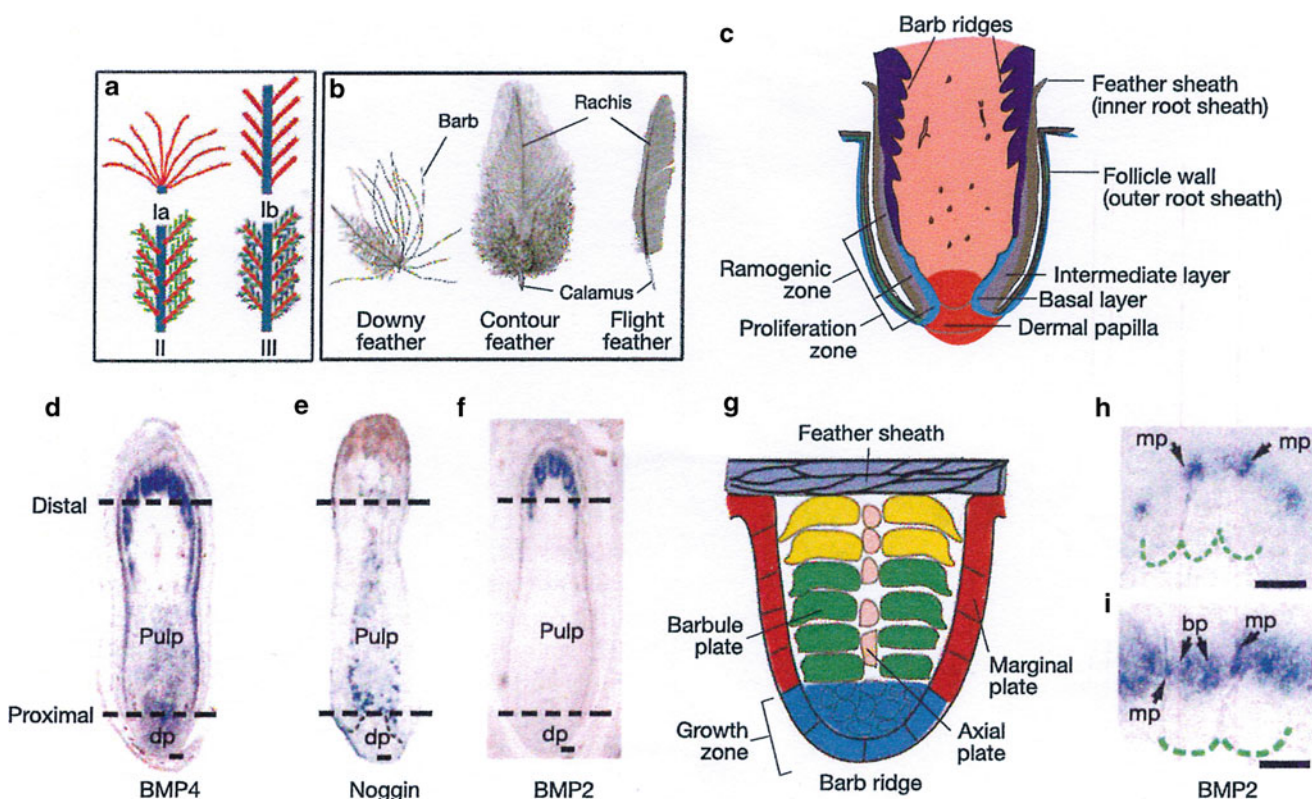


Fig. 2.5 Feather-branching morphogenesis and gene expression. (a) Diagram showing three branching levels. Level I, rachis (blue) branches into barbs (red). *Ia* radially and *Ib* bilaterally symmetric feathers. Level II, barbs branch into barbules (green); level III, barbules branch into cilia and hooklets (purple). (b) Different types of chicken feather. (c) Diagram of feather follicle structure.

(d-f) BMP4 (d), noggin (e) and BMP2 (f) expression patterns. (g) Diagram of feather barb ridge. (h, i) BMP2 in barb ridges. BMP2 is expressed first in peripheral marginal plates (mp; h) then switches to barbule plates (bp; i). dp dermal papilla. Scale bar, 100 μ m. BMP4 and BMP2 are bone morphogenetic proteins. Noggin is a modulating agent

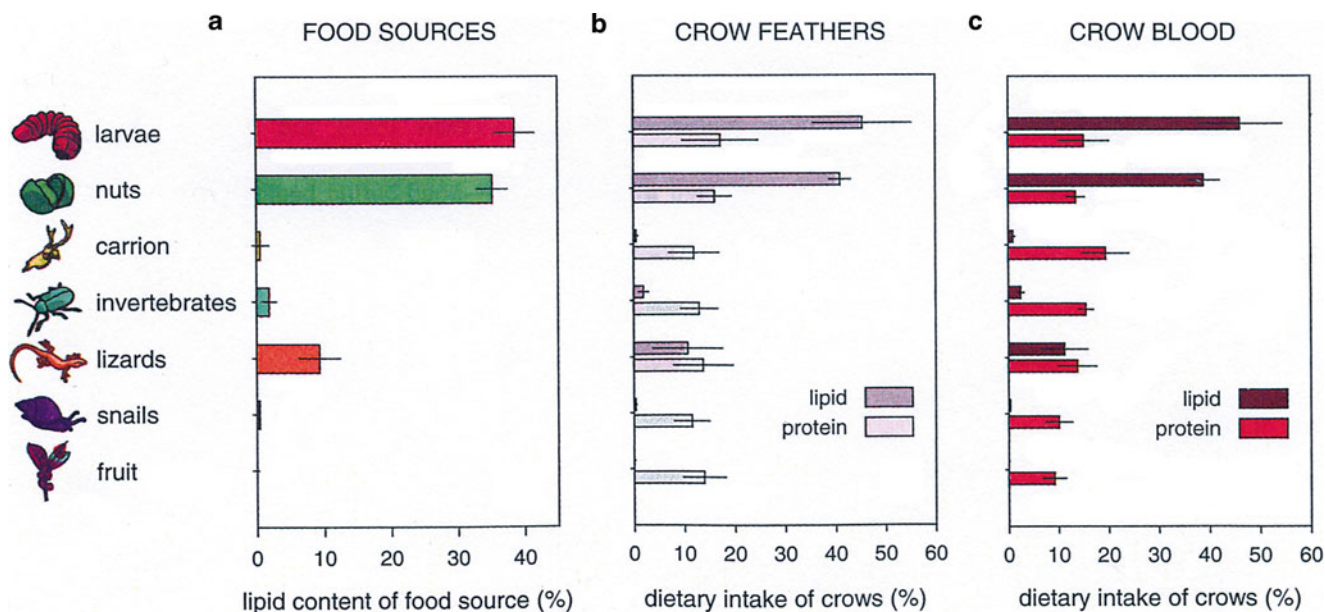


Fig. 2.6 Nutritional significance of seven different food sources for New Caledonian crows. (a) Average lipid content of food sources, as estimated through lipid extraction from food items. (b) Relative

contribution of food sources to crow diet in terms of either lipid or protein intake, as estimated on feather samples. (c) Blood samples

produced by coherent scattering of light waves from alternating layers of materials of different refractive indices. It is located in feather barbules where light is scattered from alternating layers of keratin, melanin and air. The plumage iridescence varies with the structure and organization of these layers.

The Kingfishers are known for their vibrant greens and blues, one species being called Malachite Kingfisher because it is so similar in colour to the mineral malachite, a copper carbonate. These colours are not iridescent nor are they the sole result of pigmentation. They are structural. Their feathers have a cloudy medium that consists of vacuolized keratin lying in the medulla of the feather barbs with an underlying layer of melanin. This arrangement results in the so called Tyndall's phenomenon in which short wavelengths of light are scattered. The melanin pigment occurs in the form of granules which build ordered arrays. Green is produced by a filter consisting of yellow granules, and violet by reddish-brown granules (Prum and Torres 2003; Shawkey et al. 2006). The Bee-Eaters display beautiful carmine, greenish-blue, scarlet and pink pastel shades which are rare among birds in general. In the African trogons the breast is green and the belly is red. Other species have beaks and legs of all possible colours. This unique painter's palette surpasses the rainbow extending into the ultraviolet.

Spectroscopy experiments have shown that the feathers of the Great Spotted Woodpecker reflect ultraviolet radiation. And the study of the ultraviolet reflecting properties of pigeon feathers has led to the finding that birds can see ultraviolet light which is invisible to humans. Neck feathers that appear purple to the human eye exhibit four reflectance peaks: two in the ultraviolet and one in the blue and red regions of the spectrum. The feathers that appear green to the human eye are characterized by several ultraviolet peaks and a predominant green peak (McGraw 2004).

The mechanism responsible for production of ultraviolet iridescence in feathers was uncovered in hummingbirds and bowerbirds by means of electron microscopy, spectrometry and thin-film optics (Doucet et al. 2006).

The frontiers between the chemical, physical and structural origin of colour are not always sharp and in several organs the three seem to combine in the formation of the final colour.

The complexity of colour formation has been made evident by the analysis of the chemical structure of parrot pigments in the Scarlet Macaw (*Ara macao*). This group of birds harbours unusually bright, non-carotenoid feather pigments which are lipochromes called psittacofulvins. They differ from the widely distributed carotenoids (zooerythrin and xanthoerythrin) in several physical and chemical properties. Unlike carotenoids, the pigments in parrots do not depend

on dietary input and are visible under ultraviolet light. The plumage coloration was due to four pigments with a linear polyene chain containing conjugated double bonds. Stradi et al. (2001) concluded that the rainbow colours of parrots are obtained by modulating a few endogenous yellow pigments with the feather keratin. This chemical work has been extended by Burt et al. (2010). The red, orange and yellow colours of parrot feathers are the product of psittacofulvins which are pigments known from no other organism. On the other hand in blue feathers colour is based on the microstructural arrangement of keratin, air and melanin granules. Green feathers combine structural blue with yellow psittacofulvins.

Much remains to be learned about the molecular biology of plumage coloration.

2.13 The Location of Pigments in Feathers is Guided by Proteins and Other Molecules

No order springs from nowhere but is the product of another order active at a lower level of structural organization. This is confirmed by the latest studies on cell morphogenesis during the embryonic development of the chick. In the embryo the process starts in an epidermic germ containing a dermal papilla which is surrounded by blood vessels. The papilla has a nutritious function directing the gradual change of the skin's germinative zone into a feather.

Pigments in birds are programmed concerning their origin, location and dynamics. To start with, they are mainly located in feathers instead of being dispersed throughout the skin in an irregular manner. All biochromes (melanins, carotenoids, porphyrins and others) are produced in the dermis by special cells being incorporated into the feathers during their growth. Melanin is formed in melanoblasts.

The dynamic details of pigment cell migration are being unraveled. Avian melanoblasts must be specified before they can migrate. Transmembrane receptors which guide them in their route include ephrins, endothelins and other molecules leading to their exact location on the skin along the embryo's dorsolateral pathway. Ephrins are a family of proteins known for their guidance and patterning roles in morphogenesis. The terminal site of migration depends, in part, upon extracellular matrix reorganization in which semaphorins, spondins and a long array of proteins take part.

Hence, pigment morphogenesis in birds involves a cell migration, directed by a series of specific molecules, which results in the regular integration of pigments into feather germs the ultimate result being the formation of stripes, bands and spots (Kelsh et al. 2009).

Sources of Figures

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Fig. 2.5 Yu, M. et al. 2002. The morphogenesis of feathers. *Nature* 420: 308–312 (Fig. 1 page 308).

Fig. 2.6 Rutz, C. et al. 2010. The ecological significance of tool use in New Caledonian Crows. *Science* 329: 1523–1526 (Fig. 2 page 1524).



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