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Introduction

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1.1 To the Reader

If the author of this book was to have painted the over 18,000 figures, on which this work is based, some people would have argued that he had retouched the pictures or invented details. They would assert that birds with so well-defined and extraordinary markings on their bodies, could not exist. Fortunately, the figures were painted, with the highest accuracy, by many different bird specialists who had no other intent than to convey every detail of the bird's body. No feather or claw was left out. For this reason the author is free of any intervention or distortion.

There is more to consider than the markings.

The avian body is covered with such varied colours, that these also defy imagination. The rainbow is not enough. Soft pastel shades have been introduced, by secluding pigments of well-defined chemical composition in microscopic cell organelles. These reflect light in novel ways. Other processes were added such as iridescence, which is a physical phenomenon caused by the arrangement of particular feather molecules. These biological "fireworks" were made more impressive by the location of colours, side by side, which are complementary on the light spectrum such as green–blue facing red, or yellow neighbouring indigo–blue. Moreover, these colours are often sharply delimited.

The shapes that the body assumes may be equally exquisite.

The crest may acquire exotic forms which could compete with the best hairstyles in a fashion show. The tail of some strains of Japanese fowl may attain the length of the wedding gown of a Swedish Princess. Pendular protrusions, covered with feathers, stick out from the breast hanging like pieces of jewellery.

Remarkable is that all these features: markings, colours and particular shapes, are part of geometric figures that pervade the avian body.

Starting with the eye, this is surrounded by concentric circles of increasing diameter which expand to the periphery of the head. This circularity extends to the neck, breast, tail and wings in the form of larger circles which also have well-defined centers. Not only circles, but straight lines, in the form of well-delimited stripes cross the head at the level of the eye. These build several series of parallel bands which are intersected by other parallel lines running at 90°. This criss-cross pattern also extends to the breast and the wings. This short list could be easily transformed into a long array of geometric avian patterns. A novel geometry, that is even visible in the bill and the legs, unfolds in front of our eyes giving the body configurations another meaning.

These unexpected displays of pattern have been seen as bizarre events that demanded little attention, or were interpreted using assumptions that turned out to be contradictory. This attitude resulted in much speculation and controversy. But "amazing curiosities" only exist in our minds, birds never heard of them. On the contrary, they represent key phenomena that lead to the search for the underlying atomic and molecular mechanisms responsible for the geometry.

Life seems to know no limits in its capacity of improvisation and its ability to produce secret backdoor solutions. What turns out, is that none of these surprising features seem to be fortuitous. They appear as an integral part of a rigid order and coherent geometry which is directed by simple gene interactions and molecular cascades occurring at various cellular levels, and at different times, during the organism's development.

Now, let the birds speak for themselves.

1.2 Two Centuries of Ornithology – An Impressive Contribution to Science

Ornithology is the branch of learning covering the study of birds (from the Greek *ornis*, bird and *logos*, discourse). It deals with avian species (from the latin *avis*, bird).

Mammals have, since the birth of biological science, attracted attention because they are our closest relatives. Hundreds of volumes have dealt with them.

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Other vertebrate and invertebrate groups seemed remote, but the birds caught the attention of naturalists from the beginning due to their many unique properties.

Since transatlantic voyages, and expeditions to distant islands, became more accessible to scientists in the early 1800s, there was an explosion in bird watching and specimen collecting.

Two hundred years of uninterrupted research have filled bookshelves with their documentation. This impressive contribution deserves our respect and praise, for it has been the result of exhaustive and accurate work carried out by successive generations under most difficult conditions. To obtain their results ornithologists have gone through all kinds of adventurous journeys, incredible situations and duress. They have climbed trees in the extreme humidity of rain forests waiting for hours perched on a weak tree branch that could break anytime. They put their lives at risk by climbing to the top of mountains, or by hoisting their bodies against the sharp cliffs overlooking the sea. They crossed, on sledges, the vast frozen spaces of Antarctica to learn the behaviour of penguins and walked on all fours over the dunes of deserts to follow the trails of ostriches. The reward at times was only the counting of the number of eggs in a nest.

With the advent of the jet age they covered tedious hours of travelling to reach some remote island in the Pacific where a subspecies remained to be identified. In an unfailing effort to learn more, they became more demanding, and started intruding into the private life of birds. Equipped with tape recorders, they registered their calls, songs and private conversations. Cameras were also installed inside nests to disclose family affairs and intriguing details of copulation were not left out. Radar and surveying satellites were employed to track their autumn journeys to warmer tropical areas.

The many specimens collected were preserved in the long galleries of museums which are filled with the doubtful smell of formalin and other chemicals used as preservatives. To these travails are to be added the long hours of laboratory work and of scientific writing that led to the tedious reading of proofs of the scientific articles that were finally published.

It is a staggering contribution.

Science is not written with ink, as most people believe, but is written with blood.

1.3 The Preparation of the Plates Covering Specific Bird Traits

The "Handbook of the Birds of the World" 1992–2010 (Edited by *del Hoyo*, *Elliot* and *Sargatal*) Lynx Edicions, Barcelona, Spain, has been published in 15 volumes. It assembles the contributions of leading ornithologists combined with the work of the best specialists in bird painting.

Hundreds of books have been published on birds but these usually deal with the local fauna of Europe or North America, and in some cases with that of other continents. Moreover, these books tend to consist of photographs or paintings that represent the most common species with a view of informing ornithologists in their field work.

What is unique about the "Handbook of the Birds of the World" is that it covers most species and subspecies from all over the world with emphasis on the less studied birds from different continents. But its exceptional value lies in each species, and subspecies, being painted with the utmost care including minute details. This is precious information which is often unobtainable even from the best photographs.

The 15 published volumes contain 18,300 images (additional volumes are under preparation). Each volume can contain as many as 70 plates, each plate usually covering a family and containing a variable number of species.

A careful study of each image led to the finding that many bird traits unveiled genetic and evolutionary mechanisms which so far had been bypassed. Each bird figure found to be of interest was photocopied in black and white and chosen bird species were cut out.

Relevant features which displayed the same pattern, were assembled to build groups of birds which represented a specific phenomenon. A second photocopy series was made to adjust the size of the different species because this varies drastically from family to family. The whole body was used when cutting out the bird figures, since this gives an immediate idea of the family to which the bird belongs. A third series of photocopies was carried out in colour and again each species was cut out with the utmost care and included in an appropriate new assembly.

A special copyright contract permitted the use of 200 bird figures from the "Handbook of the Birds of the World". These were supplemented by a number of figures retrieved from other works, as mentioned in the Source of Illustrations and Acknowledgements.

When searching for the occurrence of a given bird trait, among the thousands of species, a large number was collected which displayed the same feature. During the making of the final plate assemblies this number had to be reduced due to copyright considerations. Thus, only the most distinct cases are included, but many more could have been added.

The Family name was added to the scientific name to allow a rapid identification of the bird in relation to close or distant relatives.

At present the number of bird species is estimated to be about 9,000 (Burnie 2004) and circa 9,600 (Pough et al. 2005). The 18,300 images cover: species, subspecies, females, variants, photographs and partial images of body parts such as the head of a given bird. This information is based on a personal communication from the Production Department of the "Handbook of the Birds of the World".

2 The Molecular Determination of a Bird's Pattern

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

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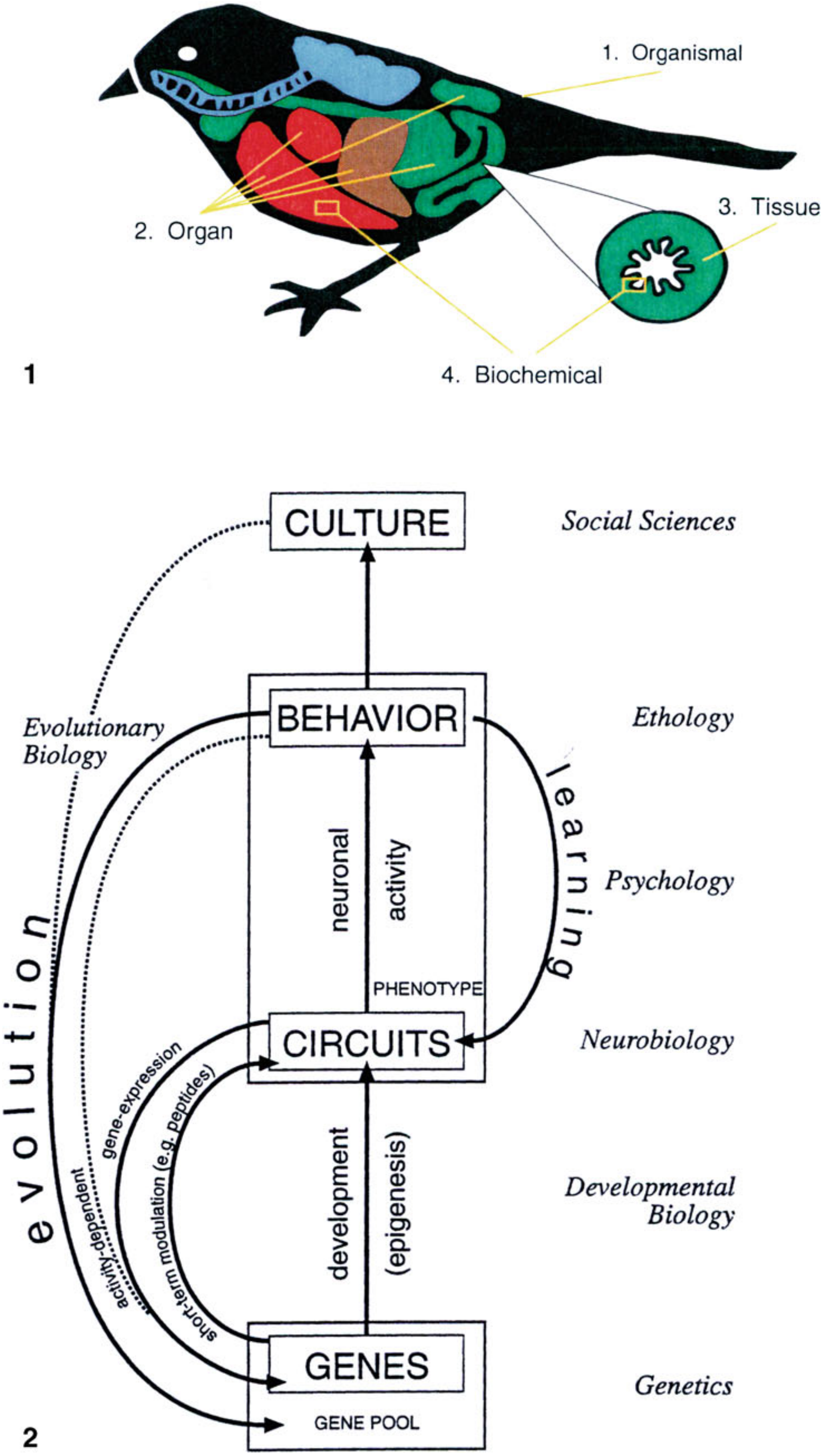


Fig. 2.1 **(1) A bird, like most other living organisms, consists of four levels of organization: (1) Organismal, (2) Organ, (3) Tissue and (4) Biochemical**. The structures and functions of these four levels result from the action of molecular processes having their origin in the DNA sequences of the 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.

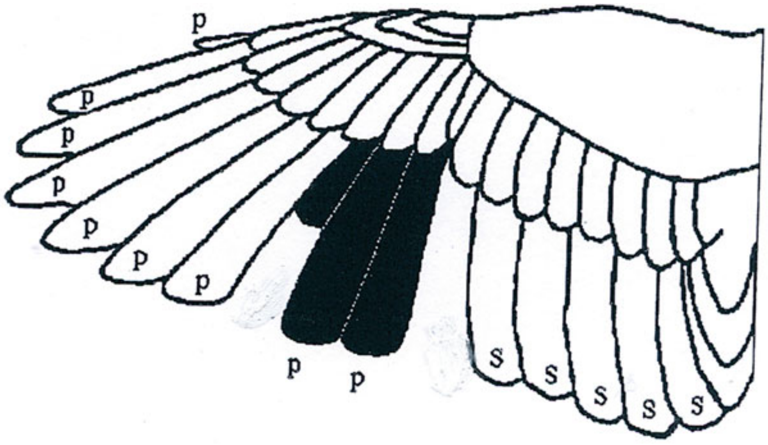
2.9 Hormones Control the Size, Shape and Colour of Feathers

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 diffentiation of sex-related morphological features such as plumage form and colour (Eckert and Randall 1978).

1



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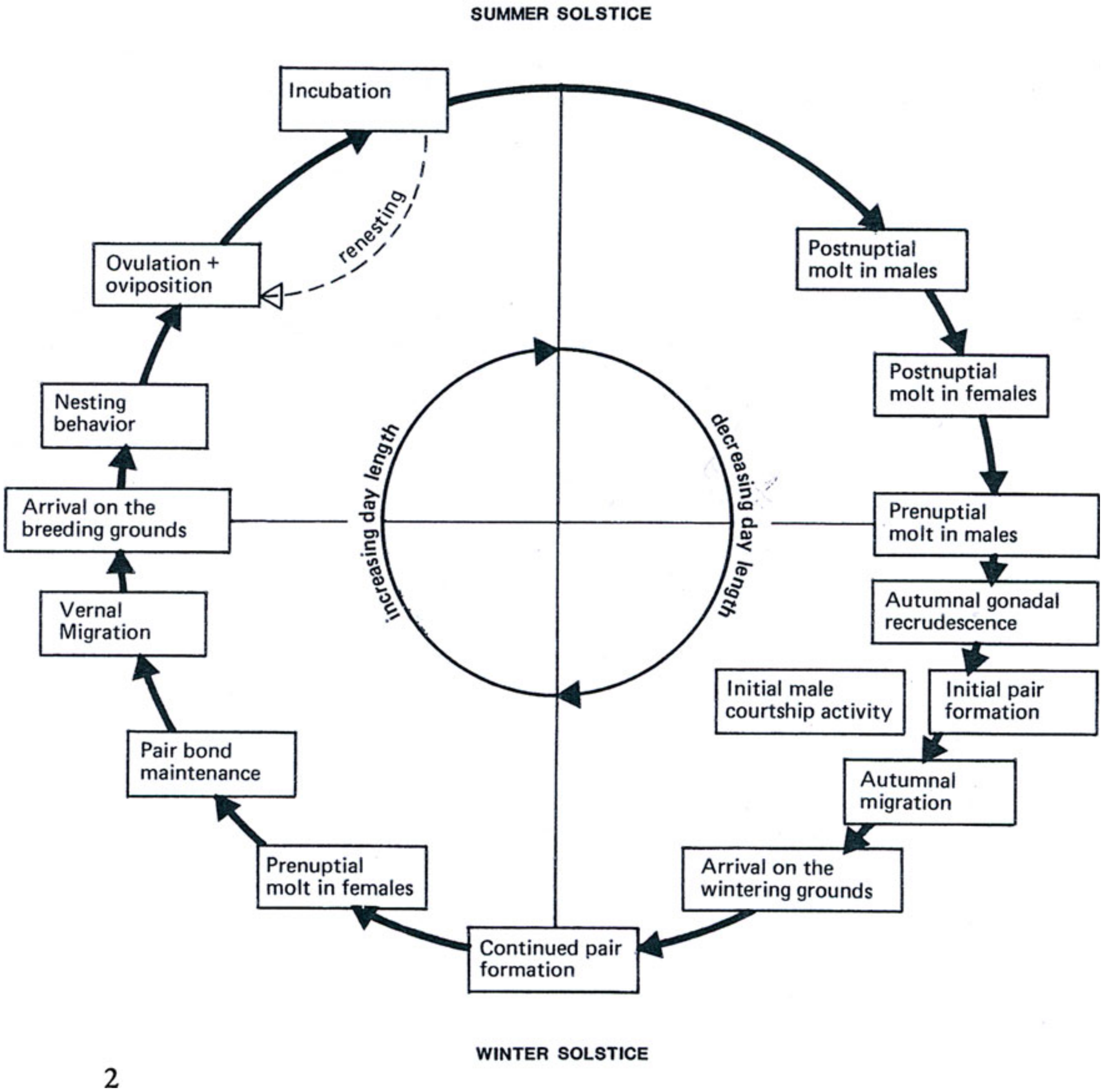

Fig. 2.2 **(1) A passerine wing in moult** (*p* primary; *s* secondary feathers). Primaries and secondaries are collectively called remiges. Dark feathers are new feathers (fully-grown or in growth). **(2) Summary of the major components of the moulting cycle of the Mallard (*Anas platyrhynchos*)**.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

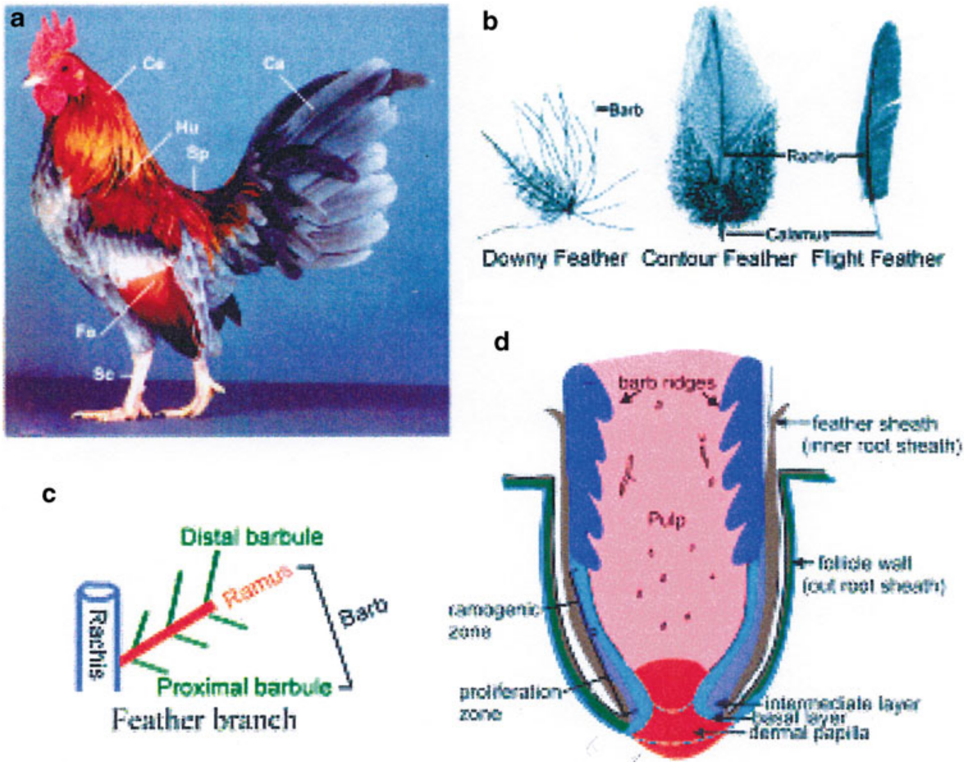

Fig. 2.3 **The basics of feathers.** (**a**) A rooster with plumage showing the different feather tracts on different parts of the body. *Ca* caudal tract, *Ce* cervical tract, *Fe* femoral tract, *Hu* humerus tract, *Sc* scale region, *Sp* spinal tract. (**b**) Major types of feathers: radially symmetric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

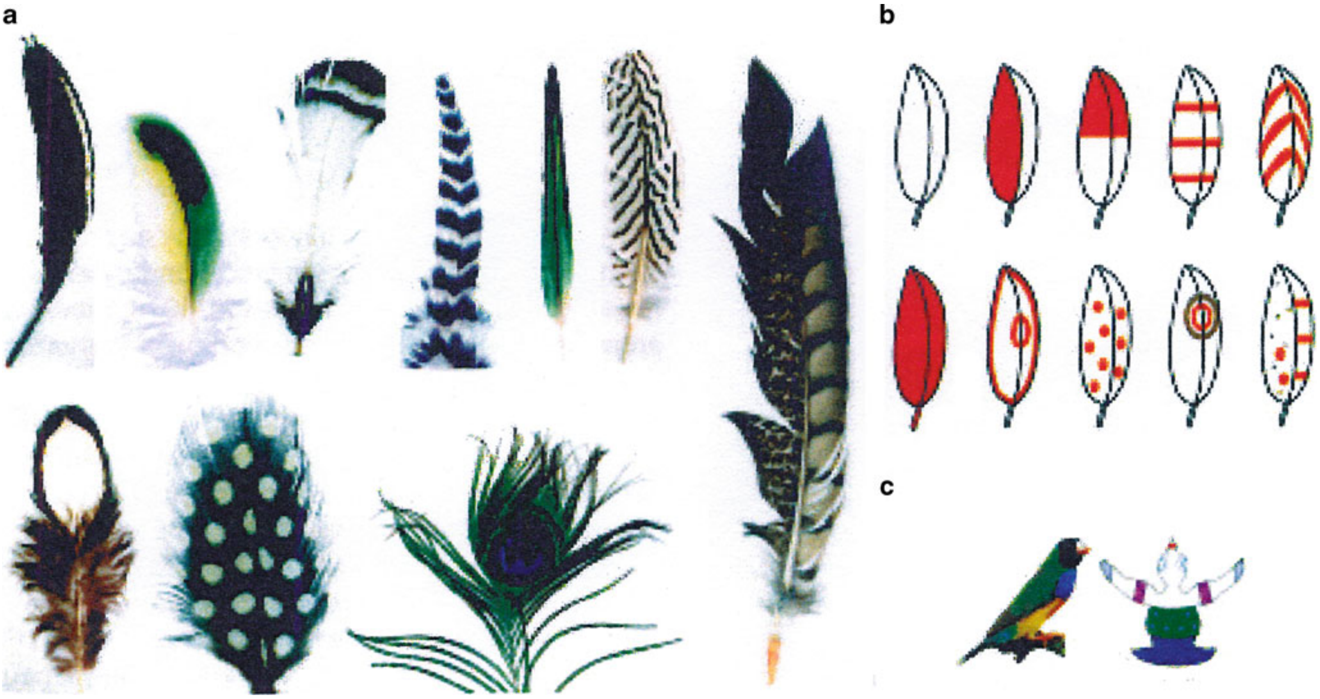

Fig. 2.4 Pigment patterns of feathers. (**a**) Representative pigment patterns within a feather. Feathers are from chicken, zebra finch and peacock. (**b**) From these, some basic patterns such as barbs, chevrons, circles and dots are derived. Note that pigments in the *left* and *right vane* are under 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. Picofulvins 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

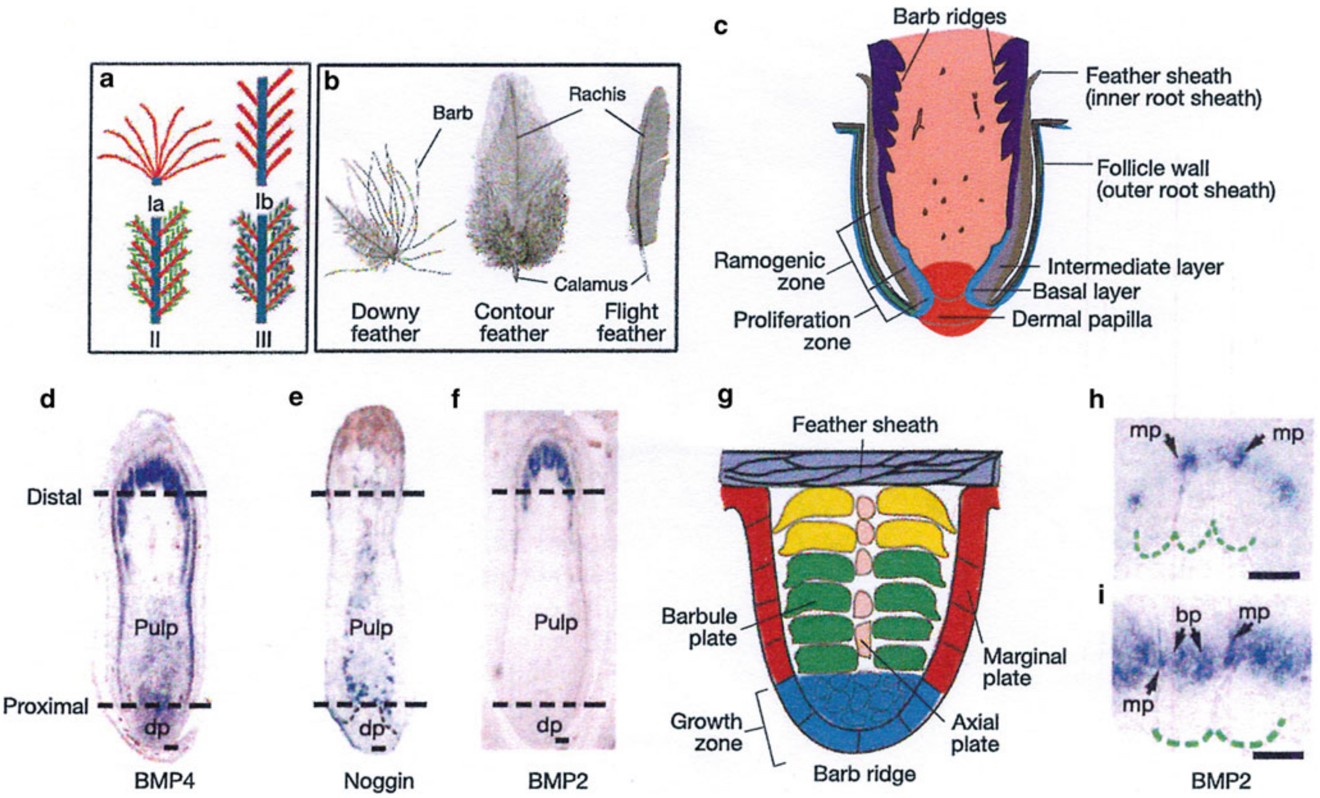

Fig. 2.5 **Feather-branching morphogenesis and gene expression.** (**a**) Diagram showing three branching levels. Level I, rachis (*blue*) branches into barbs (*red*). *Ia* radially and *Ib* bilaterally symmetric feathers. Level II, barbs branch into barbules (*green*); level III, barbules branch into 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 μm. BMP4 and BMP2 are bone morphogenetic proteins. Noggin is a modulating agent

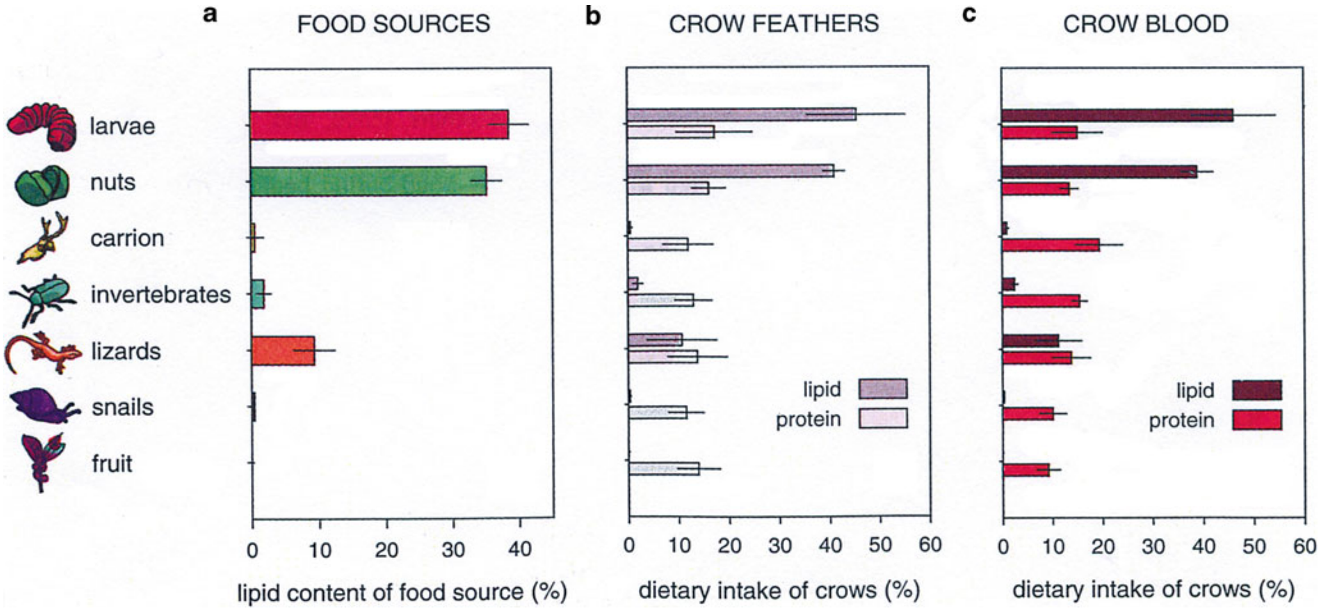

Fig. 2.6 **Nutritional significance of seven different food sources for New Caledonian crows**. (**a**) Average lipid content of food sources, as estimated through lipid extraction from food items. (**b**) Relative contribution of food sources to crow diet in terms of either lipid or protein intake, 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 Burtt 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

Fig. 2.1 **(1)** Swawson, D.L. 2010. Seasonal variation in birds: functional and mechanistic correlates. In: Current Ornithology (Thompson, C.F. Editor) *17*: 75–129 (Fig. 3.4 page 97), **(2)** After Plotkin and Odling-Smee 1981, Greenspan et al. 1994. From: Huber, H. 2000. Psychophylogenesis: innovations and limitations in the evolution of cognition. In: The Evolution of Cognition (Heyes, C. and Huber, L. Editors) 2000: 23–41 (Fig. 2.1 page 24).

Fig. 2.2 **(1)** Lind, J. et al. 2010. Impaired predator evasion in the life history of birds: behavioral and physiological adaptations to reduced flight ability: In: Current Ornithology (C.F. Thompson, Editor) *17*: 1–30 (Fig. 1.3 page 11), **(2)** Bluhm, C.K. 1988. Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. In: Current Ornithology (Johnston, R.F. Editor) *5*: 123–185 (Fig. 3 page 132).

Fig. 2.3 **(A)** Green-Armytage, S. 2000. Extraordinary Chickens. Harry N. Abrams, New York, U.S.A., **(B)** Lucas, A.M. and Stettenheim, P.R. (Editors) 1972. Avian Anatomy – Integument. Agricultural Handbook 362. Agricultural Research Services (US Department of Agriculture, Washington, D.C.) U.S.A., **(C)** and **(D)** Yu, M. et al. 2004. The developmental biology of feather follicles. Int. J. Dev. Biol. *48*: 181–191 (Fig. 1 page 182).

Fig. 2.4 (**A**, **B** and **C**) Yu, M. et al. 2004. The developmental biology of feather follicles. Int. J. Dev. Biol. *48*: 181–191 (Fig. 7 page 187).

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).

3 The Occurrence of Conspicuous Feathers at Different Body Locations and Their Genetic Interdependence

3.1 Two Long Feathers Emerging from the Tail

Ornithologists have been specially attracted by the formation of long feathers protruding from the avian tail. These birds are such elegant creatures that they fascinate the observer. But their beauty may distract from the search for the genetic processes that lie behind the formation of these structures.

The feathers are so long that in some cases they become four times the length of the body. Besides, they may be thick but also quite thin along the whole length of the feather, becoming graciously undulated and curved (Figs. 3.1 and 3.2). The variation does not stop here. In other cases the long thin feathers terminate in a thick and broad expansion resembling a spatula. The two feathers may even cross each other building an unexpected arrangement (Fig. 3.3). Moreover, the long tail feathers can have a rather even thickness along their entire length or they may be thin all the way, terminating in a minor expansion (Figs. 3.4 and 3.5).

It is evident that: (1) Two is the dominating number of extra long feathers, whereas many other numbers could have occurred. At the same time the feathers have acquired many shapes. Constancy and variation appear as the two inseparable sides of the same medal. (2) Some species belong to the same family, or to the same genus, but the 27 birds, depicted in the five figures, belong to the families: Paradisaeidae, Tyrannidae, Trogonidae, Trochilidae, Momotidae, Alcedinidae, Furnariidae, Monarchidae, Pipridae, Nectariniidae, Dicruridae, Coraciidae and Psittacidae. Not less than 13 families are represented. This means that the same genetic solution, in the form of two extra long feathers, reappears suddenly in families that are distantly located phylogenetically indicating the occurrence of periodicity.

A comparison of these families reveals the following:

1. The Birds of Paradise (Paradisaeidae) are confined to a limitied area: New Guinea, Moluccas and north-eastern Australia. On the contrary the Tyrant-Flycatchers (Tyrannidae) and the Hummingbirds (Trochilidae) cover the whole American continent from northern Canada to the extreme South of Argentina. Other families have a transversal distribution spreading along the Earth's equator, being almost pantropical (Trogonidae). There are also those which are cosmopolitan, such as the Kingfishers (Alcedinidae), being found on every continent and most latitudes.
2. Some species have a habitat restricted to tropical and humid rain forests (Birds of Paradise and Manakins, Pipridae), but others dwell in a wide variety of habitats that extend from rain forests at sea level up to mountain ranges reaching close to 5,000 m. These are the Hummingbirds (Trochilidae) and the Sunbirds (Nectariniidae). The Ovenbirds (Furnariidae) thrive in all types of vegetated habitats. The Rollers (Coraciidae) as well as the Parrots (Psittacidae) inhabit both the wet rain forest and the dried savanna.
3. The diet is equally most varied. There are omnivores (Birds of Paradise), insectivores (Drongos, Trogons and Monarch-Flycatchers), nectarivores (Hummingbirds and Sunbirds) and others which cannot do without flowers combined with fruits and seeds (Parrots).
4. When it comes to behaviour some are essentially arboreal being incapable of walking (Trogonidae), others on the other hand are known for their acrobatic flight (Monarch-Flycatchers) and Hummingbirds are easily recognized by their hovering ability. Nest building may be highly diverse stretching from the architectural skills of Ovenbirds (Furnariidae) to the simple excavation of burrows on earth banks (Motmots, Momotidae).
5. When it comes to the voice some birds are rather silent (Manakins, Pipridae), others like the Parrots emit short and unmusical sounds, whereas the Sunbirds (Nectariniidae) are known for their loud and distinct calls.

The conclusion is inescapable. The presence of two long feathers protruding from the tail in the 13 families cannot be

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Fig. 3.1 **Two long feathers protruding from the tail which are thick along the whole length of the feather**. (**1**) Ribbon-tailed Astrapia, *Astrapia mayeri*, Paradisaeidae. (**2**) Stephanie's Astrapia, *Astrapia stephaniae*, Paradisaeidae. (**3**) Strange-tailed Tyrant, *Alectrurus risora*, Tyrannidae. (**4**) Resplendent Quetzal, *Pharomachrus mocinno*, ssp costaricensis, Trogonidae. (**5**) Resplendent Quetzal, *Pharomachrus mocinno*, ssp mocinno, Trogonidae

easily correlated with any particular geographic distribution, habitat, diet or behaviour.

Contributing to elucidate this avian trait is the information gathered from the ornamental group of birds called widowbirds and bishops (genus *Euplectes*). These are widely distributed across the grasslands of sub-Saharan Africa. As Prager (2010) states: "Despite similar ecologies and general behaviour breeding *Euplectes* males show an extraordinary variation in tail ornamentation and carotenoid coloration". Males in widowbirds (but not in bishops) grow, during the

Fig. 3.2 Two long feathers protruding from the tail which are thin along the whole feather. (**1**) Emperor Bird-of-paradise, *Paradisaea guilielmi*, Paradisaeidae. (**2**) Red Bird-of-paradise, *Paradisaea rubra*, Paradisaeidae. (**3**) Raggiana Bird-of-paradise, *Paradisaea raggiana*, Paradisaeidae. (**4**) Wilson's Bird-of-paradise, *Cicinnurus respublica*, Paradisaeidae. (**5**) Magnificent Bird-of-paradise, *Cicinnurus magnificus*, Paradisaeidae

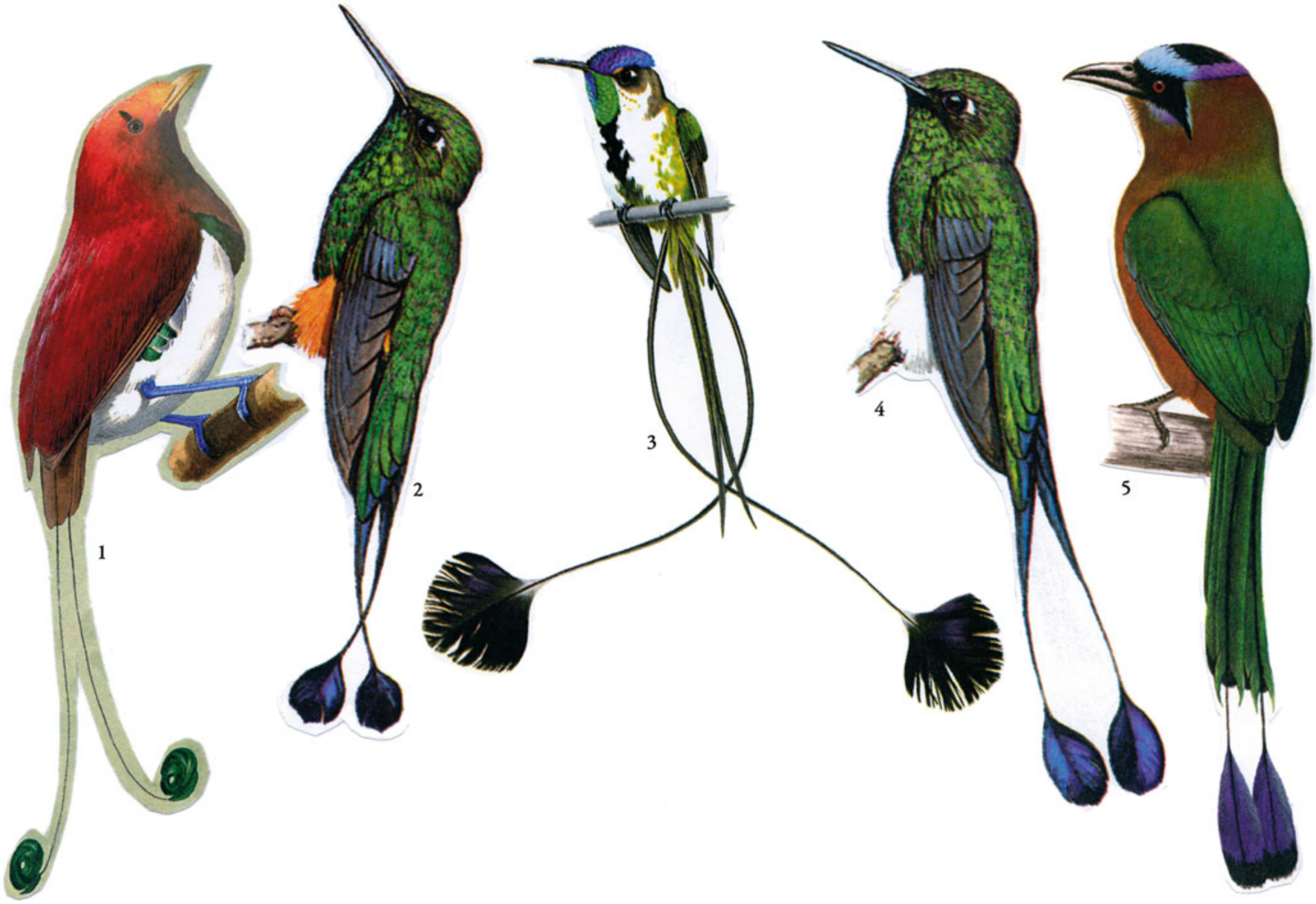

Fig. 3.3 **Two long feathers protruding from the tail which are thin but terminate in a broad expansion**. (**1**) King Bird-of-paradise, *Cicinnurus regius*, Paradisaeidae. (**2**) Booted Racquet-tail, *Ocreatus underwoodii*, ssp annae, Trochilidae. (**3**) Marvellous Spatuletail, *Loddigesia mirabilis*, Trochilidae. (**4**) Booted Racquet-tail, *Ocreatus underwoodii*, ssp melanantherus, Trochilidae. (**5**) Russet-crowned Motmot, *Momotus mexicanus*, Momotidae

breeding season, elongated black tails that may attain 50 cm, whereas females and non-breeding males retain the usual plumage (Fig. 3.6). This shows that the occurrence of long feathers is primarily an internal event.

3.2 A Bird Gets its Body Trait Whether it Likes it or Not – DNA Follows its Own Atomic Evolution

The recurrence of this body pattern has the characteristics of a well known genetic event. The same DNA sequence, can become active, leading to a protein cascade that obliges the same body pattern to reappear. The sudden revival of a given gene sequence is usually directed by genes located in the same or in other chromosomes and which follow solely the rigid molecular organization of the chromosome (Lima-de-Faria 1983, 2003; Gehring 1998).

Even the DNA does not need to change to create the same genetic solution (van der Ploeg 1990). The messenger RNA, that is transcribed from DNA, may suddenly splice differently according to its own molecular makeup and build a different RNA that will again produce the same final protein. The physical chemistry of DNA as well as that of RNA, do not ask permission to follow their own atomic rules. They present the living organism with a solution from which it cannot depart or escape.

An example may suffice to illustrate one of the molecular mechanisms that may lie behind the re-emergence of two long feathers at a given body site.

During embryonic development the program of epidermal morphogenesis leads to the formation of trichomes in flies, of hairs in mammals and of feathers in birds.

Epidermis differentiation in the fruit fly *Drosophila* results in the formation of trichomes which, like hairs and feathers, are outgrowths of the epidermis protruding from the skin surface (Abercrombie et al. 1990). Modifications of the pattern of these hairy structures in the fly are all attributable to changes in expression of the gene *shavenbaby* (*svb*). The *svb* gene encodes three overlapping proteins of different

Fig. 3.4 **Two long feathers protruding from the tail which are of rather even thickness**. (**1**) Common Paradise-kingfisher, *Tanysiptera galatea*, Alcedinidae. (**2**) Des Murs's Wiretail, *Sylviorthorhynchus desmursii*, Furnariidae. (**3**) Long-tailed Tyrant, *Colonia colonus*, Tyrannidae. (**4**) Asian Paradise-flycatcher, *Terpsiphone paradisi*, Monarchidae. (**5**) Long-tailed Manakin, *Chiroxiphia linearis*, Pipridae. (**6**) Pygmy Sunbird, *Anthodiaeta platura*, Nectariniidae

lengths: *Svb*, *Ovo A* and *Ovo B*, all three share the same DNA recognition and transcriptional-activation domains but differ in their terminal amino acids – *Svb* is the longest and *Ovo B* the shortest.

What before was called "junk" or "nonsense" DNA has turned out to be the source of the critical decisions that guide embryonic development. A substantial proportion of the RNAs transcribed from DNA, in high organisms such as the birds, have been found to be small RNAs that are translated into small peptides. These were considered before to be without genetic significance because the peptides formed consist of only 11–32 amino acids. Their dimensions are minuscule compared to those of large proteins translated from long messenger RNAs.

These peptides, which are encoded by the gene *polished rice* (*pri*), control epidermal differentiation by modifying the terminal region of the *Svb* protein. They truncate it into the smaller *Ovo A* and *Ovo B* proteins. The result is dramatic converting Svb from a repressor to an activator during embryogenesis, actually orchestrating epidermal differentiation. Kondo et al. (2010) concluded that the gene *svb* defines the spatial pattern of hairs and that the small peptides define the time at which the hairs are formed (Fig. 3.7).

Hence, the DNA molecule, by itself, as a result of its atomic construction, has the ability to transform its message into a repressor or an activator. Moreover, this process is not achieved by any complex system of messages but by a simple change in the length of the protein that has its source in the same DNA sequence. An impressive versatility is the result of simplicity.

In this connection it may be mentioned that a protein which is nonfunctional can suddenly become fully functional when activated by three *heat shock proteins* (Chap. 10, Fig. 10.2). In this case the protein does not even change in length it is solely modified by the intervention of other macromolecules.

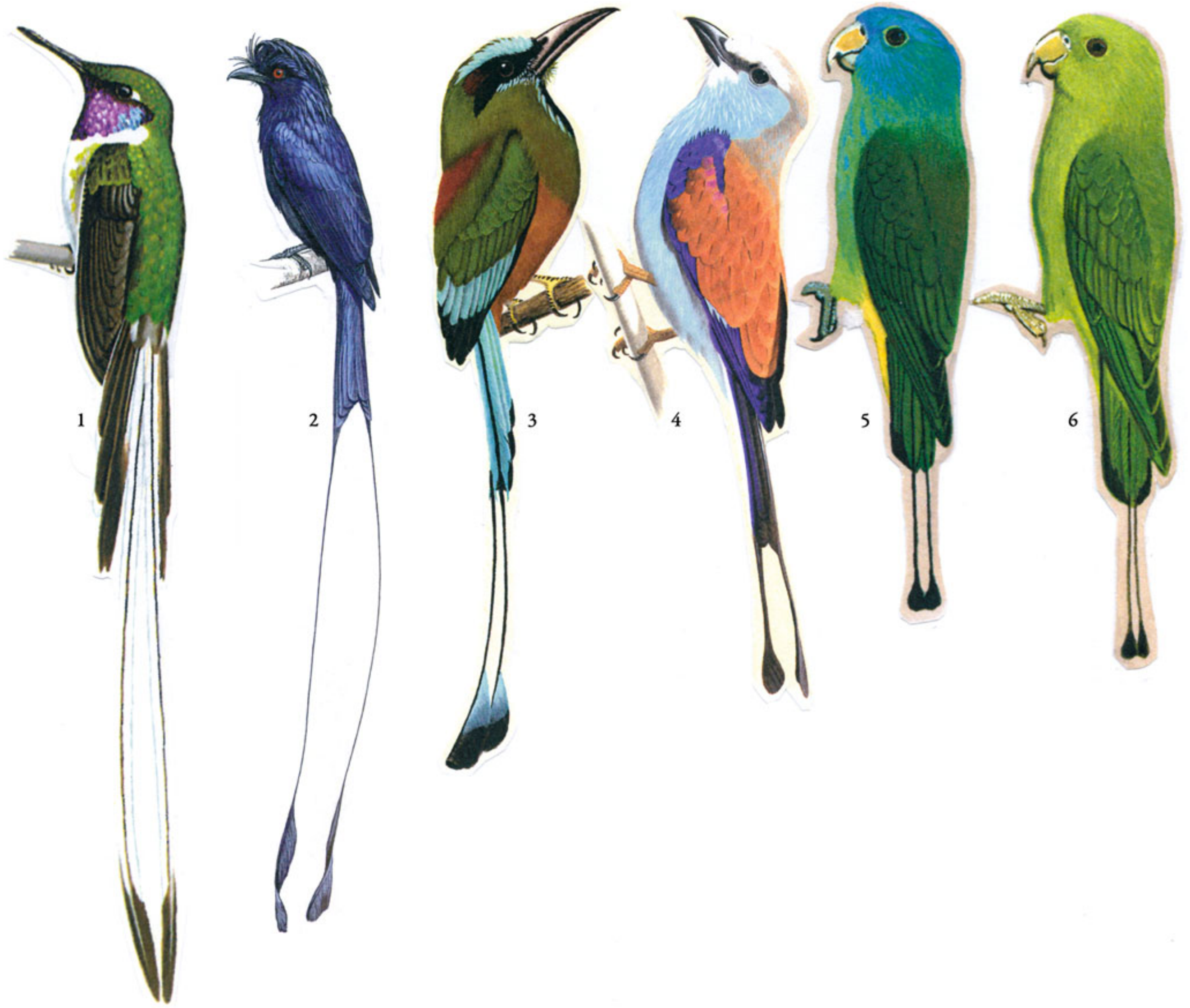

Fig. 3.5 **Two long feathers protruding from the tail which are thin and finish in a small expansion**. (**1**) Peruvian Sheartail, *Thaumastura cora*, Trochilidae. (**2**) Greater Racquet-tailed Drongo, *Dicrurus paradiseus*, Dicruridae. (**3**) Turquoise-browed Motmot, *Eumomota superciliosa*, Momotidae. (**4**) Racquet-tailed Roller, *Coracias spatulatus*, Coraciidae. (**5**) Blue-headed Racquet-tail, *Prioniturus platenae*, Psittacidae. (**6**) Green Racquet-tail, *Prioniturus luconensis*, Psittacidae

3.3 Two Long and Short Feathers Protruding from the Head

The question then arises. These two tail feathers, that are so common, are they also present at other body locations? A search among the thousands of species described by ornithologists led to the identification of birds with two feathers protruding from the head.

A striking example is the King of Saxony Bird-of-paradise, which owes its royalist name, to the two imposing and long feathers which emerge from the back of its head (two birds of the same species are shown in Fig. 3.8 for the sake of clarity). These exquisite plumes are up to 50 cm long and bear 40–50 plastic-looking small “flags” blue on the upper surface and brown on the underside.

The Rufous Night-heron and the Little Egret have two long feathers of smaller size also starting from the head. The Horned Lark got its name from the two small, but distinct, feathers that rise from its head in the form of antlers (Fig. 3.8).

We are dealing with a situation comparable to the tail feathers: (1) Only two feathers are displayed at a time. (2) The four species represented belong to three unrelated families: Paradisaeidae, Ardeidae and Alaudidae. (3) The species have quite different habitats: arboreal (King of Saxony Bird-of-paradise), aquatic or semiaquatic (Heron and Egret) and terrestrial (Lark). (4) Their habitat may be

Fig. 3.6 Tail ornamentation and body coloration are related to sex and breeding activity. Fifteen of the 17 species of widowbirds and bishops (*Euplectes* spp.). *Left panel* shows males in breeding (nuptial) plumage; *right panel* females and non-breeding males. Not included: golden-backed bishop *E. aureus* and mountain marsh widowbird *E. psammocromius*

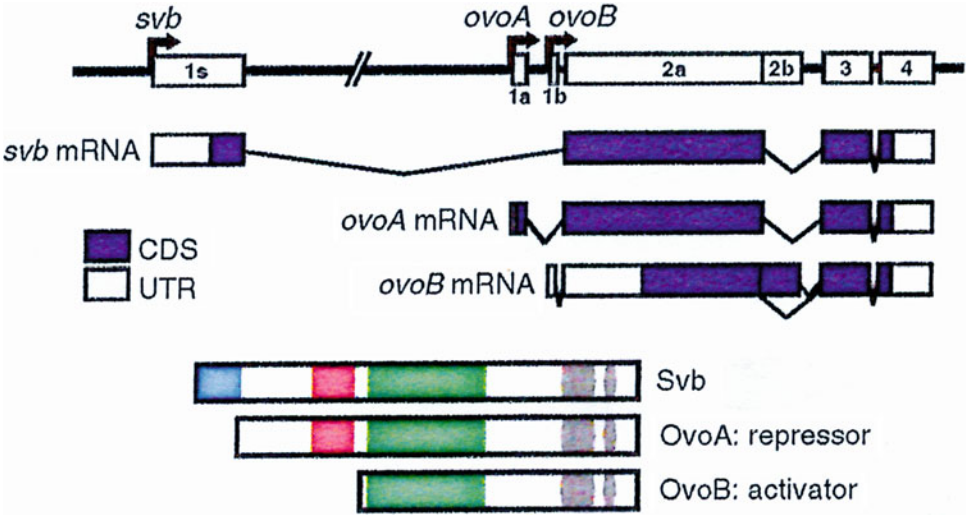

Fig. 3.7 DNA and proteins follow their own atomic evolution – a repressor is transformed into an activator by elimination of amino acids. The gene *svb* (*shavenbaby*) which defines the spatial pattern of hairy structures in the fruit fly, encodes three overlapping proteins of different lengths: *Svb*, *OvoA* and *OvoB*. The gene *pri* (*polished rice*) encodes small peptides which convert the *Svb* protein from a repressor to an activator by terminal truncation of amino acids. *mRNA* messenger RNA. Coding regions of mRNA (*CDS*) and untranslated regions of messenger RNA (UTR) are represented by blue and white boxes respectively. The *Svb*-specific protein region is in turquoise; the repression, activation and DNA binding domains are in red, green and gray respectively

Fig. 3.8 **Two feathers protruding from the head which are of different dimensions and shapes**. (**1**) King of Saxony Bird-of-paradise, *Pteridophora alberti*, Paradisaeidae. (**2**) King of Saxony Bird-of-paradise, *Pteridophora alberti*, Paradisaeidae. Two specimens of the same species are represented to show well the location of insertion and the details of the feathers. (**3**) Rufous Night-heron, *Nycticorax caledonicus*, ssp hilli, Ardeidae. (**4**) Little Egret, *Egretta garzetta*, ssp gularis, Ardeidae. (**5**) Horned Lark, *Eremophila alpestris*, Alaudidae

confined to the tropics but may extend to most regions of the globe. (5) Their food preferences and other forms of behaviour do not show immediate similarities.

A recurrence of the same genetic event which cannot be easily attributed to external factors is also expected to be involved in this case.

3.4 Two Long Feathers Arising from the Wing

Nothing is impossible. Life tells it in clear language, since it so often devises new alleys that can be hardly conceived.

Two long feathers suddenly are formed on the middle of the wings, with a length, about the double of the body size (attaining up to 78 cm). They are thin and straight, but in one species, out of 89 described in this family, the Standard-winged Nightjar, the long feathers finish in a large expansion which gives them the appearance of a flag called by ornithologists the "standard". The Pennant-winged Nightjar has also long feathers starting from the wings but lacking "standards" (Fig. 3.9).

There may be more cases available in the vast literature but in these species the phenomenon is clear-cut, as can be seen when the animal flies (Fig. 3.9).

Many extra long feathers could have been formed in this new position since every wing contains a large series of primary and secondary feathers. Yet the number two is maintained. Moreover, they have a precise wing location. In both the Standard-winged and the Pennant-winged Nightjar it is only the ninth primary feather that is elongated. Additionally, the long feathers: (1) appear only in the male, (2) are formed as breeding approaches and (3) are shed following this event being replaced by slow growing feathers. This indicates a hormonal process connected with sexual differentiation and the involvement of genes that determine the exact location and time of their emergence. The species previously mentioned are diurnal whereas Nightjars are mainly nocturnal. Their food preference is insects like that of many other families and they are distributed all over the world.

3.5 Particular Feathers Which Appear in Other Body Regions Indicating a Common Molecular Event

Nature surpasses our imagination. Besides the tail, the head and the wing particular feathers appear on the breast, the belly and the beak.

The Wild Turkey has a skin formation (called a "wattle" by specialists) which sticks out of the breast and is covered with feathers (Fig. 3.10). The Amazonian Umbrellabird and the Long-wattled Umbrellabird have large wattles descending from the breast and covered by dense black feathers. In the Bare-necked Umbrella bird the wattle hangs from the belly (Fig. 3.11). But what about the beak? In the White Bellbird a wattle grows from the upper part of the bill and this is covered with white short feathers which are described as having the "form of stars" (Fig. 3.10).

This means that particular feather formations, which diverge prominently from the usual distribution, emerge in all the main parts of a bird's body. Six species illustrate this phenomenon: Pied-crested Tit-tyrant (head), Standard-winged Nightjar (wing), Lesser Raquet-tailed Drongo (tail), Bare-necked Umbrellabird (belly), Wild Turkey, ssp merriami (breast) and White Bellbird (beak). They seem to be unrelated but were disposed along a single circle, combining the six positions, to emphasize that on the contrary they may be genetically interrelated (Fig. 3.11). Such a contention is supported by the finding that in the Herons some species, especially the day- and night-herons, have ornamental plumes on the head, the lower neck, the breast and the back. This shows that the long feathers occur within the same individual in four different positions – an indication that they are the result of a common internal molecular event. However, the feathers that appear on wattles, hanging from the bill, the breast and the belly may differ, in some way, from those being formed on the head, wing and tail (Fig. 3.11).

Another common feature of these ornamental feathers is that their growth tends to be restricted to males, they grow as the breeding season approaches and are usually shed following this developmental stage. This not only happens in the four body positions found in the herons but it is also a property (with minor variations) of the head, wing and tail feathers described previously.

To be noted is that the same gene that is responsible for the formation of an organ, such as: a leg or an eye, may lead to the production of the same organ at totally different positions in the body. In the fruit fly the gene *Antennapedia* can produce legs on the thorax but also on the head; and the gene *eyeless* can lead to the formation of eyes in: the wings, legs and antennae (Gehring 1998) (Chap. 7).

3.6 Feather Numbers Which are Multiples of Two Occur on Tail and Head

The number 2 dominates but its multiples: 6, 10 and 12 appear as well with high frequency. Obviously there are deviations from these numbers. The sequence: 2, 6 and 12 is of particular interest because it occurs both in the tail and the head.

The two long tail feathers that are typical of several species of the birds of paradise are thin like wires in the Blue Bird-of-paradise. Similar long thin feathers emerge from the tail of the Wired-tailed Manakin but instead they number 6. In the 12-wired Bird-of-paradise the equally thin feathers number 12 as testified by the name of the bird (Fig. 3.12).

Instead of being "wired" the tail feathers may be thick resulting in the same type of sequence: 2, 6, 12. As the name

Fig. 3.9 Two long feathers arising from the wing. In one species they finish on what ornithologists call a "standard" (a flag), in other related birds there is no terminal large expansion at the end of the feathers. (**1**) Standard-winged Nightjar, *Macrodipteryx longipennis*, Caprimulgidae. Male at rest and flying, to show the origin of the long feathers on the wings and their standards. The female does not grow long feathers. (**2**) Pennant-winged Nightjar, *Macrodipteryx vexillarius*, Caprimulgidae. Male at rest and flying showing long feathers starting from the wings but lacking standards. The female does not grow long feathers. (**3**) Standard-winged Nightjar. Photograph taken when in flight

Fig. 3.10 Body protuberances which are covered with feathers. These start from the breast and beak. (**1**) Wild Turkey, *Meleagris gallopavo*, ssp silvestris, Meleagrididae. (**2**) Amazonian Umbrellabird, *Cephalopterus ornatus*, Cotingidae. (**3**) Long-wattled Umbrellabird, *Cephalopterus penduliger*, Cotingidae. (**4**) White Bellbird, *Procnias albus*, Cotingidae. The wattle growing from the upper part of the bill is covered with short white feathers

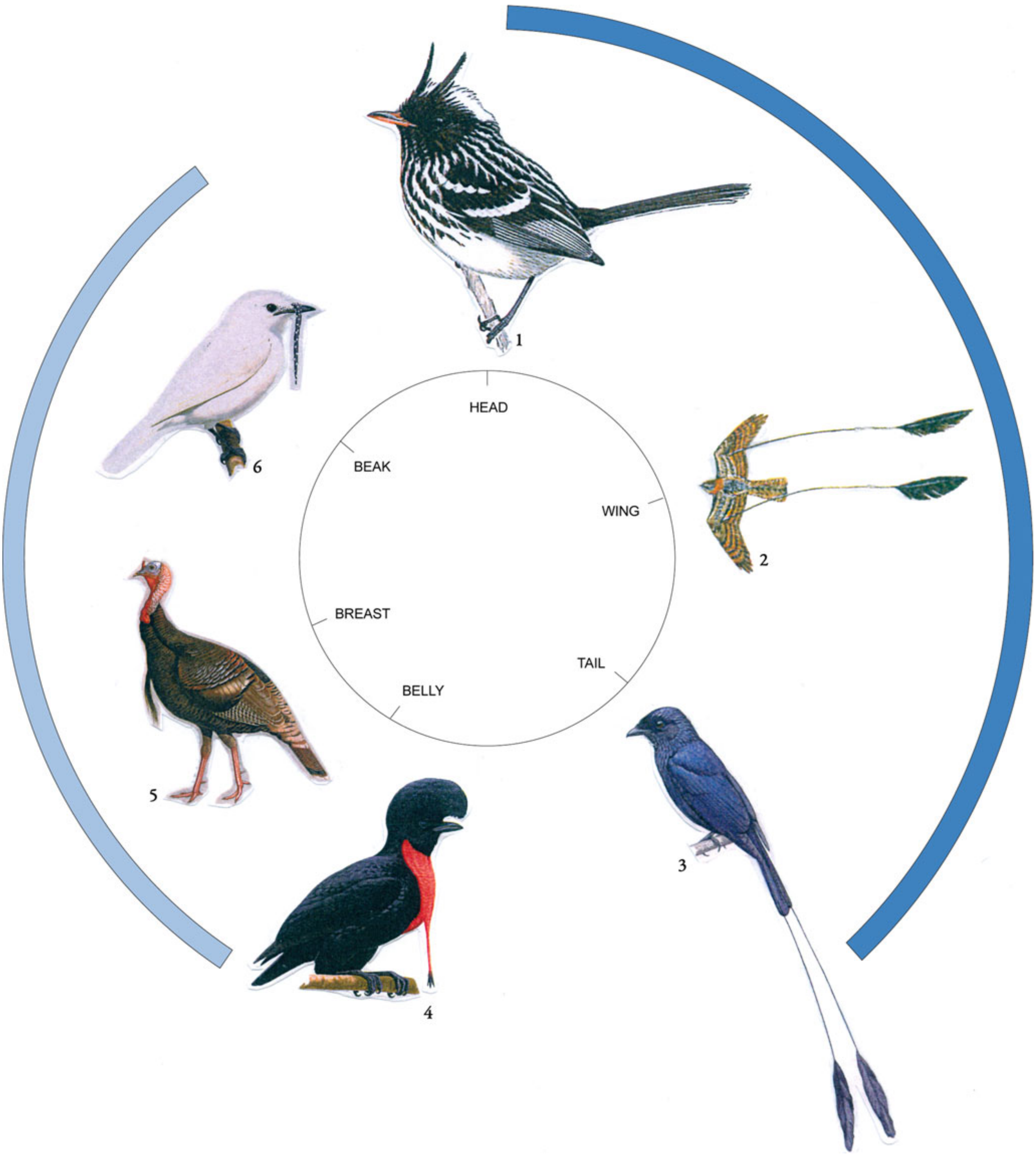

Fig. 3.11 Conspicuous feathers which stand out at five different body locations: head, wing, tail, belly, breast and beak. (**1**) Pied-crested Tit-tyrant, *Anairetes reguloides*, Tyrannidae. (**2**) Standard-winged Nightjar, *Macrodipteryx longipennis*, Caprimulgidae. (**3**) Lesser Racquet-tailed Drongo, *Dicrurus remifer*, Dicruridae. (**4**) Bare-necked Umbrellabird, *Cephalopterus glabricollis*, Cotingidae. (**5**) Wild Turkey, *Meleagris gallopavo*, ssp merriami, Meleagrididae. (**6**) White Bellbird, *Procnias albus*, Cotingidae. The feathers that appear on wattles, hanging from the bill, breast and belly, are considered to form a group separated from those being formed directly on the head, wing and tail

Fig. 3.12 Long tail feathers which occur in the multiple numbers: 2, 6 and 12. *Upper row*: birds with thin feathers. *Lower row*: birds with thick feathers. (**1**) Blue Bird-of-paradise, *Paradisaea rudolphi*, Paradisaeidae. (**2**) Wire-tailed Manakin, *Pipra filicauda*, Pipridae. (**3**) Twelve-wired Bird-of-paradise, *Seleucides ignotus*, Paradisaeidae. (**4**) Ribbon-tailed Drongo, *Dicrurus megarhynchus*, Dicruridae. (**5**) Rufous-crowned Emu-wren, *Stipiturus ruficeps*, Female, Maluridae. (**6**) Dimorphic Fantail, *Rhipidura brachyrhyncha*, Dark morph, Rhipiduridae. (**7**) Rufous Fantail, *Rhipidura rufifrons*, ssp kubaryi, Rhipiduridae (the 12th feather is hardly seen)

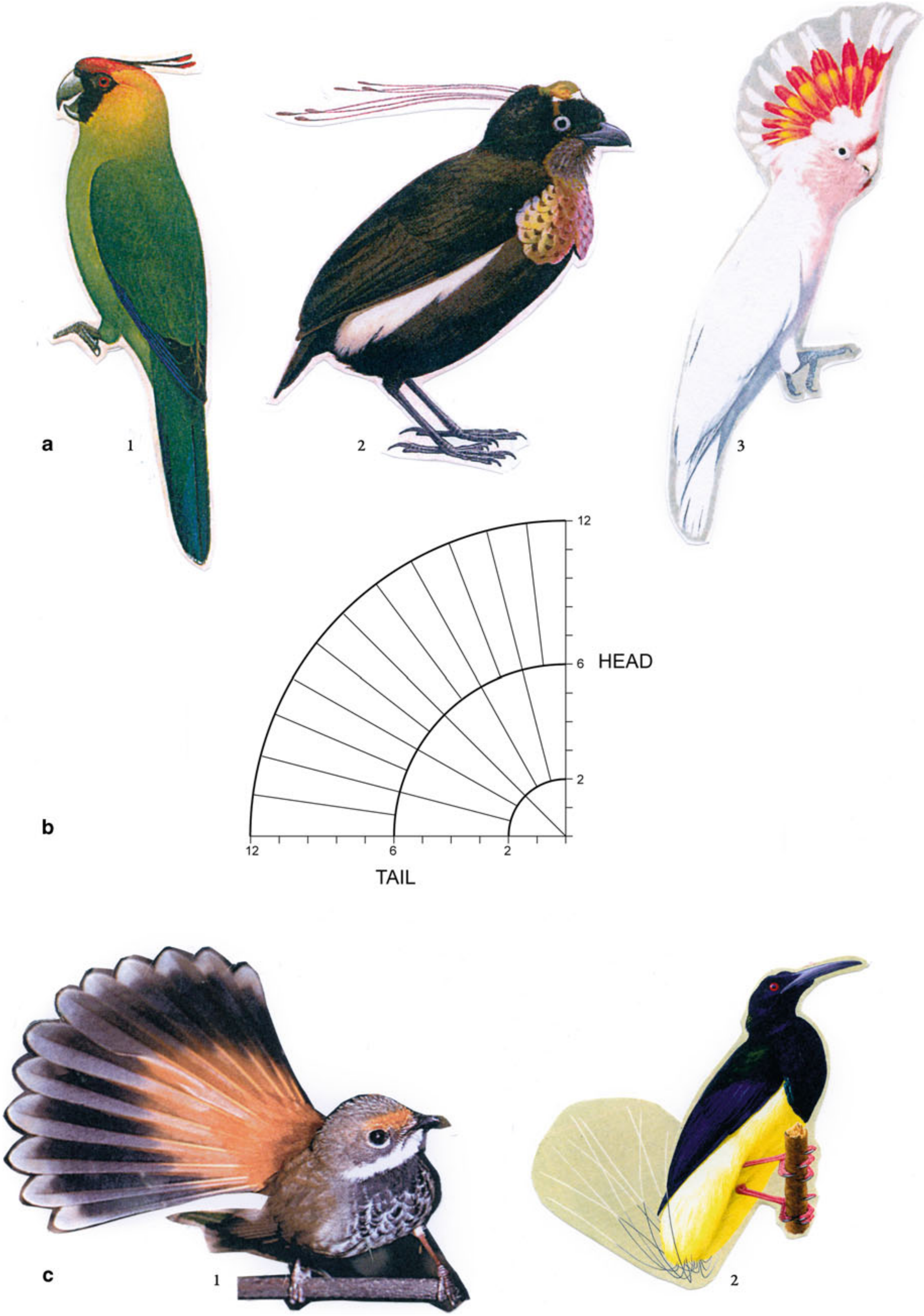

Fig. 3.13 **(a) Long feathers starting from the head occur also in the multiple numbers: 2, 6 and 12**. (**1**) Horned Parakeet, *Eunymphicus cornutus*, Psittacidae. (**2**) Foja Parotia, *Parotia berlepschi*, Paradisaeidae. (**3**) Major Mitchell's Cockatoo, *Cacatua leadbeateri*, Cacatuidae. **(b) Diagram depicting the occurrence of 2, 6 and 12 feathers both in the head and tail. (c) Twelve feathers – either thick or thin – build a fan in the tail**. (**1**) Rufous Fantail, *Rhipidura rufifrons*, Rhipiduridae. (**2**) Twelve-wired Bird-of-paradise, *Seleucidis melanoleucus*, Paradisaeidae

specifies, the Ribbon-tailed Drongo has two long feathers that resemble ribbons. The Emu-wren has 6 and the Fantails have 12. In this last case the species name also conveys the characteristic shape of the tail which looks like the fans used by ladies for centuries.

What is remarkable is that this same sequence is found with a head location. The Horned Parakeet got its name from the two feathers which stick out of its head like horns. From the head of the Foia Parotia emerge 6 and the Major Mitchell's Cockatoo displays a colourful crown with 12 (as counted from its drawing) (Fig. 3.13). These species (Figs. 3.12 and 3.13) belong to the families: Paradisaeidae, Pipridae, Dicruridae, Maluridae, Rhipiduridae, Psittacidae and Cacatuidae. Most of them have no immediate relationship with each other.

3.7 The Occurrence of Fixed Numbers in Other Animals

Before the birds occupied the Earth 135 million years ago, the invertebrates had already been there for a long time. They started to evolve about 600 million years ago (Barnes 1980). The constancy of six legs in insects is so extreme that the whole animal class is defined by their presence. Similar invertebrates, like the spiders, have eight legs which is also a fixed number.

If the insects had been found: (1) limited to a small number of species or (2) isolated in some islands of the Pacific Ocean, one would tend to explain this constancy of body pattern as being due to their isolation or any other similar factor. But no other animal group diversified more than the insects. Their species number exceeds one million, new ones are being added every day as their study proceeds. Moreover, the number of insect species alone is larger than that of all other animal and plant species combined. Yet the number 6 has been preserved.

Variation could have easily occurred because the Centipedes and the Millipedes, which are not distant relatives, have as many as 750 legs (Burnie 2004). This constancy has bewildered biologists for generations. At present, the data from molecular biology lead us at once to the homeotic genes which are known to determine the formation of legs in insects. But, although the genomes of several species, from yeast to humans, have been sequenced, including that of the fly *Drosophila* (Bork and Copley 2001), we lack knowledge of the mechanisms which have imprisoned the DNA sequences in such a way that they could not change the leg number for millions of years. Proteins are now known to intervene in gene expression but we are far from having accurate information of the processes that impose this tremendous body constancy and bilateral symmetry (Chap. 9).

Sources of Figures

Fig. 3.1 Original Plate composed of species depicted in the **HBW**: **(1)** Volume 14 – Plate 22 – Nr. 14, **(2)** 14 – 22 – 15, **(3)** 9 – 37 – 295, **(4)** 6 – 7 – 39 ssp costaricensis, **(5)** 6 –7 – 39 ssp mocinno.

Fig. 3.2 Original Plate. **HBW**: **(1)** 14 – 28 – 41, **(2)** 14 – 28 – 40, **(3)** 14 – 27 – 38, **(4)** 14 – 26 – 32, **(5)** 14 – 26 – 31.

Fig. 3.3 Original Plate. **HBW**: **(1)** 14 – 26 – 33, **(2)** 5 – 68 – 254 ssp annae, **(3)** 5 – 73 – 288, **(4)** 5 – 68 – 254 ssp melanantherus, **(5)** 6 – 24 – 8.

Fig. 3.4 Original Plate. **HBW**: **(1)** 6 – 9 – 7, **(2)** 8 – 15 – 58, **(3)** 9 – 40 – 331, **(4)** 11 – 19 – 12, **(5)** 9 – 12 – 20, **(6)** 13 – 9 – 19.

Fig. 3.5 Original Plate. **HBW**: **(1)** 5 – 73 – 294, **(2)** 14 – 10 – 5 ssp grandis, **(3)** 6 – 23 – 3 ssp bipartita, **(4)** 6 – 28 – 4 ssp spatulatus, **(5)** 4 – 39 – 117, **(6)** 4 – 39 – 118.

Fig. 3.6 Prager, M. 2010. Phylogeny and Signal Diversity in Widowbirds and Bishops (*Euplectes* spp.) Doctor's Thesis, University of Gothenburg, Department of Zoology, Gothenburg, Sweden (Illustration by Dale A. Zimmerman) (Fig. 1 page 6).

Fig. 3.7 Kondo, T. et al. 2010. Small peptides switch the transcriptional activity of shavenbaby during *Drosophila* embryogenesis. Science *329*: 336–339 (Fig. 2 page 337).

Fig. 3.8 Original Plate. **HBW**: **(1)** 14 – 23 – 22, **(3)** 1 – 29 – 37 ssp hilli, **(4)** 1 – 27 – 23 ssp gularis, **(2)** Beazley, M. 1974. The World Atlas of Birds, M. Beazley, London, UK (Fig. on page 206). **(5)** Mullarney, K. et al. 1999. Fågelguiden – Europas och Medelhavsområdets Fåglar i Fält. A. Bonniers Förlag, Stockholm, Sweden (Fig. on page 239, adult, summer).

Fig. 3.9 Original Plate. **HBW**: **(1)** 5 – 35 – 82, **(2)** 5 – 35 – 83, **(3)** Photograph on vol. 5 page 310.

Fig. 3.10 Original Plate. **HBW**: **(1)** 2 – 35 – 1 ssp silvestris, **(2)** 9 – 7 – 61, **(3)** 9 – 7 – 62, **(4)** 9 – 8 – 65.

Fig. 3.11 Original Plate. **HBW**: **(1)** 9 – 19 – 53, **(2)** 5 – 35 – 82, **(3)** 14 – 9 – 3, **(4)** 9 – 7 – 60, **(5)** 2 – 35 – 1 ssp merriami, **(6)** 9 – 8 – 65.

Fig. 3.12 Original Plate. **HBW**: **(1)** 14 – 28 – 42, **(2)** 9 – 10 – 3, **(4)** 14 – 10 – 15, **(5)** 12 – 42 – 17, Female, **(6)** 11 – 15 – 27, **(7)** 11 – 14 – 25 ssp kubaryi, **(3)** Perrins, C. 1976. Bird Life. Elsevier Phaidon, Oxford, UK (Fig. 6 page 107).

Fig. 3.13 Original Plate. **HBW**: **(A)** **(1)** 4 – 35 – 73, **(2)** 14 – 23 – 21, **(3)** 4 – 28 – 15, **(B)** Original diagram, **HBW**: **(C)** **(1)** Photograph, volume 11 on page 216, **(2)** 14 – 26 – 35.

The Evolution of the Birds

4

4.1 The Origin of Birds is Disputed – Arboreal Monkeys were not Able to Develop Wings

As several authors acknowledge the origin and evolutionary history of birds is poorly known in comparison with that of reptiles and mammals. Fossils are rare, most probably because the skeletons of birds are fragile. The well-known five fossils of *Archaeopteryx,* from the limestone deposits in Bavaria, are about 150 million years old (Upper Jurassic). But there is a gap in the fossil record until the Cretaceous (130 million years ago). *Hesperornis regalis* from this period, still retained primitive teeth, had small wings and a weak sternum. By the end of the Cretaceous the toothed birds disappeared. All the fossil species of the present era are toothless animals.

Archaeopteryx was characterized by grasping forelimbs, long tail and a skeleton resembling that of reptiles. It was capable of gliding or primitive flight since it had feathers of modern design. By late Cretaceous *Ichthyornis* had a keeled sternum allowing the insertion of bulky flying muscles and maneuverability of the tail.

This crucial transformation was little understood until new fossils were found in China with intermediate characters. A new bird species, *Sinornis santensis*, was collected in lake sediments that belong to the lower Cretaceous (135 million years old). The species has a toothed snout, a pelvis and many other primitive features that are present in *Archaeopteryx* and *Ichthyornis* but it also exhibits a broad sternum, has a wing-folding mechanism and other modern flight functions (Sereno and Chenggang 1992).

Controversy and debate have dominated in the last decade due to the discovery of feathered dinosaurs and the reexamination of the earliest fossils. The results from phylogenetic trees have also added to these disputes (Zhou 2004). The most controversial issue has been the finding of feathered dinosaurs and their close relatives, such as oviraptorosaurids and dromaeosaurids, which have been proposed to be flightless birds. Other fossils have added to the confusion. *Protoavis texensis*, a late Triassic bird is considered 75 million years older than *Archaeopteryx*. Some authors have argued that it is a chimera belonging to two different species. *Rahonavis,* a long-tailed bird from the late Cretaceous of Madagascar, is also considered a composite of avian and theropod traits. Other fossils have been added to this list of controversial birds.

It is clear that the debate is not over. There are two separate hypotheses on the origin of avian flight: (1) Terrestrial or “ground-up” coupled with the dinosaurian ancestry of birds. (2) Arboreal or “trees-down” which was linked with the thecodont origin of birds. The argument runs that the large-sized terrestrial dinosaurs could not be the ancestors of birds. Avian flight originated in the trees taking advantage of gravity (Ostrom 1986; Feduccia 1999).

One serious difficulty encountered by these assumptions resides in the fact that the monkeys have had an arboreal life, jumping down from trees, for 45 million years, without having acquired wings or wing rudiments. As Napier and Napier (1985) have pointed out: “The arboreal monkeys are the most generalized of all primates, both structurally and behaviourally. They are also the most successful in terms of wide geographic range and high population numbers”. Other monkeys, like the macaques, are ground-living, a place where they face numerous predators that they could have avoided if they had been able to fly. Both groups have diversified into not less than 242 species (Burnie 2004). Yet there are no signs that they developed wings as they continuously jump from trees or run on the ground.

At least gliding could have developed in the monkeys but it occurred in quite different mammalian orders: the marsupial gliding phalangers, the rodent gliding squirrels and the dermopterans or gliding “lemurs”. None of these animals has powered flight, they have folds of skin extending between the limbs which enable gliding. This ability is considered to have evolved independently in these distinct groups since it also appeared among the reptiles where there are gliding lizards (Savage and Long 1986).

A. Lima-de-Faria, *Molecular Geometry of Body Pattern in Birds*,
DOI 10.1007/978-3-642-25301-0_4, © Springer-Verlag Berlin Heidelberg 2012

Actually flight did emerge in the mammals, but in an independent and well-defined group. Among the 4,475 species of mammals, only the bats acquired wings (977 species). All other orders continue to run and swim, none has grown such well-developed structures and efficient flying organs.

As Zhou (2004) was obliged to conclude, in his discussion of the evolution of flight in birds, the origin of flight should be decoupled from the origin of birds if this problem is going to be understood. The present hypotheses on the origin of flight, although simplistic, have been valuable, because they obliged geneticists to ponder over the origin of this event and to investigate its underlying molecular mechanism.

The advantage of an idea, how provisory it may be, is that an idea can be superseded but the lack of an idea cannot.

4.2 The Long Journey that Led to the Establishment of Chemical Periodicity

Chemical periodicity took over a century to elucidate. Although information had been available since 1772 on the regularity of certain properties of the chemical elements, no one could think of order among the elements for 100 years.

In 1865 *Newlands* proposed his law of octaves, showing that the properties of certain elements repeated themselves and that they could be put together in groups of eight. He sent his paper to *Nature*, where it was rejected and ridiculed.

Six years passed, and in 1871, *Mendeleev* produced periodic tables in which he left empty spaces that represented elements not yet discovered, but of which he predicted the properties. His predictions were confirmed a few years later and the concept of periodicity soon became established in chemistry.

However, no chemical or physical mechanism was available that could explain such a strange property. It took 50 years more until this was elucidated. Only when the electronic organization of the atom became established in the 1920s and 1930s did it become evident that it was, not the total number of electrons, but only the number of electrons that occur in the outer shell of an atom that governs its properties.

A most significant feature of chemical periodicity, is that chemical elements exhibit similar properties, irrespective of their degree of complexity. A simple atom such as beryllium (Be, atomic mass 9.0) can have the same properties as a most complex one, such as radium (Ra, atomic mass 226,0). Both are alkaline earth metals which are silvery white, lustrous and relatively soft. The same is true for helium (He, a.m. 4.0) and radon (Rn, a.m. 220), which are both inert gases. This means that extreme changes in complexity of organization among chemical elements can lead to the display of the same basic properties. Moreover, not just one, but a package of as many as ten properties, are repeated in the elements that happen to have the same electron number in their outermost shells.

Although chemical periodicity is now firmly established and has become the basis of the interpretation of most chemical phenomena, there are irregularities. Not less than 700 different periodic tables have been published (Mazurs 1974) and these mirror the presence of exceptions and of structures that are still difficult to explain. The location of helium (He) in the tables varies with the author and copper (Cu) and chromium (Cr) do not fit easily into the periodicity charts. The length of the periods built by the elements is not constant either. Although there is variation the periodicity of the elements has become a most powerful instrument in the understanding of chemical transformations (Sanderson 1967; Greenwood and Earnshaw 1989; Atkins 1995; Scerri 2007).

4.3 From Chemical to Biological Periodicity

At present the concept of periodicity may seem as inappropriate to biologists as it was to chemists in the first half of the nineteenth century. However, the advancement of molecular biology has been so rapid that we have been obliged to revise or abandon some of our previous concepts.

A search for periodicity among living organisms discloses, that as in the case of the chemical elements, not just one property, but a series of biological functions and structures displaying periodicity. Moreover, the periodicity results, also like in the case of the single atoms, from the emergence of the same property in the simplest as well as the most complex organisms. Likewise, a small or a large amount of DNA is not a limiting factor to the emergence of the same basic structures and functions. Also, as in the case of atoms, the length of the period does not need to be always the same.

Periodicity provides an explanation of the sudden emergence of functions that had been absent in many species for millions of years of evolution. An example is the placenta. This organ appears at first in some of the most primitive invertebrates, such as the Onychophorans, turns up in fishes to disappear again. Later it is formed in other groups of vertebrates, such as amphibians and reptiles, it becomes again absent in marsupial mammals and suddenly reappears as the dominant feature of the placental mammals. In all these different organisms its function is essentially the same and it attains a degree of complexity that is not necessarily related to genetic complexity. Besides the placenta other functions display periodicity. Some of them are the recurrent emergence of the penis, the repeated appearance of bioluminescence, the punctuated form of advanced vision in invertebrates and the capacity to fly (Lima-de-Faria 1995, 1997, 2001).

4.4 The Periodicity of Flight

The Chordates, which include the vertebrates, build only one phylum. But the invertebrates have diversified into over 25 phyla. Yet in only one of them, the Arthropoda, did flight emerge, and within this phylum only the class insecta developed this ability. No other invertebrate group had shown this phenomenon before the insects, and no other invertebrate group displayed it in the future. This was not due to lack of time, as at least 600 million years have elapsed, since the invertebrates emerged. Such a punctuated appearance of this function is one of the characteristic features of biological periodicity. No other ancestral groups exhibited wings and no other invertebrate phyla that were later formed were able to fly. An additional characteristic is that flight at its origin (350–270 million years ago) attained full capacity. The fossils of the giant dragon fly *Meganeura*, which inhabited the forests of the Carboniferous period, had wings that measured 73 cm from tip to tip. Many bird species have smaller wings and the insects that live at present have wings of smaller size.

The second time flight appeared it showed no direct connection with that of insects. As the vertebrates emerged, the fishes, the amphibians and most reptiles could not fly. The flying reptiles, the pterosaurs (230–195 million years ago) had wings built by a different type of skeleton, but which were equally efficient in allowing them to fly.

The pterosaurs became extinct during the Cretaceous period leaving no survivors. Later, the situation repeated itself. The birds, which emerged 150–135 million years ago, are supposed to have as ancestors flightless reptiles, such as the Thecodonts, the main reptile group during the Triassic period (Walker 1974).

The mammals started their evolution about 100 million years ago, the marsupials appearing first around 63 million years ago and the placentals about 58 million years ago. During their long evolution the mammals diversified into over 20 orders, without any indication of flying capacity. Within this large number of flightless families and species, appeared a single order that had no direct connection with the birds or the flying reptiles, but which got highly effective wings. These were the bats which emerged about 45 million years ago. Fossils that represent intermediate stages have so far not been found, and those that exist are so well preserved that they disclose the stomach contents of the first bats (Colbert 1980).

Equally showing no signs of direct relationship to closely related species was the emergence of flight among fishes. These vertebrates arose about 425 million years ago and are represented today by a large number of species. The teleosts appeared 190 million years ago. Among them a few species fly, and do so in an environment that is adverse to their respiration, namely in air. They are obliged to return within minutes to water otherwise they would die, but their flight shows a degree of complexity considered not inferior to that of insects (Hanström and Johnels 1962; Beazley 1980).

The evolution of flight discloses that in non-related groups and on unexpected occasions, animals that did not fly gave rise to species that became aerial with high efficiency. Most significant for the understanding of periodicity, is the fact, that like in the chemical elements, the degree of complexity of the organism is not a limiting factor to the emergence of the properties, simple invertebrates like the insects, as well as the complex mammals, such as the bats, display the same high capacity to fly.

Several bird and insect species have wings but do not fly. A series of parts, organs and specific molecules must be present for flight to occur.

The comparison between insects, pterosaurs, birds, fishes and bats reveals that similar basic solutions were used in these different groups (Fig. 4.1). A coherent and rigid pattern recurred in all of them: (1) A fusiform body is present in most groups. (2) The wings are located above the center of gravity on the dorsal surface both in invertebrates and vertebrates. (3) Air-filled bones and other organs are present in several groups. (4) Antagonistic muscles and articulations are obligatory components. (5) The same source of energy, glycogen, is used by insects and birds. (6) Measurement of speed, balance and vision are controlled by the nervous systems of the different organisms, although the brain of an insect is at least 100 times smaller than that of a bat (McFarland 1981).

Fishes do not perform a passive gliding like some squirrel species do, but use powerful muscular contractions that oblige the body and the wings to vibrate like those of insects (as much as 70 contractions per second). Fishes can circle around a boat, can stop in air, and modify their flying direction at ease, as birds do (Hanström and Johnels 1962) (Fig. 4.2). The marine forms of flying fishes populating the tropical seas, such as *Exocoetus*, are part of a family (with 48 species) which have all well-developed pectoral fins. These are used in flight as gliding wings. An enlarged lower part of the caudal fin is employed in thrust while the fish is taking off from the waves. As Rayner (1986) puts it: “The flight performance can often be impressive, with speeds up to 13 m/s and glides up to 50 m being recorded”.

Later studies revealed that the fresh water fish of the African swamps *Pantodon bucholzi* and the flying hatchet fish *Gasteropelecus sp.* “undoubtedly leave the water on short flights that involve flapping of the pectoral fins”. This last flying fish has extremely well-developed pectoral muscles that make up 25% of the body weight, which is more than most birds (Davenport 1994).

Hence, there are two groups of flying fishes: (1) those in which the caudal and pectoral fins vibrate and glide and (2) those which beat the fins both during taxing and in flight. The gurnards are fish which also have greatly enlarged

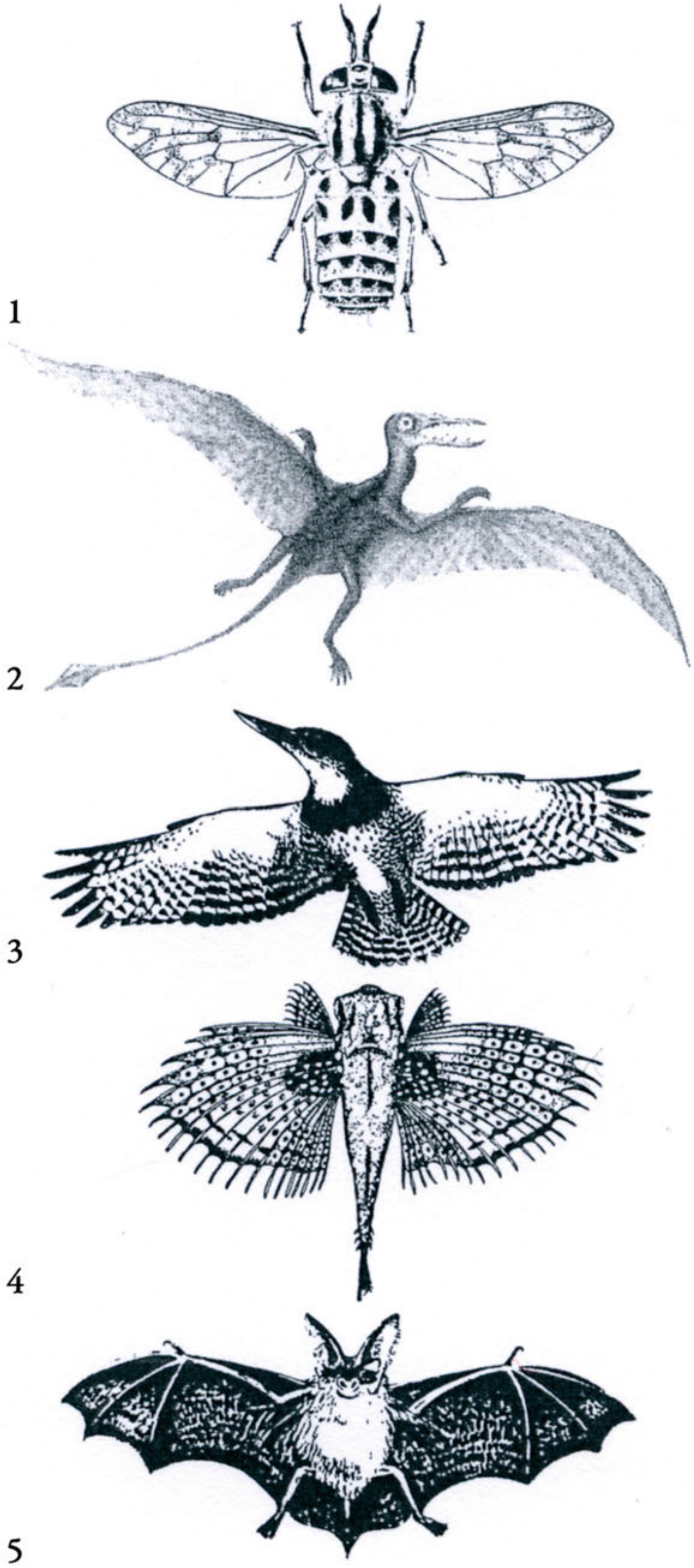

Fig. 4.1 **Periodicity of flight**. (**1**) Insect *Chrysops discalis*. (**2**) Extinct flying reptile *Rhamphorhynque*. (**3**) The bird, giant kingfisher, *Megaceryle maxima*. (**4**) Flying fish *Dactylopterus orientalis* (gurnard). (**5**) A bat (flying mammal)

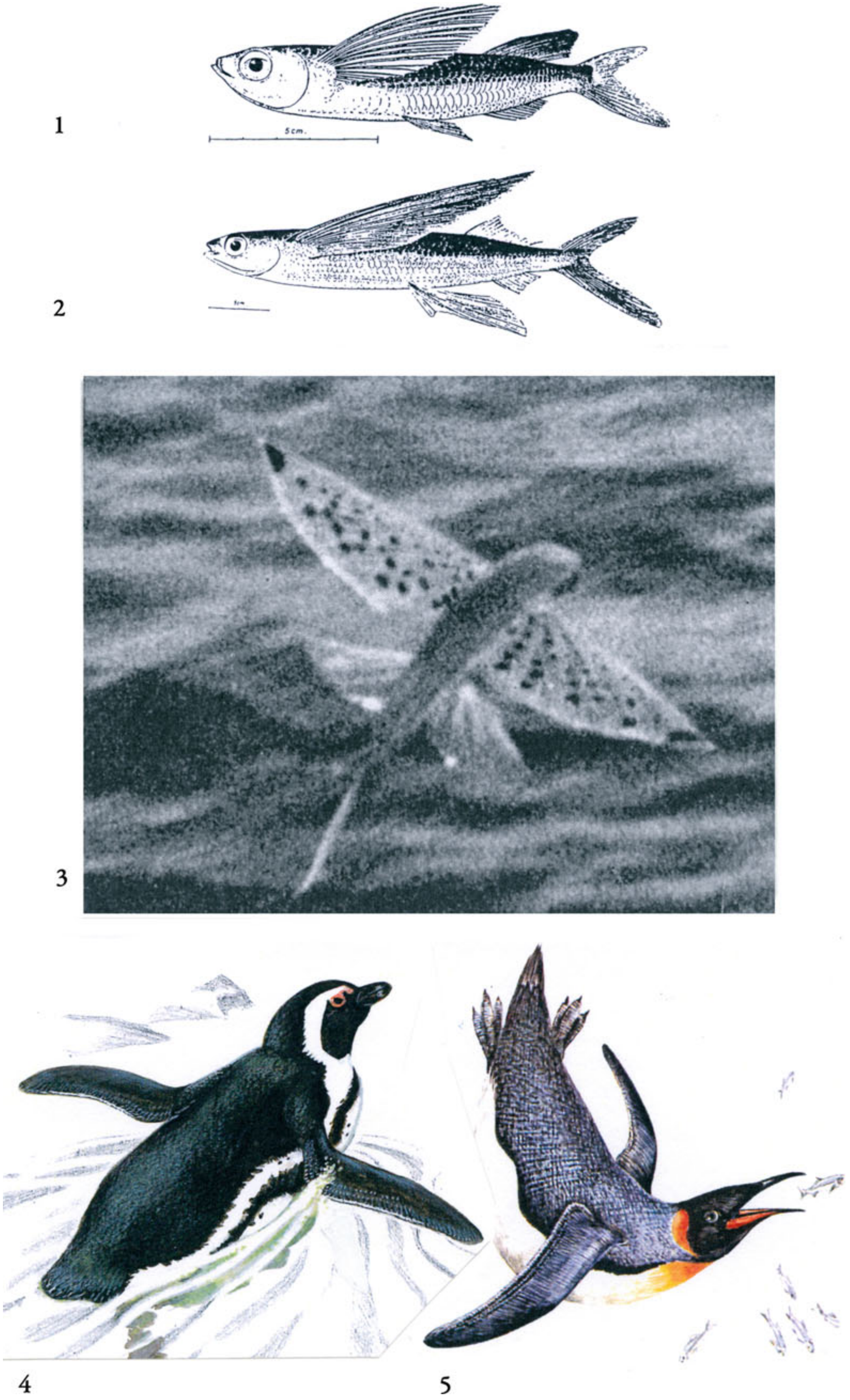

Fig. 4.2 **Flight in fishes and swimming in birds**. (**1**) The Atlantic two-winged flying fish *Parexocoetus mento atlanticus*. (**2**) The four-winged flying fish *Cypsilurus heterurus* also from the Atlantic Ocean. (**3**) A four-winged fish flying over the ocean (Photo by A. Christiansen). (**4**) A Jackass penguin coming ashore. (**5**) The King penguin *Aptenodytes patagonica* may dive to considerable depths while hunting

pectoral fins and seem to represent an intermediate stage (Greenwood and Thomson 1960; Davenport 2003).

Earlier interpretations of the origin of flight in fishes considered it to be the result of an escape from predators. More recent work has led to the conclusion that fishes travel considerably faster in air than in water. This allows a reduction in energy costs of transport, a solution used by aquatic birds and mammals, such as dolphins (Rayner 1986).

A particular feature to be considered is the skeleton of insects, that does not consist of bones and is thus different from that of vertebrates, yet allows the same solution. A corresponding situation occurs in vertebrates. They have created organs that do not either possess a bony skeleton but are equally functional. An example is the large caudal fin of whales which measures over a meter. This body organ did not exist in the ancestors of whales and has no skeleton. Yet it is hardly distinguishable, in its form and function, from the caudal fin of a fish which has a well developed bony skeleton. Hence, in vertebrates, organs that are practically identical in form and function, can be produced with or without bones (Macdonald 1984).

The periodicity of flight is characterized by the following features: (1) Flight arises without immediate predecessors in five major groups. (2) Few intermediate forms seem to have been involved or it appeared suddenly. (3) It tends to occur in a restricted class or order. (4) It consists of a coherent package of structures and functions several of them being obligatory components in all the groups. (5) The evolutionary position of the organism is not directly related to the complexity of the phenomenon. The flight of bats is not more complex than that of birds. (6) The number of wings is not either correlated to the evolutionary position of the species. Birds have only two wings, whereas insects and fishes may have four. (7) There seems to be no obligatory relationship to a specific type of environment, since fishes fly in a medium (air) adverse to their normal respiration, which takes place in water. Moreover, all mammal orders, except the bats, remained terrestrial and aquatic, and among all the aquatic and terrestrial invertebrates, only the insects conquered the air. (8) The interval at which flight has occurred is difficult to estimate due to the uncertainties in the timing of the fossil record. Yet, it is expected that the length of the period may not be always the same since this is already the case with the simple chemical elements (Lima-de-Faria 1995, 1997).

4.5 Molecular Mechanisms that may be Responsible for Periodicity and the Emergence of Coherent Structures

When a phenomenon is recognized, it cannot be expected that the mechanism responsible for its occurrence becomes immediately available. However, several main mechanisms can be considered.

Most structural genes in multicellular organisms consist of intervening DNA sequences termed introns and other sequences coding for proteins termed exons. These two types of sequences alternate and can recombine. New mosaic proteins are formed when exons located originally in other DNA sequences move to new locations. Examples are the cholesterol transport protein and the human tissue-type plasminogen activator (Südhof et al. 1985a, b; Ny et al. 1984).

Still more interesting is alternative RNA splicing since it does not change the DNA sequences of the cell. Yet the mechanism modifies the messenger RNA, the result being the formation of different proteins. Since the phenomenon is reversible this is most significant to understand periodicity: (1) It is not necessary to change the genetic constitution to produce a different protein and (2) an old protein can suddenly reappear due to the reversibility of the RNA splicing. Examples are the sarcomeric contractile protein genes. This means that new and old proteins can be formed without changing appreciably the genetic constitution of the organism (Breitbart et al. 1987; Smith et al. 1989; Van der Ploeg 1990).

The emergence of coherent packages of structures and functions that are involved in flight can be better understood in the light of the internal cascades of molecules that have been studied recently. The coherence arises from the fact that the initial production of a single molecule obliges the release of a series of other substances that follow in a cascade and which have simultaneously morphogenetic effects on a group of different tissues and organs.

Blood clotting in humans is one example of such an event. It involves more than ten proteins that follow in a rigid sequence determined by intrinsic molecular processes (Rydén and Hunt 1993). Another case with special significance for periodicity is the action of the hormone produced by the anterior pituitary, an endocrine gland located in the brain. The action of a single molecule results in radical functional changes in quite different body organs. As a result of three successive cleavages a polypeptide is carved into six hormones. The resulting amino acid sequences act on: (1) the adrenal cortex, (2) affect lipid metabolism, (3) change the pigment of the skin, and (4) modify brain function (de Duve 1984). Thyroxine in frog embryos has similar effects. Its action leads to drastic changes in (1) the heart, (2) the digestive apparatus and (3) the muscles of the larva. Moreover, new organs are built which lead to the emergence of the adult frog. These are, among others, the lungs and a complete vertebrate skeleton with adjoining muscles forming body members not present in the larva. Controls show, that in the absence of thyroxine, no organ transformations occur (Alberts et al. 1983).

The most pertinent example is the molecular cascade that results in the formation of the placenta, which is an organ that also shows periodicity. This cascade has been studied in detail. The pathway, which is strictly canalized, starts with the follicle-stimulating hormone (FSH). This increases the cellular concentration of cyclic AMP (adenosine monophosphate). As a result proteins are produced that affect the transcription of DNA. A second cascade is started by the hormone oestrogen and as a result other molecules are formed which act on the uterus and lead to the development of the placenta (Dorrington 1979).

4.6 Genetic Analysis Discloses that the Same Genes are Involved in the Flight of Insects and Birds – The Impossible Became Possible

The wing of an insect has been considered by zoologists to be analogous to that of a bird, but not homologous. The reason was that the two structures are so different that they seemed to have no relationship. Any comparison seemed impossible and unreasonable.

The recent work on embryonic development in the fly *Drosophila* and vertebrates (including birds and mammals) has disclosed that the same type of genes are responsible for the formation of corresponding regions of the body in invertebrates and vertebrates. These genes, called homeotic genes, not only control the formation of similar structures but have also maintained the same order in the chromosomes of the distantly related species. The wings of birds are mainly formed by the bones and muscles of the anterior limbs. It has been found, by molecular analysis, that the genes responsible for limb formation in the chicken are homologous to the genes that lead to the production of the wings in *Drosophila*. The results show that the wing of an insect is determined by the same type of genes that decide the formation of the wing of a bird. The analogy has become a homology since it is the product of the ordered expression of the same DNA sequences (Affolter et al. 1990; De Robertis et al. 1990; Holland 1992; Lawrence 1992; McGinnis and Kuziora 1994).

4.7 The Direct Production of Flies with Four Wings

Confirmation that combination of genes may produce suddenly a structure and function that has not been available for millions of years, is furnished by the results in *Drosophila*. A normal fly has only two wings, but molecular biologists have been able to produce flies with four wings. What is remarkable is that these flies are not monsters but are quite well-formed and their new wings are equally normal. These accesory wings are also partly functional. Moreover, contrary to the generally accepted idea on the mechanism of evolution, these flies were neither obtained by selection of individuals that originally displayed rudimentary wings, nor by random gene mutations that led to successive progenies with bigger and better wings. The flies with four wings were obtained directly, without any progressive transformation.

The studies of Lewis (1978), Bender et al. (1983), Peifer et al. (1987), Duncan (1987) and Lawrence (1992), led to the production of four wing flies by a simple molecular manipulation combining mutations occurring in the genes *bithorax* and *postbithorax* (in another set of experiments the inactivation of the gene *ultrabithorax* was involved). These genes were somatically recombined following irradiation of larvae the result being the immediate appearance in the progeny of normal flies with four perfect wings (Fig. 7.2).

Insects with four wings are known to exist in nature and to be quite common, an example is the butterflies. Moreover, the position of the wings in the butterflies is the same as in the four-winged *Drosophila*. Among the vertebrates, fishes may display four wings as well.

The implications of this molecular transformation at the chromosome level are most significant for the understanding of evolution and of biological periodicity. They reveal the following. (1) The formation of new wings is an immediate and direct process. (2) The structures appear as "ready-made" the pattern being fully coherent from the onset. (3) The structures are accompanied by the corresponding functions, such as blood flow, control by the nervous system, access to large amounts of energy. (4) The position of the wings is not accidental but occupies the dorsal part of the body. (5) The genetic transformation apparently re-enacts in days what has occurred millions of years ago.

4.8 Wings in Birds may have Appeared "Ready-Made" and As "A Surprise" to the Animal – Birds with Extra Wings Produced in the Laboratory

The genes responsible for the production of the extra wings in *Drosophila* are part of the *bithorax complex*. Of relevance is that the *bithorax complex* is a cluster of genes that are the homeotic genes (Bender et al. 1983). This means that the direct production of a normal wing or of extra wings can be expected to occur in birds, as it does in *Drosophila*, since the genes are the same. This also means that the wings in birds may have originated "ready-made", just as they do in *Drosophila*. Hence, the structural and functional solutions that the living organism suddenly gets, occur as a package independently of being of advantage to the animal, or of representing a need. In other words, the structure combined with the function emerge whether the organism likes it or not, they come as "a surprise" to the animal, that it is obliged to use.

This type of reasoning was soon confirmed by experiments carried out in different laboratories. The application of the protein *fibroblast growth factor* to the chick embryo changed the expression of *Hox* genes inducing the formation of either an additional wing or an extra leg (Cohn et al. 1997). These results demonstrated that the wings of birds can be produced at will in the laboratory (Fig. 5.3) (Chap. 5).

4.9 Evolution was not Kind to the Birds – Wings have no Prehensile Fingers, Jaws Lack Teeth and the Penis is Rare

The general assumption is that evolution leads to better and better morphological and physiological solutions. Improvement is an idea usually associated with the transformation of species into novel ones. The situations in which negative effects have resulted tend to be sidestepped or ignored. Although mentioned sometimes, they are soon forgotten in the desire to see a permanent increase in perfection.

The cases in which evolution has led to deadly ends, inefficient organs, rudimentary anatomic structures, could cover easily a treatise.

When it comes to the birds, the tendency has been to herald their magnificent wings that led to the conquest of the air space. That is true, but there is another aspect, that now emerges, which shows that evolution was not so kind to the birds. The transformation of their forelimbs into wings without prehensile digits and the formation of their jaws without teeth had unexpected consequences that seriously affected their behaviour. Still worse, most bird species have no penis, copulating by means of an ineffective cloaca.

4.10 Evolution Created Serious Limitations in Birds

The transformation of the forelimbs into wings in birds has allowed them to fly but at the same time has devoided them of a valuable instrument. The inhibition of the ability to use the forelimbs to climb, and to catch food with fingers, as other vertebrates do, may not have been mentally erased and may still today give the bird a sense of frustration, because in this connection the wings are worthless or of little help.

Another limitation occurred. The jaws, which in mammals and reptiles have well-developed rows of teeth, became devoid of this valuable instrument used in the catching of prey and grinding of food.

There are, however, ways of circumventing difficulties. Any brain's main capacity, be it that of a social ant or of a bird, is the ability to recognize the difficulties facing the individual, or the social group, automatically looking for alternative solutions. Instead birds substituted these absent instruments by beaks and feet which they use in their predatory activity.

The presence of a horny beak in place of teeth is not unique to birds. Evolution uses many sidelines, as a result the same phenomenon occurs in turtles and was also present in dinosaurs (Pough et al. 2005).

4.11 A Sense of Frustration or of Amputation may have Remained in a Bird's Mind

The relationship between the emergence of the wing and the organization of limbs has not been the same during animal evolution.

In insects, where the wing first appeared (about 310 million years ago) it developed independently, the six legs being free and having no direct contact with the wing. Later when the wing reappeared in the pterosaurs (230 million years ago) it became connected with the forelimbs. These fossil flying reptiles could continue to use their fingers which stuck out from the wings. The pterosaurs had a wing membrane supported by only one of the five fingers, which was highly elongated, the other four remaining free (Babin 1980).

The fossil *Archaeopteryx* possessed a large wing, covered with feathers, in which three digits were well separated. This means that in the early evolution of birds at least three fingers were available that later disappeared. Evolution does not seem to have always led to positive situations.

When the wing, even later, reemerged in the bats (45 million years ago), one of the digits still remained free allowing these mammals to use it in various activities.

In the birds, this reduction of the fingers took the form of a real amputation. In the modern avian wing the first digit is vestigial and two other rudimentary fingers are incorporated into the wing. The result is that the upper part of the wing has a smooth surface in which feathers cover the whole forelimb (Fig. 4.3).

No animal can move its legs, arms or fingers without a previous decision starting from the brain that commands the desired movement. Besides it is well known that in humans when an arm is amputated the brain retains the memory of this event. Amputation of a limb in humans is usually followed by a feeling that the missing limb is still present. This has been called phantom limb awareness. Most individuals who suffered amputation describe it as not creating pain (Flor et al. 2006).

A second situation occurs in which a phantom limb pain develops in which the individual may experience from only short shocks to an excruciating pain—the individual having a vivid and intense perception of the missing body part. This

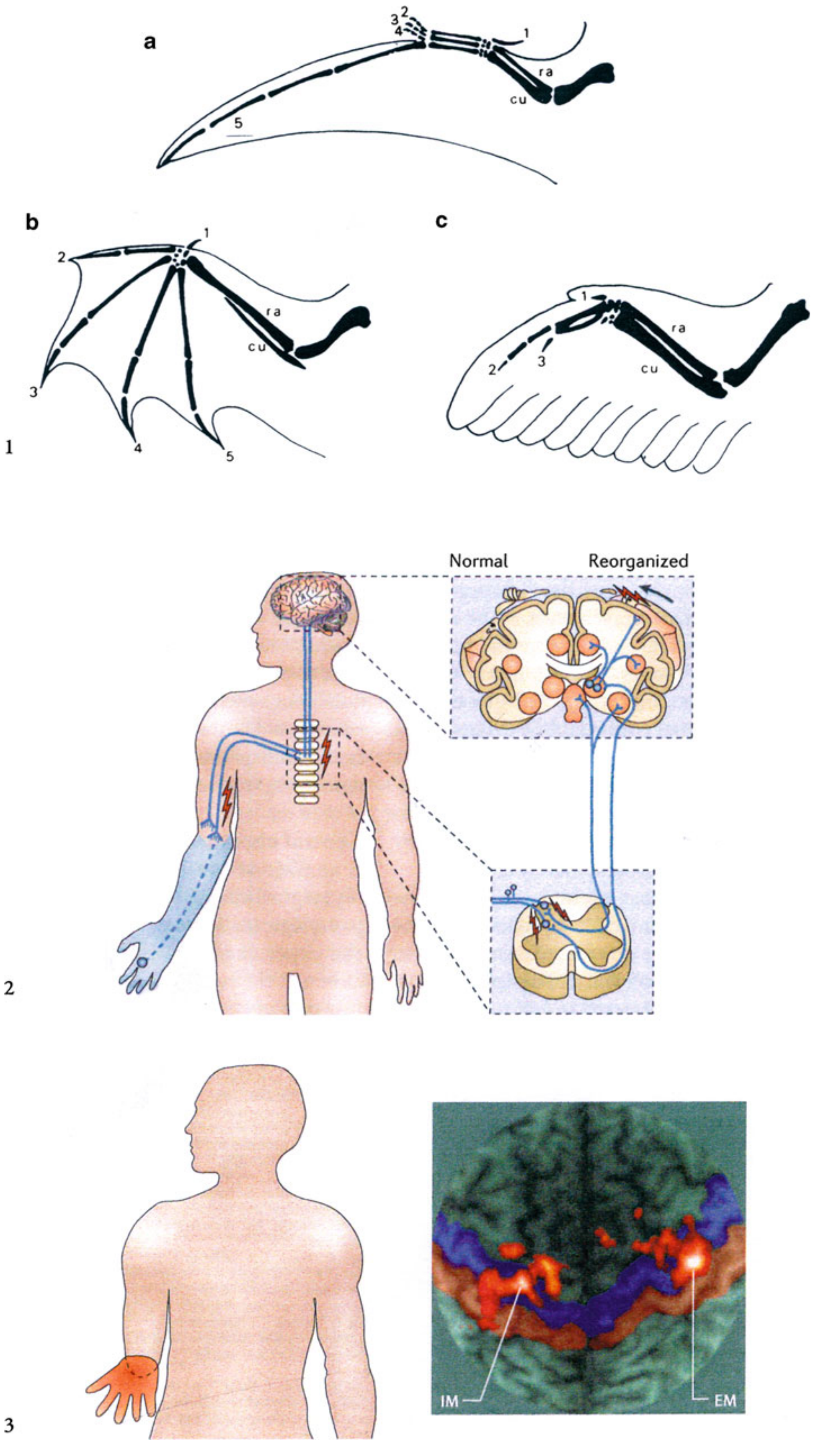

Fig. 4.3 Comparison of the wing structure in birds with amputation in humans.
(**1**) Wing structure in: a pterosaur (**A**), a bat (**B**), and a bird (**C**); ra: radius; cu: cubitus. Note the presence of: four free fingers in pterosaurs, of one free finger in bats, but the lack of prehensible fingers in the wing of adult birds. Compare with Fig. 4.4.
(**2**) **Diagram of areas involved in the generation of phantom limb pain**. The peripheral areas include the residual limb and the dorsal root ganglion, and the central areas include the spinal cord and supraspinal centres such as the brainstem, thalamus, cortex and limbic system. (**3**) **Brain correlates of the telescoping phenomenon**. The phenomenon of telescoping refers to the shrinking and retraction of the phantom towards the residual limb (*left*). The panel shows brain activation related to the imagined movement (IM) of telescoped and non-telescoped phantoms. The representation of the movement in the primary somatosensory cortex (*red shading*) follows the perceived location of the movement (opening and closing of the hand) and not the actual anatomical location (hand area). Completely telescoped phantoms create activity in the cortical region that represents the shoulder, partially telescoped phantoms in the region of the arm and non-telescoped phantoms in the hand region. EM denotes the cortical activation related to executed movements of the intact hand and indicates where the representation of the hand in the cortex is located

pain sensation is known to extend for years and is attributed to changes in the brain cortex (Flor et al. 2006).

A similar phenomenon is telescoping that is frequently observed in people who lost their hands. It refers to the perceived changes in the size and length of the phantom sensation that lead to the shrinking and retraction of the phantom towards the residual limb. This imaginative movement of the opening and closing of the hand has also been located in the brain cortex (Fig. 4.3).

Hence, it cannot be excluded that birds continue, to this day, to have the sensation that their fingers have been amputated.

Supporting this contention is the existence of a few species which have retained claws on their wings.

Along the shores of the Amazon river the Hoatzin (*Opisthocomus hoazin*) is an arboreal bird that as an adult resembles most other birds. His young, when alarmed, drop into the water and soon climb to the nest using their sharp and strong claws that stick out from the margins of their wings (Beazley 1974). The claws of the nestling Hoatzin are located in the first and second fingers (Carroll 1987) (Fig. 4.4). These appendages are not unique. Very young European coots (*Fulica atra*) are water birds that bear single claws and some species of geese carry sharp spurs on the wingedge even as adults (Perrins 2003). This means that the brain of birds retains the capacity to command the movement of finger extremities of juveniles and adults in some species. In the adult Hoatzin, as well as in most other families, this capacity of using the fingers was eliminated, which may be expected to give birds a sense of frustration or of amputation.

Three arguments can be raised against this interpretation of avian mental behaviour based on the current ideas on evolution. First, the wing is supposed to have arisen by minor successive modifications that took a long time to reach the present form. Second, a situation that arose a

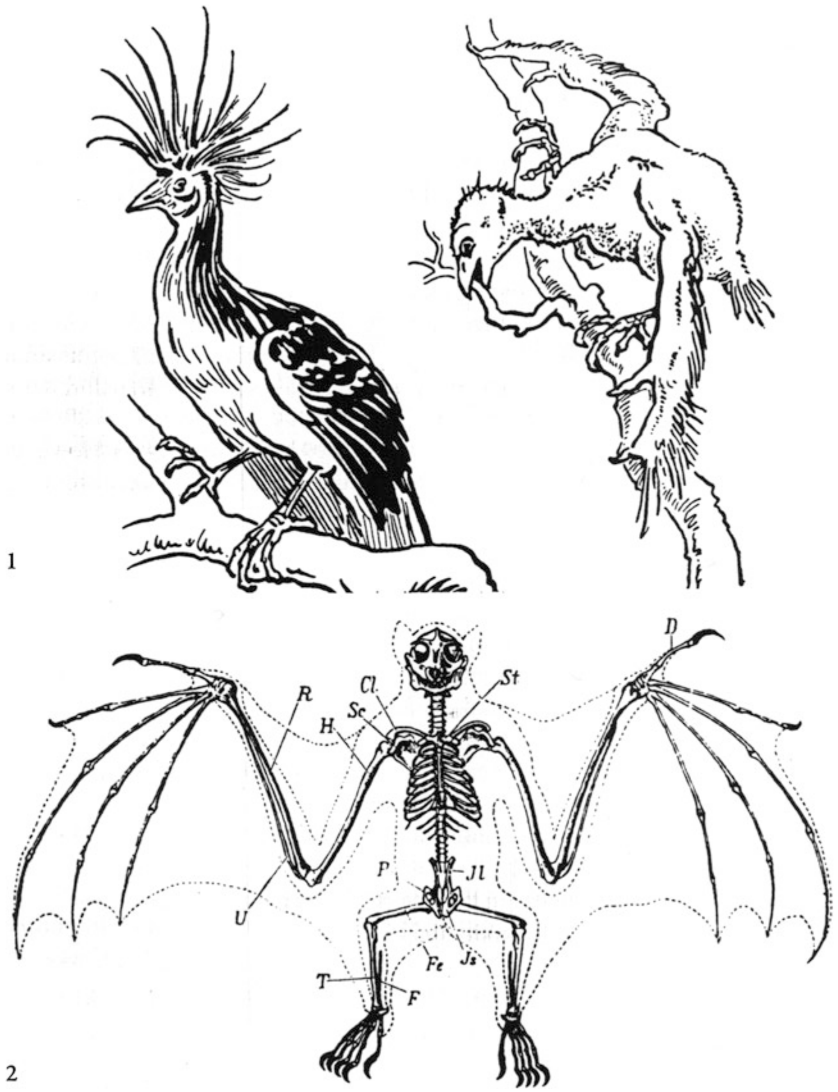

Fig. 4.4 Similarities between the wings of birds and mammals. (**1**) The bird *Opisthocomus hoazin* as an adult (*left*), and as a young (*right*) climbing by means of clawed wings. (**2**) Skeleton of the bat *Pteropus edulis* showing the two upper fingers having claws like those of the bird. In bats the upper finger stretches out of the wing (D)

long time ago may have not remained imprinted in the memory of modern birds. Third, the avian brain is different from that of humans.

The recent molecular and behavioral data do not support this argumentation. First, wings can arise by manipulation of the DNA sequences of a bird, the wings having the same structure and function known from previously existing wings (Chap. 5). Second, the transformation of the Hoatzin fingers takes place so rapidly that it occurs within the same individual, being solely the result of the development into the adult stage. One is actually dealing with the same brain, as such the memory of the elimination of the digit claws cannot be easily erased. Third, the mental ability of birds is not very different from that of chimpanzees as disclosed by the comparative behaviour of these two groups of animals (Chap. 6).

4.12 The Constant Replacement of Teeth in Vertebrates – "Actually there is Method in this Seeming Madness"

Teeth are unknown in lower chordates, such as the primitive *Amphioxus*, some fossil fishes, and in cyclostomes, like the lampreys.

In all jawed vertebrates teeth are universally present, except where secondarily lost as in birds and turtles.

The mammalian dentition helps to understand the events that took place in avian evolution.

The front teeth, called incisors, are retained in most mammals, but ruminants, like the cows, have lost the upper incisors. Primitive living mammals, like the monotremes, have entirely lost their teeth as adults and reduction of teeth is found in anteaters.

In mammals tooth renewal involves two dentitions. The first is the "milk" or deciduous dentition which lacks molars. This whole set of teeth is not permanent. At a specific signal, all these teeth start to fall at a tender age, an impressive example of a programmed cell and organ death. The formation of the second and permanent dentition follows, like the first, an anteroposterior order (Romer and Parsons 1978).

Fishes, amphibians and reptiles face a different situation in which tooth replacement continues throughout life. Teeth are constantly being formed deep within the tissues of the jaws, they grow in size and finally, through resorption at their bases, are shed, being soon replaced by a new generation of teeth. Initially this permanent replacement was considered to be chaotic but "Actually there is method in this seeming madness" (Romer and Parsons 1978). The permanent substitution of teeth takes place in a most concerted way in the form of waves that travel along the jaw at a given time. What seemed irregular turned out to be internally determined.

Recently the dental formula of mammals has been shown to be under molecular control.

The interactions required to generate a tooth are mediated by families of signaling molecules. In the mouse, coordinated restriction of signaling molecule activity, was found to be necessary to ensure appropriate tooth number. Three genes are involved: *Osr2*, *Msx1* and *Bmp4*. The gene *Osr2* represses tooth formation in the wild type by restricting the action of the *Bmp4*-*Msx1* pathway. In mouse mutants, in which the *Osr2* does not function, the *Bmp4*-*Msx1* activity is unrestricted and additional teeth are formed. This process controls the emergence and the suppression of teeth as well as their number (Fig. 4.5) (Cobourne and Sharpe 2010).

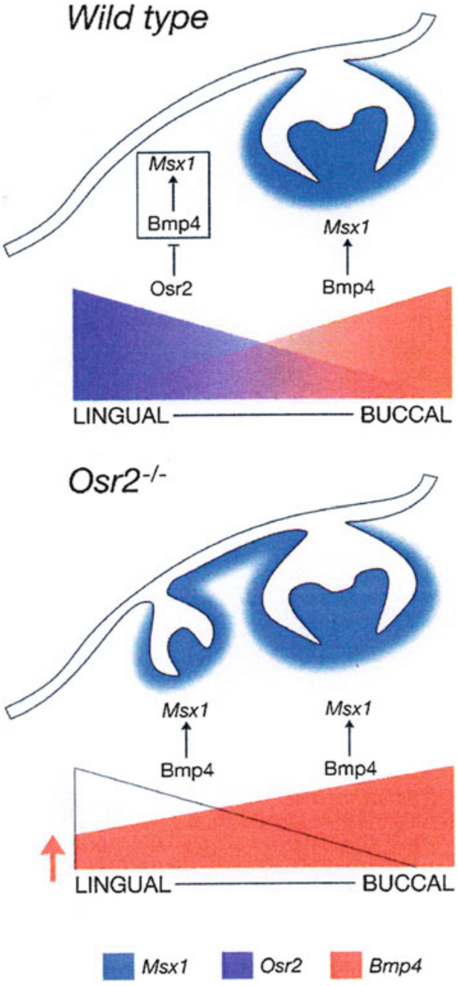

Fig. 4.5 Molecular control of tooth number across buccal-lingual dental axis. In the wild type mouse (*upper panel*), Osr2 is expressed in a lingual-to-buccal gradient across the jaw axis and restricts Bmp4-Msx1 pathway activity in the lingual region. In the absence of Osr2 function (*lower panel*), Bmp4-Msx1 activity is unrestricted and propagates mesenchymal activation for sequential tooth induction in the lingual region, with supernumerary teeth developing directly from the oral epithelium. Therefore, Osr2 is an important determinant for patterning the mammalian dentition into a single row across the jaw. *Osr2*: Mouse gene that represses tooth formation, *Msx1*: gene that encodes the protein MSX1, *Bmp4*: gene encoding a protein participating in enamel formation

During evolution the shedding of teeth was not always followed by the production of new ones, resulting in their total absence. This evolutionary trend not only occurred in the birds but also in a group of mammals that have little resemblance to birds—the gigantic baleen whales.

Most species of whales have large and ferocious teeth, but unexpectedly, the largest animals that ever lived on earth—the blue whales—(attaining lengths of 33 m), have no teeth. All other baleen whales are also toothless. However, teeth are present as vestigial buds in their embryos (Macdonald 1984, 2002).

The question may not sound pertinent, but does the adult conserve an imprint in its memory of this earlier existence of teeth? How much does one retain, in its brain, early experiences? In humans this problem has long ago been addressed and dealt with by psychologists and psychiatrists. They seem to agree that early experiences contribute to an important part of the adult behaviour.

Humans, whales and birds may not be very different in this, as in other respects. This problem leads us to the comparison between the genomes of humans and birds which has established a high degree of similarity between *Homo sapiens* and *Gallus gallus* (red jungle fowl, Fig. 5.1).

4.13 Most Bird Species Lack a Penis But in Flatworms this Organ is Highly Developed

A unique feature of birds is the seasonal increase in volume of their ovaries and testes and of the ducts associated with them. In winter the ovary of domestic quails weighs 15 mg and the oviduct 20 mg whereas in the breeding season they may reach 6,000 mg and 5,000 mg respectively. In several species the increase in the size of the testes is dramatic, it can multiply by 200–300 times in spring.

In this respect evolution was generous but when it came to the process of copulation the situation was reversed. Both sperms and eggs are ejected into cavities that, in both sexes, finish in an opening—the cloaca. Copulation consists on bringing together the male and female cloacae, a rather inefficient system. The result is that copulation lasts only a few seconds and must be repeated many times in succession.

There are not less than 9,000 species of birds but only in some groups: storks, flamingos, ducks, gallinaceous birds, and a few others, is there a penis. The absence of a copulatory organ occurs in over 97% of birds (Briskie and Montgomerie 2001; Wesolowski 1999; Frey 1995). When present the penis develops from the cloaca as an erectile protrusible phallus being evaginated by muscular action. The ostrich's penis can attain the size of 20 cm.

This means that among thousands of species that lack a penis, suddenly this organ arises in a most unexpected way. The phenomenon is, however, not new. An extensive study revealed that throughout the evolution of invertebrates and vertebrates the penis has appeared and disappeared in a periodic way independent of animal complexity (Lima-de-Faria 1995). (1) Gnathostomulids are marine worms that are hermaphroditic but cross-fertilize. They possess a penis that is stiffened by a stylet. During copulation the animal injects sperm packets into its partner. (2) Another animal group, the flatworms, have a well developed penis located in a genital atrium. (3) Among the molluscs *Busycon* species, display a large penis seated in the frontal part of the body. An equally long penis is present in *Buccinum undatum*, a sea dweller (Margulis and Schwartz 1982). (4) There is a sudden occurrence of a well developed penis in the insects. The dragonflies copulate by means of such an organ (Romoser 1973). (5) Among the crustaceans, barnacles (*Balanus*) are known to have a long penis. Some of these marine animals are hermaphroditic, but cross fertilization is usually the rule. The testes are located in the cephalic region and the two sperm ducts unite within a penis which upon protrusion out of the body reaches a distant individual acting as female (Barnes 1980). (6) Unlike human females, marsupials possess a double vagina; the males may have a double penis, whereas humans and other placental mammals, have only one (Macdonald 1984). (7) In flatworms this organ is as complex as in mammals. It consists of: a cirrus (the protruding part of the penis), genital atrium, ejaculatory duct, prostate gland, seminal vesicle, and vas deferens.

Hence, a most complex organ has come and gone during the whole animal evolution, maintaining the same basic organization and function. With the emergence of the avian body, the penis was suddenly inhibited reappearing sporadically in a narrow number of animals. One is dealing with a periodic event comparable to the emergence of the wing or the teeth. The sudden appearance and disappearance of the penis is to be searched for in the evolution of the chromosome's DNA.

Sources of Figures

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Fig. 4.2 **(1)** **(2)** Lima-de-Faria, A. 1995. Biological Periodicity. Its Molecular Mechanism and Evolutionary Implications. JAI Press, U.S.A. (Fig. 6 page 26), **(3)** Hanström, B. and Johnels, A.G. 1962. Benfiskar. In: Djurens Värld (Hanström, B. Editor) vol. 6 Fig. 265 page 312, Norden AB, Malmö, Sweden, **(4)** Perrins, C. 2003. The New Encyclopedia of Birds. Oxford University Press, Oxford, UK (Fig. 10 page 52), **(5)** Perrins, C. 1976. Bird Life. An Introduction to the World of Birds. Elsevier Phaidon, London, UK (Fig. King penguin page 60).

Fig. 4.3 **(1)** Babin, C. 1980. Elements of Palaeontology. J. Wiley, New York, U.S.A. (Fig. 18.31 page 326), **(2)** and **(3)** Flor, H. et al. 2006. Phantom limb pain: a case of maladaptive CNS plasticity? Nature Reviews, Neuroscience *7*: 873–881 (Figs. 1 and 3 pages 876 and 879).

Fig. 4.4 Lima-de-Faria, A. 1995. Biological Periodicity. Its Molecular Mechanism and Evolutionary Implications. JAI Press, U.S.A. (Fig. 5 page 23).

Fig. 4.5 Cobourne, M.T. and Sharpe, P.T. 2010. Making up the numbers: the molecular control of mammalian dental formula. Seminars in Cell and Developmental Biology *21*: 314–324 (Fig. 6 page 321).

5 The Bird Genome and the Molecular Determination of Wings, Legs and Beaks

5.1 What is a Genome

The genome is the total set of genetic information carried by an individual or cell. But the following specifications are to be taken into account:

1. The genetic information is not restricted to the chromosomes of the nucleus but it is also present in cytoplasmic organelles such as the mitochondria and chloroplasts (in plants) which have their own chromosomes also containing DNA.
2. Chromosomes consist of DNA and proteins but it is their DNA that carries the genetic information.
3. However, DNA alone cannot make use of the code words that are written along its base sequences. The activation of DNA, leading to its replication and transcription, only takes place when proteins intervene. If DNA were to be sent to another planet no one would know what to do with an isolated DNA molecule. It is only when specific proteins interact with DNA that this macromolecule becomes alive.
4. The term genome had earlier been defined as being the total set of genes. However, at present it is known that structural genes, those that lead to the production of proteins, only occupy about 3% of the total DNA in humans (Strachan and Read 1996; Brown 1999). The remaining fraction of 97%, which before was called junk or nonsense DNA, has turned out to consist of introns, transposons, DNA satellites and other sequences which are of utmost importance in maintaining gene function and chromosome order.
5. The chromosome of higher organisms consists, besides DNA of two types of proteins: histones that are atomically coupled to DNA along most of its length, and structural proteins that build the chromosome's scaffolding. The behaviour of these proteins regulates the expression of the DNA sequences and, as a consequence, is highly responsible for determining the kind and number of structural genes, and other DNA sequences, that become active or are repressed at a given time of the organism's development.
6. Each gene has turned out to be a highly ordered molecular structure. A gene begins with a promoter followed by a transcription initiation site and a translation initiator codon, and is closed by a translation terminator codon and a transcription terminator sequence. There is so far no information on how this sequence originated and how it was maintained as a result of atomic interactions. Still less understood is another gene feature. Genes consist of exons (coding sequences) separated by introns (non-coding sequences). The exons are later translated into proteins whereas the introns are usually not part of this process. Most genes contain a few exons but some genes may consist of as many as 118 exons (Christiano et al. 1994). The way these exons increased to such a high number is not known. Still more difficult is to understand how they were able to produce during this evolution molecularly coherent proteins. One tends also to forget that some genes do not code for proteins but code only for a specific RNA, which means that they evolved in other ways which remain to be elucidated.
7. Many species have been the object of DNA sequencing in the last 10 years. Thus, the code written along about three billion nucleotides, that build the human genome, has been deciphered (Baltimore 2001), but we continue to be highly ignorant of the way the sequences are organized into such a well-defined and coherent unit as a chromosome (Lima-de-Faria 2003, 2008a).

5.2 The Unity of the Chromosome Remains a Question Mark

The initial optimism led to the assumption that the knowledge of the base sequences along all the chromosomes of an organism would unveil most of its genetic properties and open the door to the treatment of many diseases. The result

A. Lima-de-Faria, *Molecular Geometry of Body Pattern in Birds*,
DOI 10.1007/978-3-642-25301-0_5,

turned out to be different. This optimism derived from the general assumption that the chromosome is a chaotic structure an idea that still prevails. Once one knew the sequences, one would know the way they would interact.

But the chromosome's DNA is not a string of bases functioning in a molecular vacuum. The bases are not distributed at random along the chromosome. Some bases tend to be much more frequent at various stretches along the DNA which results, among other things, in areas of higher guanine-cytosine contents. Also, there are gene-rich areas along the chromosome and genes with similar functions tend to be clustered. This gene association related to function, is already present in viruses and it extends from bacteria to humans (Fritsch et al. 1980).

The association of the DNA with proteins, building what are called nucleosomes, has also turned out to be nonrandomly distributed (Segal et al. 2006).

Moreover, the chromosome has not changed its basic organization, and molecular properties, since the protozoans arrived, demonstrating a unity of organization that has defied our efforts to analyse it. The chromosomes that are observed in humans today, have gone, during 1 billion years, through an untold number of drastic translocations, inversions and other rearrangements, yet they continue to be undistinguishable in their main properties and functions from those of a single cell organism such as an *Amoeba*.

It is the discovery of the preservation of this wholeness, and the unfailing maintenance of the unity of structure and function, that constitute the present challenge. Before these central properties are unravelled the chromosome—although we have it in the test tube—will continue to pose many questions concerning its long-range molecular effects and its behaviour as a unit in space and time (Lima-de-Faria 2008a).

5.3 What was Revealed by Sequencing the Chicken Genome – Humans and Birds are Genetically Similar

The "International Chicken Genome Sequencing Consortium" (2004) was able to present an extensive analysis of a draft sequence of the red jungle fowl *Gallus gallus* genome, which is considered to have diverged from the mammalian genome about 310 million years ago.

The following main results were:

1. The draft sequence has led to an estimated 20,000–23,000 genes. The number of chicken genes given in Fig. 5.1 is 17,709. This reduced figure has to do with the realization that there are different types of genes. In this case it is mainly those that were relevant to the establishment of the homology with humans that were included. This discrepancy is also evident in other species. The numbers predicted by the "Human Genome Rough Draft" (2001) led to 31,780 (Public sequence) and 39,114 (Celera sequence) (Bork and Copley 2001). Since then the number of human genes has been estimated to be close to 20,000 (Pennisi 2003). On Fig. 5.1 the number of human genes is considered to be 21,787. What is of importance is that both in chicken and humans the number of genes is of the same magnitude—around 20,000.
2. There is a nearly threefold difference in size between the chicken and human genomes (approximately one billion versus about three billion base pairs) which reflects a reduction in repeated content of various sequences.
3. Chicken-human aligned segments tend to occur in long blocks where gene order was conserved.

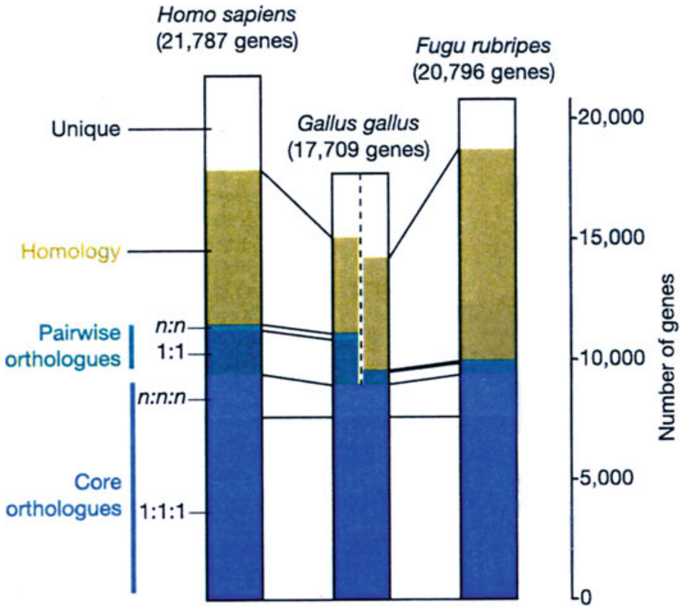

Fig. 5.1 **Chicken (*Gallus gallus*) genes classified according to their predicted evolutionary relationships with genes of two other model vertebrates (*Fugu* and human).** Forty-three percent of the chicken genes are present in 1:1:1 orthology relationships for the three species. *Fugu rubripes*, Bony fish. Orthologues are genes found in different species which have originated from a single ancestral gene

4. The chicken 78 chromosomes (diploid number) differ in size, building two groups of macro- and microchromosomes. In this last class synonymous substitutions are elevated.
5. Alignment of the chicken and human genomes identifies 70 million bases that are supposed to function similarly in both species.
6. A total of 571 non-coding RNA genes belonging to over 20 gene families were identified in the chicken genome. These are mainly microRNAs and small nucleolar RNAs which are found in the introns of protein coding genes.
7. About 60% of chicken protein-coding genes have a single human orthologue (homologous sequence that has conserved gene order and orientation) revealing a high gene homology between the two species.
8. Genes that are conserved between humans and chickens are also conserved in fish (Fig. 5.1).

There are so many gene similarities between birds and humans that, after over 300 million years, the genes cannot only be recognized as being the same but retain similar base sequences and are supposed to function similarly.

The similarities of the avian genome extend not only to fish but also to amphibians. The western clawed frog *Xenopus tropicalis* has about 1.7 billion base pairs on ten chromosomes. By comparing homologous sequences it was estimated that this species contains 20,000–21,000 protein coding genes. Of interest is that the *X. tropicalis* genome displays long stretches of genes which are colinear with human and chicken genes (Hellsten et al. 2010).

5.4 Genome Sequencing of a Wild Bird Discloses That Song Behaviour is Dependent on RNA Expression in the Brain

The draft assembly of the song bird zebra finch genome has been completed (Warren et al. 2010). The sequenced genome spans 1.2 billion base pairs with a total of 17,475 genes representing about 90% of the expected total gene content. This is the first passerine bird to be sequenced but portions of the genome remain unknown (Balakrishnan et al. 2010).

The overall structures of the genomes are similar in zebra finch and chicken, but they differ in: (1) many intrachromosomal rearrangements, (2) lineage-specific gene family expansions, (3) the number of certain types of retrotransposons and (4) mechanisms of sex chromosome dosage compensation.

Of special interest is that song behaviour, in this wild bird, engages gene regulatory networks in the brain, altering the expression of non-coding RNAs, microRNAs, transcription factors and their targets. Besides, rapid molecular evolution has occurred in the songbird lineage of genes that are regulated during song experience (Warren et al.2010).

The sequencing of the genome opens the doors into brain function. Musical behaviour can now be followed at the molecular level.

5.5 Comparison of Large and Small Chromosomes in Birds

Avian chromosomes show a distinctive difference in size. There is a small number of large macrochromosomes and numerous microchromosomes that are so small that some of them are close to the resolution power of the light microscope. For this reason this minor class has been difficult to study at the molecular level.

The chick genome has only 1.1 billion base pairs on 39 chromosome pairs (haploid number). By analyzing patterns of nucleotide substitutions in two sets of chicken-turkey sequence alignments Axelsson et al. (2005) found that chicken microchromosomes account for only 18% of the total female genome but they harbor about 31% of chicken genes. The guanine to cytosine content of the DNA is higher in microchromosomes and these replicate their DNA earlier than the macrochromosomes.

A small size, and a minor amount of DNA, is not necessarily associated with genetic insignificance.

5.6 How to Obtain a Bird With Extra Wings and Legs – Genes Interact With Specific Proteins Producing Normal Wings and Legs

Fruit flies and other insects were found in nature with extra legs and extra wings. The phenomenon extended to the vertebrates and specifically to the birds. The spontaneous occurrence of cocks and ducks with four legs was reported long ago but remained a curiosity (Fig. 5.2).

Three types of results changed this approach. First, the genes responsible for wing and leg formation were identified. Second, by genetic manipulation extra legs and wings could be produced in insects. Third, genes remained conserved in invertebrates and vertebrates disclosing unsuspected homologies between the most distant groups. It is thus not surprising that it soon became possible to produce experimentally birds with extra wings and legs, although such a feat was considered before impossible.

Research in this area started by implanting leg grafts in chick embryos, expressing a gene called *Tbx4*, which developed into toe-like digits when placed in the wing. Wing grafts expressing another gene *Tbx5* developed into wing-like digits when placed into the leg. These results indicated that the two genes participated in specifying limb identity,

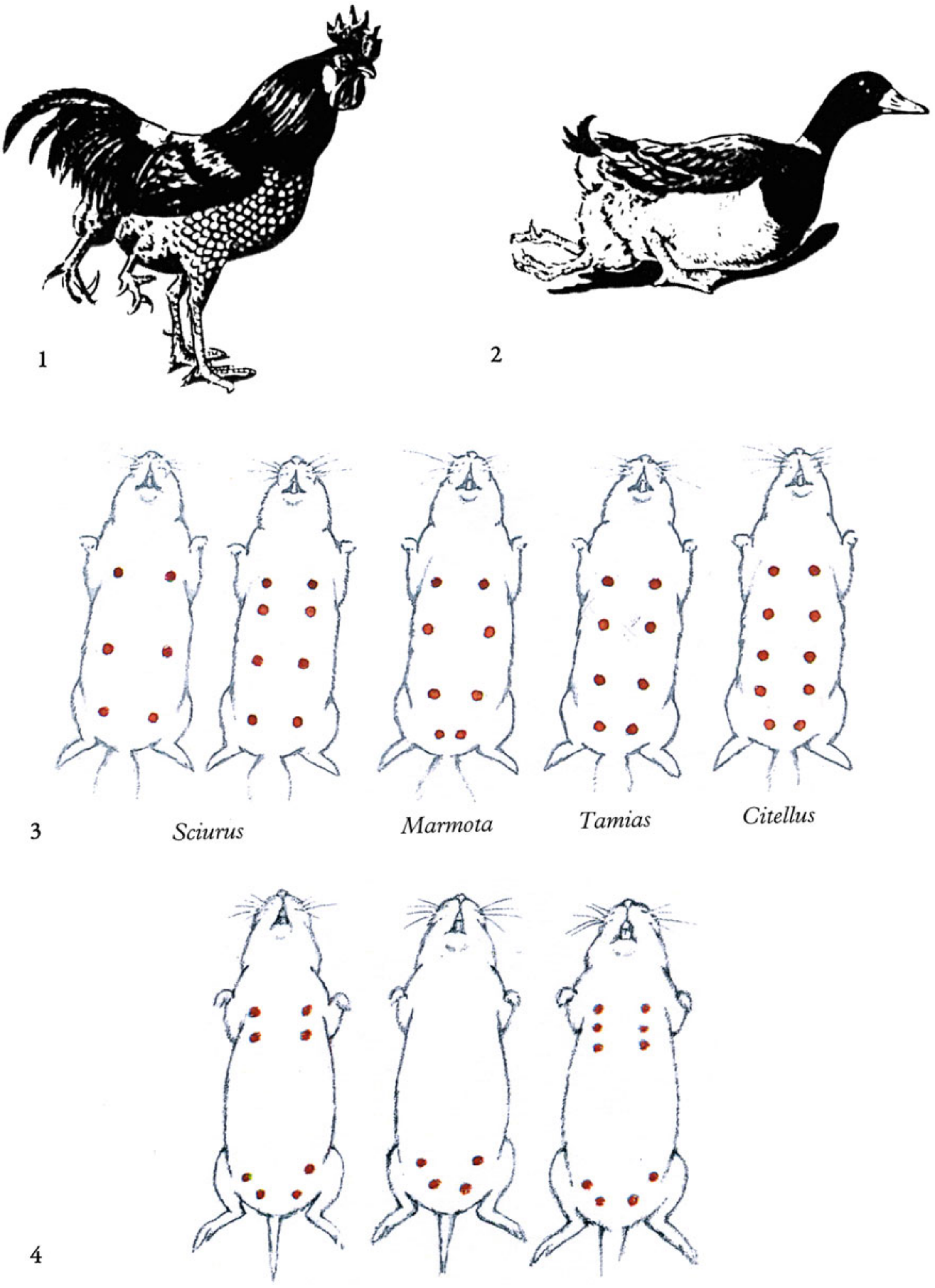

Fig. 5.2 **(1) and (2) Spontaneous occurrence of a cock and a duck with four legs. (3) Nipple positions in four different species of European squirrels. (4) Nipple positions of field voles (*left*), pine voles (*centre*) and the Muskrat (*right*)**

their expression inducing leg cells to become wing cells as well as wing cells to become leg cells (Ohuchi et al. 1998; Isaac et al. 1998; Logan et al. 1998).

Subsequent experiments disclosed that these genes, which are two members of the *T-box* (*Tbx*) gene family, are essential regulators of limb outgrowth and are tightly linked to the activity of three signaling proteins that are necessary for limb outgrowth and patterning. Of these proteins, *fibroblast growth factor* (FGF) and *bone morphogenetic protein*, are the most important. The initial experiments indicated that *Tbx4* and *Tbx5* genes were critical for promoting limb outgrowth, but they did not establish cell-fate determination. It is at this stage that the intervention of the proteins became evident.

5.7 Whether Wings or Legs are Formed Depends on the Change in Position of a Protein

Cell determination was changed when the *protein fibroblast growth factor* was combined with the gene *Tbx4* resulting in the production of extra wings or extra legs in the chicken. Implantation of fibroblast growth factor beads (opposite somite 21) gave rise to an extra wing in 70% of cases and an extra leg in 20% of cases. When the gene *Tbx4* was injected, before this protein was implanted, the percentage of legs produced increased to 54% and wing formation decreased to 26% (Fig. 5.3) (Rodriguez-Esteban et al. 1999).

The role of the protein *fibroblast growth factor* became better defined when Cohn et al. (1997), using *Hox* genes which influence the position of limb formation by encoding plate mesoderm along the body axis, made local applications of this protein to the prospective flank of a chick embryo. They found that the same population of flank cells could be induced to form either a wing or a leg, this event being accompanied by changes in the expression of three *Hox* genes. To determine whether cells that formed additional wings constituted a separate population from cells that formed additional legs, a bead soaked in *fibroblast growth factor* was implanted in the flank at two opposite locations. Following the local applications of this protein to the

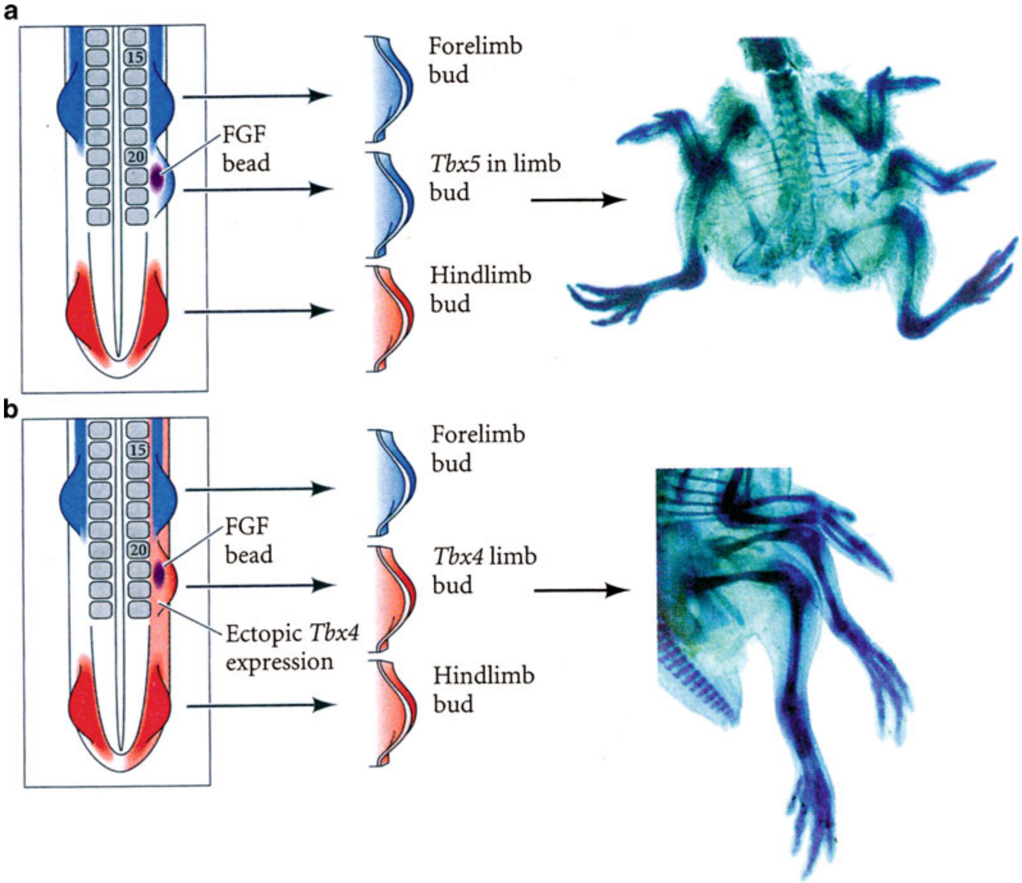

Fig. 5.3 Genetic intervention leading to the formation of a bird with four wings or four legs. Respecification of forelimb into hindlimb by ectopic expression of Tbx4 leading to the formation of an extra limb out of its normal place. (**A**) An FGF-secreting bead opposite somite 21 usually induces a Tbx5-expressing limb but that forms a new wing. (**B**) If the entire flank is experimentally made to express Tbx4 (by infecting it with a Tbx4-expressing virus), the FGF-induced limb bud expresses Tbx4, and often becomes a leg. (After Rodriguez-Esteban et al. 1999; photographs courtesy of J.C. Izpisúa-Belmonte.) *Tbx4* and *Tbx5* are genes affecting limb formation. *FGF*, Fibroblast growth factor, *Ectopic expression*, Out of place formation

anterior flank resulted in an extra wing, whereas the application to the posterior flank induced an extra leg (Fig. 5.4).

What emerges from this combined experimentation is the following:

1. The same genes determine the emergence of homologous limbs, *i.e.* wings and legs.
2. The number of wings or legs can be determined in birds. The final result is that *Tbx-5* is expressed in wings and *Tbx-4* is expressed in legs (Isaac et al. 1998).
3. The action of these specific genes must be combined with that of equally specific proteins to obtain these transformations.

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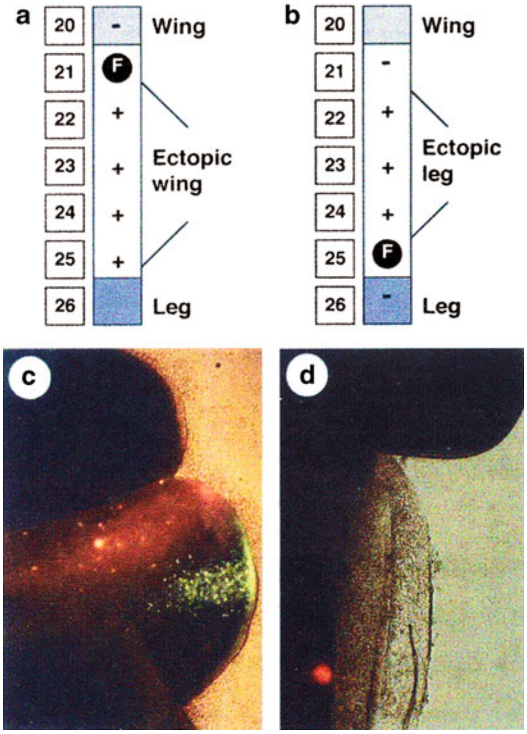

Fig. 5.4 Induction of extra wings or legs depends on location of growth factor in bird embryo. FGF induces bidirectional transformations in flank cell fate to induce ectopic wings and legs. (**a**, **b**) Lateral plate mesoderm with FGF bead (F) placed in anterior flank opposite s21 (**a**) a position that generally results in ectopic wing formation, or in posterior flank opposite s25 (**b**) a position that generally results in ectopic legs. (**c**) Triple exposure photomicrograph of ectopic limb bud to reveal positions of fluorescent cells 72 h after implantation of a FGF bead opposite s25. At the time of bead implantation, flank cells were labelled with Dil (*red*) opposite s22, and DiA (*green*) opposite s23. Cells from both positions have contributed to the ectopic limb bud (**d**). (**d**) Double-exposure photomicrograph of a normal chick embryo in which flank cells opposite s22 had been labelled with Dil 48 h earlier. Labelled cells remain in the flank as a small patch. There is no contribution to the limb buds. *FGF*, Fibroblast growth factor, *Ectopic*, Out of place formation, *s21*, *s25*, *s23* and *s22* somites or body compartments, *Dil* and *DiA*, Fluorescent dyes

5.8 Great Variation in Beak Morphology – The Same Evolutionary Solution Occurred in Distant Islands and also on the Mainland

It is believed that ancestral finches had “general-purpose bills” similar to that found at present in the chaffinch. Finches inhabit the remote and small islands of the Pacific Ocean, such as Galapagos and Hawaii, but have established themselves in vast land masses like Madagascar, on the Indian Ocean, and the Caribbean region of Central America.

Darwin’s finches, as they are usually called, are considered to have the following characteristics: (1) They provide the “best-known example of an adaptive radiation in birds”. (2) The variety of feeding specializations have evolved within a short time of less than 5 million years. (3) They evolved from a single ancestral finch species.

The 14 species known from the Galapagos islands have similar plumage but differ greatly in bill morphology and feeding habits: (1) narrow beak (insect eating), (2) thick beak (seeds), (3) sharp-beaked (blood), (4) wood-pecker (insects), (5) tree finches (insects and seeds) and (6) Vegetarian finch (only leaves and fruits) (Perrins 2003).

There are about 22 surviving species of Hawaiian Honeycreeper finches. They have been divided into five groups according to the shape of their beak and food specialization: (1) straight short beak (flowers), (2) slightly curved beak (leaves), (3) strongly decurved bill (bark-pickers), (4) short heavy sometimes curved at tip (seed and fruits), (5) long curved but also short narrow bill (nectarivores) (Grant and Grant 2008) (Fig. 5.5).

The island of Madagascar has a landmass that is larger than Sweden as well as that of the Italian Peninsula. The vangids of Madagascar display an equally impressive variation in bill shape that is a copy of that found in the Caribbean, the Galapagos islands and Hawaii. The 12 species of Madagascar vangids have long thin decurved to extremely thick and heavy beaks as well as long and short thin bills (Fig. 5.5).

Perrins (2003) summarizes the whole situation in the following way:

1. *Darwin*’s finches may have originated from a Caribbean species, since most of their close relatives are found in this region of Central America.
2. These relatives also display a great diversity of bill types: The bananaquit has a thin decurved bill feeding on nectar, whereas bullfinches have large, seed-crushing bills.
3. Common to all species is that they build domed-shaped nests similar to those of the Galapagos islands.

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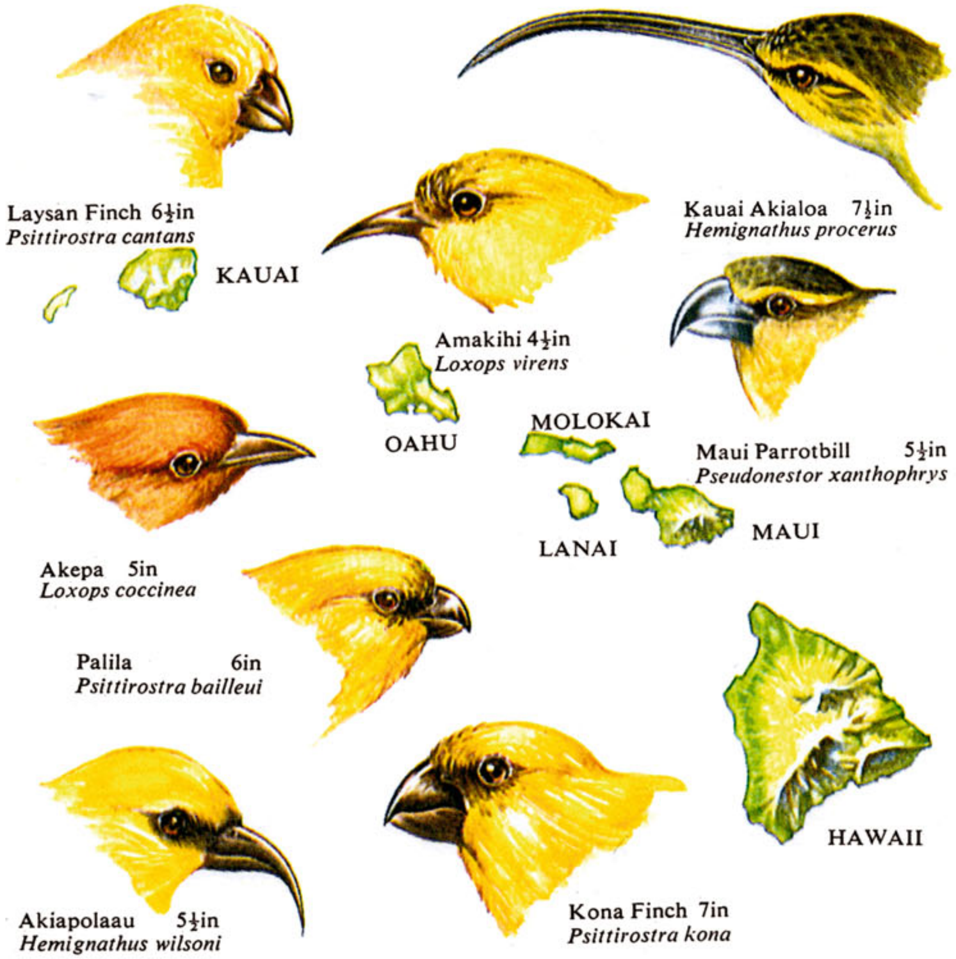
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Amakihi 4½in
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Maui Parrotbill 5½in
Pseudonestor xanthophrys
LANAI
MAUI
Akepa 5in
Loxops coccinea
Palila 6in
Psittirostra bailleui
HAWAII
Akiapolaau 5½in
Hemignathus wilsoni
Kona Finch 7in
Psittirostra kona

2

5.9 How to Recreate Beak Evolution – Proteins Shape the Beaks of Ducks and Finches

Ornithologists have been most attracted by the multiple forms of the avian beak due to its morphological specializations and its relationship with feeding habits (Pough et al. 2005). For this reason Galapagos finches became used as the perfect example of the present interpretation of evolution (Patel 2006). As a consequence the variation of their beaks has been considered to be the result of "ecological forces", the dimensions of each species beak (length, depth and width) being crucial for life style and survival. Selection was considered to be the main agent that changed the relative success of birds with various beak shapes (Grant and Grant 2002).

However, well-defined molecular pathways have now been found that furnish another explanation.

Abzhanov et al. (2004, 2006) and Wu et al. (2004) have uncovered the molecular mechanism deciding the three-dimensional shape of a bird's beak. This is made up of multiple facial prominences: frontonasal, maxillary, lateral nasal and mandibular, which are coordinated during development composing the beak (Fig. 5.6).

Wu et al. (2004) concentrated on later beak morphogenesis during the moulding of the frontonasal mass prominence by comparing proliferation zones of chickens and ducks that have distinct beak shapes. They found that there is only one proliferative zone in the frontonasal mass of chickens, but there are two in ducks, these growth zones being associated with the *bone morphogenetic protein four* activity. Moreover, they were able to produce beaks that imitated those in nature by modulating the activity of the bone protein. The different beak shapes arising in nature depend on whether and when this signaling molecule is turned on during development.

To start with, Abzhanov et al. (2004) performed a comparative analysis of various growth factors in finch species of the genus *Geospiza*. The *bone morphogenetic protein 4* (*BMP4*), is a cell-cell signaling protein. The expression of this gene in mesenchyme of the upper beaks, strongly correlated with deep and broad beak morphology. When the same gene was misexpressed in chicken embryos this bone protein caused morphological transformations paralleling the beak morphology of the finch species *Geospiza magnirostris*.

The same authors compared beak development in embryos of six species of finches, the morphology of the beak ranging from: (1) sharp, (2) broad and deep, (3) long pointed. Gene expression in the beak correlated with the increasing depth and width of beaks seen in the species investigated.

In a later study Abzhanov et al. (2006) used complementary DNA microarray analysis of the transcripts expressed in the beak primordia to find genes whose expression correlated with specific beak morphologies. Calmodulin, a molecule involved in mediating calcium signaling, is expressed at higher levels in the long and pointed beaks of finches than in more robust beak types. *In situ* hybridization validated this observation by artificially replicating these results in the chick. The higher levels of calmodulin led to the elongation of the beak in the chick providing a molecular explanation for its independent growth along different axes. A simple molecule is directing the evolution of distinct beak shapes (Fig. 5.6).

Pennisi (2004) in her comments on the work of *Abzhanov* and collaborators and of *Wu*'s team writes: "Today, these song birds are often cited as a perfect example of how new species arise by exploiting ecological niches. Now developmental biologists have added a new twist to this classic story. Two research teams have discovered that a protein normally associated with the development of the skull and other bones is one of the molecules that tailors the shapes of beaks." She could not have been more explicit..

Fig. 5.5 **(1) "A bill for every purpose"**. "The ancestors of the Honeycreeper family arrived on the Hawaiian archipelago to find a wealth of different vegetation zones. In this isolated and largely unexploited habitat, the honeycreepers managed an unrivalled degree of divergence, evolving to fill niches usually taken by other groups of birds. However, such opportunism had its penalties; of the 22 honeycreeper species, eight made fateful commitments to their chosen way of life and overspecialization led to their extinction. The 14 surviving species are more generalized feeders, but still display an astonishing range of adaptation, from the long, curved beaks and brush-tipped tongues of the nectarsippers, through the straight, slender beaks of the insectivorous species, to the stout, crunching bills of the seed-eaters. On Hawaii, the Akiapolaau, *Hemignathus wilsoni*, a rare, perhaps extinct, species apes the woodpecker by using its stout lower mandible to hammer and lever off bark. Its long decurved upper mandible then probes for exposed insects" (Beazley 1974, page 217). **(2) The vangids of Madagascar displaying a comparable variation in bill shape**

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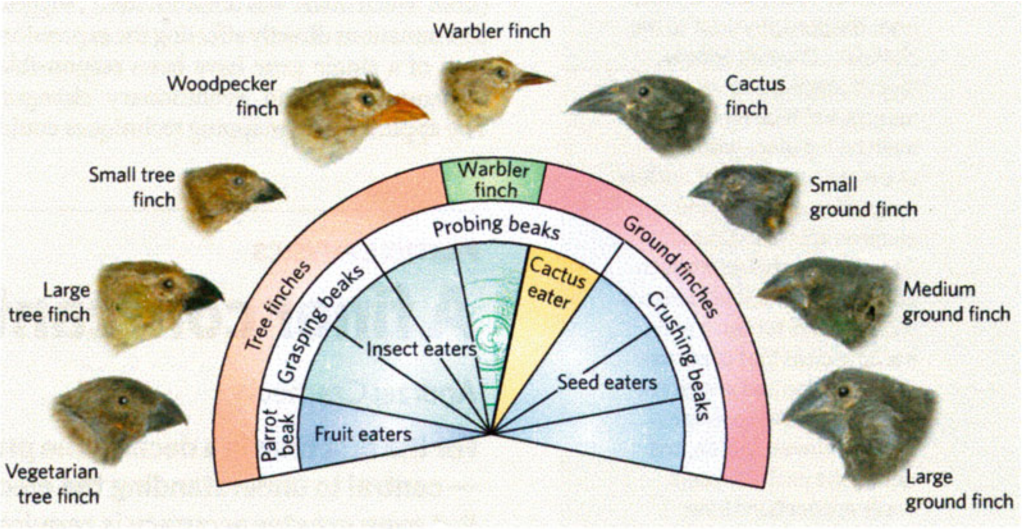

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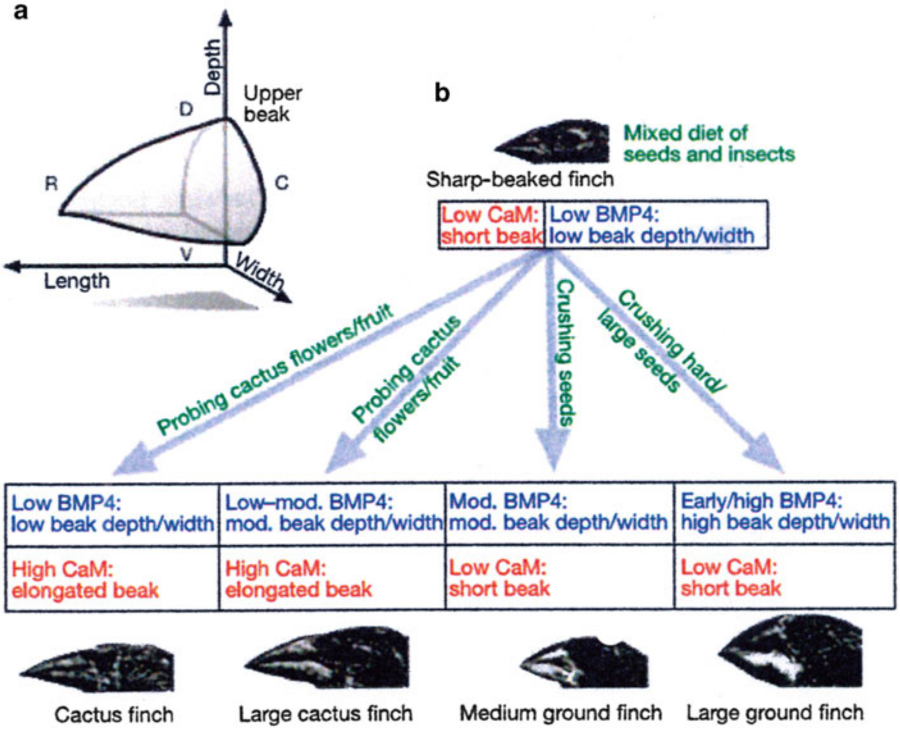

Fig. 5.6 How to recreate beak evolution by protein intervention (1) The evolutionary radiation of Darwin's finches. The species depicted here have all arisen from a common ancestor, but have evolved a remarkable diversity of beak shapes and sizes. They exploit different food sources. The work of Abzhanov et al. implicates upregulation of the calmodulin-dependent signalling pathway in the evolution of the long, pointed beak of the cactus finch. (Finch specimens provided by the Museum of Vertebrate Zoology, Berkeley.) **(2) BMP- and CaM-dependent signalling regulates growth along different axes, facilitating the evolution of distinct beak morphologies in Darwin's finches**. (**a**) Developing avian beak is a three-dimensional structure that can change along any of the growth axes. (**b**) A beak of the sharp-beaked finch reflects a basal morphology for *Geozpiza*. The model for BMP4 and CaM involvement explains development of both elongated and deep/wide beaks of the more derived species. Abbreviations: *C* caudal, *D* dorsal, *R* rostral, *V* ventral, *BMP* Bone morphogenetic protein, *CaM* Calmodulin, a protein involved in mediating calcium signalling

Sources of Figures

Fig. 5.1 International Chicken Genome Sequencing Cosortium (incl. L. Andersson and H. Ellegren). 2004. Sequence and comparative analysis of the chicken genome provide unique perspectives on vertebrate evolution. Nature *432*: 695–715 (Fig. 5 page 700).

Fig. 5.2 **(1)** and **(2)** Shepherd, W. 1939. Science Marches On. Harrap, London, UK (Plate 19 page 193), **(3)** and **(4)** Macdonald, D. and Barret, P. 1993. Collins Field Guide, Mammals of Britain and Europe. Harper Collins Publishers, London, UK (Nipple positions Plates 48 and 60).

Fig. 5.3 From Gilbert, S.F. 2000. Developmental Biology. Sinauer Ass., U.S.A. (Fig. 16.6 page 508). After Rodriguez-Esteban, C. et al. 1999. T-box genes *Tbx4* and *Tbx5* regulate limb outgrowth and identity. Nature *398*: 814–818 (Fig. 3 page 816).

Fig. 5.4 Cohn, M.J. et al. 1997. *Hox 9* genes and vertebrate limb specification. Nature *387*: 97–101 (Fig. 1 page 98).

Fig. 5.5 **(1)** Beazley, M. 1974. The World Atlas of Birds. M. Beazley Publishers Ltd, London, UK (Fig. on page 217), **(2)** From: Grant, P.R. and Grant, B.R. 2008. How and Why Species Multiply. The Radiation of Darwin's Finches. Princeton University Press, Princeton, U.S.A. (Plate 31 facing page 123). After: Yamagishi, S. and Kanao, K. cited in: Yamagishi, S. and Honda, M. 2005. Tracking the route taken by Rufous Vangas. In: S. Yamagishi, ed., Social Organization of the Rufous Vanga: the Ecology of Vangas—Birds Endemic to Madagascar. Kyoto University Press: 141–162, Kyoto, Japan.

Fig. 5.6 **(1)** Patel, N.H. 2006. How to build a longer beak. Evolutionary changes in the beaks of Darwin's finches have been instrumental in the adaptive radiation of these birds. The molecular basis for variation in beak size and shape is opening up to investigation. Nature *442*: 515–516 (Fig. 1 page 515), **(2)** Abzhanov, A. et al. 2006. The calmodulin pathway and evolution of elongated beak morphology in Darwin's finches. Nature *442*: 563–567 (Fig. 4 page 565).

The Mental Ability of Birds Takes Many Forms

6

6.1 Cognition and the Use of Tools

When observing with binoculars birds perched on some tree top or telephone pole, they do not convey the impression of a high mental ability. It is usually their bright colours and melodic song that attract the birdwatcher. However, they are capable of the most exquisite forms of behaviour and can surmount difficult situations surpassing mammals in many respects.

The list of their abilities is long indeed.

Europeans usually become distressed and overwhelmed when they are obliged to recognize that several of their inventions were made centuries before by the Chinese. The same with the birds. They solved problems posed by their environment, long before humans appeared on the planet.

The Birds-of-paradise use their feet as tools to hold and manipulate food. They easily extract the edible part from capsular fruits harvesting them in a most effective way. The Goldfinch (*Carduelis carduelis*) when presented with food at the end of a string can use its feet and bill to successively lift it close to its mouth, finally eating the prey. The Hooded crow (*Corvus cornix*) goes one step further. After seeing Eskimos setting lines through holes on the ice for catching fish, it rapidly learned the devise and alone used the same lines to catch the fish. Another example of independent learning is the way Blue tits started opening milk bottles that had their tops covered with foil. They easily perforated the capsules to get a meal and the novel technique spread rapidly among the other members of the species. Like in mammals, the storing of food as a reserve for the winter is a regular habit among the Nutcracker and the Siberian jay (Perrins 1976).

The last decades have seen an upsurge in the study of cognition in birds.

Tools have been defined as external objects, used in the attainment of an immediate goal, by extending the function of the hand, mouth, beak or claw (Lawick-Goodall 1970). Examples are: (1) A vulture breaking an egg by hitting it with a stone. (2) Insertion of twigs in crevices by the Woodpecker finch of the Galapagos islands. (3) Leaf manufacture in Caledonian crows. These are true tool cases which are different from borderline situations such as a gull dropping an egg from a rock. It turned out that the use of tools in birds was much more common than previously thought. Over 120 cases of tool use were reported in 104 species with 39 assigned to the true tool category (Lefebvre et al. 2002).

The crows (Corvidae) are so mentally advanced that they have been compared to the great apes. Many species cache food during periods of seasonal abundance. Western Scrub jays are able to remember where they have hidden it but also are aware of its perishable condition and take adequate measures to eat it in time. Extractive foraging includes dropping of mussels from the air until the shell breaks and hammering with the beak on walnuts and acorns.

Ravens obtain insect larvae from holes in wood. Their hook tools are made by trimming twigs in a complex series of steps. Most corvids form long-term pairs that extend thoughout the life of the two sexes and show many other forms of social behaviour.

In many ways the cognitive capacity of corvids is on a level similar to that of the great apes including: causal reasoning, imagination, flexibility and prospection. There is an impressive similarity of high mental ability in the two distant groups of animals (Fig. 6.1) (Emery and Clayton 2004; Seed et al. 2009).

In a review comparing the social cognition of primates and birds Marler (1996) states that: “there are more similarities than differences between birds and primates”.

6.2 Migration was a Highly Innovative Process that Demanded New Solutions

Migration is usually considered as an activity distinct from other forms of behaviour dealing with mental ability. From the beginning, migration was interpreted in terms of

A. Lima-de-Faria, *Molecular Geometry of Body Pattern in Birds*,
DOI 10.1007/978-3-642-25301-0_6, © Springer-Verlag Berlin Heidelberg 2012

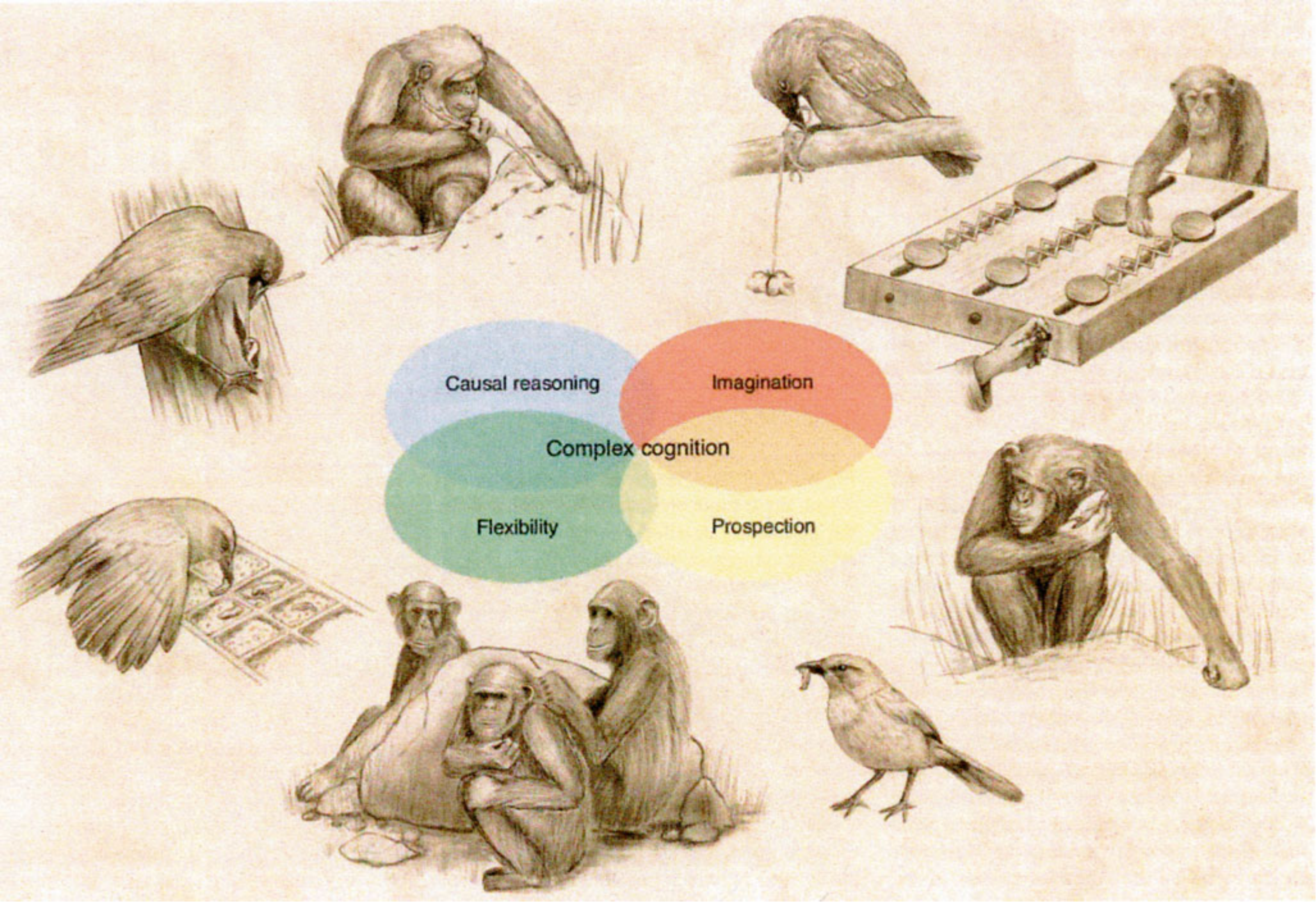

Fig. 6.1 **Illustration of the four nonverbal cognitive tools displayed by corvids and apes, which are considered as the basis of complex cognition: (1) Causal reasoning**: tool use in New Caledonian crow and in chimpanzee. **(2) Imagination**: insight in ravens and role taking in chimpanzees. **(3) Flexibility**: flexible memory for degraded and fresh food items in western scrub jays and tactical deception in apes. **(4) Prospection**: western scrub jays recaching food and chimpanzees carrying stone tools

concepts that prevailed in the 1800s and that still pervade many present interpretations of behaviour and evolution.

Migration tended to be regarded as a natural event. It should be realized that when birds emerged in evolution they did not start necessarily by migrating. This was an elaborate process that depended on the acquisition of: (1) much empirical experience, (2) assembling of learning and (3) coherent combination of dispersed information. No bird in the Cretaceous (130 million years ago), or even several millions of years later, is expected to have started to fly from the North to the South Polar regions, every year, as the Arctic Tern (*Sterna paradisaea*) does during migration, covering up to 15,000 km. Another species, the short-tailed shearwaters (*Puffinus tenuirostris*) makes an annual migration between the North Pacific and its breeding grounds in South Australia which requires a round trip of more than 30,000 km (Pough et al. 2005). Such long and hazardous routes are not expected to have been discovered and established overnight.

Research in many areas, which has included the chemistry and physics of the bird's ultramicroscopic anatomy, has disclosed that migration represents one of the best examples of innovation and improvisation. The birds have been obliged to solve problems to follow new routes, as the geography of the earth, its magnetic field, and other parameters changed drastically as the years passed.

6.3 Landmasses have Moved Across the Earth's Surface

When Alfred Wegener proposed in 1915 the hypothesis on continental drift it was rejected as impossible. His suggestion was that earth's continents had at one time been joined in two supercontinents. His conclusion was based on a large study of the distribution of fossils and rocks in different parts of the planet. According to him the continents had once been joined and later separated, moving in different directions. The original supercontinent has been called Gondwana.

It is now evident that the earth consists of a series of plates which are in constant motion moving at speeds of up to 100 mm per year. The first direct measurements of plate movements were made by using laser stations around the world and astronomical telescopes. One of the figures obtained was 60 mm per year (Doyle et al. 1994).

6.4 The Emergence of New Continents, Seas and Deserts

Our planet is a highly dynamic celestial body. As a consequence the face of the earth has changed in an unrecognizable way. A single land mass covered a fraction of its surface 240 million years ago. By 200 million years ago this mass started to separate into individualized continents, but as late as 120 milllion years ago South America and Africa built a single land unit. North America was attached to what later would become Europe, India was close to Antarctica, and the Mediterranean and the Baltic Seas did not exist yet.

This was the land scenario that birds faced when they were already well-developed as a separate animal group.

Since then, the changes of the landscape became equally dramatic. Africa collided with Europe creating on this impact the mountainous Alps. The Mediterranean Sea has dried out and been replenished with water several times. Moreover, about 3,000 years B.C. its surrounding lands were covered by dense and luxuriant forests that have successively disappeared due to human intervention. The deserts, like the Sahara, have increased. The cave paintings found in this area of Africa depict a dense vegetation and animal life that has since then retreated into the center of the African continent (Attenborough 1987; Honour and Fleming 2002).

These geological and geographic transformations had a large impact on the distribution of the fauna and the flora. As a result the birds have been confronted, throughout their evolution, with a geography and landscape that changed slowly but demanded new solutions.

6.5 Birds are Faced with Challenges – The Earth's Magnetic Field is Under Constant Change

Like the sun, the earth has a magnetic field which has its origin in the core. The result is the formation of a magnetic dipole building a north–south axis.

The magnetic field of the earth is under permanent change which derives from the movement of electric currents in its interior. Its variations are periodic and have resulted in the change of the position of the magnetic poles with time, as well as of the intensity of the magnetic field. Over the last 200,000 years the reversals of the field polarity resulted in the sharp displacement of the magnetic poles. This event tended to occur every 5,000 years (Zirker 2009). At some locations the magnetic field may change daily due to the earth's rotation, or monthly in connection with the moon's position (Fig. 6.2).

Hence, the birds are faced permanently with new challenges concerning their orientation in relation to the magnetic field which they have learned to use in their migrations. Besides, since the position of the poles has been reversed throughout the last millennia, this has interfered with a bird's capacity to use the magnetic field. Moreover, as migration became imperative due to changes in habitat they soon discovered solutions that allowed them to circumvent novel obstacles.

6.6 The Night Sky, with its Stars, Tells the Birds their Latitude – The Star Compass

An intensive research on migration has led to the present evidence. To start with, birds have a compass that allows orientation. Secondly this anatomical instrument is used: (1) in orientation related to the geomagnetic field, (2) in guidance connected with the sun's position on the horizon, (3) to access skylight polarization distribution and (4) in the sorting out of star configurations.

The existence of the magnetic compass in birds was first demonstrated in European robins. They preferred their migratory direction even in cages and responded to a shift in magnetic North with a corresponding changing in their headings. Standard bar magnets produce much stronger magnetic fields than the Earth's field. When these magnets were placed on homing pigeons their navigation was disrupted (Lohmann 2010).

Sun orientation was demonstrated by placing starlings in an experimental aviary in which the position of the sun could be altered by means of mirrors. The light of the sun at sunset is polarized and it has also been shown that it functions as a cue in orientation (Baker 1980; Muheim et al. 2006).

The ability to navigate by the stars was discovered in experiments with warblers which were allowed to observe the night sky in a planetarium. When exposed to the star constellations that prevailed at the time of their southerly migration they followed their direction.

Novel experiments were designed, using songbirds, to control the flight by the stars during overnight migration. The height of the Pole Star telling them the latitude. Songbirds that migrate at night, when placed in a cage, jump in their migratory direction. Twenty blackcaps (*Sylvia atricapilla*) and 34 pied flycatchers (*Ficedula hypoleuca*) were enclosed in a planetarium at the University of Aarhus, Denmark. Using infrared sensors it could be ascertained that the birds jumped in a south-southwesterly direction which is their normal route. When the stars in the planetarium were flipped to the south, the birds jumped north-east. This was taken as confirmation that they use the stars as a compass to find the north (Fig. 6.3) (Mouritsen and Larsen 2001).

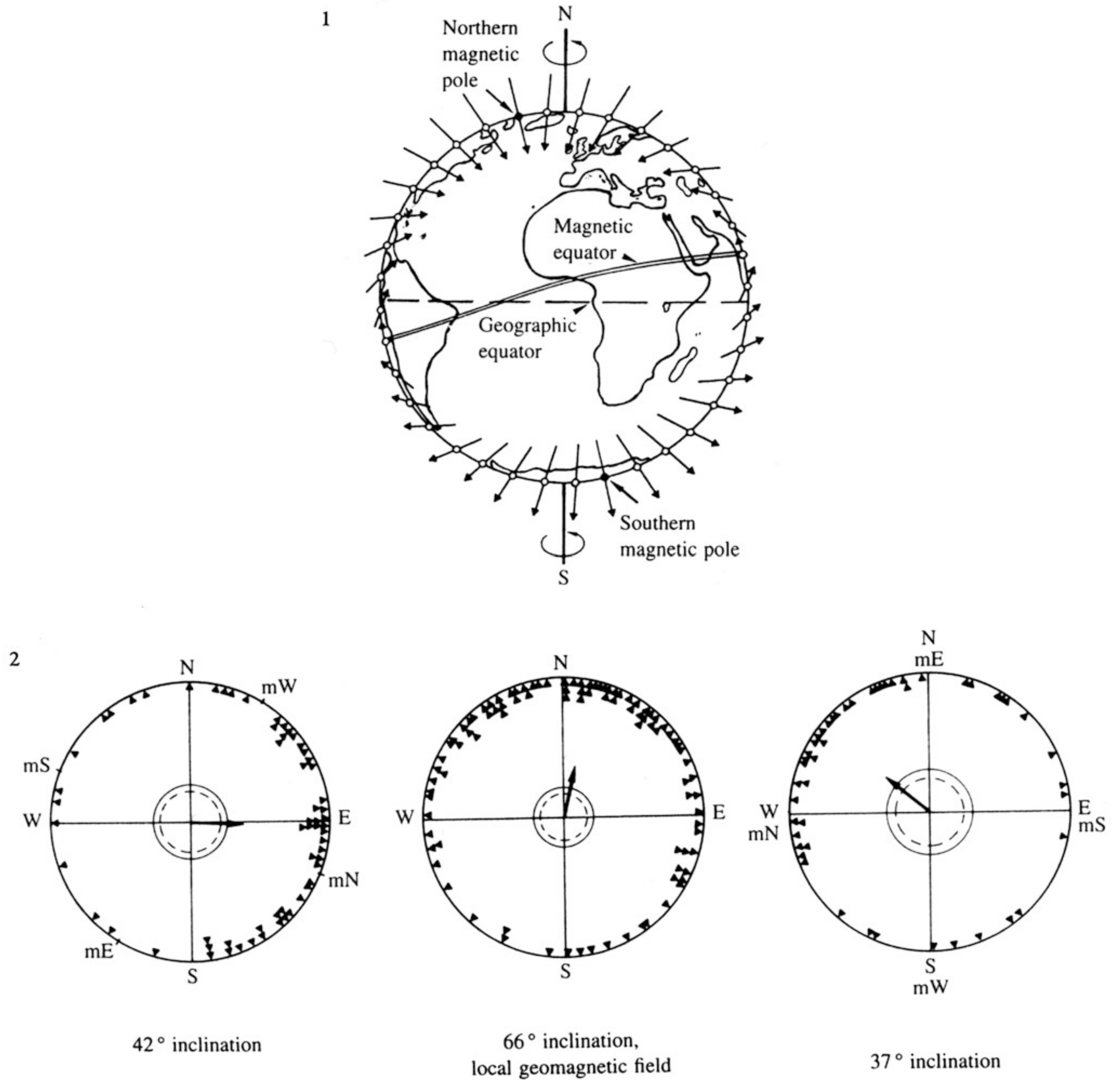

Fig. 6.2 Magnetic orientation in birds. (**1**) Schematic view of the earth and the geomagnetic field. (**2**) Orientation of European robins: when magnetic north (mN) is deflected, the birds alter their preferred direction accordingly. The symbols at the peripihery of the circle indicate the bearings of single test nights, the *arrows* represent the mean vectors with the length proportional to the radius of the circle = 1. The two inner circles mark the 5% (*dashed*) and the 1% significance border

6.7 The Physical Basis of the Magnetic Compass and the Evolution of Bird Migration

Experiments have been designed to access the relative importance of the different compass mechanisms and the situations in which the magnetic field has shifted in alignment relative to natural celestial cues.

During the period that precedes migration the birds rely mostly on celestial cues but during migration the magnetic field becomes the primary source of information. Adding to this plasticity of mental activity, is the capacity to recalibrate the magnetic compass. Birds exposed to the dual perception of the celestial and magnetic patterns alter their activity as disclosed by the comparison of animals kept in cages or allowed a view of the entire sunset sky where polarized light is emitted.

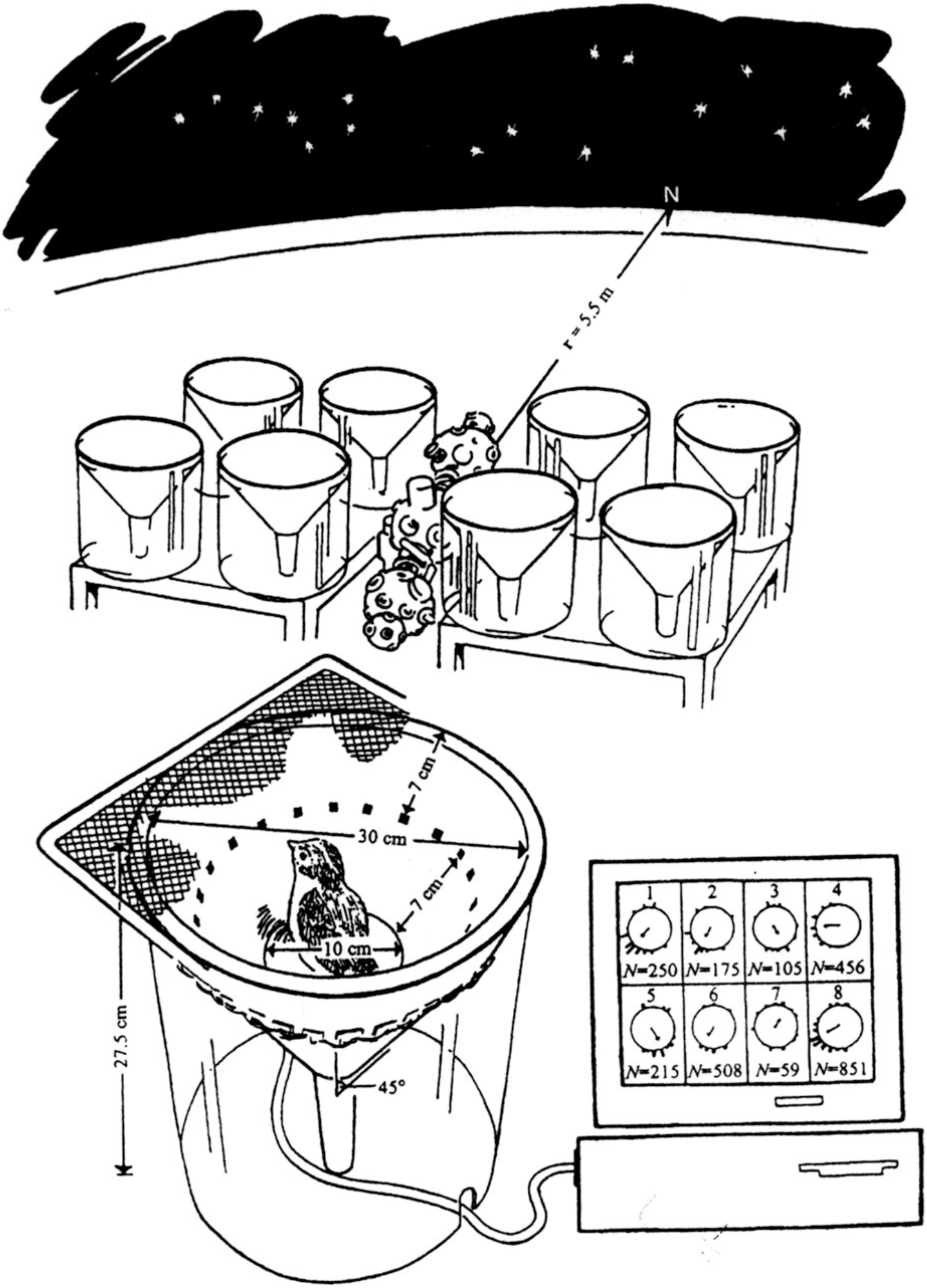

Fig. 6.3 **Migrating birds use star compass**. Sketch of the experimental equipment and set-up in the planetarium which led to the confirmation that birds use stellar cues during migration

Magnetoreception is based on microscopic particles of magnetite, an iron mineral Fe_3O_4. The inherent program coding for a general direction and distance to be travelled, is located on the upper part of the beak and nasal cavity. Compass orientation is disrupted by local anaesthesia of these body regions where the iron-based receptors are located.

Another study of magnetoreception indicates that it may also be based on spin-chemical processes involving electrons in specialized photopigments. The magnetosensitive process would take place in the eye due to photon absorption. Both systems lead into the realm of elementary particles disclosing that bird behaviour is no longer an abstract area but has a physical basis that can be pinpointed to the photon and electron levels (Muheim et al. 2006; Wiltschko et al. 2010; Rodgers and Hore 2009).

A bird's capacity to innovate has led to the use of new breeding regions and the movement to survival areas in the non-breeding season, attesting what several authors call the evolution of bird migration (Fig. 6.4) (Salewski and Bruderer 2007; Boyle and Conway 2007).

6.8 One-Eyed Sleep in Ducks and Brain Activity

In birds, eye movements can be quite independent in each eye, which is not the case in mammals. By the beginning of the 1400s it had already been noticed that some bird species slept with open eyes. It took over 500 years to investigate this phenomenon in detail.

When birds feel safe they sleep with both eyes closed and the two hemispheres of the brain participate in this process. Under dangerous situations they keep watch with one eye.

Mallard ducks usually sleep in rows of four. The birds on both extremities of the row, had the eye facing away from the center of the group, open most of the time, avoiding the attack by predators. Birds in the central part of the row felt safe and opened their eyes without directional preference. Recordings of electrical activity of their brain showed that the hemisphere receiving input from the open eye was more active than the sleeping hemisphere. This ability to use only one hemisphere when sleeping exists also in aquatic mammals that must alternate between breathing at the surface and sleeping under water (Pough et al. 2005).

6.9 Active Cooperation Among Birds Leads to Class Distinction

Another aspect of high mental ability is the development of cooperation which attains advanced forms of behaviour.

The cooperative breeding of the Woodswallows is characterized by the presence of breeding and non-breeding mature individuals which help each other build a social group. This behaviour assumes refined forms with the creation of a working class of birds called "helpers". These are non-breeders which assist in the defense of the nest and in attacking predators. They also function as nurses. They feed the nestlings of the senior breeding pair and when the young leave the nest they continue to supervise them. We are dealing with the formation of hierarchy and class distinction.

Hierarchy in birds takes many forms showing up when they build flocks. Groups of up to ten homing pigeons were followed using *GPS* (Global Positioning System) devices capable of capturing movement decisions resulting in a detailed mapping of individual dynamics. Birds tended to copy consistently the directional behaviour of a leader (Nagy et al. 2010).

The establishing of hierarchies is also notorious among the Australasian Babblers in connection with the asserting of territory. Such behaviour includes submissive display, threat, chasing and alarm-calling and is connected with the building of large nest colonies with densities of 20 nests per 90 m^2.

With Grey-crowned and White-browed Babblers most animals of the group take part in nest building and class formation occurs. Juveniles remain in the territory of their parents during the first year and become "helpers" of the group during the following season. Other families use cooperative breeding such as Bee-eaters and Cockatoos.

Over 2,400 warblers were ringed and monitored in the Seychelles islands for a period of 17 years. It was found that although some warblers can breed independently others are subordinates functioning as helpers. Due to the ability of female breeders to modify the sex of their progeny by various means, the helpers were found to consist mainly of daughters (Komdeur 2003).

Sociability may extend to other behaviour forms. Cormorants, at a time when they form flocks consisting of many thousands, develop collective fishing. The birds cooperate by getting distributed on the water in a fan-shape formation and by advancing towards the fish shoals in unison.

6.10 To Cope with Water Refraction Birds are Obliged to Make Corrections

The high mental ability of birds becomes also evident in their way of fishing. Predation of fish is widespread occurring in penguins and cormorants but these are mainly underwater feeders.

Kingfishers plunge into the water to catch their prey located many times at the bottom of a river or lake. Light reflection and refraction at the surface would lead them to

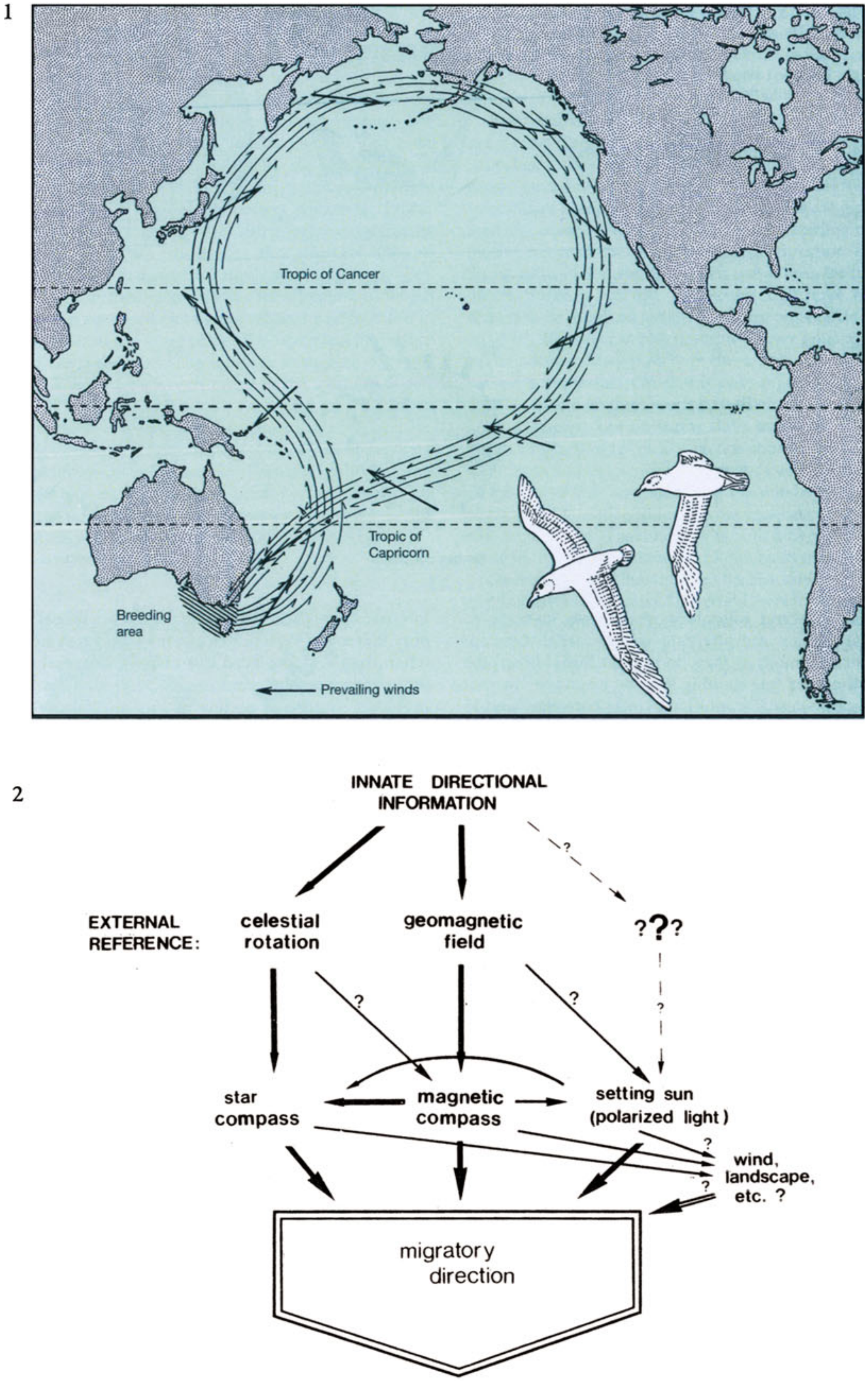

Fig. 6.4 **Internal and external sources that affect migratory direction**. (**1**) The migratory path of the short-tailed shearwater *Puffinus tenuirostris*. As this species migrates from its Australian breeding area to its northern range, it takes advantage of prevailing winds in the Pacific region to reduce the energy cost of migration. This migration route covers over 30,000 km. (**2**) Interaction of the various orientation cues in migratory orientation. The *question marks* indicate relations that are not yet fully understood. The *dashed lines* mark a relation that is contemplated

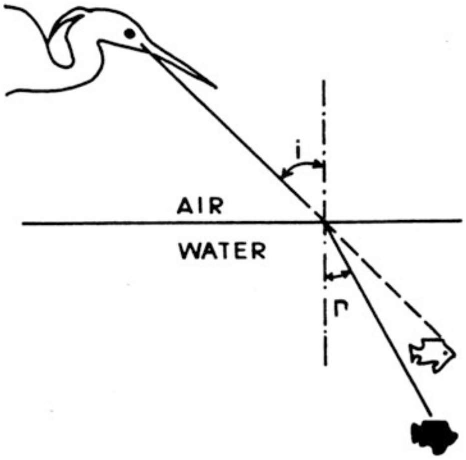

Fig. 6.5 **Prey capture in water birds demands visual compensation for refraction**. Light refraction at the air/water interface in accordance with Snell's law causes the apparent image (*white fish*) to be seen somewhere along the line of refraction, i.e., above the real fish (*black*)

miss their prey. They face problems in their fishing which they have solved. As revealed by laboratory experiments they can compensate for these optical difficulties, catching prey successfully under water by adjusting the angle of diving.

Birds that strike at submerged prey must take into account prey position, movement, depth, distance and other factors. All these calculations are made by herons, kingfishers, little egrets and other species coping with refraction over a wide range of prey positions by making corrections of the incident angles (Fig. 6.5) (Katzir 1993; Kral 2003).

6.11 Song Learning in Birds Depends on the Concentration of a Protein in their Brain and the Action of Hormones

Genetic aberrations of the human gene *FoxP2* impair speech production. The protein encoded by this gene is essential for the full articulation of the human language. Mutations of *FoxP2* cause verbal disorders.

Human speech, and learned vocalizations in songbirds, bear behavioral and neural parallels. Like human youngsters, songbirds learn to vocalize by imitating the sounds of their elders. When zebra finches learn to sing, or adult canaries change their song, there is an increase in *FoxP2* levels in the bird's brain. If the amount of this protein is reduced, by using virus-mediated RNA interference, there is a disruption in bird song which becomes more variable and imprecise as that of controls. Humans and birds seem to employ similar molecular pathways in vocal learning (Haesler et al. 2007).

Other molecules, such as hormones, participate in the song process (Shen et al. 1995). Neural conversion of androgen to estrogen by the enzyme aromatase is an important step in the development and expression of masculine behaviour in birds. Non-songbirds have low levels, whereas songbirds, such as zebra finches, possess high levels of aromatase activity. The mapping of the distribution of aromatase messenger RNA, by *in situ* hybridization, revealed its widespread expression in the brain of these birds. The presence of estrogen receptors in the brain of several avian species has turned out to be unique to songbirds (Gahr et al. 1993).

Dopamine is a modulatory transmitter in the brain. In songbirds dopamine is released into a part of the brain and its levels are linked to social contexts and type of singing. This activity is due to the gene *avian zenk*. Kubikova et al. (2010) cloned, from zebra finch brain DNA, all avian dopamine receptors. These were found to be highly expressed in the brain. They concluded that dopamine receptors may be involved in song development and social behaviour.

6.12 The Starling Owned by Mozart Whistled the Theme of his Concerto

Wolfgang Amadeus Mozart (1756–1791) is well known for his symphonies, operas and concertos. Less known is that he owned a starling that he purchased on May 27, 1784 as recorded in his book of expenditures.

The European starling (*Sturnus vulgaris*) has been known since Antiquity for its vocal talents. This bird possesses a rich repertoire of calls and songs composed by whistles and other sounds. It also copies the sounds of other animals, including human speech. This has been checked by recent experiments involving captive birds.

Mozart listened attentively to the starling's song which delighted him. When he wrote for the piano a fragment of what the bird was whistling he noted, to his surprise, that it was similar to the beginning of the last movement of his Piano Concerto in G Major (K 453). The starling had learned the theme from the concerto but sang it in its own key (Fig. 6.6).

A few years later the starling died. Mozart was so attached to the bird that he wrote a poem which he recited at its funeral (West and King 1990).

Fig. 6.6 Wolfgang Amadeus Mozart was the owner of a pet starling. He recorded a musical fragment the bird was singing. Mozart expressed pleasure at hearing the starling's song—"Das war schön!" (that was beautiful)—because it sounded like the beginning of the last movement of his Piano Concerto in G Major, K. 453. Somehow the bird had learned the theme from Mozart's concerto

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Fig. 6.2 Wiltschko, W. and Wiltschko, R. 1996. Magnetic orientation in birds. J. Exp. Biol. *199*: 29–38 (Figs. 1 and 2 page 30).

Fig. 6.3 Mouritsen, H. and Larsen, O.N. 2001. Migrating songbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass. J. Exp. Biol. *204*: 3855–3865 (Fig. 2 page 3859).

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Fig. 6.5 Katzir, G. 1993. Visual mechanisms of prey capture in water birds. In: Vision, Brain, and Behaviour in Birds (Zeigler, H.P. and Bischof, H.-J. Editors), MIT Press: 301–315, London, UK (Fig. 17.1 page 303).

Fig. 6.6 (**1**) Salter, L. 1978. The Gramophone Guide to Classical Composers and Recordings. Salamander Books Ltd., London, UK (Fig. on page 132), (**2**) Burton, P. and Hayman, P. 1977. Fåglar och Fågelliv i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. on page 103), (**3**) West, M.J. and King, A.P. 1990. Mozart's starling. American Scientist *78*: 106–114 (Musical notes page 112).

How to Redesign the Body Pattern of an Organism 7

7.1 A Sophisticated Genetic Technology Opened the Way

Molecular biology is such an advanced science when compared to other biological disciplines, that it has created a sophisticated language of its own filled with difficult terms and many abbreviations. To the uninitiated reader it may sound at times like a foreign language. It is thus appropriate to avoid, as much as possible, technical words in the description of the observations and experiments that led to the elucidation of many obscure biological phenomena.

A marriage of embryology with a sophisticated genetic technology has led to a deeper understanding of the pathways taking place between the DNA molecules, located in chromosomes, and the body structure of the adult organism. As usual, what was considered impossible became possible, and what seemed irrelevant, or fancy, turned out to be the key to the molecular cascades that canalize embryonic development and lead subsequently to the emergence of the adult pattern. The road map of organism development was the product of an intense toil in laboratories spread around the world carried out by the last generation of molecular cytogeneticists. The simpler the results seem to be, the more work at the laboratory bench and serious thought lie behind them.

7.2 Early Evidence on Drastic Structural Transformations – Feet on the Head

Since Bateson's work (Bateson 1894) it became known that one structural element may be transformed into another. In animals the antennae of an insect could be modified to a foot and the eye of a crustacean could be transformed into an antenna. This phenomenon had been described by Goethe (1749–1832) in plants. Transformation of stamens into petals occurred regularly in roses and ranunculus, as well as the transformation of sepals into petals (Fig. 7.1).

Bateson proposed the term *Homeosis* which was defined as a change of something into the likeness of something else. Homeo derives from the Greek word which means *alike*. The examples that Bateson collected included: (1) Sawfly (*Cimbex*), the antenna was transformed to a foot. (2) Moth (*Zygaena*), transformation of a hind leg into a hind wing. (3) Crab (*Palinurus*), transformation of an eye to an antennalike structure. (4) Additional ribs in humans by transformation of the seventh cervical vertebra to a first thoracic vertebra with a rib. (5) Humans with supernumerary nipples and mammae on the front of the trunk. (6) Homeotic variations affecting the body plan, even more profoundly, were changing radial symmetry. Normal starfishes have five arms and are radially symmetrical but Bateson described six-armed starfishes in *Asterias rubens*.

Later, it was found that in mammals, such as squirrels and voles, nipples vary in body location and number in different species (Fig. 5.2).

7.3 The Homeobox Genes – Formation of Identical Organs at Different Body Locations

The homeobox is a highly conserved DNA segment of 180 base pairs encoding a conserved DNA binding protein of 60 amino acids (the homeodomain).

The homeobox genes (also called homeotic and *Hox* genes) turned out to be the determinants of a universal principle of specification of the body plan (Gehring et al. 2009). The mutations arising in homeotic genes lead to the development pattern of an organism to be replaced by a different, but homologous one. The homeotic mutations in *Drosophila*, and other species, cause the formation of an identical organ at a different body location.

In organisms with bilateral symmetry the anteroposterior axis is specified by the *Hox* genes. These genes are arranged in the same order along the chromosome as they are

A. Lima-de-Faria, *Molecular Geometry of Body Pattern in Birds*,
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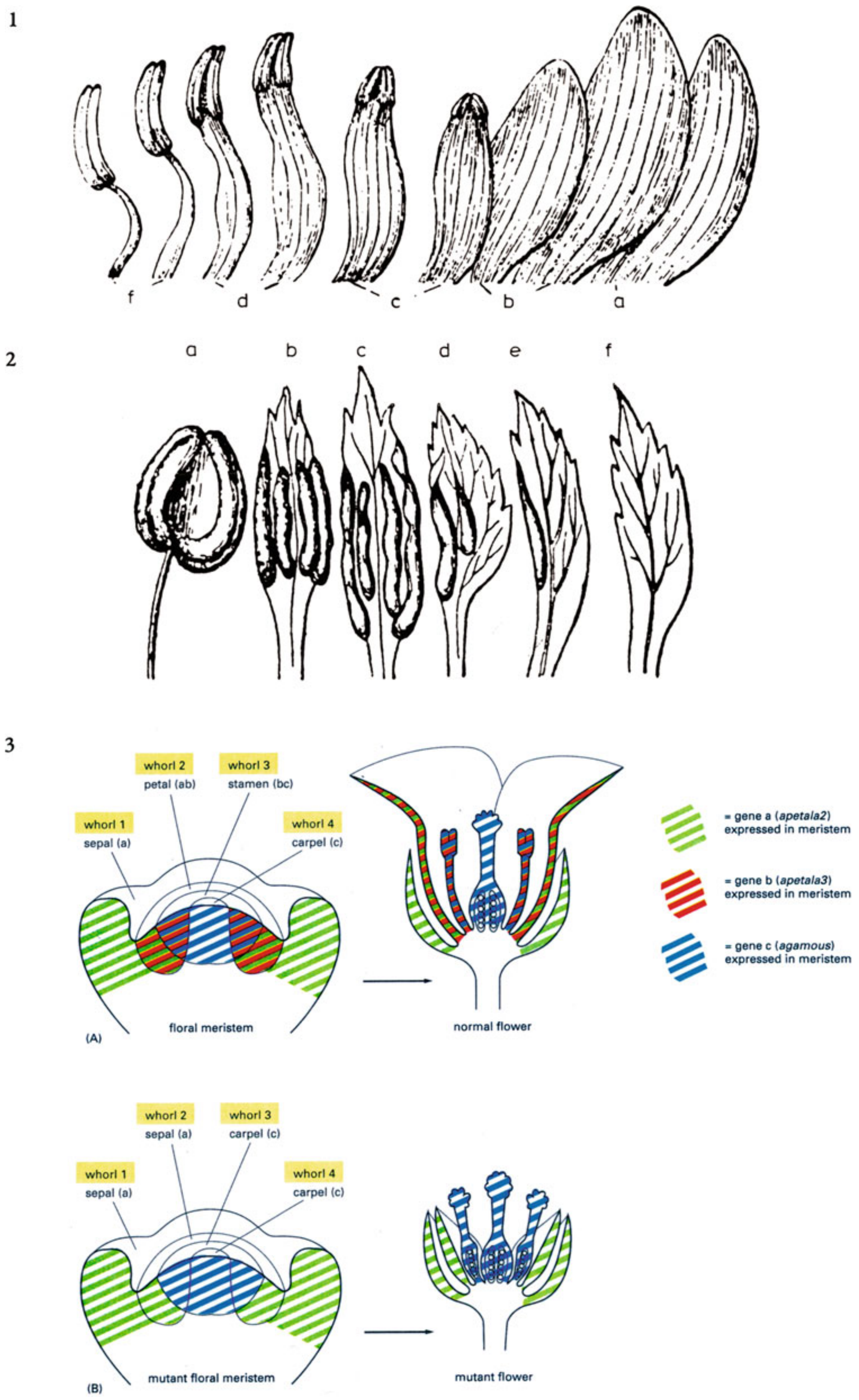

Fig. 7.1 **The genes that specify the order of flower parts are the same that decide the body organization of birds and flies—the homeotic genes**. (**1**) Transformation of petals into anthers in the flower of *Nymphaea alba*. a and b, normal petals. c, beginning of pollen formation at the top. d, more advanced stages of the transformation. f, normal anthers. (**2**) Regressive transformation of the anther (a) into a petal with the shape of a leaf (f) in the genus *Rosa*. (**3**) Homeotic selector gene expression in an *Arabidopsis* flower. (**A**) Diagram of the normal expression patterns of three genes which code for gene regulatory proteins. The colored shading on the flower indicates which organ develops from each whorl of the meristem. (**B**) The patterns in a mutant where the *apetala3* gene is defective. Because the character of the organs in each whorl is defined by the set of homeotic selector genes that they express, the stamens and petals are converted into sepals and carpels

expressed along the anteroposterior axis specifying the corresponding body regions. This has been called the colinearity rule.

Ordered *Hox* clusters were found first in the fruit fly by Lewis (1978) and later in mammals by Boncinelli et al. (1988). They turned out to be present as well in birds, frogs and humans (Carrasco et al. 1984; McGinnis et al. 1984a, b). Subsequently they were discovered in the squid *Euprymna* and in the primitive chordate *Amphioxus* (Callaerts et al. 2002; Garcia-Fernandez and Holland 1994) establishing their general occurrence among invertebrates and vertebrates.

The original *Hox* cluster has been split into two gene complexes: the *bithorax* and the *Antennapedia* by a chromosomal rearrangement in the fruit fly, but in other insects it has remained intact. The head and anterior thoracic segments are specified by the *Antennapedia* complex whereas the posterior thoracic and abdominal segments are specified by the *bithorax* complex genes.

Mouse and human *Hox* genes are also arranged in a colinear order but they occupy four complexes on different chromosomes whereas the invertebrates have a single *Hox* complex (Fig. 7.2). Significant is that the *Hox* genes do not act alone, microRNAs also participate in their function (Bender 2008). This class of RNAs has turned out to make crucial decisions in map reading during embryonic development.

Homeobox genes in the plant *Arabidopsis* provide positional information necessary for controlling cell specification and pattern formation. Besides they function as molecular markers in the establishment of both apical-basal and radial symmetries (Lu et al. 1996) (Fig. 7.1).

What could hardly be contemplated a few years ago is that the genes that decide the body segmentation of a fly, are the same that decide the formation of the vertebral column in humans and birds as well as the sequential arrangement of flower parts in plants. These master genes are the homeotic genes.

7.4 Geneticists Transformed Curiosities into Valuable Developmental Keys – Eight-Legged and Four-Winged Flies were Produced

The first homeotic mutant in the fly *Drosophila* was found in 1915. It was named *bithorax* because it showed partial duplication of the thorax and turned out to consist of a number of closely linked genes. A deletion of the entire *bithorax complex* resulted in all abdominal segments becoming transformed into second thoracic segments. As a result of an intensive study Lewis (1978, 1992) concluded that: (1) There seemed to be one gene primarily required for each body segment. (2) The genes were arranged along the chromosome in the same order in which they were expressed along the anteroposterior axis of the organism. (3) This colinearity rule applied to other species. (4) A gene primarily expressed in a given segment tended to be expressed in the more posterior segments.

It became evident that the genes of the *bithorax complex* removed the legs from the abdominal segments, leaving only three pairs of legs on the three thoracic segments, which is the normal situation in insects. By inactivating the gene specifying the first abdominal segment Lewis and collaborators obtained eight-legged flies, which usually have only six legs.

In the flies which are found in nature the third thoracic segment forms only small balancers instead of wings. As a result normal flies have only two wings. By inactivating the *ultrabithorax* genes, it became possible to convert the balancers into a second pair of wings producing a fly with four well shaped and large wings (Bender et al. 1983; Lawrence 1992) (Fig. 7.2). The butterflies are insects whose body consists regularly of four wings. Hence, one was recreating in the laboratory a situation which occurred in nature in other insect species. Actually evolution was being repeated by experimental means and at will.

From these results it was concluded that the homeotic genes specify the order inherent to the construction of the fly deciding the route of development and evolution.

Subsequently the first homeotic mutant causing the transformation of an antenna to a leg was collected in nature, proving that this transformation also could occur spontaneously. Later this mutant was induced by X-rays and neutron irradiation. The gene responsible for this mutation was called *Antennapedia* and found to be associated with a chromosome rearrangement (Fig. 7.3) (McGinnis et al. 1984a).

7.5 The Antenna to Leg Transformations

Transgenic flies were obtained by fusion of the heat-shock promoter to the gene *Antennapedia*. Initially the transgenic flies had normal antennae but by refining the experiments large legs with claws appeared on the head (Fig. 7.4). Gehring (1998) and collaborators concluded that *Antennapedia* was a master control gene directing leg morphogenesis. It functioned as a single switch that activated the leg developmental pathway creating a cascade of molecular events in which several hundred genes participated.

The understanding of the function of *Antennapedia* became better elucidated by the discovery of a mutant called *Contrabithorax* which has the opposite effect on the

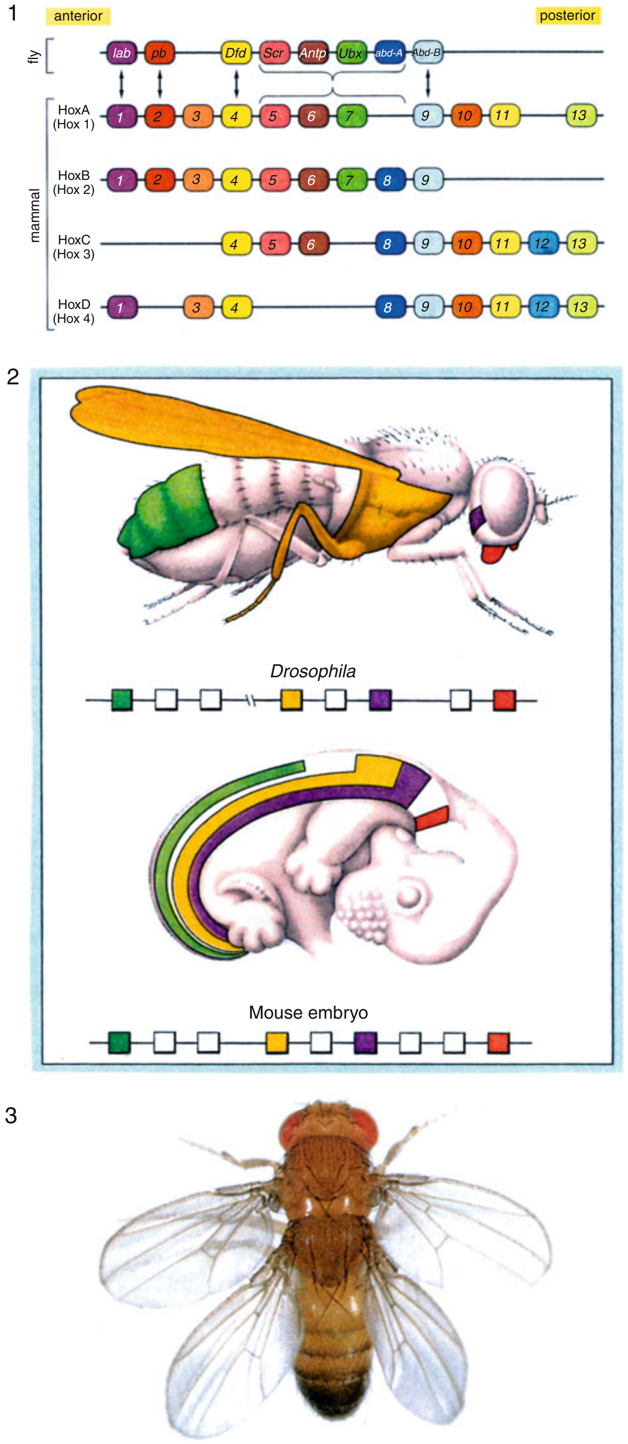

Fig. 7.2 Combination of homeotic genes leads to the production of flies with four wings. (**1**) The *Hox* gene cluster of an insect compared with the Hox complexes of a mammal. The genes of the *Antennapedia* and *bithorax complexes* of *Drosophila* are shown in their chromosomal order in the top line; the corresponding genes of the four mammalian (mouse or human) Hox complexes are shown below, also in chromosomal order. Genes with the most anterior expression domains are to the left, those with the most posterior expression domains to the right. The five complexes are aligned so that genes with the most closely corresponding sequences lie in the same column. The parallelism is not perfect because apparently some individual genes have been duplicated and others lost since the complexes diverged. (**2**) The genes shown in the above figure encode transcription factors crucial to development and are conserved from insects to mammals. Even the chromosomal positions of these genes (*squares*) and the portions of the animal they influence during development (color coded) have been conserved. These genes are called *homeotic* genes in flies and *Hox* genes in mammals but they are homologous. (**3**) Four-winged fly, produced by combining *bithorax* and *postbithorax* gene mutations. A normal fly (shown above from the side) has only two wings

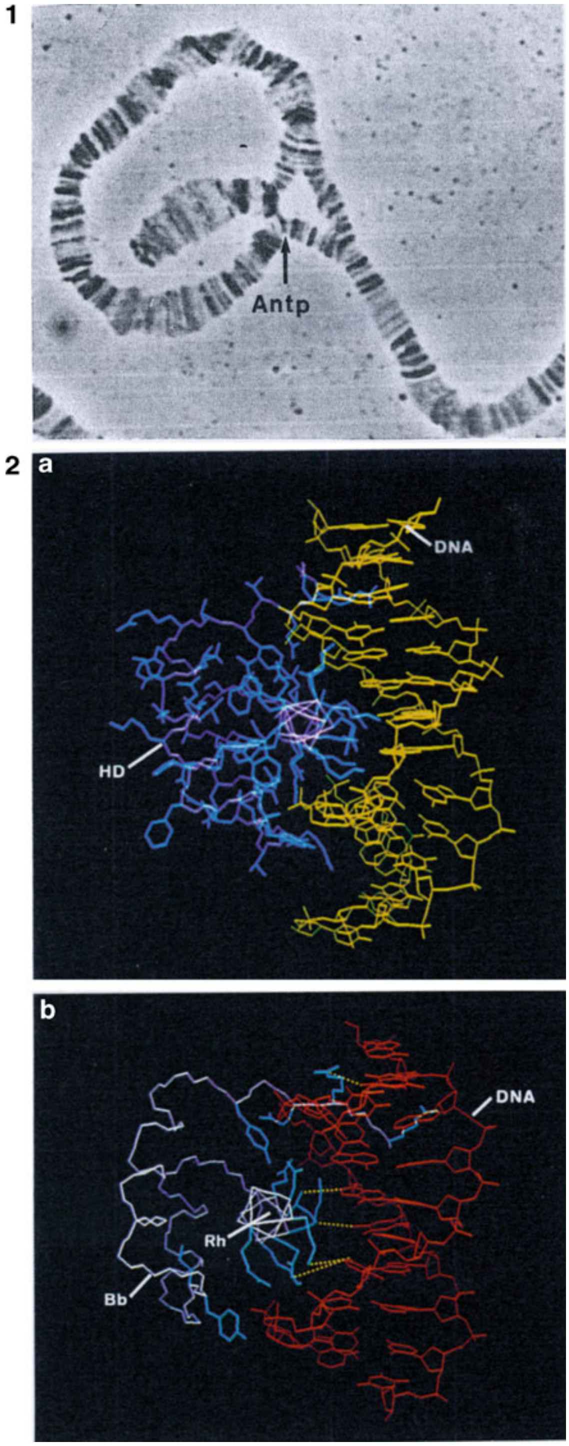

Fig. 7.3 **(1) Localization of the *Antennapedia* gene in the giant chromosomes of the fruit fly *Drosophila*.** The *Antennapedia* gene (*Antp*), is located at the proximal breakpoint (arrow) of the inversion (In($_3$R)*Antp*$^{\mathrm{LC}}$). Courtesy of R.L. Garber. **(2) The homeodomain is a protein of 60 amino acids encoded by the homeotic genes which is seen here binding to its DNA molecule.** Structure of the *Antennapedia* homeodomain-DNA complex as determined by nuclear magnetic resonance spectroscopy. (**A**) Structure with all side chains represented. DNA (*yellow*), homeodomain (*HD*), backbone (*magenta*), amino acid side chains (*blue*). (**B**) Homeodomain-DNA contacts. DNA (*red*), homeodomain backbone (*Bb, magenta*), amino acid side chains contacting DNA (*blue*), direct contacts between amino acids and specific bases (*yellow dotted lines*). Courtesy of K. Wüthrich and M. Billeter

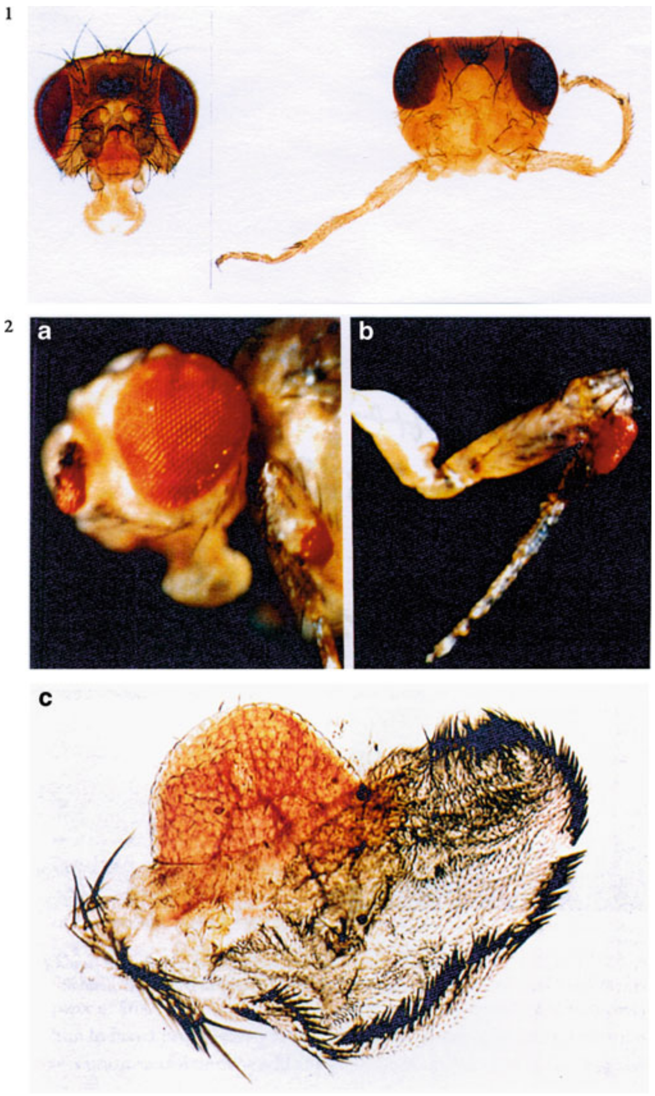

Fig. 7.4 **(1) Antennae are transformed into middle legs in the mutant *Antennapedia*.** The head of a normal (wild-type) fruit fly on the *left* is compared to the homeotic *Antennapedia* mutant head on the *right*. **(2) Induction of additional eyes on the antennae, legs, and wings of a transgenic fly by expression of the normal eyeless gene**: (**A**) additional eyes on the antenna and the foreleg; (**B**) higher magnification of an eye induced on the tibia of the foreleg; (**C**) large eye on wing

structure of the fly. It produces four balancers instead of the four wings that are the result of the action of *bithorax*. *Contrabithorax* was associated with a complex rearrangement in the chromosomes and collaborated with *Antennapedia* in the formation of the body pattern of the fly (Hafen et al. 1984).

7.6 Eyes Formed on Wings, Legs and Antennae – The Unity of Body Construction

Outside these gene clusters other homeobox genes have been discovered, the most interesting being *eyeless*, which corresponds to the mutation *Small eye* in mice and to *Aniridia* in humans (Quiring et al. 1994). Following a series of experiments transgenic flies were obtained in which eyes were formed on the wings, legs and antennae (Fig. 7.4) (Halder et al. 1995). The eyes are real eyes because they are identical in structure and contain functional photoreceptors. This means that a single master control gene can start the cascade of eye development which involves not less than 2,500 other genes needed for eye formation (Gehring 1998).

It turns out from these experiments that:

1. A single gene *eyeless* is the switch for a developmental molecular cascade.
2. Hundreds of other target genes are under its hierachical command which implies an impressive order in gene action.
3. This fly gene has its functional homologue in mice and humans, a proof of the conservation of its structure and function from invertebrates to vertebrates.
4. The gene *Antennapedia* is also expressed in the eye imaginal disc where it induces cell death. However, if this situation is prevented by genetic engineering these cells form little wings in the eye region an indication that this gene also controls wing formation.
5. As demonstrated by Bachiller et al. (1994) there is a conservation of a functional hierarchy between mammalian and insect homeobox genes.
6. The fact that eyes can be formed in most areas of the body, and are true morphological and functional structures, and that little wings can form in the eye, implies a remarkable unity of body construction. Hence, the eye cannot be separated from the wing or from the leg. This unity seems to be the key to our understanding of the emergence of the body pattern in birds.

7.7 Mouse Genes Produce Eyes in Flies – The Importance of Eye Genes

Hox genes have turned out to be functional homologues of the homeotic *Drosophila* genes, as demonstrated by an experiment in which *Hox* genes of the mouse were introduced into flies. The mouse vector induced antenna to leg transformation in adult flies. Moreover, the mouse *Pax-6* (*Small eye*) gene was able to induce eyes in the fly (Fig. 7.5) (Halder et al. 1995; Callaerts et al. 1997). There is an extensive nucleotide sequence homology between the fly *eyeless,* the mouse *Small eye* and the human *Aniridia* genes.

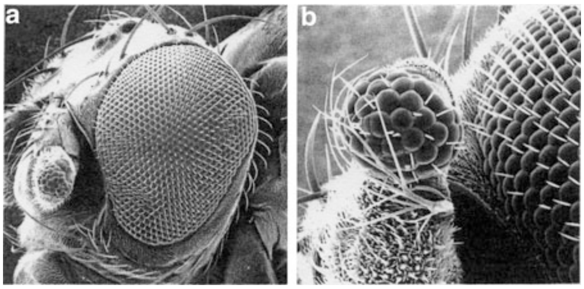

Fig. 7.5 The mouse gene *Pax-6* (small eye) was introduced into the fruit fly, inducing an eye on the antenna of this species. (**A**) overview of the head showing the large normal eye and the minor eye induced by the mouse gene. (**B**) the similarity of structure between the normal and the induced eye is seen in this higher magnification. Scanning electron micrograph by G. Halder and A. Hefti

This result reinforces the unity of body construction which extends from flies to humans and gives more weight to the primary role of the eye in shaping body structure.

7.8 The Wing of the Fly and the Human Fingers are Controlled by the Same Proteins

Another set of genes has added to the establishment of the basic genetic similarities between flies and humans, a homology that a few years ago would be considered out of question. The family of proteins called *Hedgehog* controls and patterns almost every aspect of the vertebrate body plan including: cell growth, survival and fate. It functions as a single morphogen because its action depends on the type of cell encountered, its dose at a given site and the time at which it acts.

The name *Hedgehog* derives from the short and spiked appearance of the cuticle of the mutants in the fruit fly. These genes impaired or changed development of the larval body plan (Nüsslein-Volhard and Wieschaus 1980). *Hedgehog* genes were later found and cloned in other invertebrates and vertebrates including the chicken *Gallus gallus*, the mouse and humans.

The vertebrate set of genes has been divided into three subgroups: the *Desert* (*Dhh*), *Indian* (*Ihh*) and *Sonic* (*Shh*) *hedgehogs*. Both in invertebrates and vertebrates *Hedgehog* binds to a receptor called *Patched*, the result being a signaling cascade leading to the expression of a series of target genes.

The *Hedgehog* proteins control multiple development processes, *Shh* being the most important signaling molecule due to its broad spectrum of action during early vertebrate embryogenesis. It decides the patterning of the left-right

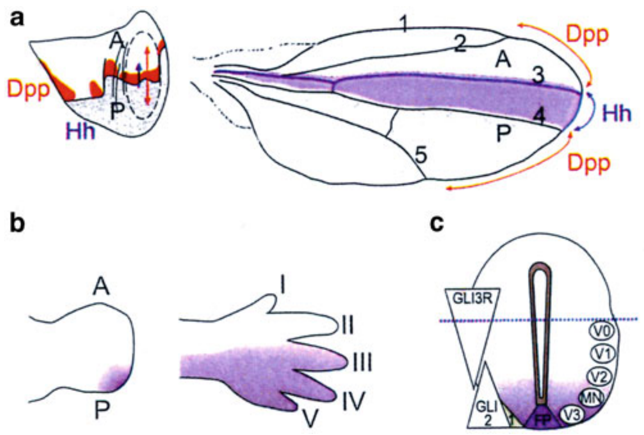

Fig. 7.6 The proteins from *Hedgehog* genes pattern both the wing of a fly and the human fingers. *Hh*, *Hedgehog* gene from the fruit fly. *Shh*, *Sonic Hedgehog* corresponding human gene. (**A**) Hh acts both directly and indirectly to pattern the *Drosophila* wing imaginal disc. (*Left*) Hh activates decapentaplegic (dpp; red) at the anterior side of the A-P boundary of the imaginal disc, which diffuses into and patterns both A and P compartments (red arrow). Hh (blue) also acts directly to pattern the anterior compartment close to the A-P boundary. (*Right*) Adult wing showing the regions derived from the anterior (A, *top*) and posterior compartment (P, *bottom*, shaded), and the regions patterned by Dpp (red arrows) and Hh (blue color, between wing veins 3 and 4). (**B**) Shh has a similar role in anterior-posterior patterning of the distal elements of vertebrate limbs and in specifying digit identity (roman numerals). (**C**) Time and dose-dependent action of Shh. The gradient of Shh (blue color) emanating from the notochord (not shown) and floor plate (FP) progressively defines five different neuronal subtypes in the ventral neural tube

and dorso-ventral axes of the embryo. This same protein influences the pattern of the distal elements of the limbs. Significant, in this connection, is that *Hedgehog* acts both directly and indirectly to pattern the *Drosophila* wing at the same time that one of its proteins (*Shh*) has a similar role in anteroposterior patterning of the distal elements of the vertebrate limbs, such as specifying the five digits of the vertebrate hand (Varjosalo and Taipale 2008). A remarkable conservation of homology exists between the formation of an insect wing and the fingers of our hands. The same genetic and molecular pathways, with intervening minor modifications in the signaling mechanisms, lead to astounding pattern differences (Fig. 7.6).

7.9 Feather Development is also Controlled by One of these Proteins

Even more important for our understanding of the body pattern in birds is that the activity of *Sonic Hedgehog* (*Shh*) has helped to clarify the molecular basis of chicken feather morphogenesis. During early feather development *Shh* is expressed early in epithelial placodes. As development proceeds it appears in the marginal plates of the feathers. The bird's epithelium segregates into two domains, the placode and interplacode. Later these give rise to the barbs and the space between the barbs of the feathers. By using retroviral vectors Ting-Berreth and Chuong (1996) could assert that *Sonic Hedgehog* mediates key interactions between the epithelium and mesenchyme during feather morphogenesis. The molecular pathway starts by induction of a placode accompanied by dermal condensation. Soon a short feather bud develops which grows into a long bud and later, by invagination, builds a feather filament enclosed in a follicle. Following cell differentiation and specifically localized cell death, the mature feather emerges with its rachis, barbs and barbules.

7.10 Moving from Gene Constructs to Embryonic Development – The Avian Molecular Clock

It was now time to test the novel genetic tools for their effect during the fly's embryonic development and their expression in the adult. Two organisms had previously furnished much information on the molecular processes taking part during embryogenesis. They were as disparate as a simple worm and a frog, but they were treasure troves.

The worm *Caenorhabditis elegans* was transformed into a valuable object of research by Brenner (1974). It was chosen because its haploid genome size is 8×10^7 base pairs, about half of that of the fruit fly, and the whole animal consists of only 1,031 somatic cells in the adult male and a variable number of germ cells. What turned out to be of importance from the point of view of development was that out of the 1,031 somatic cells 111 undergo programmed cell death (in the hermaphrodite 113). This is a highly ordered event in which cells are obliged to commit suicide without external influences. Moreover, *C. elegans* although it has a fixed pattern of cell division, cellular interactions play a major role in cell differentiation. Such cell interactions were demonstrated by killing adjacent cells with a laser microbeam and examining their fate (Wood et al. 1988, Salser and Kenyon 1994).

The embryological experiments that had been carried out in frogs and other organisms had involved centrifugation, transplantation, localized destruction and other methods. They led to the conclusion that the antero-posterior pattern was controlled by two organizing centers, one anterior and one posterior. Later results confirmed a model in which two opposing morphogenetic gradients with an anterior and a posterior position were responsible for the formation of the head plus thorax and for the abdominal regions, respectively. The anterior determinant was found to be the *bicoid* gene and the *nanos* gene was involved in specifying the posterior region (Fig. 7.7) (Carrasco et al. 1984; Shepherd et al. 1984).

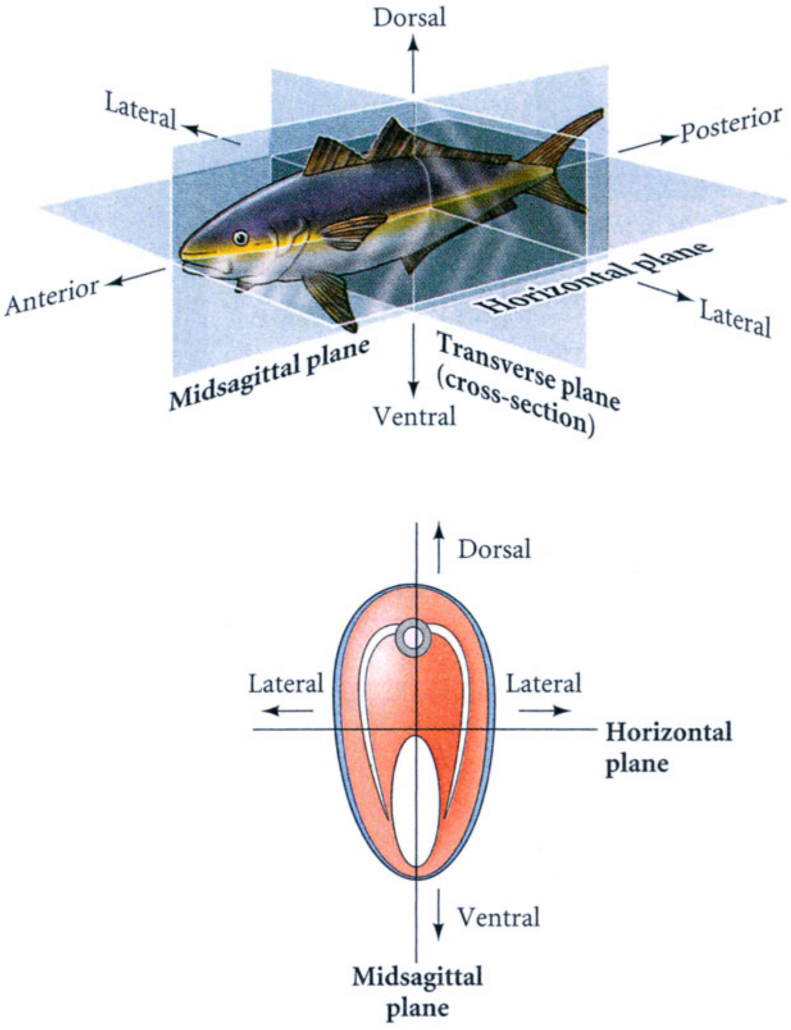

Fig. 7.7 The axes that become evident in the adult animal are present in the embryo. These are the foundations of the future body plan. Representation of the axes of a bilaterally symmetric animal such as a fish or a bird. A single plane, the midsagittal plane, divides the animal into left and right halves. Cross sections are taken along the anterior-posterior axis. Humans are subjected to the same type of symmetry consisting of the three axes: anteroposterior, dorsoventral and right-left (lateral). “Somehow, the embryo knows that some organs go on one side and other organs go on the other” (Gilbert 2000)

The order directing development was reinforced by a third component. A molecular clock linked to somite segmentation was found to be active in avian embryos. The most obvious segments of the vertebrate embryo are the trunk somites or compartments which give rise to the vertebral column and associated muscles. In chickens there is a rhythmic expression of two avian genes (*c-hairy 1* and *IFng*) responsible for a molecular clock linked to somite segmentation (McGrew et al. 1998; Holley 2007).

7.11 The Formation of Stripes Already in the Embryo

Stripes are most common in the adult plumage of birds and also are part of various organs in mammals such as the tail of the ring-tailed lemur (*Lemur catta*) with its sharp black and white bands. For this reason the well-defined stripes that turned out to be present in the embryo of the fruit fly were an intriguing discovery.

It soon turned out that gene regulation not only occurred in the DNA, but also at the RNA and protein levels. Surprisingly the RNA transcripts were distributed in the embryo building distinct stripes. Experiments using immunolocalization showed that the *fushi tarazu* protein was also expressed in stripes and had a most precise gene expression in nerve cells (Scott and Weiner 1984; Hiromi and Gehring 1987; Rivera-Pomar and Jäckle 1996).

Additionally, the gene *Antennapedia* is transcribed in the embryo, at an early stage, as a single stripe corresponding to the second thoracic segment, no expression being detected in the antenna region of the head. The *Antennapedia* protein accumulates mainly in the three thoracic segments and latter at other regions of the embryo and larva (Schneuwly et al. 1987).

The order that dominates since the early stages of the embryo proceeds according to the following main pathways. The body plan starts with the morphogenetic gradients, then is subdivided into broad domains by the *gap* genes, these are followed by *pair-rule* genes which produce segmentally repeated units, lastly *segment-polarity* genes divide it into compartments in a stepwise manner (Fig. 7.8).

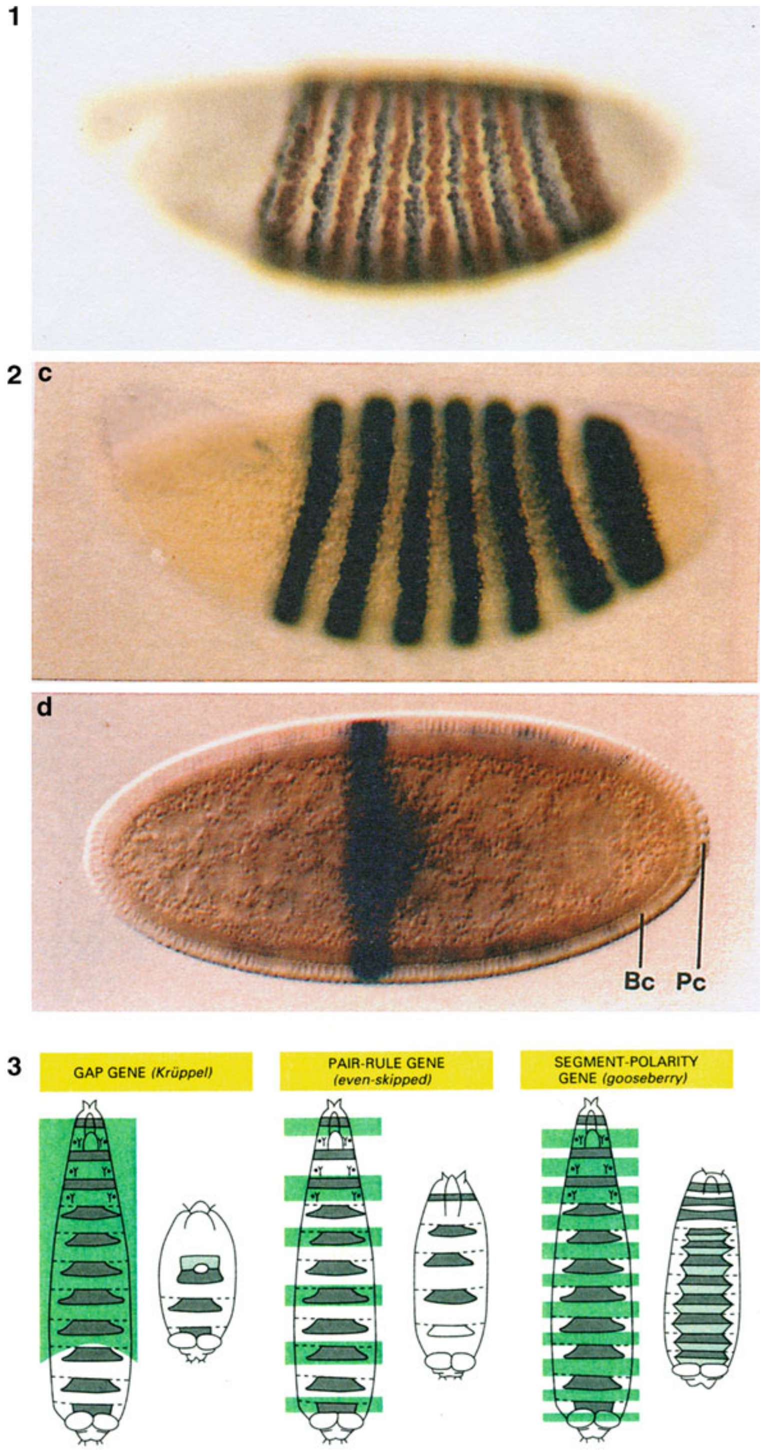

Fig. 7.8 The action of specific genes results in the formation of stripes in the embryo and larva. (**1**) The patterns of the gene products in *Drosophila*. The expression of *ftz* (*brown*) and *eve* (*grey*) in the cells of the embryo. The stripes of *ftz* and *eve* expression narrow from the posterior margin and sharpen anteriorly as they intensify. (**2**) Steps in pattern formation during embryonic development of *Drosophila*: (**C**) expression of the *fushi tarazu* messenger RNA in a repetitive pattern of seven stripes at the preblastoderm stage; (**D**) expression of the *Antennapedia* mRNA in a unique pattern of a single stripe at the blastoderm stage. *Bc* blastoderm cells, *Pc* pole cells. Anterior is always to the left and dorsal at the top. (**3**) Examples of the phenotypes of *Drosophila* mutations affecting the three types of segmentation genes. In each case the areas shaded in *green* on the normal larva (*left*) are deleted in the mutant or are replaced by mirror-image duplicates of the unaffected regions (Modified from C. Nüsslein-Volhard and E. Wieschaus, Nature 287: 795–801, 1980. 1980 Macmillan Magazines Ltd.)

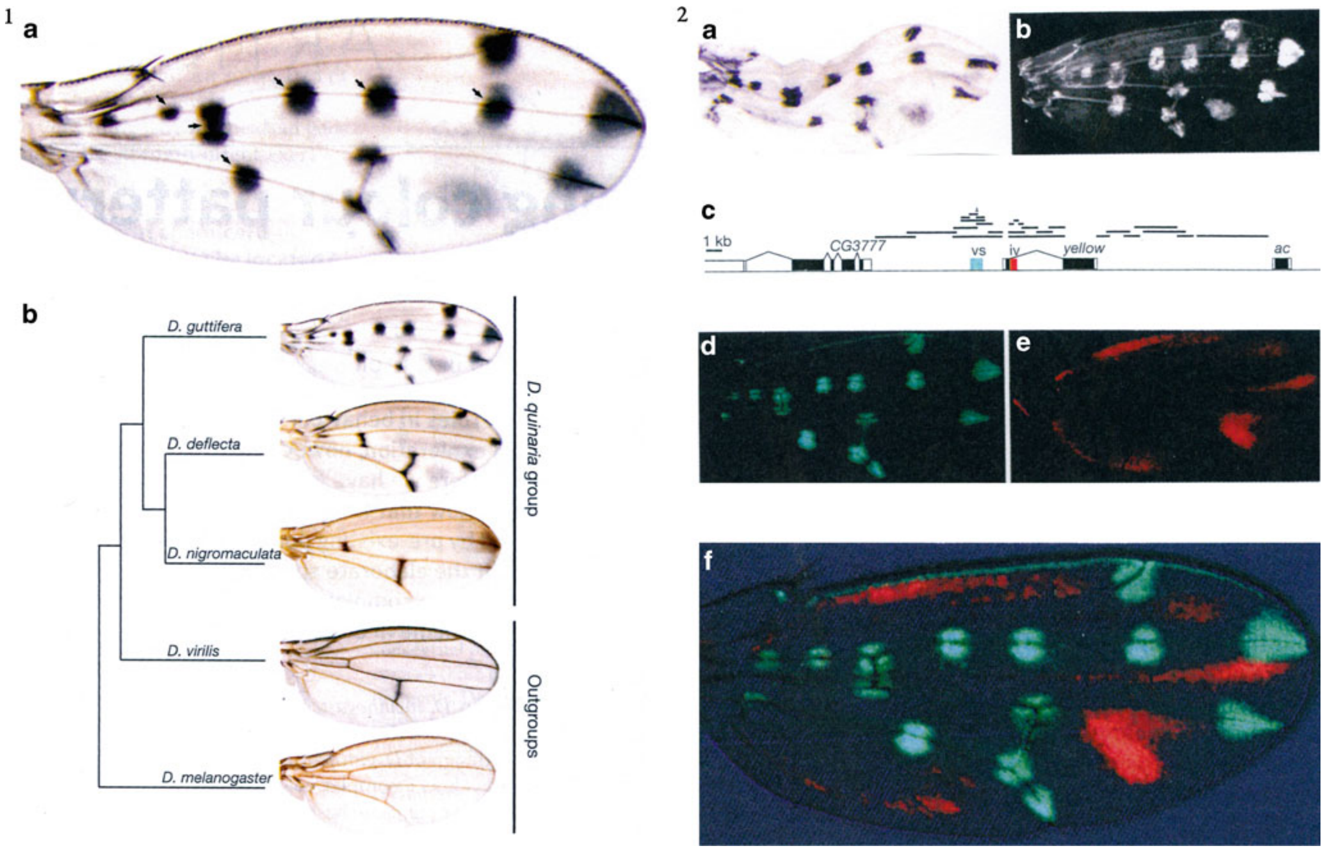

Fig. 7.9 (**1**) **The *Drosophila guttifera* wing exhibits a complex pigmentation pattern**. (**a**) The wings of *D. guttifera* display 16 vein-associated spots and four intervein shades; six vein-spots are associated with campaniform sensilla (*arrows*). (**b**) Phylogenetic tree showing the relationships of species bearing different elements of the wing pigment pattern (crossveins, longitudinal wing tips, and campaniform sensilla). The *D. guttifera* pattern is the most complex in that it bears the most pattern elements. **(2) Two *yellow* CREs encode the elaborate *D. guttifera pattern***. (**a**) *In situ* hybridization detecting *yellow* gene expression. The expression pattern of *yellow* mRNA transcripts foreshadows the adult melanin pattern in the pupal *D. guttifera* wing at stage P10. (**b**) Immunohistochemical localization of the Yellow protein. Yellow expression in late pupae foreshadows the adult pigment pattern. (**c**) The 42-kb *yellow* locus. The turquoise box represents the *vein spot* CRE (vs), and the red box marks the location of the *intervein shade* CRE (iv). Top bars depict the DNA fragments screened for enhancer activity in pupal wings. (**d**) The *vein spot* CRE drives nuclear eGFP reporter protein expression in all 16 vein-associated spots in a transgenic *D. guttifera* pupal wing. (**e**) The *intervein shade* CRE drives cytoplasmic DsRed reporter protein expression in all intervein shades in a transgenic *D. guttifera* pupal wing. (**f**) Merged image of *vein spot* CRE and *intervein shade* CRE activity in a double-transgenic *D. guttifera* pupal wing. *CRE*, enhancer and regulatory element controlling the expression pattern of the gene *yellow*

7.12 The Spacing of Feathers is Directed by a Protein

The origin of periodicity in the patterning of animal structures has been a debated question. Recently it has been approached at the molecular level (Jiang et al. 1999). In animals, as well as plants, structural elements are often repeated at relatively regular intervals, such as vertebra, teeth and feathers. An effort was made to elucidate the location, number and size of these repetitive elements. These authors compared the development of feathers *in vitro* and *in vivo* and concluded that the size determination is an intrinsic and a self-organizing process. The emergence of periodic patterning in these organs was attributed to a mechanism involving reaction diffusion in which *bone morphogenetic protein* (BMP) was antagonized by the presence of *Noggin* (an embryonic inducing factor). The size, number and spacing of feathers was considered to be modulated by morphogens and receptors.

Werner et al. (2010) identified a morphogen responsible for the induction of the spot pattern in several species of *Drosophila*. The morphogen production is localized by a pre-pattern of positional information. Besides, they found, by using DNA constructs and fluorescence technology, that two enhancers of the *yellow* gene were involved in the pigmentation pattern. The protein derived from the *yellow* gene is required for the formation of black melanin on fly wings and bodies (Fig. 7.9).

7.13 Change of Gene Action During Development – A Single Gene is Important but not Almighty Since an Antenna can Regenerate into a Leg

Not surprisingly, the homeotic action may change during development, indicating what is called at present an epigenetic effect. For instance, the antenna of a stick insect or a lobster, if it is amputated, will be regenerated instead to a leg. This means that without changing the genetic constitution of the organism, since one is dealing with the same individual, a secondary body development (during the process of regeneration) transforms the gene action resulting in the emergence of a leg in place of an antenna. Thus, the original genetic information carried in the DNA sequences of the chromosomes can be altered during the adult body construction.

The outer as well as the inner environment change during the many cell divisions that lead to tissue and organ differentiation. During this process gene function may be modified. Human identical twins can be different from each other exhibiting quite different finger prints despite the fact that they have the same set of genes in their genomes (Hood 2002). In other human identical twins, one individual may be left-handed and the other right-handed (Fig. 9.1) (Müntzing 1961).

The problem of whether cells retain their original epigenetic memory during differentiation has recently been studied using different types of mouse stem cells. Aged cells had a limited efficiency and fidelity of reprogramming the tissue pattern (Kim et al. 2010).

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Fig. 7.3 Gehring, W.J. 1998. Master Control Genes in Development and Evolution: The Homeobox Story. Yale University Press, London, UK ((**1**) Fig. 2.10 page 33; (**2**) Plate 5).

Fig. 7.4 **(1)** Gehring, W.J. 1998. Master Control Genes in Development and Evolution: The Homeobox Story. Yale University Press, London, UK (Plate 1 facing page 110), **(2)** Halder, G., Callaerts, P. and Gehring, W.J. 1995. Induction of ectopic eyes by targeted expression of the *eyeless* gene in *Drosophila*. Science *267*: 1788–1792, with permission from the American Association for the Advancement of Science (AAAS), Washington, D.C. U.S.A.

Fig. 7.5 Gehring, W.J. 1998. Master Control Genes in Development and Evolution: The Homeobox Story. Yale University Press, New Haven, U.S.A. (Fig. 13.7).

Fig. 7.6 Varjosalo, M. and Taipale, J. 2008. Hedgehog: functions and mechanisms. Genes and Development *22*: 2454–2472.

Fig. 7.7 Gilbert, S.F. 2000. Developmental Biology. Sinauer Associates Inc. Publishers, Sunderland, MA, U.S.A. (Fig. 8.7 page 229).

Fig. 7.8 **(1)** Lawrence, P.A. 1992. The Making of a Fly. Oxford, Blackwell, London, UK (Plate 4.1 Facing page 108), **(2)** Gehring, W.J. 1998. Master Control Genes in Development and Evolution: The Homeobox Story. Yale University Press, London, UK (Plate 3), **(3)** From Alberts, B. et al. 1994. Molecular Biology of the Cell. Garland, New York, U.S.A. (Fig. 21.60 page 1088).

Fig. 7.9 Werner, T. et al. 2010. Generation of a novel wing colour pattern by the Wingless morphogen. Nature *464*: 1143–1147 (Figs. 1 and 2 page 1144).

The Molecular Geometry

8

8.1 What is Geometry?

Geometry is by definition "The branch of mathematics that deals with points, lines, planes and solids, and examines their properties, measurement, and mutual relations in space" (Webster 1976). A complementary definition is: "Geometry is tantamount to order and compelling logic in the edifice of our thoughts and speculations" (Oechslin 2010).

In the case of the body pattern of birds, the geometry is so evident that there is no need for speculations.

8.2 Mathematicians and Physicists Know that there is not One, but Several Geometries – Euclidean and Non-Euclidean Geometries

Nothing is known of Euclid's life and the dates of his birth and death: 325–250B.C. are uncertain. But his book "The Elements" has remained the reference work on geometry for over 2,000 years. It was written in 13 volumes (1–6 on plane geometry, 7–9 on the theory of numbers, 10 on irrationals, 11–13 on solid geometry). Other extant works attributed to him are two treatises on music: "Section of the Canon" and "Harmonica". Music, like geometry, is also based on order and as such was not left outside his working domain (Hornblower and Spawforth 1999).

Geometry contains an element of beauty, due to its harmony and simplicity. In 1847 an edition was made of the first six volumes of the "Elements" by colouring in yellow, red, blue, black and white all the numerous figures. The purpose was to make this work more appealing and easier to grasp by students of mathematics (Byrne 1847) (Reprinted 2010).

The Euclidean geometry deals with circles, triangles and other geometric figures drawn on a flat two-dimensional surface. In this type of geometry one measures the exact dimensions of a circle or the value of the angles in a triangle. When the same triangles and circles are laid out on the surface of the Earth, they do not obey the ordinary flat Euclidean geometry. On the curved surface of the Earth, the square of the hypotenuse of a right-angled triangle is smaller than the sum of the squares of the two sides. Still more strange is that on the Earth's surface, the sum of the interior angles of a triangle is more than 180°, and the circumference of a circle of radius r is less than $2\pi r$ (Ohanian 2009). In a spherical structure another geometry applies which is called non-Euclidean geometry.

In 1915 Albert Einstein (1879–1955) developed his general theory of relativity. He had found that his relativity concept required that the space of the universe be considered a non-Euclidean space. It needed the type of geometry devised by the mathematician Georg Riemann (1826–1866) who had changed the concepts of distance and curvature into a multidimensional geometry. For Einstein space-time might have a different geometry at different locations and he created a curved space-time geometry that fitted his expanded view of relativity.

8.3 Molecular Geometry is Multidimensional

Relativity dealt solely with physical phenomena, and these are well-known for not being as complex as biological ones. Physical and chemical processes regulate the organization and function of biological structures. However, at the cell level additional factors are involved. These are: (1) The transmission to the progeny of the same basic pattern by means of a chemically organized structure, the chromosome. (2) The temporal development of a fertilized cell leading to an embryo and later to a full grown organism; events that are directed by specific macromolecules. (3) The modification

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of the animal's body structure and function by chemical and physical agents of internal and external origin.

Hence, the geometry that is patent in living organisms cannot obey the few dimensions that are enough for mathematicians and physicists. It must include a higher number of dimensions. The three-dimensional space of a sphere and the inclusion of time as a fourth dimension are not sufficient. Three other dimensions: inheritance, development and environment interference, need to be added if one is to understand the geometry displayed by living organisms. All these three processes have for a long time been known to be molecular and the latest data obtained from molecular biology have only reinforced this information. Hence, we are dealing with a geometry that is strictly molecular and which is multidimensional involving not less than seven components.

8.4 Molecular Geometry is Dynamic and Ephemeral – Yet it Persists

Every figure drawn in the "Elements" of Euclides, or any other book, is always an approximation. If one draws a sphere or makes a dice, neither the sphere, nor the dice, are totally accurate. There is always a molecule missing on one line or corner. The ideal sphere, and the ideal dice, only exist in our minds.

Thus, the representation of the Euclidean geometry found in books contains already an inaccuracy that cannot be avoided by the biological geometry. The circle on the crest, or the breast, of a bird, has always some minor deviation, or some molecule, that does not fit exactly in the whole.

Besides, this geometry displayed by the feathers, or any other body part, is affected by other variables such as the external and internal environments (*e.g.* length of day light and hormones, respectively). Moreover, the shape of the feathers, their colour, and their consistency, are modified all the time as the individual grows from the juvenile to the adult stage. The molecular geometry of a bird's body is highly dynamic.

The feathers may even be shed after a specific period in the life of the animal, the local geometry simply disappearing. Nothing could be more ephemeral than molecular geometry. Yet it persists, it is repeated every generation and maintains the same overall pattern. This is due to being directed by the same genetic information. This information is located in the nucleotide sequences of the individual's DNA.

Most important is that DNA knows nothing about geometry. Its four bases that are repeated millions of times along the chromosomes never heard of geometry and never saw the final geometric product *i.e.* the bird or any other living organism that they contributed to shape. The final shape of any living body is locally dictated by proteins, small RNAs and other molecules which carry in them the final atomic configurations that make the critical decisions. They have had their origin in DNA but during the long process of embryonic development, and of the formation of young and adult stages, it is the final configurations of proteins, and of other minor molecules, which are responsible for actually determining the geometric shape of the individual.

8.5 Every Bird is a Lesson in Geometry

The wing is the structure that has been envied for centuries by humans.

At least 60 millions of years ago birds have made the atmosphere of the earth their main domain of action, which was barred to humans until a century ago. Not only the capacity to fly but several other features put the birds apart.

First, being mainly diurnal, birds can be seen soaring over mountain peaks or gliding along deep valleys. They see everything from above like a pilot seating on the cockpit of a helicopter or a jet aeroplane. For them geography is the order of the day. It is thus not surprising that with the millions of years that they have had at their disposal they learned how to migrate as far as from polar to polar region and are able to memorize the local map of their birth place with an accuracy that seems to surpass that of a surveying satellite.

Second, the wing by itself would not be enough to give birds the prominent position that they have. Bats and insects also fly. Bats lack attractive colours and are mainly active at night which impedes a close observation. Many insects, such as the butterflies and the dragonflies fly by day, exhibiting their impressive colours. Their wings and body are measured in millimeters, whereas the wingspan of an albatross is 3.5 m. Birds are on our scale.

Third, a person not familiar with zoology will easily recognize a bird as being a bird, but will have difficulty in accepting that a mouse and a giant whale are mammals. This is because birds are much more uniform in their body construction building a well delimited animal group. An ostrich, a falcon and a minute hummingbird can be easily recognized as birds. Romer and Parsons (1978) in their extensive study of the vertebrate body were obliged to conclude that "most birds are rather uniform in basic anatomic features". Variation has led to over 9,000 species but has occurred within a rigid anatomical frame from which birds could not depart. Rigidity and plasticity are not incompatible.

Fourth, while mammals usually walk on four legs birds are biped, like humans, exposing the front and back of their body when walking or at rest. The result is that their body pattern becomes evident. It turns out that every bird is a lesson in geometry. Every organ from the head to the tail and the feet, discloses a regular distribution of parallel lines, bands, stripes, markings and other tracings. To these are added numerous circles and semicircles which are concentric or have centers located in relation to specific body parts. Together they create a unique form of biological geometry.

8.6 Emblematic Birds and Crystals do not Lie

A careful search was undertaken of species that revealed a trait having geometric significance. This was not a difficult task because, as stated before, every bird is a lesson in geometry. But as with any other biological process, a phenomenon is more evident in certain species than in others. The specimens that suddenly reveal a pattern, that leaves no doubt about its significance, are the emblems that guide the researcher in his effort to uncover a possible coherence among the vastness of variation. Once a well-defined pattern is found similar traits turn out in other species. They do not take time to appear and to confirm the general occurrence of the initial finding.

However, be aware, first impressions may delude. Soon a phenomenon with just opposite meaning turns out to be equally distinct. Never retract, or "sweep under the rug" a trait that seems to diverge, or contradict, the initial finding. Nature is built on antagonistic situations and antithetical principles as revealed by the properties of most phenomena in the world of physics, chemistry and biology. One should not forget that matter and antimatter are already part of the original construction of the universe (Alfven 1966) and that, at the biological level, antigens are counteracted by antibodies.

It is these opposing processes that create the intermediate situations found most of the time. It is these which have bewildered and confused bird specialists for generations. Intermediate forms are everywhere and as a consequence give us no guidance. The situations that from the beginning seem to be exceptional, are so because they are rare. But they turn out to be like the crystals which show up suddenly among the many amorph forms of matter. Crystals do not lie, because they concretize an underlying order that cannot be denied, and the same is true of emblematic biological forms that expose a given trait in an uncompromising and palpable way.

However, nothing should be discarded, since every biological trait is the manifestation of an underlying specific molecular mechanism. The intermediate forms need to await inclusion. Once the main lines of the molecular processes are established it will become easier to incorporate them into a general scheme of avian pattern where they will find their proper place.

8.7 The Uniqueness of the Avian Eye – It Surpasses the Human Eye

Birds are known for their unusual vision.

It starts with the skeleton. The skull is far more rounded than that of reptiles, showing a notable increase in the size of the braincase and of the orbits where the eyes are located.

Bird eyes are relatively large when compared with those of other vertebrates. This is evident already in the embryonic stage where the avian eye is much larger than that of humans (Fig. 8.1). As the adult stage is reached the difference is maintained. In the Common Starling the eyes account for 15% of its head mass, while in man for only 2%. The Ostrich eye, with its 5 cm in diameter, is the largest of all terrestrial animals.

The field of vision is very wide (more than 300°) but the zone of binocular vision is narrow being widest in owls (60°–70°). Compared with reptiles the avian brain has a highly developed optic lobe in agreement with its advanced optical system (Fig. 8.1).

The interior of the eye contains several particular structures. Some birds have a second fovea which is an area of high receptor cell density in the retina. A particular feature is the pecten, a pleated sheet of tissue located inside the vitreous body, supposed to supply nutrients to the retina. The retina has a high density of light receptor cells. In the human fovea the density reaches 200,000 receptors/mm, a figure which is twice and five times higher in the House Sparrow and Common Buzzard.

Like reptiles, birds have a scleral ring formed by 12–15 cartilaginous plates. These plates build a wall around the eye. The partial immobility imposed by the scleral ring is compensated by the head rotating as much as 270° (owls).

The cones are the most abundant colour receptors in the retina. Each contains an oil droplet coloured by carotenoids, supposed to enhance colour perception. These cells surpass the human eye allowing birds to discriminate ultraviolet and polarized light.

The combination of all these features makes the bird's eye an exceptional organ. Still more exceptional is the finding that the body's geometry appears to be inseparable from the position of the eye.

8.8 The Eye – A Focus of the Bird's Body

In invertebrates the eye takes many forms and may occur in highly variable numbers which run from single ones to hundreds of them. The insects may have simple eyes but

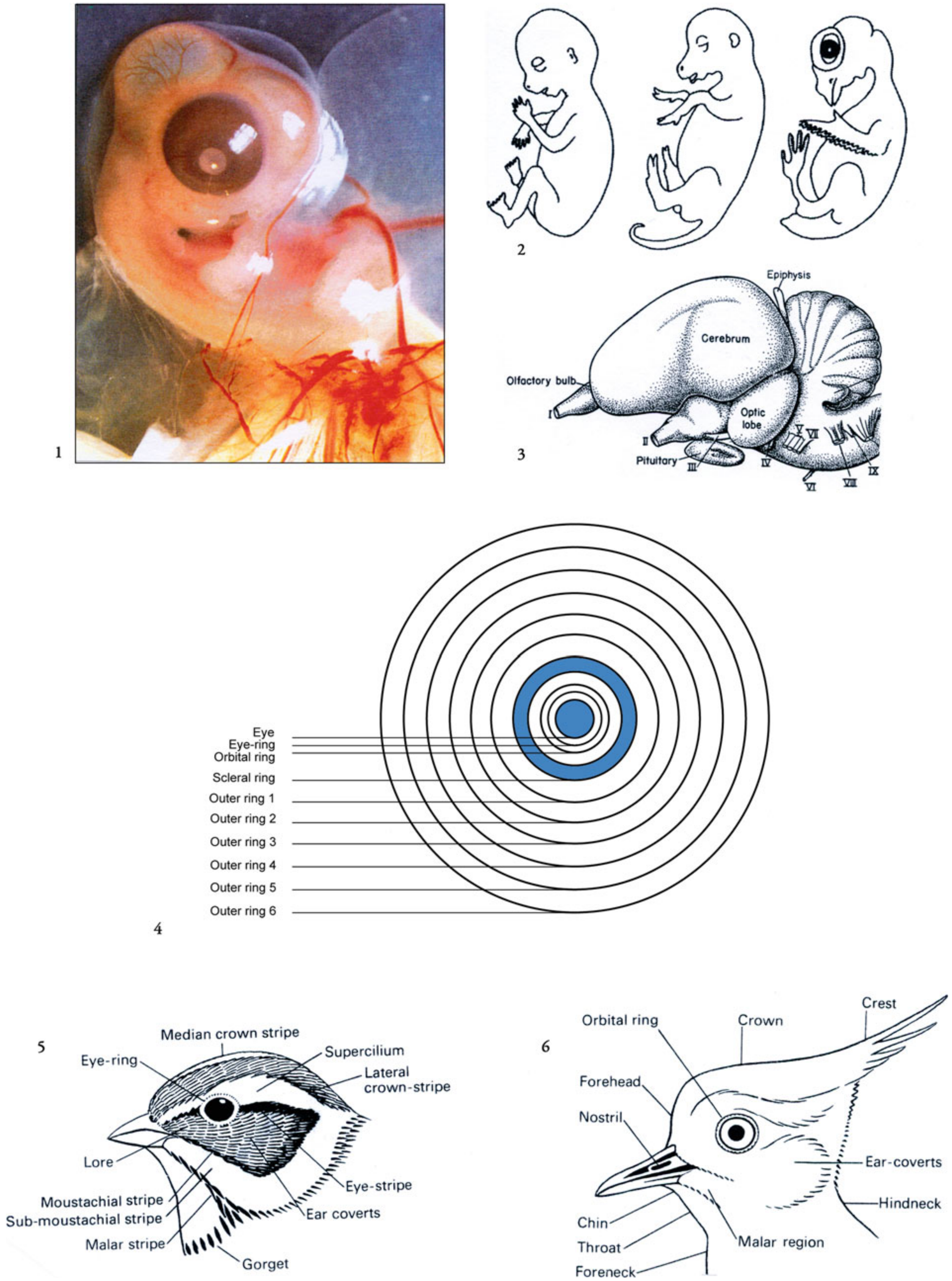


Fig. 8.1 **The unique properties of the avian eye**. (**1**) A seven-day-old hen embryo. The eye has developed a large lens (Photo). (**2**) Comparison of the embryonic development of: human, calf and chick, showing the disproportionate size of the bird's eye. (**3**) Lateral view of the brain of a goose (*Anser*) with a most developed optic lobe. (**4**) Concentric rings encircle the eye and extend to the whole head. Diagram of the circles surrounding a bird's eye according to the morphological details depicted by ornithologists. The scleral ring is in the cranium (Fig. 8.2). Outer rings 1–6 encircle the eye of the Asian Barred Owlet (Fig. 8.33). (**5**) Head of bird with eye-ring. (**6**) Head of bird with orbital ring

these may combine into large organs consisting of hundreds of eye units.

The bird eye is not only a potent instrument of vision but its original circularity extends to the head in the form of concentric rings of larger and larger diameter. These in turn spread to other parts including the breast, the wings, the tail and the beak. Moreover, from the eye start semicircular stripes and other markings that point to its primary role in the formation of the body pattern.

8.9 The Circularity of the Eye

From the beginning of the skeleton's formation a circularity accompanies the eye. The anatomy of a bird's skull discloses the presence of a particular feature: a scleral ring consisting of small plates distributed as a perfect circle and in which the eye is encased (Fig. 8.2).

The eye is known to be partly spheroidal, presenting a circular shape on the outside. Ornithologists have described in detail two concentric rings which are seen, in several species, surrounding the iris. They called them the Eye-ring and the Orbital-ring (Fig. 8.1).

Unexpectedly, this circularity extends to the whole head starting by an increase in the diameter of concentric rings which have their centre in the focal point of the iris. Such rings are most conspicuous in a number of species. The Nyasa Lovebird, the White-eyed Slaty-flycatcher and the Hairy-crested Antbird display a sharp white ring at an appreciable distance from the eye which increases successively in diameter as it reaches the Spectacled Eider. The name betrays the sensation that the bird wears spectacles.

One could expect that the diameter of the rings would not increase further, but in the Spotted Wood-owl they get larger again occupying the whole frontal part of the head. In another variant (Madagascar Red Owl) the rings become transformed into a near semicircle which is delimited by a dark sharp line (Fig. 8.2).

If one is in doubt of the role of the eye in circularity, another still more unexpected picture emerges which leads one to become perplexed. The Black Monarch together with the White-headed Steamerduck and the Southern Pochard display a semicircular white band that starts at the very eye. Complementing this evidence the Torrent Duck, the Rock Partridge and the Oriental Pratincole have a black band which also originates in the eye (Fig. 8.3). In the six cases the band could not be better delineated.

The families involved (Figs. 8.2 and 8.3) are: Psittacidae, Muscicapidae, Thamnophilidae, Anatidae, Strigidae, Tytonidae, Monarchidae, Phasianidae and Glareolidae.

8.10 Rings Around the Eye Extend to the Whole Head

The Ringed Teal, the Little Pied Cormorant and the Ross's Gull display a semicircular black ribbon that starts at the upper part of the beak or on the middle of the head (Fig. 8.4).

The participation of the top of the head becomes evidenced by the occurrence of a coloured circle which appears as a patch at the top of the head. This starts as a small circle that is darkly coloured in the Black-and-white Hawk-eagle and the Flame-crested Manakin, but it may be accompanied by a larger concentric white circle, as seen in the Blue-crowned Motmot, the Common Blue Tit and the Shore Plover (Fig. 8.5).

The centre of the inner and outer circles at the top of the head is not the eye. Instead it is located on an axis that runs throughout the bird's body from the head to the tail.

Life is full of antagonistic solutions and a bird, or any other living organism, is a prisoner of this general property. This feature becomes even more evident as we analyse the patterns that occur in other parts of the body.

8.11 Horizontal and Vertical Stripes that Cross the Eye are Accompanied by Others which Run Above and Below it

One is obliged to go back to the eye because other markings reveal again its position as a primary centre of pattern distribution. A white stripe either starts at the eye or runs across it. The stripe follows a direction that goes from the bill or the eye to the lower back of the head. It has a near horizontal position when the bird is at rest. The White-eared Sibia, the Scaly-throated Foliage-gleaner and the Black-chinned Honeyeater are representatives of this situation (Fig. 8.6).

Starting from the upper part of the bill and running to the lower back of the head there are other white stripes. These pass quite close to the upper part of the eye but do not traverse it, being parallel to those that cross the eye. Examples are: Yellow-breasted Boatbill, Chestnut-crowned Babbler, White-browed Chat-tyrant and White-browed Woodswallow (Fig. 8.7).

But the same type of white stripe may run instead from the base of the bill in the direction of the back of the head, not crossing the eye but passing below it, tending to maintain a parallel position to the two previous types of stripes: Blue-headed Quail-dove, Variegated Antpitta and Spotted Puffbird. The position of the three types of white stripes tends to be horizontal (Fig. 8.8).

White and black colours often substitute one another in the same body area in many birds, and in other species black

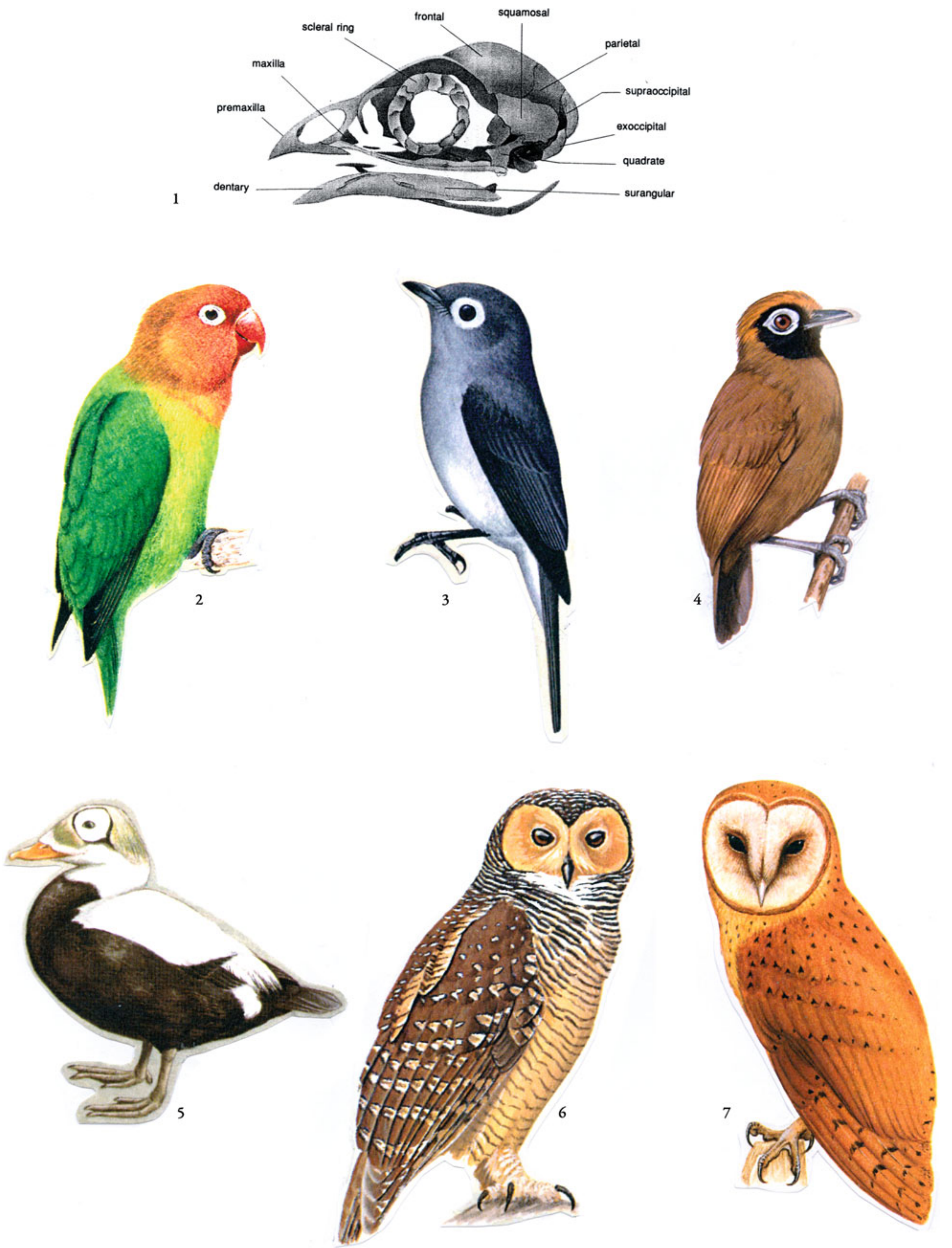


Fig. 8.2 Increase in diameter of the circle which occurs around the eye. (**1**) Cranium of a bird showing the scleral ring consisting of 14 segments. (**2**) Nyasa Lovebird, *Agapornis lilianae*, Psittacidae. (**3**) White-eyed Slaty-flycatcher, *Melaenornis fischeri*, Muscicapidae. (**4**) Hairy-crested Antbird, *Rhegmatorhina melanosticta*, ssp brunneiceps, Thamnophilidae. (**5**) Spectacled Eider, *Somateria fischeri*, Anatidae. (**6**) Spotted Wood-owl, *Strix seloputo*, Strigidae. (**7**) Madagascar Red Owl, *Tyto soumagnei*, Tytonidae

Fig. 8.3 **Head displaying a semicircular white line (*upper row*) and a semicircular black line (*lower row*) starting in all cases from the eye**. (**1**) Biak Monarch, *Monarcha brehmii*, Monarchidae. (**2**) White-headed Steamerduck, *Tachyeres leucocephalus*, Female, Anatidae. (**3**) Southern Pochard, *Netta erythrophthalma*, Female, Anatidae. (**4**) Torrent Duck, *Merganetta armata*, ssp turneri, Anatidae. (**5**) Rock Partridge, *Alectoris graeca*, Phasianidae. (**6**) Oriental Pratincole, *Glareola maldivarum*, Glareolidae

stripes occupy the position of white ones. The black regions are like the "negatives" of the white ones.

When contemplating Fig. 8.9 one has the impression that some leading artist, such as Pablo Picasso (1881–1973) or Salvador Dali (1904–1989), in their realistic or surrealistic fashion, could have painted these birds, using their precise drawing power in a burst of imagination. But no, they were painted by an artist having only the desire to convey every detail with full accuracy. This impression derives from the presence of a solid black stripe which originates at the base of the bill, crosses the eye and finishes at the lower part of the head or close to it. This striking painting, that seems to be made by a brush full of black ink, is present in: Swallow-tailed Bee-eater, Slender-billed Oriole, Common Green Magpie, White-crested Laughingthrush and Eurasian Penduline-tit (Fig. 8.9). The position of these stripes is also horizontal or quasi-horizontal.

Other black stripes are found running below the eye or above it as seen in the Veracruz Quail-dove and the Tree-toed Parrotbill. To remove any doubts about the constancy of this pattern the Masked Duck displays on the same head three black stripes: one over the eye, a second across it, and a third below the eye. All are parallel to each other and tend to be horizontal (Fig. 8.10).

Why not implement a contrary orientation. Instead of horizontal stripes let them be vertical. These as well could have been painted by some distracted artist who suddenly looked at the model instead of concentrating on the bird. As a result brush strokes full of black ink, were splashed over the head in a different direction. The vertical black stripes run across the eye in the Inland Dotterel and the Northern Scrub-robin (Fig. 8.11), are located in front of the eye or close to it in the Bearded Parrotbill and the Mascarene Parrot. Besides, they run across the eye being accompanied by parallel stripes

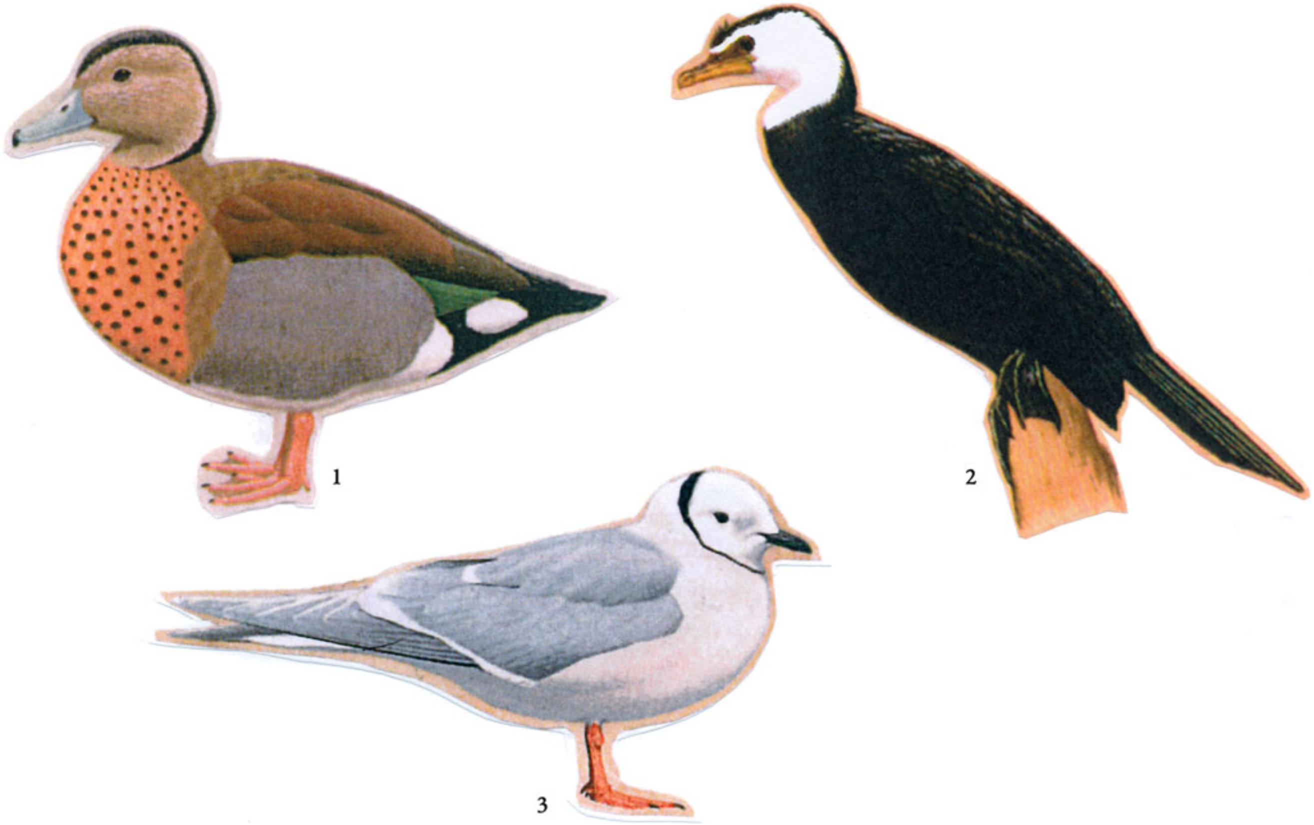


Fig. 8.4 **A black line runs along the periphery of the head building a semicircle**. (**1**) Ringed Teal, *Callonetta leucophrys*, Anatidae. (**2**) Little Pied Cormorant, *Phalacrocorax melanoleucus*, ssp brevirostris, Phalacrocoracidae. (**3**) Ross's Gull, *Rhodostethia rosea*, Laridae

which are located in the middle and back of the head: Orange-headed Thrush and American Kestrel (Fig. 8.11).

These birds belong to the most diverse families. White stripes: Timalidae, Furnaridae, Meliphagidae, Monarchidae, Pomatostomidae, Tyrannidae, Artamidae, Columbidae, Formicariidae, Bucconidae. Black stripes: Meropidae, Oriolidae, Corvidae, Timaliidae, Remizidae, Columbidae, Anatidae, Paradoxornithidae, Charadriidae, Petroicidae, Psittacidae, Turdidae, Falconidae.

One is confronted with a situation of the same type as the occurrence of two long feathers on the tail (Chap. 3) in which over 10 different families displayed the same body-pattern.

8.12 The Circularity of the Crest and its Division into Three Distinct Sections

If Euclid of Ancient Greece could have come back to life he would have been delighted to find the geometric figures of his book being drawn on the body of birds, in the most striking colours and sharp lines.

The large orange crest of the Guianan Cock-of-the-rock, builds a semicircle demarked by a sharp brown-black semicircle that could have been taken out of any geometry book (Fig. 8.12). A photograph of the same species shows that in other specimens this semicircle starts on the frontal region as a black line, becomes brownish in the middle, and turns red as it ends on the back of the head. Concentric with this semicircle is another one which covers the periphery of the crest and is a pure white (Fig. 8.13).

A semicircular crest is also found in the Royal Flycatcher which would be envied by any mathematician. During display the crest opens like a fan, surprising the observer with colours and shapes which are most attractive. A broad deep blue band demarks its external circularity. This is followed by a bright orange area in which large and small blue circular patches tend to occupy concentric semicircles but located in a less regular way (Fig. 8.13).

Imposing crests bordered by different types of semicircular markings are to be seen in: Long-tailed Hornbill, Grey Crowned Crane and the Victoria Crowned-pigeon (Fig. 8.12).

It turns out that this compact circularity is only a disguising curtain. Behind it, the crest turns out to be divided into three well delimited sections: an anterior, a median and a posterior. The species that betray this underlying division are: Topknot Pigeon, Grey-crested Helmet-shrike, Pitt Shag and Spotted Shag. The pigeon from eastern Australia has a crest which consists of three parts: a white-grey brush on the

Fig. 8.5 Concentric circles of increasing diameter occur on the top of the head. (**1**) Black-and-white Hawk-eagle, *Spizastur melanoleucus*, Accipitridae. (**2**) Blue-crowned Motmot, *Momotus momota*, Momotidae. (**3**) Common Blue Tit, *Cyanistes caeruleus*, Paridae. (**4**) Flame-crested Manakin, *Heterocercus linteatus*, Pipridae. (**5**) Shore Plover, *Charadrius novaeseelandiae*, Charadriidae

Fig. 8.6 White stripe at eye level. (**1**) White-eared Sibia, *Malacias auricularis*, Timaliidae. (**2**) Scaly-throated Foliage-gleaner, *Anabacerthia variegaticeps*, Furnariidae. (**3**) Black-chinned Honeyeater, *Melithreptus gularis*, Meliphagidae

Fig. 8.7 **White stripe above eye**. (**1**) Yellow-breasted Boatbill, *Machaerirhynchus flaviventer*, Monarchidae. (**2**) Chestnut-crowned Babbler, *Pomatostomus ruficeps*, Pomatostomidae. (**3**) White-browed Chat-tyrant, *Ochthoeca leucophrys*, Tyrannidae. (**4**) White-browed Woodswallow, *Artamus superciliosus*, Artamidae

forehead, a separate median region, and on the nape a second brush which is rusty and black. This division into three sections becomes quite distinct in the Shags in which the median region of the crest lacks large feathers and is accompanied on both sides by groups of feathers that stick out prominently (Fig. 8.14).

This clear cut division of the crest belongs to a special class of phenomena. They display in an irrefutable way a situation that cannot be denied but that at first sight looks like an insignificant exception. Appearances betray. Instead the novel feature turns out to be of general occurrence when an exhaustive search is made. This is confirmed by the existence of species which have crests with only one of the three types of location. The California Quail and the Crested Auklet have a prominent crest situated only on the forehead, the Green Peafowl and the Crested Pigeon have it sticking out in the median region, and the Northern Lapwing and the Jerdon’s Baza on the posterior region of the head (Fig. 8.15).

Fig. 8.8 **White stripe below eye**. (**1**) Blue-headed Quail-dove, *Starnoenas cyanocephala*, Columbidae. (**2**) Variegated Antpitta, *Grallaria varia*, Formicariidae. (**3**) Spotted Puffbird, *Nystactes tamatia*, Bucconidae

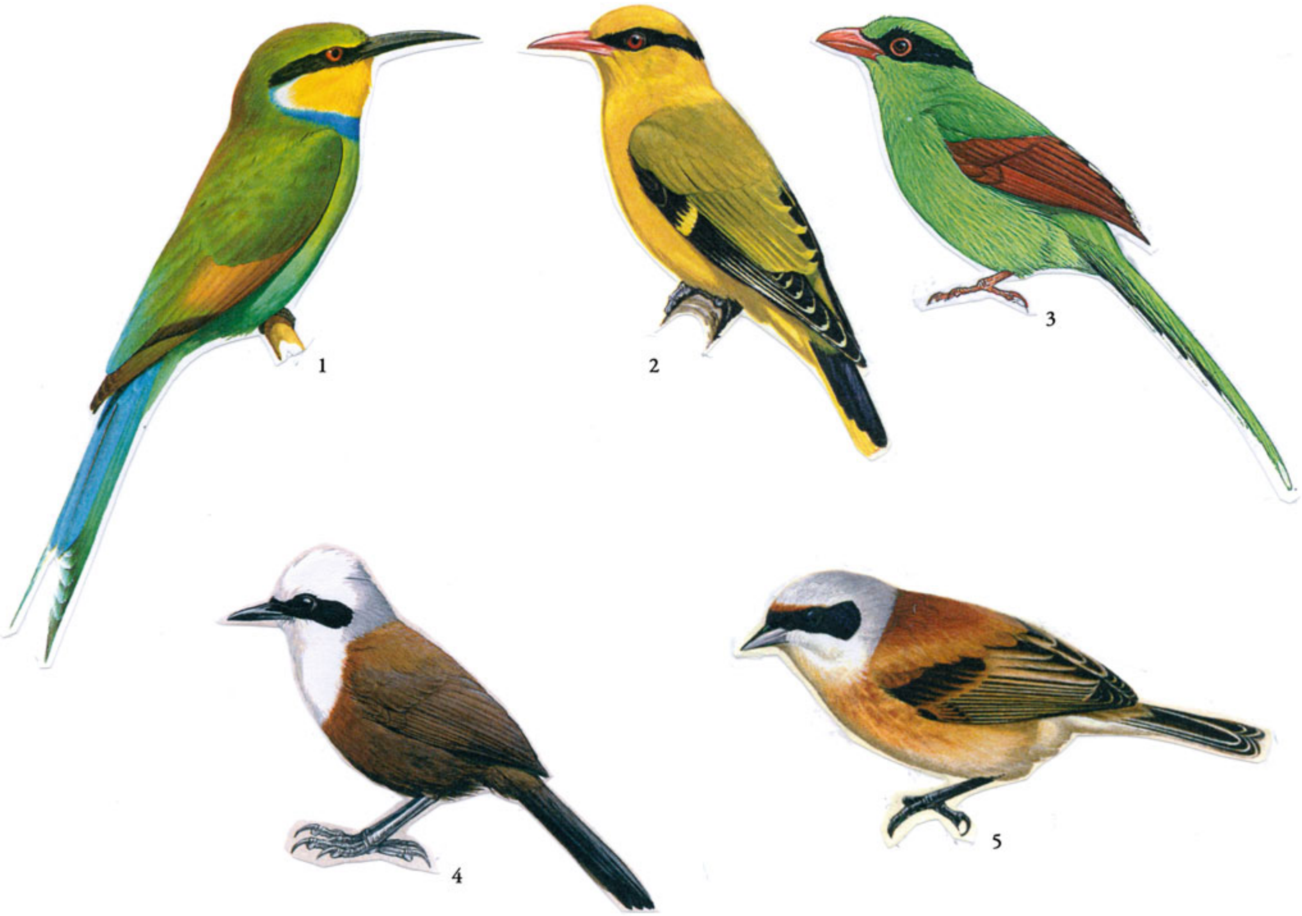


Fig. 8.9 **Black stripe at eye level and crossing the eye**. (**1**) Swallow-tailed Bee-eater, *Merops hirundineus*, Meropidae. (**2**) Slender-billed Oriole, *Oriolus tenuirostris*, Oriolidae. (**3**) Common Green Magpie, *Cissa chinensis*, Corvidae. (**4**) White-crested Laughingthrush, *Garrulax leucolophus*, Timaliidae. (**5**) Eurasian Penduline-tit, *Remiz pendulinus*, Remizidae

Fig. 8.10 **Black stripe located below, across and above eye**. (**1**) Veracruz Quail-dove, *Geotrygon carrikeri*, Columbidae. (**2**) Masked Duck, *Oxyura dominica*, Female, Anatidae. (**3**) Three-toed Parrotbill, *Paradoxornis paradoxus*, Paradoxornithidae

These species belong to the families: Cotingidae, Tyrannidae, Columbidae, Prionopidae, Phalacrocoracidae, Odontophoridae, Alcidae, Phasianidae, Charadriidae and Accipitridae (Figs. 8.13, 8.14 and 8.15).

8.13 Single, Double and Multiple Rings Around the Throat, Breast and Belly

Descending from the head, the same geometry prevails, taking the form of equally well defined circular ribbons and stripes some of them forming nice “necklaces” around the whole neck. They tend to be parallel to each other.

Andean Hillstar, Collared Puffbird, Radjah Shelduck and Zoe’s Imperial-pigeon have a single black collar, that may be thick or thin, but is sharp in its outlines and descends from the throat to the breast and belly (Fig. 8.16).

A double ring descends also from the throat to the breast and the belly in the Collared Hill-partridge, Blue-black Kingfisher, Double-banded Courser and Three-banded Plover (Fig. 8.17).

These rings further increase in number becoming as many as 22 and may start from the front of the head extending to the throat, the breast and the belly (Little Bronze-cuckoo and Horsfield’s Cuckoo). In the Red-legged Crake the stripes start only on the lower part of the breast and cover the belly. In these cases all the stripes are parallel to each other and tend to build an angle of 90 degrees with the head-tail axis (Fig. 8.18).

8.14 Throats, Breasts and Bellies with Stripes Following the Head-Tail Axis

Again, we face an antagonistic situation. In other species the breast stripes have a position that crosses at right angles those just described.

These long dark lines consist of small patches of colour that are aligned longitudinally. They build slightly irregular but continuous streaks which tend to run parallel to each other (Streak-breasted Honeyeater, Kashmir Nutcracker and Varied Sittella, Fig. 8.19). If we were in doubt about the continuity of these streaks, this is dispelled by the dark blue and black ribbons of the Common Blue Tit and the Great Tit (Fig. 8.19). The broad streak of the Great Tit running from head to tail removes any uncertainty about the presence of a line following the head-tail axis.

Families represented, on Figs. 8.16, 8.17, 8.18 and 8.19, are: Trochilidae, Bucconidae, Anatidae, Columbidae, Phasianidae, Alcedinidae, Glareolidae, Charadriidae, Rallidae, Cuculidae, Meliphagidae, Corvidae, Neosittidae and Paridae.

Fig. 8.11 **Nearly vertical black lines with four different locations in relation to the eye. They appear: in front of it, running across, starting at the eye, and at its back**. (**1**) Inland Dotterel, *Peltohyas australis*, Charadriidae. (**2**) Bearded Parrotbill, *Panurus biarmicus*, Paradoxornithidae. (**3**) Northern Scrub-robin, *Drymodes superciliaris*, Petroicidae. (**4**) Mascarene Parrot, *Mascarinus mascarinus*, Psittacidae. (**5**) Orange-headed Thrush, *Zoothera citrina*, ssp cyanota, Turdidae. (**6**) American Kestrel, *Falco sparverius*, Female, Falconidae

8.15 The Wing has a More Complex Circularity

An apparently insignificant trait is a white mark set against a dark background, in the wing of some bird species (Fig. 8.20). It would have passed unnoticed if it had not displayed some particular properties. The comparison of birds from different families shows that the white mark: (1) increases in size, starting as a negligible small patch and attaining the form of a ribbon that runs along most of the wing. (2) The patch apparently rotates, moving from a partly transversal to a longitudinal direction which follows the main body axis. Species and families are: White-winged Cliff-chat (Turdidae), Yellow-bellied Hyliota (Sylviidae), Seychelles Magpie-robin (Turdidae), Hooded Robin (Petroicidae), Brown-throated Wattle-eye (Platysteiridae) and Crimson-breasted Shrike (Malaconotidae) (Fig. 8.20).

The wing can be analysed when the bird is at rest exposing its upper part, or when the animal flies allowing to see both its upper and under sides.

At rest, the wing shows parallel black and white stripes which tend to be circular and which are located at right angles to the main body axis. In this case a contrary orientation of the

Fig. 8.12 **The semicircular shape of the crest**. (**1**) Guianan Cock-of-the-rock, *Rupicola rupicola*, Cotingidae. (**2**) Andean Cock-of-the-rock, *Rupicola peruvianus*, Cotingidae. (**3**) Long-tailed Hornbill, *Tropicranus albocristatus*, Bucerotidae. (**4**) Grey Crowned Crane, *Balearica regulorum*, Gruidae. (**5**) Victoria Crowned-pigeon, *Goura victoria*, Columbidae

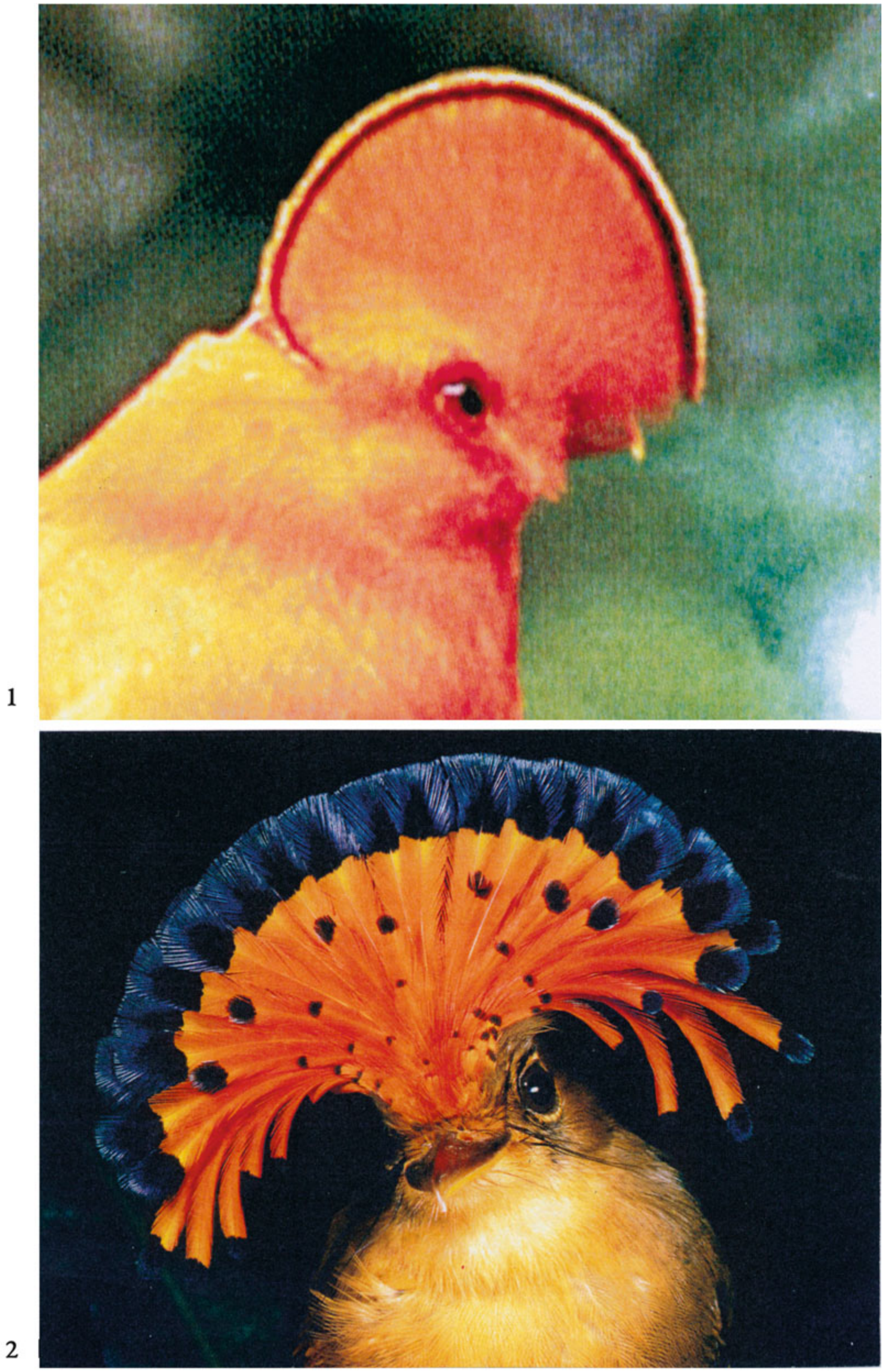


Fig. 8.13 Semicircular crests with several concentric inner semicircles. (**1**) Guianan Cock-of-the-rock, *Rupicola rupicola*, Cotingidae. (**2**) Royal Flycatcher, *Onychorynchus coronatus*, Tyrannidae (Photographs)

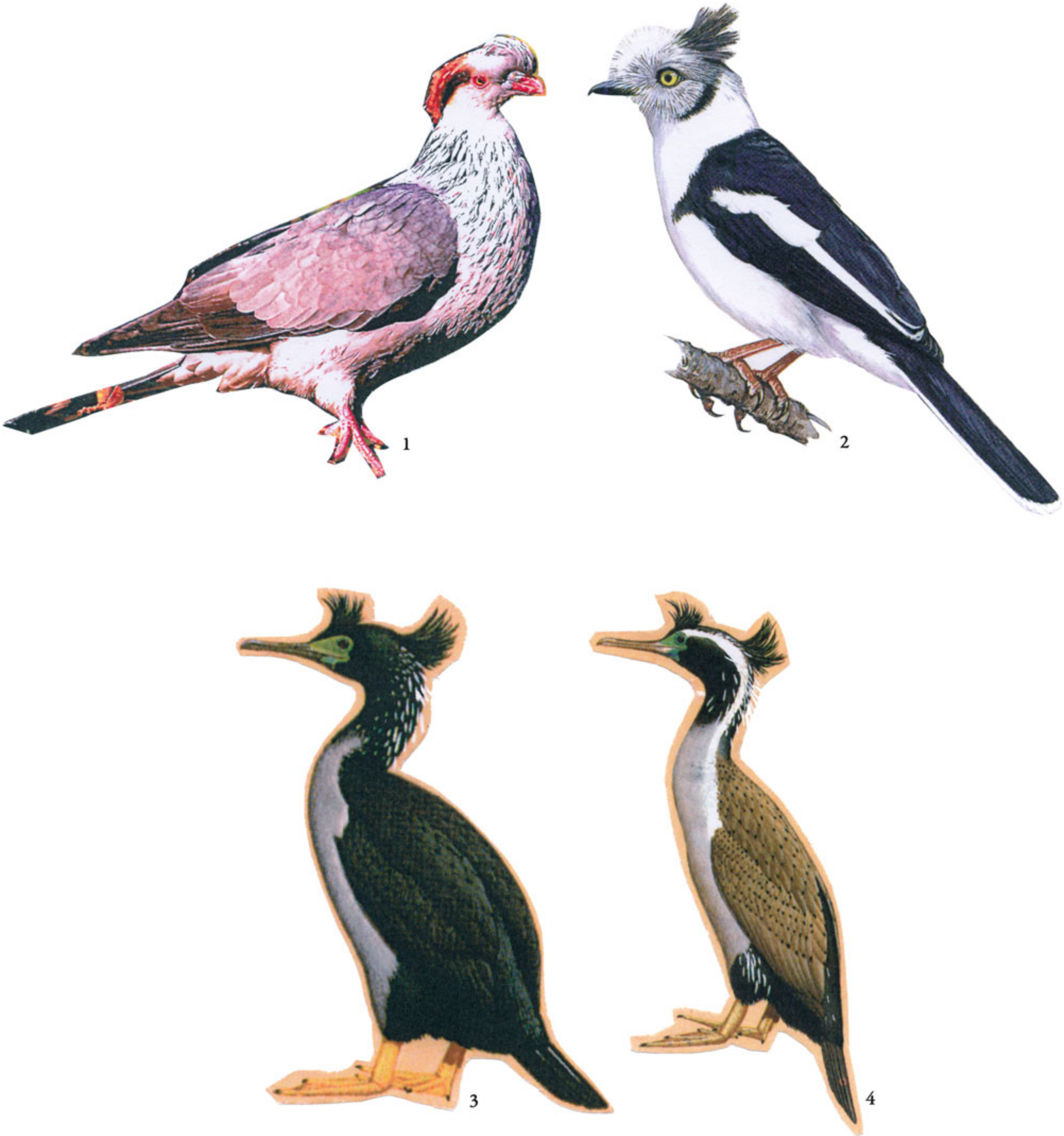


Fig. 8.14 **The natural division of the crest into three distinct parts: anterior, median and posterior**. (**1**) Topknot Pigeon, *Lopholaimus antarcticus*, Columbidae. (**2**) Grey-crested Helmet-shrike, *Prionops poliolophus*, Prionopidae. (**3**) Pitt Shag, *Phalacrocorax featherstoni*, Phalacrocoracidae. (**4**) Spotted Shag, *Phalacrocorax punctatus*, Phalacrocoracidae

pattern is also present, which could hardly be more evident than in the Great Northern Diver (Gaviidae). A criss-cross of lines results from the circular transversal stripes being intersected at 90° by long longitudinal lines (Fig. 8.21).

When the bird flies, the exquisite patterns of the wings, can be seen from above and below. The situation is more complex, but circularity prevails and it may extend from the head and the breast to the wing. Two contrasting directions are again present. On one hand, parallel lines of alternating dark and light colours run in a direction that follows the span of the wing. On the other hand these are intersected by partial circles that appear at the ends of the wings. Actually these two distinct patterns flow into each other smoothly building large parallel arches that cover each wing in agreement with its shape (Fig. 8.22).

Fig. 8.15 Crest with three different locations: anterior (*upper row*), median (*middle row*) and posterior (*lower row*). (**1**) California Quail, *Callipepla californica*, Odontophoridae. (**2**) Crested Auklet, *Aethia cristatella*, Alcidae. (**3**) Green Peafowl, *Pavo muticus*, Female, Phasianidae. (**4**) Crested Pigeon, *Ocyphaps lophotes*, Columbidae. (**5**) Northern Lapwing, *Vanellus vanellus*, Charadriidae. (**6**) Jerdon's Baza, *Aviceda jerdoni*, Female, Accipitridae

Fig. 8.16 **Single ring around throat, breast and belly**. (**1**) Andean Hillstar, *Oreotrochilus estella*, Trochilidae. (**2**) Collared Puffbird, *Bucco capensis*, Bucconidae. (**3**) Radjah Shelduck, *Tadorna radjah*, Anatidae. (**4**) Zoe's Imperial-pigeon, *Ducula zoeae*, Columbidae

Fig. 8.17 **Double ring around throat, breast and belly**. (**1**) Collared Hill-partridge, *Arborophila gingica*, Phasianidae. (**2**) Blue-black Kingfisher, *Todiramphus nigrocyaneus*, Alcedinidae. (**3**) Double-banded Courser, *Smutsornis africanus*, Glareolidae. (**4**) Three-banded Plover, *Charadrius tricollaris*, Charadriidae

Fig. 8.18 **Concentric rings starting from the lower part of the breast, or from the head, covering the whole belly**. They build an angle of 90° with the head-tail axis. (**1**) Red-legged Crake, *Rallina fasciata*, Rallidae. (**2**) Little Bronze-cuckoo, *Chrysococcyx minutillus*, Cuculidae. (**3**) Horsfield's Cuckoo, *Cuculus horsfieldi*, Female, Cuculidae

8.16 The Bands and Concentric Semicircles of the Tail

The circularity of the wing extends to the tail. This can be easily discerned in the flying Merlin in which the tail opens in the shape of a fan and displays seven semicircular white rings alternating with dark ones (Fig. 8.23). The same pattern, of seven alternating dark and white bands is seen in the Eurasian Sparrowhawk where the curvature of the rings is less pronounced (Fig. 8.22). Two birds, which are at rest, have spread their tail feathers in the form of a fan. The male capercaillie and the Palawan Peacock-pheasant exhibit a pattern that could not be more explicit. In the tail of both species four concentric rings can be discerned consisting of lines and markings. Two rings, in the Palawan Peacock-pheasant, result from the association of two series of over 20 dark blue patches which are themselves circles surrounded by yellow lines (Fig. 8.23).

In other birds the number of tail bands follows a sequence that extends from 2 to 14 when the tail is seen from above. The six species that build this series belong to the family Accipitridae (Fig. 8.24). When the tail is seen from the underside a similar sequence of increasing band numbers occurs. The members of the series belong, as well, to the same family: the Trogonidae (Fig. 8.25).

It is difficult or impossible to see the underside of the tail when most birds are painted in profile and at rest. In the families, where the upper side as well as the underside could be inspected, lines following the head-tail axis, were not identified on the tail, or there was only a faint indication of their existence.

8.17 Rump, Legs and Beak are also Part of the Body's Geometry

The rump is not easy to study because most birds have been drawn in profile, making the rump's pattern less evident.

This is not the case in some species in which the rump has a white mark that contrasts sharply with the dark feathers that surround it.

This white band may be thin or broad and is usually semicircular, the direction of the ring following that of the other parts

Fig. 8.19 **Throat, breast and belly with slightly interrupted stripes tending to run parallel to each other and along the head-tail axis (*upper row*). Single dark stripe following the head-tail axis (*lower row*).** (**1**) Streak-breasted Honeyeater, *Meliphaga reticulata*, Meliphagidae. (**2**) Kashmir Nutcracker, *Nucifraga multipunctata*, Corvidae. (**3**) Varied Sittella, *Daphoenositta chrysoptera*, Neosittidae. (**4**) Common Blue Tit, *Cyanistes caeruleus*, Paridae. (**5**) Great Tit, *Parus major*, Paridae

of the body (Fig. 8.26). Families represented are: Hydrobatidae, Trochilidae, Apodidae, Hirundinidae and Alcidae.

What about the legs and the beak? Do they remain outside the geometry?

Marks on the legs are difficult to find or to access. This derives from them being often obscured by the body of the bird which is the primary object of attention when representing a given species.

Legs may have different colours being: red (Rufous Night Heron, Red-legged Crake), black or grey (Wired-tailed Manakin), yellow-orange (Shore Plover), and having other shades.

The Greater Flamingo *Phoenicopterus ruber* has legs which are red along their entire length but the Chilean Flamingo *Phoenicopterus chilensis* has grey legs with a red mark on the knees and red feet. The same red marks occur on the knees of the Saddlebill which has black legs and besides has red feet. In both regions the red colour is sharply delimited. In the Little Egret the legs are black. Suddenly, when approaching the feet they become yellow, at the same position in both legs, and this colour extends to the feet (Fig. 8.27).

In the drawings used to illustrate the many volumes on birds, the legs seem to have been the part of the body on which least attention has been focused. This situation may change in the future.

For the beak there are no difficulties. The circularity of the bill rests on the following evidence:

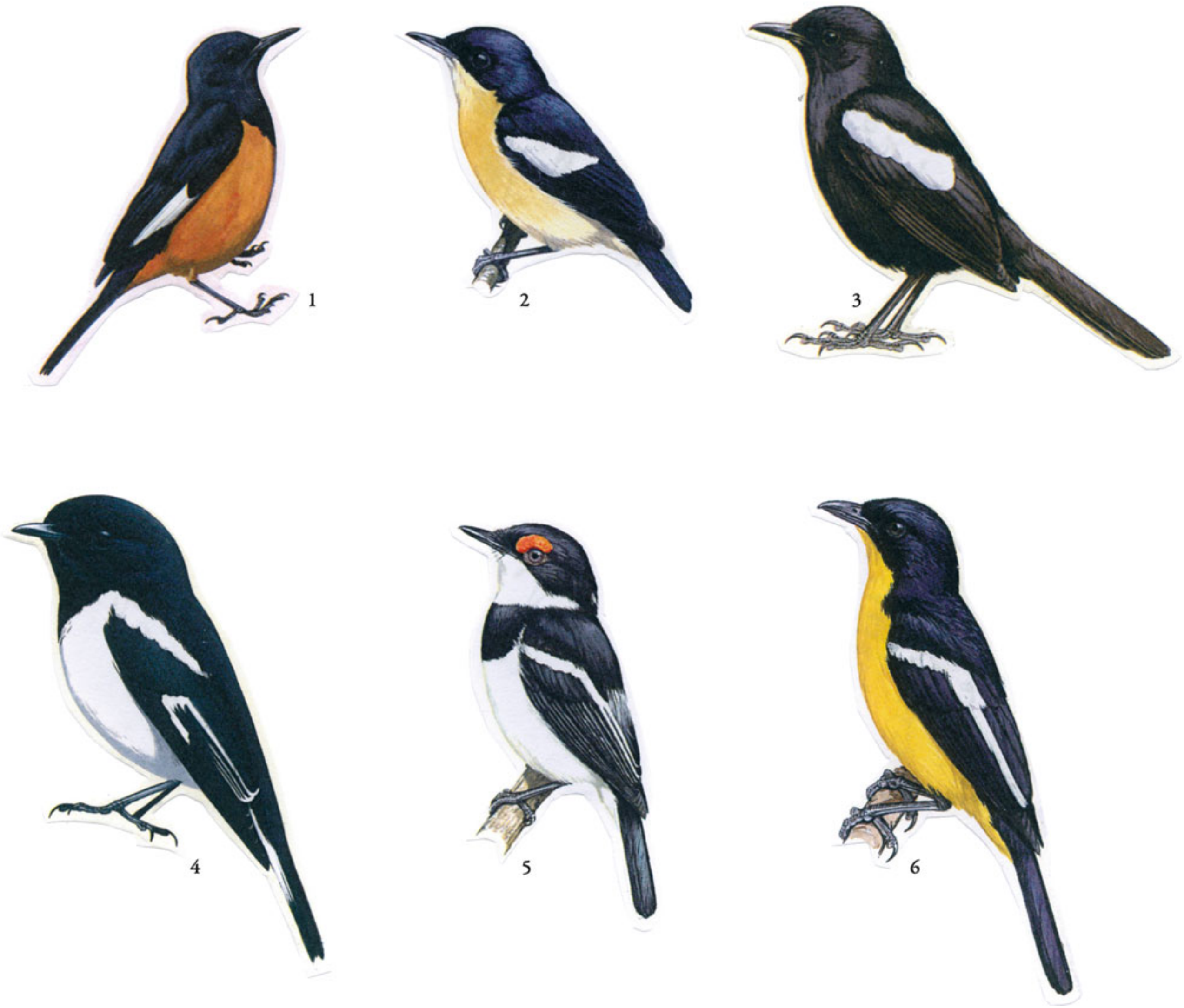


Fig. 8.20 **Wing with white mark, that increases in size and is partly aligned with the head-tail axis**. (**1**) White-winged Cliff-chat, *Thamnolaea semirufa*, Turdidae. (**2**) Yellow-bellied Hyliota, *Hyliota flavigaster*, Sylviidae. (**3**) Seychelles Magpie-robin, *Copsychus sechellarum*, Turdidae. (**4**) Hooded Robin, *Melanodryas cucullata*, Petroicidae. (**5**) Brown-throated Wattle-eye, *Platysteira cyanea*, Platysteiridae. (**6**) Crimson-breasted Shrike, *Laniarius atrococcineus*, Malaconotidae

1. Many species have distinct bands which are: white, black, red and yellow (Fig. 8.28).
2. These occupy positions along the beak from its end to its base *i.e.* the bands are located far away, at intermediate sites or close to the bird's eye. In two Flamingo species there is a black area which successively becomes located further away from the eye (Fig. 8.29).
3. Some are straight bands but others show a curvature that is concentric with the circles present around the eye in other species.
4. The number of curved bands on the bill may be one but may increase to become as many as seven (Luzon Tarictic Hornbill) (Fig. 8.28).
5. The bill may have a straight form which increases in size going from a short pointed structure to a long needle-like organ (Fig. 8.30). But in a vast number of species it is decurved. It starts as a short and sharp bend but may attain impressive lengths. The curvature is usually directed downwards, but life easily creates opposite solutions in which the beak becomes also very long but directed upwards (Sword-billed Hummingbird) (Fig. 8.31). The bill's circularity becomes more evident when one considers the series of forms aligned on Fig. 8.32. Starting with a strong down curvature that gives the bill the shape of a semicircle, it becomes successively less curved attaining a straight form. The reverse process leads to the beginning of an upright curvature that also tends to approach a complementary semicircle. This upwards, and circular, orientation is most distinct in the Common Crossbill (Fig. 8.32). In this bird the two mandibles behave independently, being

Fig. 8.21 **Wing at rest with black and white parallel stripes. They form semicircles that build an angle of 90° with the head-tail axis. In other species these are accompanied by streaks that instead run along the body axis building a criss-cross pattern as in Nr. 5.** (**1**) Barnacle Goose, *Branta leucopsis*, Anatidae. (**2**) Large-billed Antwren, *Herpsilochmus longirostris*, Thamnophilidae. (**3**) Grey-banded Babbler, *Robsonius sorsogonensis*, Timaliidae. (**4**) White-winged Magpie, *Urocissa whiteheadi*, Corvidae. (**5**) Great Northern Diver, *Gavia immer*, Gaviidae

Fig. 8.22 **Flying wing showing parallel dark and light stripes which build an angle of 90° with the head-tail axis. As the stripes approach the periphery of the wing they tend to become semicircular**. (**1**) Hoopoe, *Upupa epops*, Upupidae. (**2**) Lesser Spotted Woodpecker, *Dendrocopos minor*, Picidae. (**3**) Common Barn-owl, *Tyto alba*, Tytonidae. (**4**) Eurasian Sparrowhawk, *Accipiter nisus*, Accipitridae. (**5**) Eurasian Sparrowhawk, *Accipiter nisus*, Female, Accipitridae (Photo)

directed in opposite directions, an indication that they are under the control of different genes. Another case in which the two mandibles have different shapes and lengths is found in the Black Skimmer (Fig. 8.28).

This bill series reveals that a semicircle is opposed by another but inverted semicircle, and that these are apparently divided by a straight line that functions as the diameter of a full circle.

Fig. 8.23 **Tail displaying concentric semicircles**. (**1**) Merlin, *Falco columbarius*, Falconidae (Photo). (**2**) Lanner Falcon, *Falco biarmicus*, Falconidae (Photo). (**3**) Male capercaillie, *Tetrao urogallus*, Tetraonidae. (**4**) Palawan Peacock-pheasant, *Polyplectron emphanum*, Phasianidae (Photo)

8.18 Surprisingly the Circularity Extends to the Whole Body in Single Birds

The different parts of the bird's body have disclosed an uncompromising geometry that is dominated by circles, semicircles, parallel straight lines, and concentric rings. These parts seemed to be isolated from each other. But actually they are not.

What is significant is that, in a number of species, the circularity that starts at the eye can be seen expanding to the whole body within the same individual.

The body pattern of the Asian Barred Owlet displays such a situation. From the top of the head to the end of the tail concentric rings, which begin around the eyes and continue to the upper part of the head, expand successively into the breast, the belly, the wings, and finally to the tail. The spread of the concentric rings from the eye to the whole head are better seen in Sjostedt's Owlet (Fig. 8.33). This total pattern conveys the image of a drop of rain falling on the quiet surface of a lake. The concentric ripples, that it builds on the water, get larger and larger until they encounter the margins putting an end to their movement.

This total circularity of the body has another example in the Ruff (Fig. 8.33). It is difficult to find a more extreme geometry than that built by the 14 concentric circles that appear in the large feathers that surround its neck. Like the drop of water falling on the lake these circles are slightly closer to each other on the interior part and the distance between them has a tendency to increase as they expand into the end of the feathers. Additionally, there is a less distinct circle around the eye, and the black "comb" over the head is divided into two partial semicircles. Moreover, the concentric circles expand into the wings. In the black feathers of the breast this pattern is less evident.

In the Banded Kingfisher (Fig. 8.33) the total circularity of the body is also evident. Significant is that, like in the Asian Barred Owlet, it starts at the eye from which

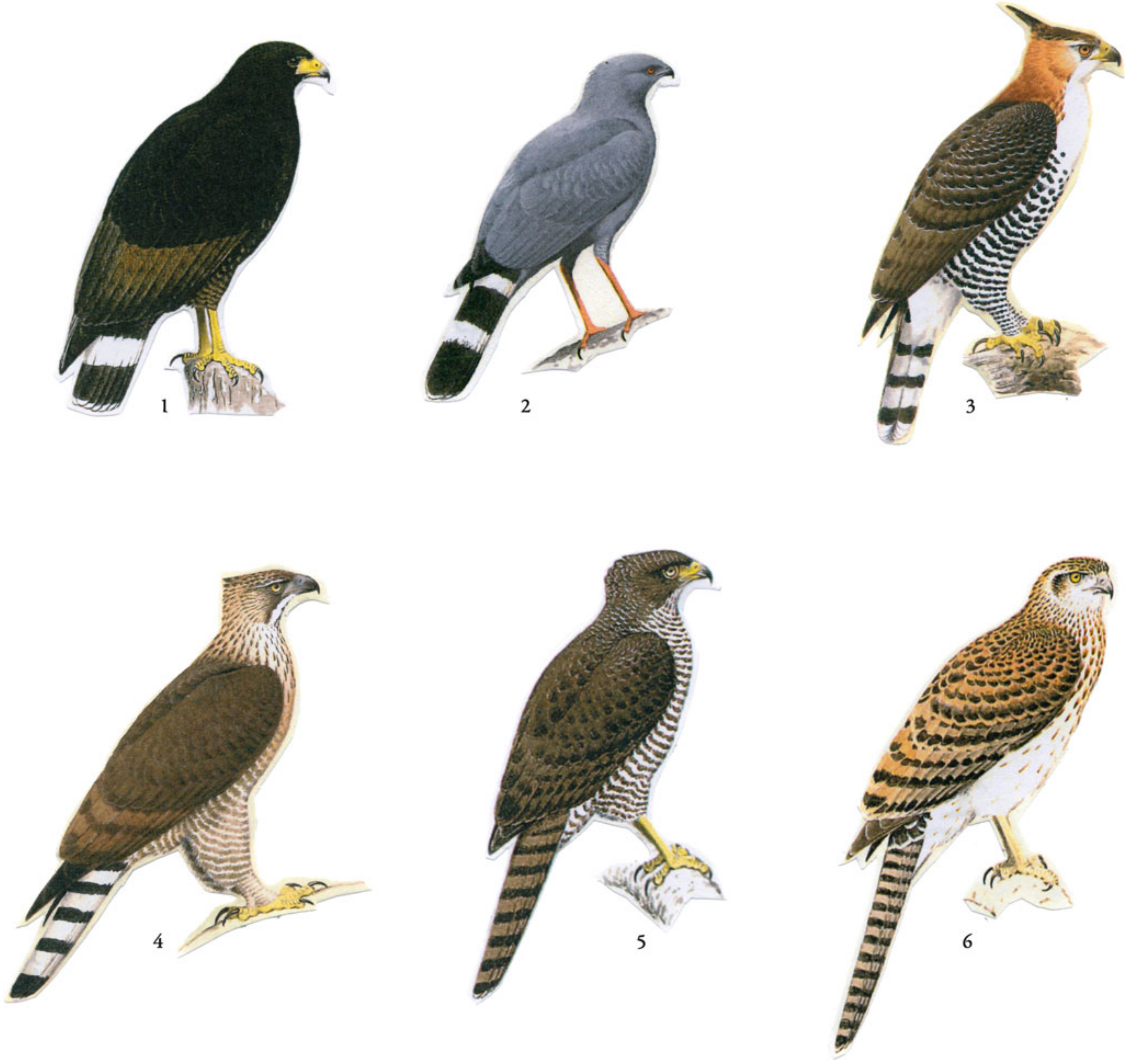


Fig. 8.24 **Tail seen from above with black and white (*or light coloured*) marks which increase in number, building a series of stripes located at right angles with the main body axis**. (**1**) Mangrove Black Hawk, *Buteogallus subtilis*, Accipitridae. (**2**) Crane Hawk, *Geranospiza caerulescens*, Accipitridae. (**3**) Ornate Hawk-eagle, *Spizaetus ornatus*, Accipitridae. (**4**) Mountain Hawk-eagle, *Spizaetus nipalensis*, Accipitridae. (**5**) Madagascar Serpent-eagle, *Eutriorchis astur*, Accipitridae. (**6**) Doria's Hawk, *Megatriorchis doriae*, Accipitridae

concentric rings spread over the whole head, the breast, the wings, the rump and the tail. Only the thick and long red bill is left out. Again, like the ripples on the water, the concentric rings are closer to each other near the eye and as the distance from the eye increases they get further apart. This is better seen in the breast (Fig. 8.33). In the birds it is not their skin, but the extremities of the feathers, that impose limits to this apparent wave.

Total body circularity is also to be seen in the Spotted Eagle-owl. In this photograph it is close to landing on the branch of a tree. All its body is a pageantry of parallel lines and concentric semicircles. Every pattern appears to start on the eye. Around it can be seen minor concentric circles which lead to a large black one that delimits the frontal part of the head. These continue, without interruption along the frontal part of the body and even into the feathers

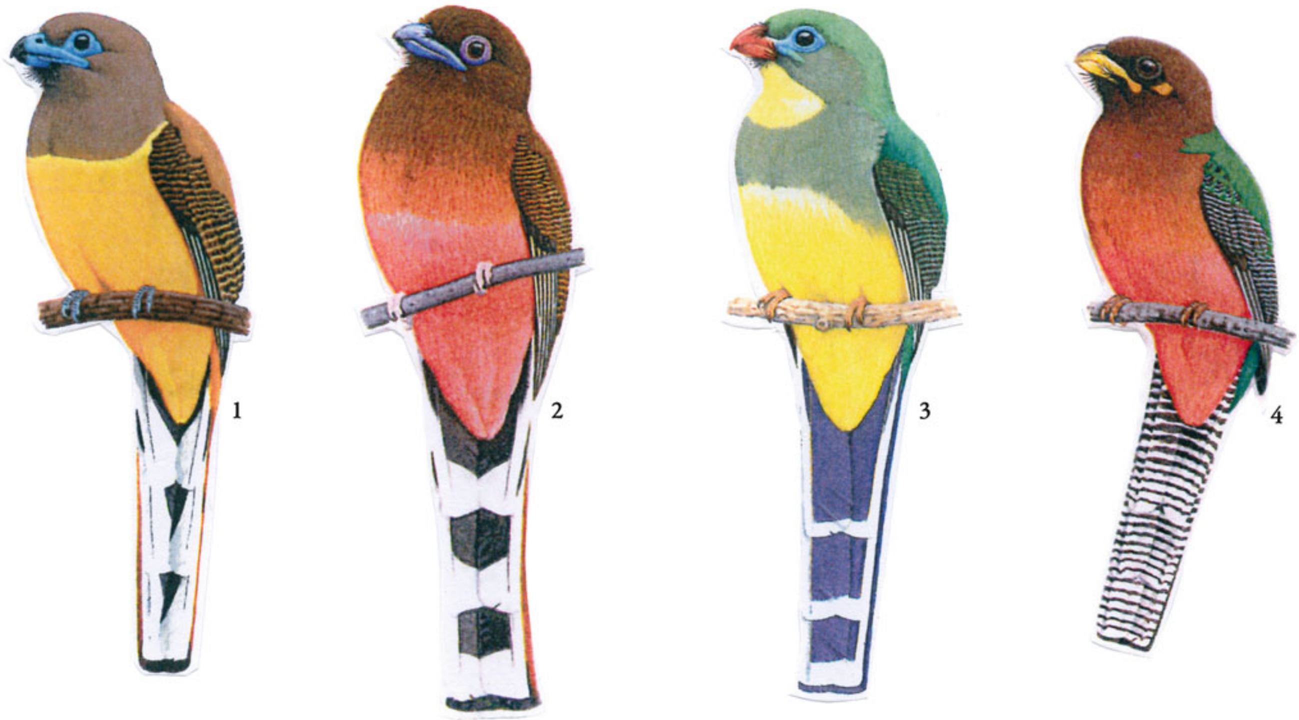


Fig. 8.25 **Underside of tail with parallel white and black stripes, which increase in number and are located at right angles to the main body axis.** (**1**) Red-naped Trogon, *Harpactes kasumba*, Trogonidae. (**2**) Red-headed Trogon, *Harpactes erythrocephalus*, Female, Trogonidae. (**3**) Javan Trogon, *Apalharpactes reinwardtii*, Female, Trogonidae. (**4**) Bar-tailed Trogon, *Apaloderma vittatum*, Female, Trogonidae

that cover part of the legs. The tail is partly covered by the tree branch separating it into two parts. It builds also a semicircular fan on which there are five concentric light coloured bands alternating with dark ones. The wings are of special interest because the upper parts, closer to the head, consist of a whirl of tiny parallel and partly circular stripes. The central and lower parts of the wings have an equally impressive geometry. Between 6 and 7 broad and distinct stripes cover their whole surface being first slightly inclined to the main axis of the body but, as they approach the extremities, they tend to be circular. The circularity of the tail and that seen partly in the wing have centers located at different sites: one above the head (wing) and the other on the middle of the body (tail) (Fig. 8.34).

In two other cases the whole body pattern is evident when the bird is flying (Crested Kingfisher) and when it spreads its wings (Greater painted snipe). Every feather from the head to the tail seems to participate in the geometry (Fig. 8.34).

Another sight is the Great Hornbill when it alights on the trunk of a tree, to take a short rest, with its broad wings and tail fully expanded. The two wings build three circles which are nearly concentric: (1) a white peripiheral band, (2) a median black broad space and (3) an interior narrow white band. The tail, opening like a fan has two concentric rings: the outermost which is white and a broad one which is black. Let us not be tempted by this impressive photo. It is to be noted that, in this species, the centers of the rings on the wing and the tail are not located at the same site. The center of the wing pattern is located close to the eye, whereas that of the tail is far below on the rump (Fig. 8.34).

Last, but not least, the male Golden Pheasant, during courtship, fluffs up his feathers, normally kept on the side of the head. Their base is located quite close to the bird's eye and build a semicircle, around it, when they are expanded. Besides, 12 concentric rings can be discerned on the feathers, their center being located close to the top of the head. This feather pattern produces an astounding picture of circularity emanating seemingly as a wave from the eye (Fig. 8.35).

8.19 The Body Pattern of Birds Condensed in a Geometric Disk

The geometric disk synthesizes the structural evidence collected on the avian body (Fig. 8.36). There has been no need to use one's imagination or to invent any details. The pattern displayed by birds is so clear-cut and so astonishingly exquisite, that it surpasses the wildest fantasy.

Fig. 8.26 **Rump with a broad or narrow white band**. (**1**) Guadalupe Storm-petrel, *Oceanodroma macrodactyla*, Hydrobatidae. (**2**) Festive Coquette, *Lophornis chalybeus*, Trochilidae. (**3**) White-rumped Spinetail, *Zoonavena sylvatica*, Apodidae. (**4**) White-eyed River Martin, *Pseudochelidon sirintarae*, Hirundinidae. (**5**) Razorbill, *Alca torda*, Alcidae

The disk has its origin in the following features: (1) Already in the embryo the eye has a preponderate size and position, dominating other organs. (2) In the adult the eye is surrounded by circles that are concentric. (3) These increase successively in diameter covering the whole head and extending to the crest. (4) Other types of semicircular lines start from the eye. (5) Wings, tails, throat, breast and belly also display circular concentric patterns. (6) Beaks and legs show markings indicating the presence of this circularity. (7) The circularity that starts around the eye apparently spreads as a wave to other parts of the body in single birds.

A process contrary to circularity is evident at the eye level. White and black stripes cross the eye and are accompanied by others, above and below it. These stripes tend to have a horizontal position and to be parallel to each other (Figs. 8.6, 8.7, 8.8, 8.9 and 8.10). Similar black stripes having a vertical position cross the eye and are present on both sides of it (Fig. 8.11).

All these eye features build the central core of the disk in which the eye occupies its focus. The eye is accompanied by its many concentric circles and horizontal and vertical lines, which extend into the rest of the head.

The crest does not either disguise its circularity. Its semicircular form is evident and is accompanied by distinct concentric rings that occur mainly at its periphery (Figs. 8.12 and 8.13). It comes as a revelation that the crest is divided into three regions: anterior, median and posterior. The key to this differentiation is furnished by birds which have, on the top of their heads, a crest that consists of developed anterior and posterior parts but in which the median region is undeveloped

Fig. 8.27 **Legs with coloured bands on the knees, feet and lower part of legs**. (**1**) Chilean Flamingo, *Phoenicopterus chilensis*, Phoenicopteridae. (**2**) Saddlebill, *Ephippiorhynchus senegalensis*, Ciconiidae. (**3**) Little Egret, *Egretta garzetta*, ssp garzetta, Ardeidae

or less distinct (Fig. 8.14). Once these cases were found it was not difficult to discover species in which only the anterior, or the median, or the posterior region developed a crest (Fig. 8.15). Due to its natural position on top of the head, the crest occupies the upper sector of the disk.

The wing comes next. In a bird at rest, it shows concentric rings that spread over most of this organ and these are crossed by parallel lines building a mosaic, as best seen in Fig. 8.21. Thus, both circularity and straight lines, at right angles, are found here. The wing seen from the underside, when the animal flies, displays also circularity but its pattern is more complex. Besides not so many species have been painted during flight, as a result an extensive study of the underpart of the wing must be carried out before it is included in the disk.

In the rump can be seen white circular bands of different thicknesses which are formed against a dark background (Fig. 8.26).

Characteristic of the tail is that circular bands are most distinct on it (Fig. 8.23), but so far there is no evidence that they are crossed by lines at right angles. Their lack may be attributed to most birds being painted with the tail at rest hiding its details. For the legs it could be argued that they are usually so thin that there is no space for vertical or transversal stripes. However, the ostrichs have long and thick legs which easily would permit the formation of such stripes. The fact that only transversal marks have been detected on the legs leaves this question open, as in the case of the tail.

The throat, breast and belly could not be more explicit in their display of geometry. Each body part was awarded a separate sector in the disk for the sake of clarity. Their patterns have been for years a source of delight to bird watchers due to the multiple rings which descend from the throat to the belly in the form of colourful collars (Figs. 8.16, 8.17 and 8.18). This circularity is not alone. It is traversed by long stripes that run along the head-tail axis and which become especially thick along the frontal region (Fig. 8.19).

Should the beak be left out? Has it any geometry that fits into the general pattern? At first sight it seemed that the beak, like the legs, were outgrowths of the body that were outside this process. But first impressions deceive. Every component of an animal body is part of its structural unity. Each organ is a product of the embryonic development and cannot be separated from it being a prisoner of its rules. When carefully inspected, many species show distinct marks on the beak that occupy different positions along its length. These marks, like the stripes on other parts of the body, are: (1) as many as seven along the same bill, (2) run parallel to each other and (3) their position seems to be related to the eye (Figs. 8.28 and 8.29). To simplify matters, each beak

Fig. 8.28 **Beaks with coloured stripes and well delimited black and red areas. Their surface appears as a fraction of a circular line which occurs at a successively increasing distance from the eye**. (**1**) Amsterdam Albatross, *Diomedea amsterdamensis*, Diomedeidae. (**2**) Atitlan Grebe, *Podilymbus gigas*, Podicipedidae. (**3**) Razorbill, *Alca torda*, Alcidae. (**4**) Horned Puffin, *Fratercula corniculata*, Alcidae. (**5**) Reddish Egret, *Egretta rufescens*, Ardeidae. (**6**) Masked Tityra, *Tityra semifasciata*, ssp costaricensis, Female, Tyrannidae. (**7**) Black Skimmer, *Rynchops niger,* Rynchopidae. (**8**) Luzon Tarictic Hornbill, *Penelopides manillae*, ssp subniger, Bucerotidae

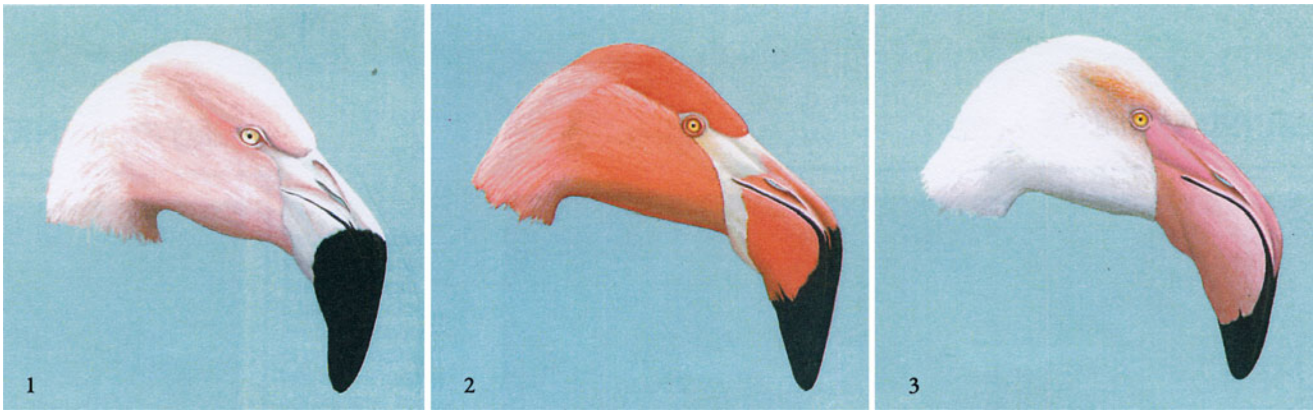


Fig. 8.29 Bill with well defined black area becoming successively located further away from the eye. (**1**) Chilean Flamingo, *Phoenicopterus chilensis*, Phoenicopteridae. (**2**) Greater Flamingo, *Phoenicopterus ruber*, ssp ruber, Phoenicopteridae. (**3**) Greater Flamingo, *Phoenicopterus ruber*, ssp roseus, Phoenicopteridae

was represented as a triangle displaying an observed marking or group of markings.

The reduction of the body pattern, of over 8,000 species of birds, to simple geometry may be regarded as an extreme simplification if not a distortion. However, every phenomenon in nature has to be simple in its foundations otherwise it would never work. The disk, exposing simplicity, may function as an incentive, and a working basis, to better uncover the order that underlies embryonic development in birds and the atomic pathways that lead to formation of the juvenile and adult body patterns (Fig. 8.36).

The strongest argument in favor of the disk's validity is that the structural unity that it represents is in agreement with the unity of genetic action. It was experimentally demonstrated that the eye is a master organ leading to the formation of the same structure and function at different body locations. Eyes emerge on the head, antennae, wings and legs. Besides, wings are able to build eyes (Chap. 7).

The combination of the structural and the genetic information produces a coherent picture of pattern organization in birds.

8.20 The Geometric Disk – Like any Figure of Geometry – Represents a Simplification of Biological Reality

Ornithologists may find the disk unworthy of their long and painstaking work, which has concentrated on collecting so many valuable details, because their great labour is now compressed into a single figure.

Besides a disk is two-dimensional. A sphere, which is three-dimensional, would seem more appropriate to represent the pattern of a bird's body. In some families the birds are called "ballbirds" because their body is actually spheroid. On purpose the sphere was avoided because the information so far gathered is considered to be preliminary. A three-dimensional representation has to await more data and a better coordination with the molecular level. The disk, if it has any value, it will be superseded by future research, suffering additions and adjustments.

It should not be forgotten that molecular geometry at the same time that it is preserved from generation to generation, is dynamic and ephemeral. With age the feathers bleach, with sexual development they acquire other shapes and colours and they are shed at regular intervals – a concretization of their ephemeral existence. Moreover, we are far from knowing how the embryonic development becomes transformed into the final body pattern. For instance, there is ignorance of the atomic processes that direct the different pigments to their exact final body locations.

8.21 What About the Intermediate Cases?

The plates of this work are covered with emblematic examples that expose their structural significance due to the sharpness of their patterns. But what about the many other cases in which the geometry is not so clear? They are often intermediate situations that are not to be discarded.

The great lesson that genetics teaches us is that a phenomenon that was originally discovered in a single species turned out to be of general occurrence when other animals or plants were carefully analysed. The examples are as many as one would like to gather. The rules of inheritance were first discovered in plants but soon were found to apply to guinea pigs and to humans. The genetic code is nearly universal. The organization of DNA and proteins, in chromosomes, is the same in all organisms which have a cell nucleus. Sex chromosomes and accessory chromosomes which were discovered initially in a few species are found everywhere.

Fig. 8.30 **Straight beaks increase in length**. (**1**) Greater Antillean Elaenia, *Elaenia fallax*, Tyrannidae. (**2**) Azure Tit, *Cyanistes cyanus*, Paridae. (**3**) White-headed Marsh-tyrant, *Arundinicola leucocephala*, Tyrannidae. (**4**) Taiwan Yuhina, *Yuhina brunneiceps*, Timaliidae. (**5**) Northern Flicker, *Colaptes auratus*, Picidae. (**6**) Red-headed Woodpecker, *Melanerpes erythrocephalus*, Picidae. (**7**) Marbled Godwit, *Limosa fedoa*, Female, Scolopacidae. (**8**) Great Sapphirewing, *Pterophanes cyanopterus*, Trochilidae

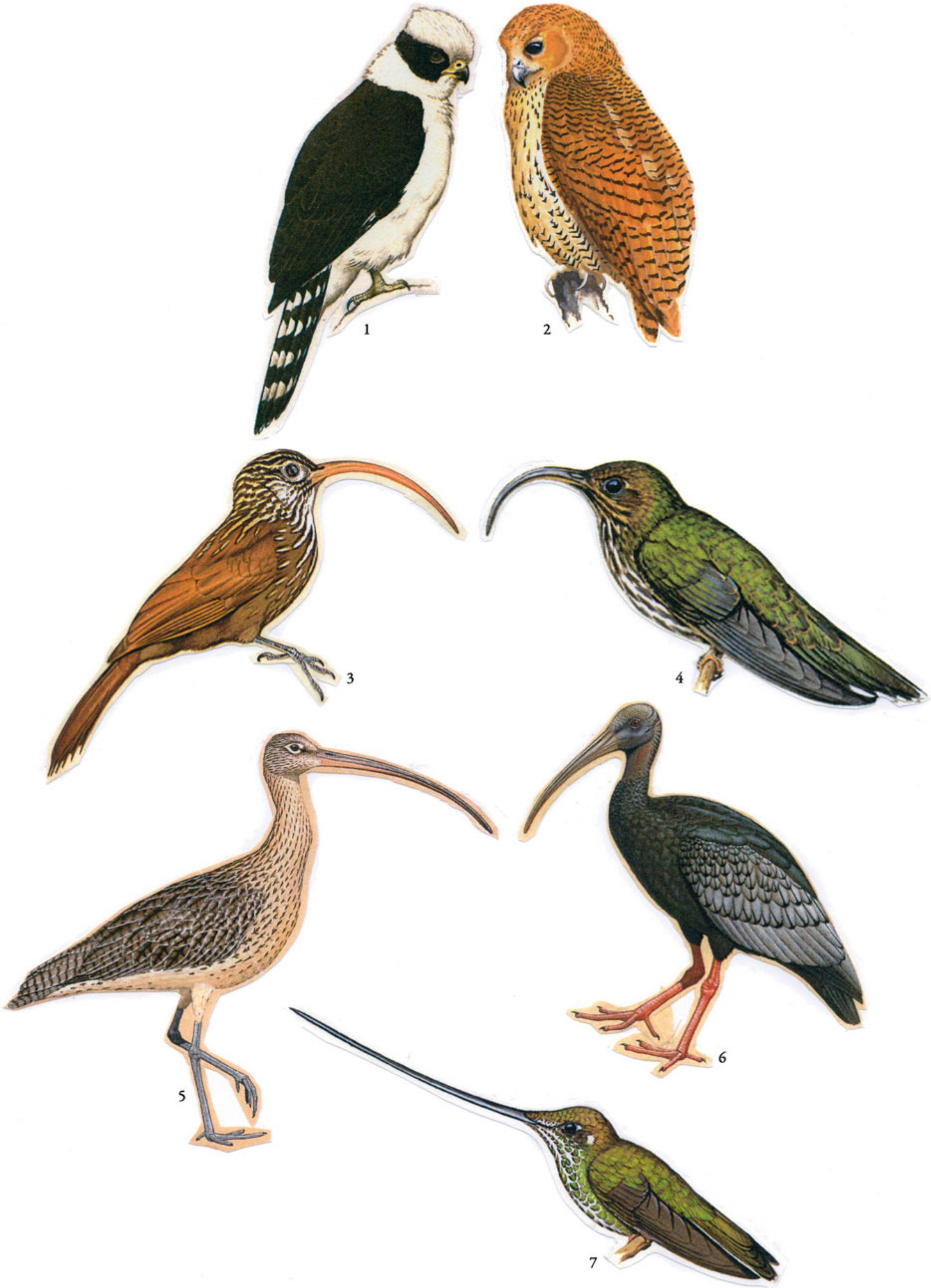


Fig. 8.31 **Curved beaks increase in length**. (**1**) Laughing Falcon, *Herpetotheres cachinnans*, Falconidae. (**2**) Pel's Fishing-owl, *Scotopelia peli*, Strigidae. (**3**) Red-billed Scythebill, *Campylorhamphus trochilirostris*, Dendrocolaptidae. (**4**) White-tipped Sicklebill, *Eutoxeres aquila*, Trochilidae. (**5**) Far Eastern Curlew, *Numenius madagascariensis*, Scolopacidae. (**6**) Giant Ibis, *Pseudibis gigantea*, Threskiornithidae. (**7**) Sword-billed Hummingbird, *Ensifera ensifera*, Female, Trochilidae

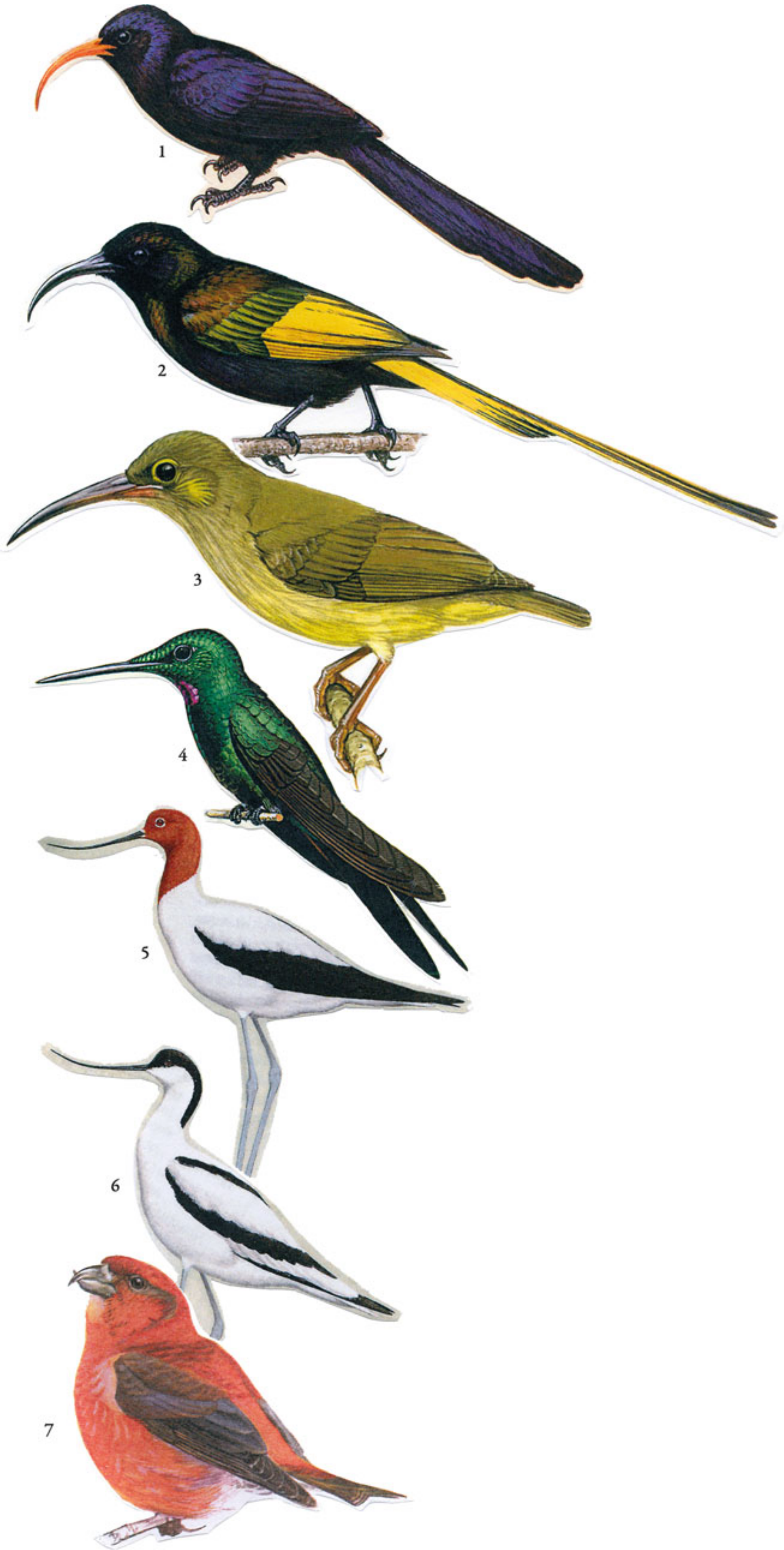
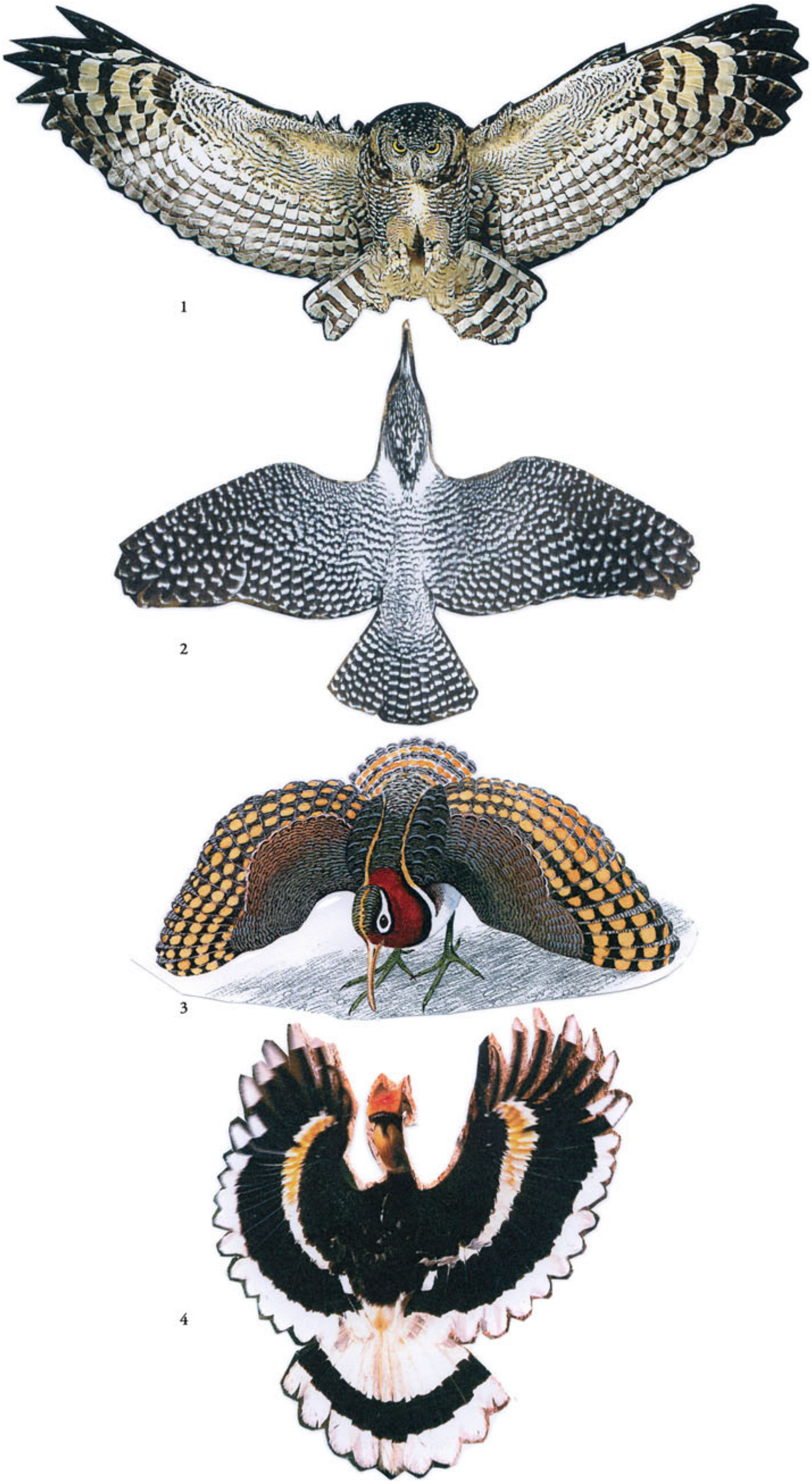


Fig. 8.32 The circularity of the beak. A sharply down curved form approaching a semicircle is followed by successively less down curved inclinations which lead to a straight bill. The beak also bends in the opposite direction forming a light up curve and it may even attain a more upward shape which comes close to a section of a semicircle. This results in an inverted position which is complementary to the down curved form. (**1**) Abyssinian Scimitarbill, *Rhinopomastus minor*, ssp cabanisi, Phoeniculidae. (**2**) Golden-winged Sunbird, *Drepanorhynchus reichenowi*, Nectariniidae. (**3**) Yellow-eared Spiderhunter, *Arachnothera chrysogenys*, Nectariniidae. (**4**) Empress Brilliant, *Heliodoxa imperatrix*. Trochilidae. (**5**) Red-necked Avocet, *Recurvirostra novaehollandiae*, Recurvirostridae. (**6**) Pied Avocet, *Recurvirostra avosetta*, Recurvirostridae. (**7**) Common Crossbill, *Loxia curvirostra*, Fringillidae

Fig. 8.33 **Whole body pattern characterized by a general circularity. The circles start around the eye, spreading like a wave. They extend to the upper part of the head and become distributed over the whole body, building parallel stripes that cover the throat, breast, belly, wing and tail**. (**1**) A drop of water falling on a tranquil surface. (**2**) Ruff, *Philomachus pugnax*, Scolopacidae. (**3**) Banded Kingfisher, *Lacedo pulchella*, Female, Alcedinidae. (**4**) Asian Barred Owlet, *Glaucidium cuculoides*, Strigidae. (**5**) Sjöstedt's Owlet, *Glaucidium sjostedti*, Strigidae

Fig. 8.34 Circularity extending to most body parts – wings seen from below and above. (**1**) Spotted Eagle-owl, *Bufo africanus*, ssp africanus, Strigidae (Photo). (**2**) Crested Kingfisher, *Megaceryle lugubris*, ssp lugubris, Alcedinidae (Photo). (**3**) Greater painted snipe, *Rostratula benghalensis*, Rostratulidae, Female. (**4**) Great Hornbill, *Buceros bicornis*, Bucerotidae (Photo)



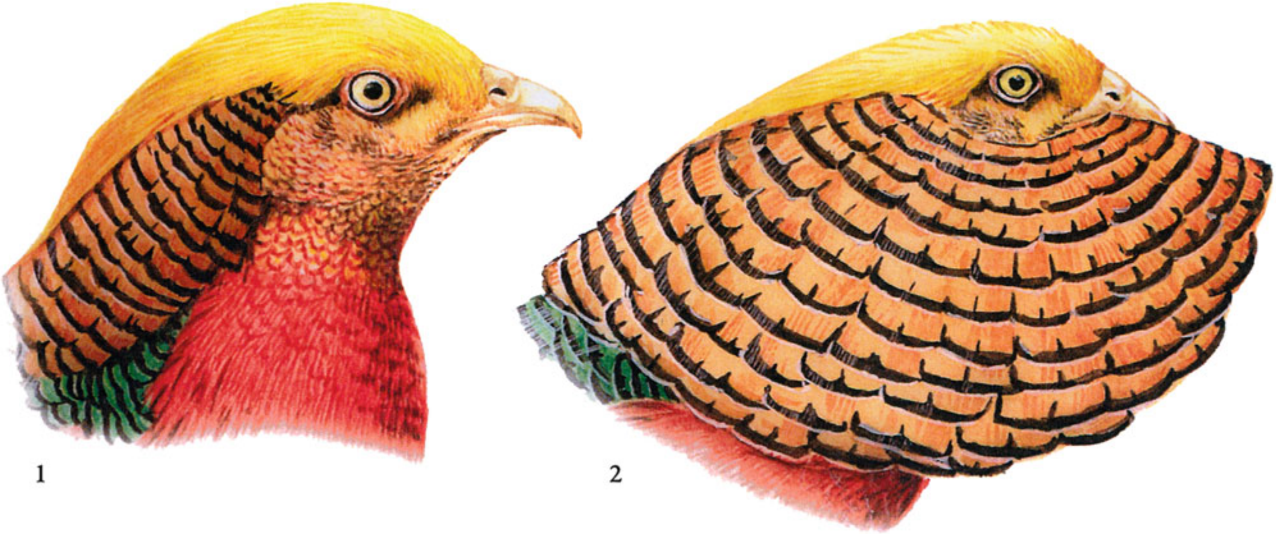


Fig. 8.35 **Among the Phasianidae, the pheasants are particularly noted for their courting displays**. Male Golden pheasants can suddenly expand cloaks of feathers normally drawn up on the side of the head (**1**) to create an impressive ruff effect (**2**). Twelve concentric rings can be discerned spreading from the eye as an apparent wave. Golden pheasant, *Chrysolophus pictus*, Phasianidae

As Jacques Monod (1910–1976), a leading geneticist, put it: “What applies to fruit flies is equally valid for humans and elephants”. The discovery of birds with a clear cut geometry led also to find other species which displayed the same phenomenon, although in a less overt way, establishing its general occurrence. The intermediate situations are not to be placed outside the main patterns revealed by the apparently exceptional cases.

At the chromosome level there are already antagonistic processes at work and these could not be erased during animal development leading to the adult stage. It became evident, from the analysis of the geometric patterns, that these were also contradictory – the eye being surrounded by concentric circles at the same time that it was traversed by straight lines. The intermediate situations, which are expected to be the most common feature of the bird pattern, are considered to be the result of the contradictory molecular processes. In these a full decision did not occur either in one or another direction, and as a consequence the pattern became blurred or less distinct. In other situations several patterns may have become superimposed creating a more complex picture.

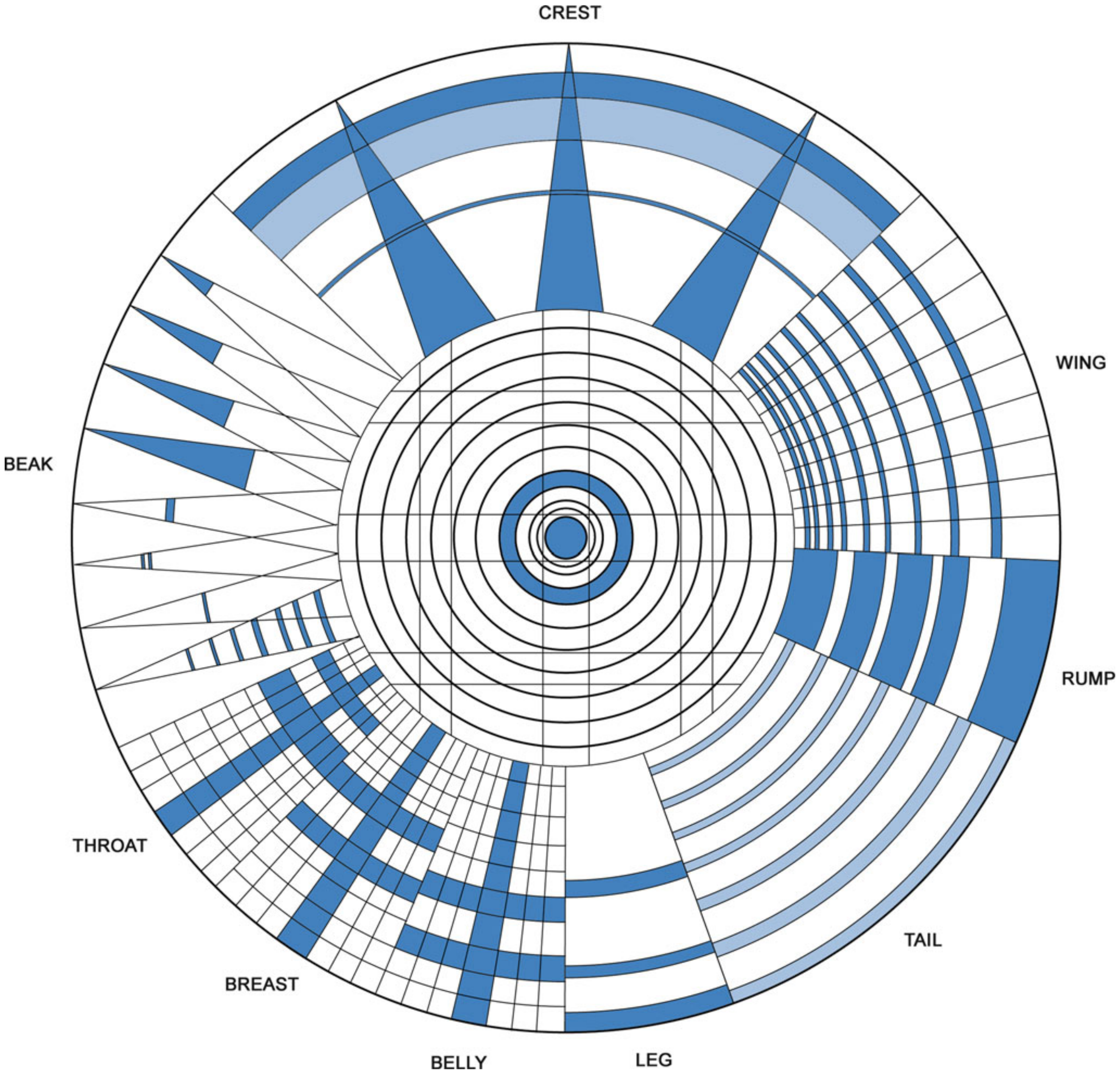


Fig. 8.36 **Disk synthesizing the information on the geometry of body pattern collected from the analysis of over 8,000 species of birds**. The eye occupies the central section of the disk, since it turned out to be the focal point from which depart: concentric rings, semicircles, parallel lines, and other geometric figures. This geometry is displayed by the whole avian body extending from the head's crest to the tail and the legs. In the disk the distribution of the bird's structural regions follows their natural position in the body which is reduced to a circle. The features depicted in the different structural sections of the disk are those that were found to be most evident in the bird species analysed.The genetic information available discloses that the pattern can be correlated with molecular cascades which originate in specific DNA sequences. These are responsible for the emergence and shaping of the body structures. Moreover, feather pigments, which are the main components of the concretization of the geometry, due to the figures that they form, turn out to be guided by proteins during their ordered migration. Additionally, genetic manipulation has led to the demonstration that eye genes are keys to the understanding of the unity of body organization.The geometric disk represents a simplification of the biological reality, just as every figure of Euclidean geometry is a simplification of the physico-chemical world. The simplicity of the disk may seem provocative but any basic phenomenon must be simple otherwise it would have never worked.All rights reserved covering this original Figure and all the original Plates. These can only be reproduced with permission of the Author or his heirs, being accompanied by: (**1**) The complete text of the Figure caption. (**2**) A citation as follows: Lima-de-Faria, A., 2012, “Molecular Geometry of Body Pattern in Birds”, to be accompanied by Figure Number, Page Number, Publisher, City, Country. (**3**) Consent will only be given for reproduction of the entire unmodified image

Sources of Figures

Fig. 8.1 (**1**) Burton, R. 1987. Egg. Nature's Miracle of Packaging. William Collins, London, UK (page 108, left side), (**2**) Raff, R.A. 1996. The Shape of Life. University of Chicago Press, Chicago, U.S.A. (Fig. 6.4 page 194, From Haeckel, E. 1874), (**3**) Romer, A. and Parsons, T.S. 1978. The Vertebrate Body. Saunders Co., Philadelphia, U.S.A. (Fig. 406 page 390), (**4**) Original diagram, (**5**) and (**6**) Snow, D.W. and Perrins, C.M. 1998. The Birds of the Western Palearctic, vol. 1. Oxford University Press, Oxford, UK (page XXVI, only part of figure).

Fig. 8.2 Original plate composed of species depicted in the **HBW** (**1**) Volume 1, Plate on page 43, (**2**) Volume 4 – Plate 43 – Nr. 171, (**3**) 11 – 1 – 7 ssp fischeri, (**4**) 8 – 69 – 204 ssp brunneiceps, (**5**) 1 – 49 – 124, (**6**) 5 – 12 – 94 ssp wiepkeni, (**7**) 5 – 3 – 12.

Fig. 8.3 Original plate. **HBW**: (**1**) 11 – 23 – 54, (**2**) 1 – 43 – 52 Female, (**3**) 1 – 48 – 108 Female, (**4**) 1 – 44 – 66 ssp turneri, (**5**) 2 – 43 – 11 ssp graeca, (**6**) 3 – 34 – 12.

Fig. 8.4 Original plate. **HBW**: (**1**) 1 – 44 – 61, (**2**) 1 – 23 – 34 ssp brevirostris, (**3**) 3 – 53 – 47.

Fig. 8.5 Original plate. **HBW**: (**1**) 2 – 21 – 224, (**2**) 6 – 24 – 9, (**3**) 12 – 56 – 52, (**4**) 9 – 14 – 42, (**5**) 3 – 39 – 61.

Fig. 8.6 Original plate. **HBW**: (**1**) 12 – 20 – 281, (**2**) 8 – 25 – 183, (**3**) 13 – 51 – 146.

Fig. 8.7 Original plate. **HBW**: (**1**) 11 – 26 – 86, (**2**) 12 – 27 – 5, (**3**) 9 – 36 – 285, (**4**) 14 – 16 – 8.

Fig. 8.8 Original plate. **HBW**: (**1**) 4 – 13 – 160, (**2**) 8 – 73 – 26, (**3**) 7 – 3 – 7.

Fig. 8.9 Original plate. **HBW**: (**1**) 6 – 26 – 7, (**2**) 13 – 55 – 17, (**3**) 14 – 33 – 50, (**4**) 12 – 16 – 211, (**5**) 13 – 1 – 1.

Fig. 8.10 Original plate. **HBW**: (**1**) 4 – 13 – 145, (**2**) 1 – 50 – 141 Female, (**3**) 12 – 25 – 3.

Fig. 8.11 Original plate. **HBW**: (**1**) 3 – 39 – 63, (**2**) 12 – 25 – 1, (**3**) 12 – 37 – 3, (**4**) 7 – F9 – Mascarene Parrot, (**5**) 10 – 62 – 113 ssp cyanota, (**6**) 2 – 26 – 32 Female.

Fig. 8.12 Original plate. (**1**) Perrins, C. 1976. Bird Life (page 23), **HBW**: (**2**) 9 – 9 – 71 ssp sanguinolentus, (**3**) 6 – 37 – 19, (**4**) 3 – 5 – 1, (**5**) 4 – 16 – 185.

Fig. 8.13 Original plate. **HBW**: (**1**) 9 – 9 – 70 (Photo on page 42), (**2**) 9 – 29 – 202 (Photo on page 179).

Fig. 8.14 Original plate. **HBW**: (**1**) 4 – 26 – 304. Photograph on page 64, (**2**) 14 – 7 – 2, (**3**) 1 – 23 – 33, (**4**) 1 – 23 – 32.

Fig. 8.15 Original plate. **HBW**: (**1**) 2 – 39 – 7, (**2**) 3 – 60 – 16 Female , (**3**) 2 – 59 – 154, (**4**) 4 – 9 – 97, (**5**) 3 – 35 – 1, (**6**) 2 – 3 – 3 Female.

Fig. 8.16 Original plate. **HBW**: (**1**) 5 – 63 – 206, (**2**) 7 – 3 – 9, (**3**) 1 – 43 – 48, (**4**) 4 – 26 – 297.

Fig. 8.17 Original plate. **HBW**: (**1**) 2 – 49 – 83, (**2**) 6 – 14 – 38, (**3**) 3 – 33 – 6, (**4**) 3 – 38 – 41

Fig. 8.18 Original plate. **HBW**: (**1**) 3 – 11 – 23, (**2**) 4 – 61 – 33, (**3**) 4 – 59 – 18 Female.

Fig. 8.19 Original plate. **HBW**: (**1**) 13 – 40 – 25, (**2**) 14 – 35 – 74, (**3**) 12 – 50 – 1, (**4**) Burton, P. and Hayman, P. 1977. Fåglar och Fågelliv i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. page 17). (**5**) Burton, P. and Hayman, P. 1977. Fåglar och Fågelliv i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. page 16).

Fig. 8.20 Original plate. **HBW**: (**1**) 10 – 68 – 193, (**2**) 11 – 47 – 140, (**3**) 10 – 73 – 259, (**4**) 12 – 38 – 24, (**5**) 11 – 12 – 27, (**6**) 14 – 3 – 19 – Yellow morph.

Fig. 8.21 Original plate. (**1**) Svensson, L. et al. 1999. Fågelguiden. Albert Bonniers Förlag, Stockholm, Sweden (Fig. page 45), **HBW**: (**2**) 8 – 55 – 111, (**3**) 12 – 11 – 137, (**4**) 14 – 33 – 49, (**5**) 1 – 10 – 3.

Fig. 8.22 Original plate. (**1**) Burton, P. and Hayman, P. 1977. Fåglar och Fågelliv i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. page 122), (**2**) Burton, P. and Hayman, P. 1977. Fåglar och Fågelliv i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. page 121), (**3**) Burton, P. and Hayman, P. 1977. Fåglar och Fågelliv i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. page 154), (**4**) Burton, P. and Hayman, P. 1977. Fåglar och Fågelliv i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. page 139), (**5**) Pedersen, J. and Svensson, L. 2009. Fågelsång. Bokförlaget Max Ström, Sweden (Fig. Nr. 030).

Fig. 8.23 Original plate. (**1**) Gensbol, B. and Straav, R. 1984. Rovfåglar i Europa. Nordstedts, Sweden (Photo page 264), (**2**) del Hoyo, J. et al. (Editors) 1992. Handbook of the Birds of the World, vol 2 (1994). Lynx Edicions, Barcelona, Spain (Photo page 221), (**3**) Perrins, C. 2003. The New Encyclopedia of Birds. Oxford University Press, UK (Fig. 7a page 187), (**4**) Burnie, D. 2004. Animal. DK, Dorling Kindersley, London, UK (Photo page 295).

Fig. 8.24 Original plate. **HBW**: (**1**) 2 – 16 – 165, (**2**) 2 – 15 – 152, (**3**) 2 – 22 – 235, (**4**) 2 – 22 – 228, (**5**) 2 – 8 – 73, (**6**) 2 – 14 – 146.

Fig. 8.25 Original plate. **HBW**: (**1**) 6 – 2 – 7 Female, (**2**) 6 – 3 – 14 Female, (**3**) 6 – 2 – 4 Female, (**4**) 6 – 2 – 3 Female.

Fig. 8.26 Original plate. **HBW**: (**1**) 7 – F1 (page 18), (**2**) 5 – 51 – 79, (**3**) 5 – 40 – 46, (**4**) 9 – 62 – 2, (**5**) 3 – 59 – 4.

Fig. 8.27 Original plate. **HBW**: (**1**) 1 – 38 – 2, (**2**) 1 – 33 – 15, (**3**) 1 – 27 – 23.

Fig. 8.28 Original plate. **HBW**: (**1**) 1 – 12 – 2, (**2**) 1 – 11 – 7, (**3**) Jonsson, L. 1992. Fåglar i Europa. Wahlström och Widstrand, Stockholm, Sweden (Fig. page 295), **HBW**: (**4**) 3 – 60 – 21, (**5**) 1 – 27 – 14, (**6**) 9 – 47 – 409 Female, ssp costaricensis, (**7**) 3 – 58 – 1, (**8**) 6 – 40 – 34 ssp subniger.

Fig. 8.29 Original plate. **HBW**: (**1**) 1 – 38 – 2, (**2**) 1 – 38 – 1 ssp ruber, (**3**) 1 – 38 – 1 ssp roseus.

Fig. 8.30 Original plate. **HBW**: (**1**) 9 – 18 – 35, (**2**) 12 – 56 – 54, (**3**) 9 – 37 – 293, (**4**) 12 – 3 – 16, (**5**) 7 – 40 – 148, (**6**) 7 – 26 – 38, (**7**) 3 – 42 – 31 Female, (**8**) 5 – 65 – 226.

Fig. 8.31 Original plate. **HBW**: (**1**) 2 – 24 – 10, (**2**) 5 – 11 – 91, (**3**) 8 – 38 – 51, (**4**) 5 – 45 – 2, (**5**) 3 – 42 – 38, (**6**) 1 – 35 – 7, (**7**) 5 – 65 – 225 Female.

Fig. 8.32 Original plate. **HBW**: (**1**) 6 – 34 – 8 ssp cabanisi, (**2**) 13 – 13 – 54, (**3**) 13 – 22 – 127, (**4**) 5 – 61 – 193, (**5**) 3 – 31 – 6, (**6**) 3 – 31 – 4, (**7**) Jonsson, L. 1992. Fåglar i Europa. Wahlström och Widstrand, Sweden (Fig. page 522).

Fig. 8.33 Original plate. (**1**) The original source of this picture could not be traced, (**2**) Svensson, L. et al. 1999. Fågelguiden. Albert Bonniers Förlag, Stockholm, Sweden (Fig. page 157), **HBW**: (**3**) 6 – 10 – 18 Female, (**4**) 5 – 16 – 143, (**5**) 5 – 16 – 142.

Fig. 8.34 Original plate. **HBW**: (**1**) 5 – 10 – 75 (Photograph page 89), (**2**) 6 – 21 – 88 (Photograph page 139), (3) Perrins, C. 2003. The New Encyclopedia of Birds. Oxford University Press, UK (Fig. page 247), **HBW**: (**4**) 6 – 39 – 28 (Photograph page 476).

Fig. 8.35 Perrins, C. 2003. The New Encyclopedia of Birds. Oxford University Press, UK (Fig. page 180).

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9 The Symmetry of Birds Emerges as the Expression of an Uninterrupted Atomic Order

9.1 The Birds have Spoken

The initial section of this work called "To the Reader", finished with the sentence: "Now, let the birds speak for themselves". Their body traits spoke louder and in a more assertive way than any writer could convey. Their geometric "language" has no parallel in any other animal group.

But what about the bilateral symmetry of a bird? From where does it come? And how is it related to the geometric figures?

Moreover, how deep goes this order, so patent at the body level? And how general is it?

Information is already available that furnishes answers to these questions indicating that order is found at every level which has been carefully investigated by using the latest tools available to molecular biology.

9.2 The Avian Bilateral Symmetry and its Internal Asymmetry

So far we have not considered one of the central features of the avian body—its bilateral symmetry.

Symmetries are an integral part of geometry. The two cannot be separated.

Symmetry is defined as the "Similarity of form or arrangement on either side of a dividing line or plane". "Thus a figure has symmetry with respect to a point called the center of symmetry or with respect to a line called the axis of symmetry" (Webster 1976). This relationship to points, lines and planes makes it inseparable from geometry.

The bilateral symmetry is easily obtained, by dividing a circle into two parts, by drawing its diameter—two half circles are formed that create a figure with a bilateral symmetry. If instead a circle is divided, by four equidistant diameters, it produces a figure with a radial symmetry composed of eight sections. The birds, like all other vertebrates, are prisoners of a bilateral symmetry. The two main symmetries found in animals and plants are the bilateral and the radial (*e.g.* starfishes).

The external appearance of a bird is so symmetrical that bird specialists, when they draw or paint a species, represent the bird in profile. They take for granted that the other half is identical.

Externally birds have two eyes, two wings and two legs, but internally the avian body does not obey this bilateral symmetry. They have two kidneys and two testes but one heart, one liver and only one functional ovary.

This bilateral condition follows the head-tail axis (Fig. 7.7) which is the product of the morphogenic gradients consisting of RNAs, proteins and other molecules that existed already in the fertilized egg and which further direct the shape of the embryo (Gilbert 2000). The symmetry is not an abstract event but has a molecular basis.

But where, and when, did this symmetry originate, since it pervades the shape of most living organisms? How could it hold such a firm grip on their organization throughout millions of years of evolution?

9.3 Nothing Essentially New Arose at the Biological Level

The generally accepted view is that biological forms are new (McMenamin 1987). However, every level of evolution is dependent on the previous one. No form or function seems to arise de novo. It is becoming evident that every pattern and function is inherent to a previous one where it appears in a simpler state. The new level of evolution arises by the formation of combinations of the initial components. The examples are many. (1) Photosynthesis as it occurs in green plants is an elaborate process that involves specialized organelles in the cell, the chloroplasts. But photosynthesis can take place in living organisms under simpler conditions. Bacteria and blue-green algae do not contain chloroplasts but are none the less photosynthetic. Minerals are one step

A. Lima-de-Faria, *Molecular Geometry of Body Pattern in Birds*,
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earlier. Under ultraviolet light some iron salts dissolved in water can fix carbon dioxide into small organic molecules such as formic acid. This is one of the processes in photosynthesis. (2) The bacteria that live in the root nodules of leguminous plants can fix nitrogen. Sand-titanium dioxide can also fix nitrogen when some iron is added to this complex. Irradiation by sunlight of this mineral results in small amounts of nitrogen being converted into ammonia, a major chemical in the formation of amino acids (Cairns-Smith 1986). (3) Calvin (1983) has studied the transition from naturally occurring inorganic catalysts to biologically generated specific catalysts. The evolution of a catalyst, exemplified by the iron atom, can be traced from the inorganic aqueous ferric ion to the haem molecule, and finally to the enzyme catalase. Briefly, the iron atom alone rapidly oxidizes in the presence of water molecules and shows a variety of oxidation states. Haem is the nonamino acid portion of hemoglobin, a respiratory protein of the red blood cells, in which the iron atom combines with oxygen. Catalase occurs in blood and contains haematin. Its activity involves the oxidation and reduction of the iron in the molecule. The noteworthy aspect is that the aqueous ferric ion (Fe^{3+}) has a catalytic activity of 10^{-5}, whilst that of haem is 10^{-2} and of catalase 10^{5}. The haem group per se does not create any new function, but rather it exerts a more rapid potentiating action than pure iron. This also holds true for catalase since it produces a more rapid and greater action than that of haem. The combination of iron with amino acids results in a highly canalized event.

Similar considerations apply to numerous metals that are an integral part of the cell's most important macromolecules. These include: zinc (zinc finger proteins), cobalt (vitamin B_{12}), nickel, copper, molybdenum, vanadium, magnesium (chlorophyll). These minerals, or mineral components, are known to confer upon the proteins and other molecules their main functions. As a result many complex cellular processes have their origin in the simple properties of single atoms.

These successive chemical transformations, which are accompanied by many similar ones, support the contention that nothing essentially new arose as biological evolution emerged. What looks new to us are the specific combinations that seem unrelated only because they are so severely canalized into a narrow and limited number of atomic channels.

9.4 The Uninterrupted Transfer of Symmetries from Elementary Particles to Humans

Symmetries are a clear cut example of a phenomenon whose origins can be traced to a still earlier level of organization—that of the dawn of matter.

Symmetries are inherent to the organization of elementary particles since they already exist in the neutrino.

The discovery of many new elementary particles has led to the finding that neutrinos are either right-handed or left-handed and that their spin of rotation can be clockwise or counter-clockwise. Since atoms result from the combination of elementary particles, it is perhaps not surprising that the carbon atom is also either right-handed or left-handed. At the next level of organization this phenomenon is evident among the minerals: quartz crystals, for example, occur as left- and right-handed structures (Fig. 9.1).

As one reaches the cell, the proteins are constituted by amino acids, which also occur in left and right forms.

When performing a chemical synthesis in the laboratory a 50:50 mixture of right-handed and left-handed forms is usually produced. Though sugars and amino acids in solution occur in these two proportionate forms, this is not so in cells. One of the two tends to prevail. The sugars occurring in living organisms belong mainly to the right form, whereas the amino acids found in tissues are usually restricted to the left form. An interesting case is provided by DNA. Most DNAs are right-handed but at very high salt concentrations, they form left-handed helices. The backbone of the left-handed structure assumes a zigzag look, hence the term Z-DNA (Hill and Stollar 1983).

These macromolecules in turn build organs which are also left-handed and right-handed. This is already the case in plants in which cross sections of flowers show left- and right-handed divergence. As one reaches the invertebrates it could be ascertained that mollusc shells have also these two forms, whose origin can be traced to the earliest egg divisions of the animal. Moreover, humans do not fall outside this universal type of symmetry. One egg twins are usually most similar in morphological and functional characters but they may differ in the symmetry of their hair distribution and the use of their hands. One of them may have a left-handed form, while the other a right-handed one (Fig. 9.1).

The existence of right-handed and left-handed forms in higher organisms is taken to mean that they do not represent an accidental event. The continuity of the phenomenon from elementary particles, to atoms, to minerals, to molecules and to macromolecules implies the existence of an auto-evolutionary process that could not be erased and is sustained as far as the human species (Lima-de-Faria 1988).

Besides the right-handed and left-handed symmetry there is the bilateral symmetry which was just mentioned. This is equally powerful since no bird species (among the over 9,000) is known to depart from it. But the birds did not create it. It is a general feature of all vertebrates and goes back to the invertebrates and plants. It even extends to the one cell organisms—the protozoa. Still earlier, the bilateral symmetry is already present in the crystals of argirodite

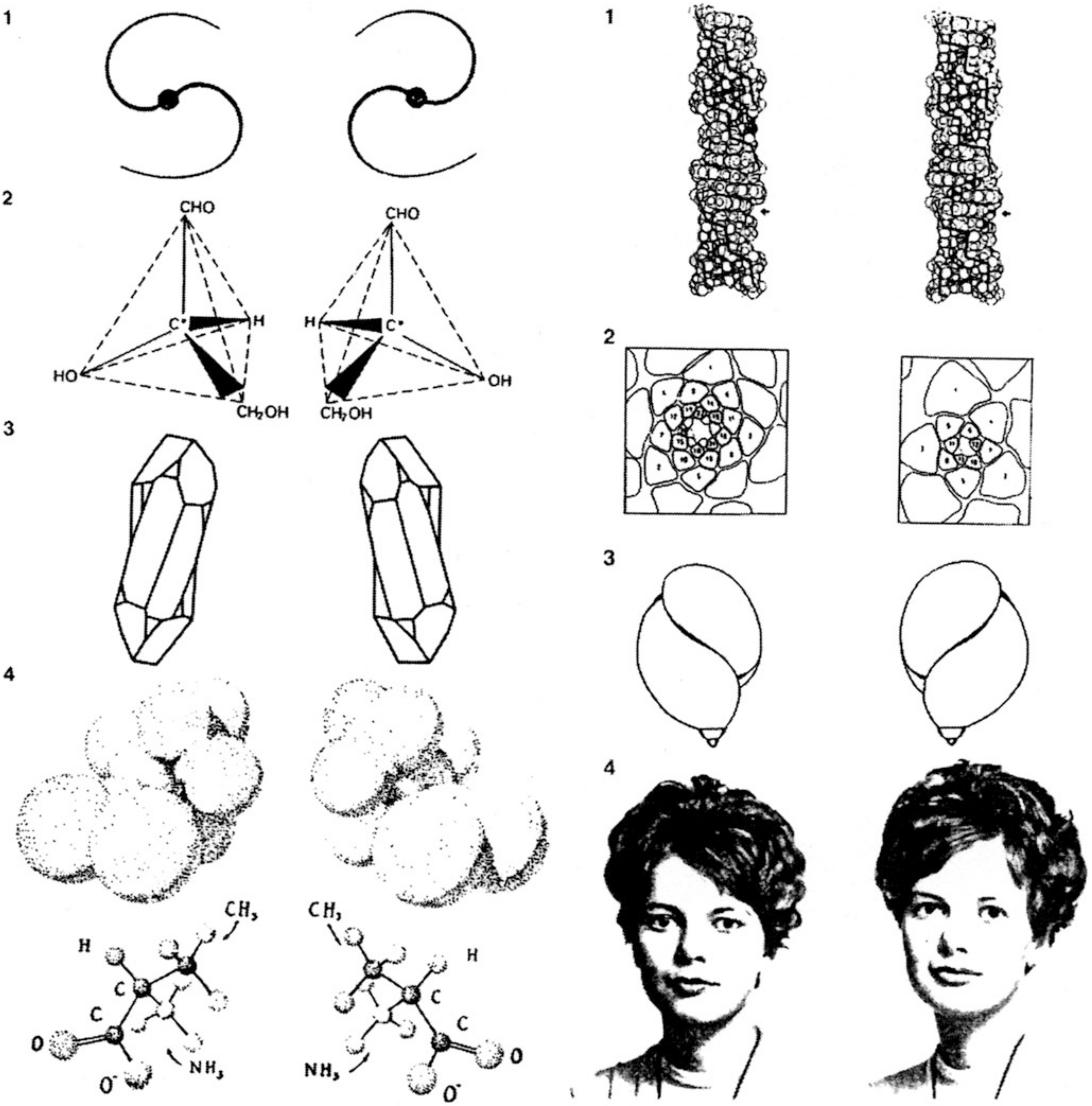

Fig. 9.1 The uninterrupted transfer of symmetries from the dawn of matter to today's organisms. Occurrence of left-handed and right-handed structures from galaxies to humans.
Left column (**1**) Spiral galaxies of the S-type (*left-handed*) and Z-type (*right-handed*). (**2**) Carbon atom bonds in left-handed and right-handed glyceraldehyde. (**3**) The mineral quartz in the left and right forms. (**4**) The amino acid alanine in the left and right form. *Right column* (**1**) DNA in its left (Z configuration) and right forms. (**2**) Sections through plant shoots (conifer *Araucaria excelsa*) showing spiral divergence left- and right-handed. (**3**) Shells of the snail *Limnaea* showing left and right orientation. (**4**) The identical twins Monica and Gerd. Monica is left-handed and has the forelock to the right. Gerd is right-handed and has the forelock to the left. They are mirror images of each other

(Ag_8GeS_6) and calcite ($CaCO_3$). Moving to the elementary particles, one finds that mesons are formed by quark-antiquark pairs in which symmetry changes are involved (Mulvey 1979). Again, another type of symmetry has its roots at the mineral level and has reached the human body in an unaltered state (Lima-de-Faria 1998a, b).

9.5 DNA Knows Nothing about Symmetries and did not Seem to have been Able to Create Novel Ones

The symmetries in living organisms are neither created by the bases and the sugars that build the DNA molecule nor by the phosphorous backbone of this macromolecule. The genetic code does not contain direct information for the symmetries of living structures. For this reason it is not able, by itself, to dictate symmetries.

It may be recalled that the message of the code is restricted to information leading to the building of nucleotides and of single amino acids. The reading occurs in groups of three nucleotides, called codons, each group representing an amino acid in the resulting protein. In some cases RNAs of different sizes are produced directly which do not give origin to proteins. There is no direct message for other types of molecules.

Moreover, it is not widely recognized that the cell can neither put together protons, neutrons and electrons, nor build a metal atom. Simply put, the iron of hemoglobin and the magnesium of chlorophyll do not derive from any information in the genetic code.

As remarked by Weinberg (1989) “Iron can be neither created nor destroyed by living cells.” This also applies to sulfur, copper, zinc and other elements. These elements are present in many proteins whose primary function depends on them. For example, zinc-containing proteins number more than 200. They constitute a family called zinc-finger proteins that function as transcription factors (Sluyser et al. 1993). The metals and other elements occurring in cells have their origin in the mineral world.

9.6 Mineral Structures, which have no Genes, Produce the Same Ordered Patterns Found in Living Organisms

The molecular processes involved in the patterns of living organisms become better elucidated by the finding that comparable patterns occur in atomic structures that lack genes. This resemblance is not accidental but turns out to have a common atomic basis.

The various symmetries, found in the body plan of animals and plants, occur in the crystals of minerals, which do not contain DNA or RNA (Fig. 9.2).

This situation exposes the limitations of the code and focuses on the need to consider pure atomic events acting at other levels. The sixfold symmetry found in water crystals is the sole result of the properties inherent to the hydrogen and oxygen atoms, that are the only components of snow crystals. These crystals are highly symmetrical six branched structures. The rays irradiate from a center and form constant angles of 60° with one another. As the crystal grows secondary branches arise. But these branches continue to form at 60° to the primary ones. The water molecules are able to ramify a third time, creating delicate tertiary branches. These continue to grow on the same plane, as the rest of the crystal, and form again at 60° angles. The dominant hexagonal symmetry pervades the whole water crystal imparting it with a unique regularity. Hence the sixfold symmetry, of a flower like that of the lily *Lilium bulbiferum*, or of the body of an invertebrate such as that of the starfish *Leptasterias hexactis*, existed before DNA arrived and can be produced by some of the simplest atoms: hydrogen and oxygen.

Another area that elucidates the atomic origin of symmetries is the spontaneous formation of atomic and molecular alternatives. Mineral chemistry already shows that symmetry transformations are the result of simple atomic processes. Graphite and diamond, provide a prime example of two minerals that consist solely of carbon atoms, yet have totally different properties and symmetries. Carbon is the hardest known mineral and crystallizes in octahedra or cubes, whereas graphite is one of the softest minerals and forms tabular crystals of hexagonal outline.

9.7 The Final Pattern of a Living Organism Appears to Be Dependent on Atomic Processes Far Removed from the Genetic Code

At present a number of laboratories participate in a large effort to discover the genes which control the ordered patterns present in the body of animals and plants. However, in the last years, several authors have become aware of the limitations of the gene analysis and have pointed out that the problem of embryonic morphogenesis, to be well understood, demands to be complemented with other sources of information.

Mutations in single genes, lead to drastic changes in the shape of the organism. Such a genetic effect has been demonstrated for the left-handed and right-handed forms of shells of the freshwater snail *Limnaea* (Fig. 9.1). The determination of one of the symmetry forms occurs at the second egg division and is due to a gene inherited maternally (Freeman and Lundelius 1982).

The flowers of the plant *Linaria vulgaris* have normally a bilateral symmetry and are one-spurred, but forms occur with fivefold radial symmetry being five-spurred. Belonging to the same family is *Antirrhinum majus*, in which the flowers have normally a bilateral symmetry. This plant has been studied extensively from the genetic point of view.

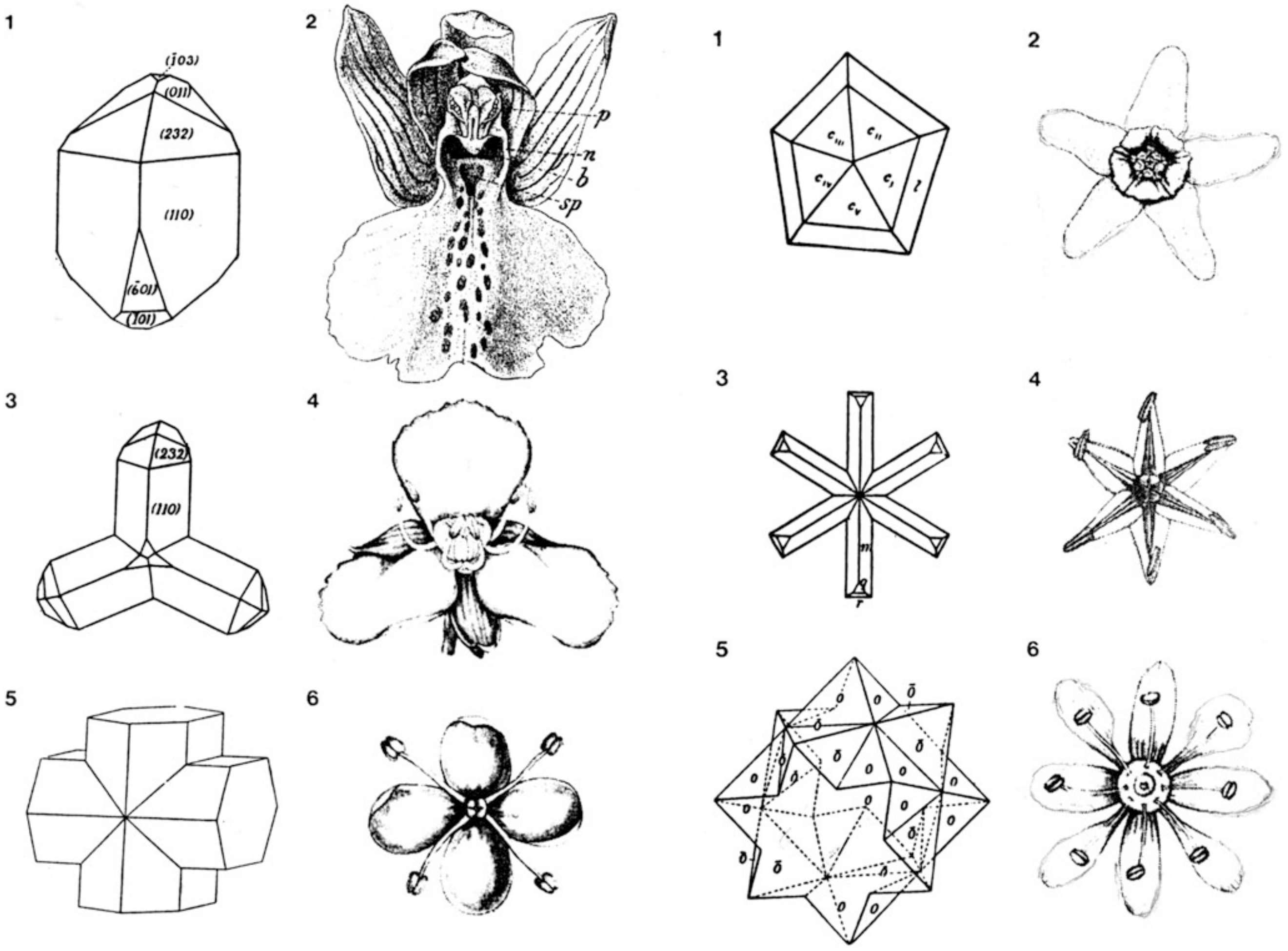

Fig. 9.2 The symmetries displayed by plants and animals existed in the minerals before DNA arrived. *Left part*—Incorporation of 2 to 4 components into minerals and flowers. (**1**) Single crystal of argirodite displaying bilateral symmetry (Ag_8GeS_6). (**2**) Flower of the orchid *Orchis Morio* whose symmetry is also bilateral. (**3**) Combination of three crystals around a center in argirodite. (**4**) Flower with three petals of *Alisma plantago aquatica*. (**5**) Staurolite ($FeAl_4Si_2O_{10}(OH)_2$) cruciform twin crystals. (**6**) Male flower of *Ilex aquifolium* with four petals and four stamens. *Right part*—Incorporation of 5 to 8 components into minerals and flowers. (**1**) The association of five crystals in marcasite (FeS_2). (**2**) Flower with five parts of *Cynanchum Vincetoxicum* (Family Asclepiadaceae). (**3**) Six crystals formed around a center in arsenopyrite (FeAsS). (**4**) Flower of *Scilla autumnalis* with six petals. (**5**) Association of crystals in galena (PbS) consisting of two octahedrons building 16 vertices. (**6**) Male flower of *Acer platanoides* with 16 parts (eight petals and eight stamens). Compare with Fig. 9.3

Flowers with a regular fivefold corolla arise by a mutation involving a single gene (Fig. 9.3).

Recently, the reversal of left-right forms in mice has been found to be related to a mutation of a gene that controls embryonic polarity (Yokoyama et al. 1993). The homeotic genes also produce regulatory proteins which are involved in the emergence of the bilateral symmetry in the chicken, the mouse and humans (Yokouchi et al. 1991).

Ryan et al. (1998) have studied at the molecular level the genes that participate in left-right symmetry in the chick, mouse and the toad *Xenopus*. They investigated the transcription factor *Pitx 2* which occurs in these species and that has a homologue in humans. Several signalling molecules disappear before morphological variants are visible in these embryos, but the expression of *Pitx 2* is maintained throughout embryogenesis directing the morphological movements that give rise to left-right structures. However, as these authors point out “much is yet to be learned about how multiple extracellular signals are transduced, propagated and maintained ultimately leading to visceral asymmetry”. It is at this final stage of molecular action that pure atomic events are expected to be the critical determinants (Lima-de-Faria 1997, 2008b).

These results, are bringing us closer to an understanding of the emergence of symmetries in living organisms. The gene is only the bearer, and the carrier, of the atomic order that already determined mineral symmetries.

The pattern of a living organism appears to be dependent on atomic processes that combine the information from the genetic code with that of the mineral atomic order. The

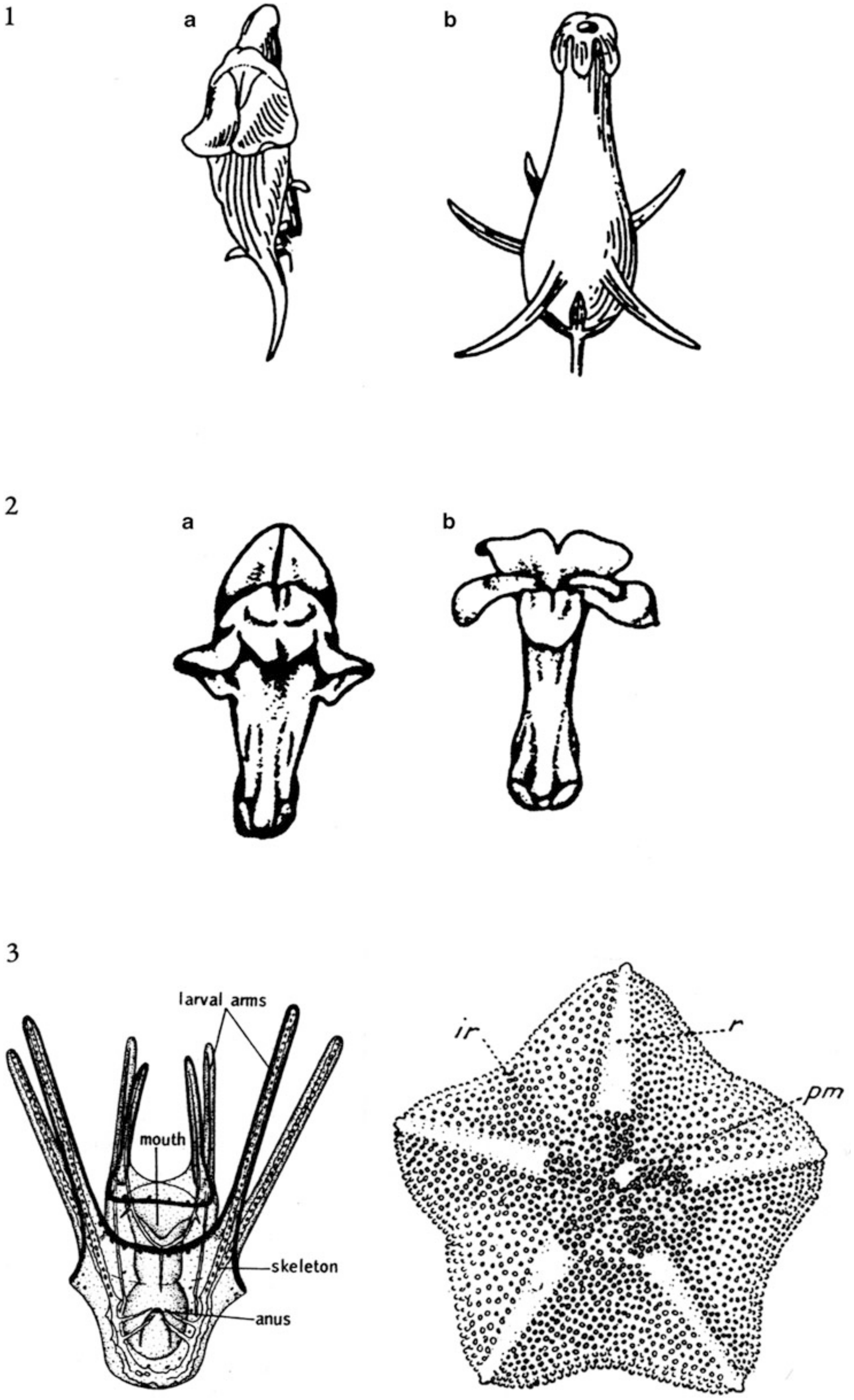

Fig. 9.3 **Symmetry changes in plants and animals**. (**1**) Normal bilateral one-spurred flower of *Linaria vulgaris* (common toadflax) (a) and the five-spurred mutant with fivefold symmetry which is seen also in the upper part of the flower (b). (**2**) Normal bilateral flower of *Antirrhinum majus* (snapdragon) (a) and the mutant with fivefold symmetry (b). (**3**) Most Echinoderm larvae have a bilateral symmetry whereas the adults display a fivefold radial symmetry. This means that the symmetry change takes place within the same individual. Left, larva of the sand dollar *Fibularia craniola*. Right, adult of the starfish *Palmipes membranaceus*. Compare with Fig. 9.2. Both the bilateral and the fivefold symmetries of animals are found in minerals

picture that emerges is that the chromosome's DNA and its proteins are mainly using the atomic processes that the minerals employed billions of years before the cell arose. This may be the reason why living organisms do not seem to have been able to create novel types of symmetries.

9.8 Pure Symmetries are Thought to have only Existed in the Very Beginning of the Universe

In Nature we never see perfect symmetries but only approximations. Modern physics has an explanation for this phenomenon. According to Pagels (1982), extreme symmetry and extreme simplicity become only evident at ultrahigh energies. As Pagels points out, "all the interactions we see in the present world are the asymmetrical remnant of a once perfectly symmetrical world". This symmetrical world occurs only at very high energies: so high that the only occasion at which they existed was in the first nanoseconds at the origin of the universe.

What remains as a source of bewilderment is that throughout the evolution of matter biological symmetries were not eliminated but persisted apparently intact. All plants and all animals, including humans, are shaped following a basic type of symmetry that prevailed since the first elementary particles were formed. It is to be noted that this symmetry is never total, humans have two lungs and two testes but only one heart and one liver. Besides one's left eye is not exactly alike one's right eye, the same is the case with a right or a left hand. Within the dominating symmetry there is place for a local asymmetry.

Again, permanence dominated at the same time that it allowed variation displaying an elusive frame.

Sources of Figures

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Fig. 9.3 Original plate. (**1**) and (**2**) Gustafsson, Å. 1979. Linnaeus' peloria: the history of a monster. Theor. Appl. Genet. 54: 241–248 (Fig. 2 page 243, Fig. 4 page 245), (**3**) (**Left**) Barnes, R.D. 1980. Invertebrate Zoology. Saunders College, Philadelphia, U.S.A. (Fig. 19–48 page 979), (**3**) (**Right**) Yung, E. 1920. Traité de Zoologie des Animaux Invertébrés. Edition Atar, Paris, France (Fig. 163 page 146).

Order is Present at Every Level But is not Total 10

10.1 The Genetic Code and the Translation Apparatus have Evolved in an Ordered Way

The genetic code is the molecular system by which the information present in DNA is correctly transformed into that of proteins. Groups of three nucleotides in DNA specify the amino acid sequence of the proteins.

As Bacher et al. (2004) point out: "Although the genetic code was discovered some 40—odd years ago, there are still numerous questions as to how it arose and evolved." Initially it was considered by F. Crick a "frozen accident," but soon it was found to have evolved leading to several examples of altered forms, such as in mitochondria. Studying the relationships between amino acids and nucleotides Lacey et al. (1993) concluded that "the genetic coding system is certainly not random; rather it appears to be based on character relationships between amino acids and their anticodon nucleotides." The same view was recently expressed by Itzkovitz and Alon (2007) who stated, on the same grounds, that: "The genetic code has been shown to be nonrandom."

The translation apparatus, by which the information in DNA is passed to RNA and subsequently leads to protein assembly, has also had its own evolution. According to Liljas (2004) it started with an "early RNA world" in which the central components were all RNA molecules that later evolved to produce the different types of known RNAs and proteins.

10.2 The Chromosome Maintains its Original Information by a Series of Efficient Repair Mechanisms

Repair mechanisms are at the basis of chromosome and cell order. T.A. Brown (1999) puts it in clear language: "In view of the thousands of damage events that genomes suffer every day, coupled with the errors that occur when the genome replicates, it is essential that cells possess efficient repair systems. Without these repair systems a genome would not be able to maintain its essential cellular functions for more than a few hours before key genes became inactivated by DNA damage. Similarly, cell lineages would accumulate replication errors at such a rate that their genomes would become dysfunctional after a few cell divisions."

The chromosome has created, not one, but a series of mechanisms, by which it has ensured the maintenance of its original DNA pattern. However, it did not confine its intervention to this level. The DNA message, in the form of RNA, could easily distort the primary script. The final protein, obtained from this RNA, could also misrepresent the RNA message. The result is that the chromosome extended the repair and adjusting capacity to the RNA and protein levels, imposing strict order at every functional step.

There are different categories of DNA repair: (1) Direct repair converts each damaged nucleotide to its original structure. (2) Base excision is obtained by its removal and resynthesis of the DNA at this site. A similar mechanism does not remove the damaged base but acts on larger areas of DNA. (3) Mismatch repair corrects errors of replication by excising a piece of single-stranded DNA, containing the distorted sequence, and filling in the resulting gap. (4) Non-homologous end-joining leads to the repair of double-strand breaks (Brown 2007).

DNA polymerases participate in the proof-reading mechanism that ensures that DNA replication occurs with a minimum of mistakes. Proof-reading is the activity possessed by some of these enzymes which enables them to replace a misincorporated nucleotide during DNA copying. The fidelity of copying is of the order of one error in every 10^9 base pair replications. A protein, called p53, that exerts a tumor-suppressing function, has been found to facilitate DNA repair (Tanaka et al. 2000; Lozano and Elledge 2000). A highly conserved pathway to repair DNA is the base excision repair pathway which is known to be found from bacteria to humans (Robertson et al. 2009).

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10.3 The Integrity of RNA is Maintained by the Elimination of Defective Molecules

RNA is essential for most basic cellular processes. It participates in key events, such as protein synthesis, which demands the collaboration of messenger RNAs, ribosomal RNAs and transfer RNAs. Moreover, a battery of small RNAs, which are too small to code for proteins, regulate a variety of other cellular processes.

The integrity of RNA must be maintained at all costs, otherwise there would be no cell that could function properly.

RNA surveillance is actually a form of quality control of the RNA. Once this molecule has been made, it moves across the nuclear sap to the pores of the nuclear envelope arriving finally in the cytoplasm. This is a long journey filled with difficulties.

The scrutinizing system consists of molecular assemblies that specifically control the quality of the messenger RNAs and it involves numerous steps, both inside and outside the nucleus (Culbertson 1999).

There is a first quality control at the level of the DNA which is performed by ten proteins that mediate its decay. In this process the messenger RNAs are monitored for errors that arise during gene expression. Base substitutions often cause chain termination. This results in the building of nonsense RNAs. These RNAs, which code for protein fragments, are recognized and eliminated (Lykke-Andersen et al. 2001).

The next step is the export of the messenger RNA. This is mediated by a transport receptor that binds to the messenger by means of adaptor proteins. This RNA-protein complex moves to the pores of the nuclear envelope. Here it interacts with a second type of proteins which are at the gates of the membrane. The messenger RNA assembly is then subjected to quality control by a nuclear surveillance mechanism so that aberrantly assembled RNAs are degraded before they are delivered to the cytoplasm (Cole 2001; Stutz and Izauarralde 2003) (Fig. 10.1).

A third quality control takes place when the RNA arrives at the cytoplasm where several types of mechanisms dispose of it or degrade aberrant molecules (Fasken and Corbett 2005).

Not only the messenger RNA, but other types of RNAs, such as non-coding RNAs, have their nuclear export controlled by association with specific proteins during their journey to the cytoplasm (Cullen 2003).

The final result is that defective proteins become a rarity. These molecular mechanisms, which impose functional coherence, have been conserved from yeast to humans (Vinciguerra and Stutz 2004).

10.4 Correction and Repair of Proteins

Molecular chaperones facilitate the correct assembly of proteins. To be noted is that they are not components of the assembled structures, i.e. they only help and supervise. Moreover, they do not convey information either for polypeptide folding or for the assembly of multiple polypeptides into a single protein. Instead, they function by binding to specific structural features that are exposed only in the early stages of assembly. The main function of chemical chaperones is to inhibit unproductive assembly pathways that would lead to incorrect structures (Becker et al. 2003).

Ten years ago protein repair was considered plausible but had not yet been fully demonstrated. The last 5 years have seen the accumulation of data, originating from different laboratories, that turned it into a general phenomenon.

Heat shock proteins are a group of proteins present in all cells in all life forms. They are produced when a cell undergoes various types of environmental stresses such as heat, heavy metals, ultraviolet radiation and others. Experiments with bacteria and a long array of organisms including humans, disclosed that heat shock proteins are fundamental in intracellular protein repair and work by preventing protein aggregation and assisting denatured proteins to refold (Fig. 10.2) (Cakmak 2009).

In plants, like *Arabidopsis*, the formation of abnormal amino acid residues is a major source of spontaneous protein damage in cells. The protein *PIMT* (L-isoaspartyl methyltransferase) combats protein misfolding and in this way eliminates deleterious protein products (Ogé et al. 2008).

10.5 Hierarchical Determination of Molecular Transit in the Cell

No molecule enters the cell, or the nucleus, without being checked for its structure. Subsequently, following its admission, it is guided to the site where it will perform its chemical reaction. Besides, this process is hierachical. A plethora of diversified molecules participate in it but some have more to decide than others.

Transport of macromolecules between the nucleus and the cytoplasm is regulated by a whole “machinery” which directs this transit at three main different levels: (1) There is a permanent entry and exit of molecules from the nucleus across the nuclear pores. Specific cellular factors and macromolecular complexes regulate this bidirectional trafficking of RNA and protein cargoes. (2) Regulation is further accompanied by the modulation of the expression (or function) of single cargoes and transport receptors. (3) The final

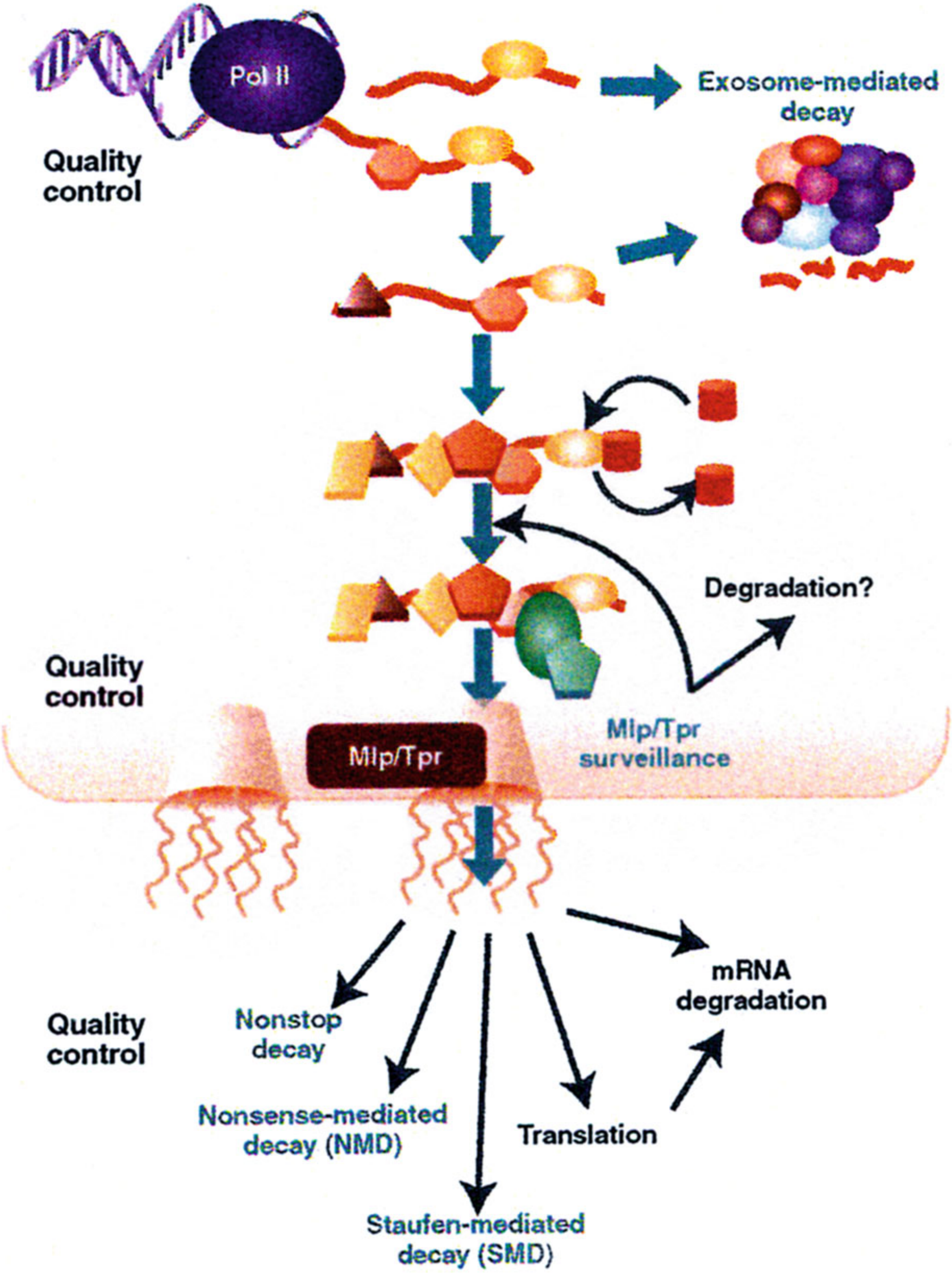

Fig. 10.1 **The export of RNAs is quality controlled**. The quality control of the coding messenger RNA occurs at three separate levels: (**1**) Immediately after transcription on the chromosome there is an "exosome"-mediated decay directed by several proteins (*top right*). (**2**) Later the RNA gets associated with another protein which directs it to the pores of the nuclear envelope, where a second quality control occurs (*middle bar*). (**3**) On arrival at the cytoplasm (lower part of figure) the RNA goes through a series of decay processes that dispose of aberrant molecules. Damaged molecules are excluded from translation into proteins

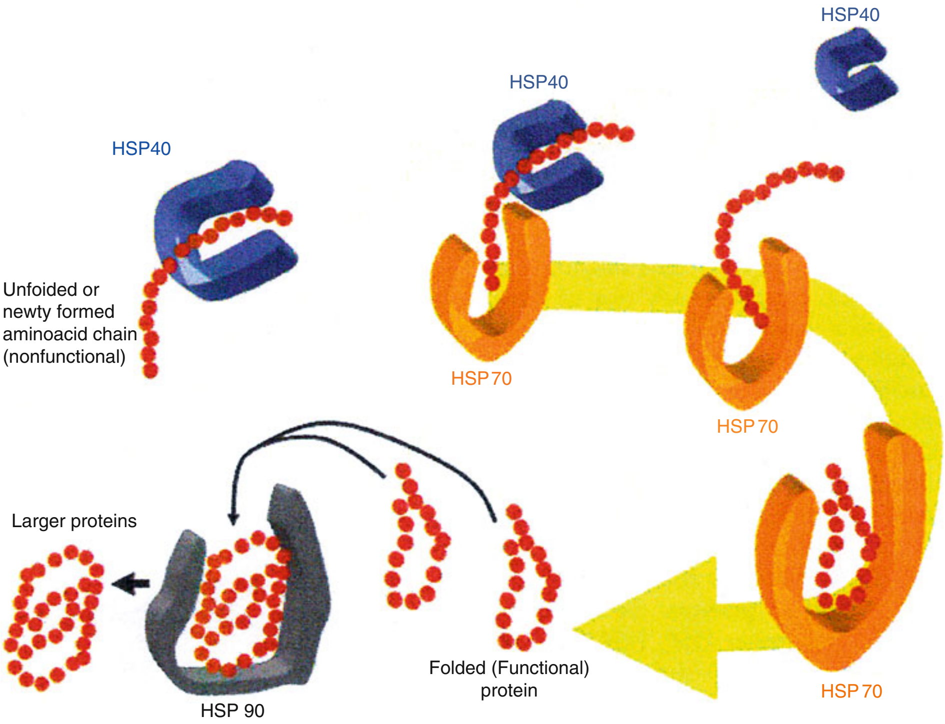

Fig. 10.2 **How a group of proteins activates others which were dormant**. The action of the *heat-shock proteins*: HSP40 (*blue*), HSP70 (*yellow*) and HSP90 (*black*), leads to the transformation of an unfolded protein (in the form of a newly translated amino acid chain represented by a string of small red circles), which is nonfunctional into a folded protein that is functional (*lower left corner*)

step is achieved by the cargo molecules displaying signals which are recognized by the transport receptors. Transport receptors are central to nuclear import and export since they deliver the RNAs and proteins to their exact destination in the cell. The result being a highly ordered transit in both directions (Fig. 10.3) (Terry et al. 2007).

The trafficking of molecules in the cell, which before was described as a most chaotic process in which the molecules moved erratically in all kinds of directions, turns out to be guided and controlled at every level.

10.6 Nuclear Architecture Regulates Gene Expression

The human genome contains about 21,000 genes located in about 3.2 billion base pairs of DNA which are compacted 400,000-fold fitting within a nuclear volume of about 1,000 cubic microns. This means that the genetic information is partly sequestered during this extreme packaging.

DNA replication, DNA repair and transcription are dependent on how much of the DNA is accessible at a given site in the nucleus. The nuclear architecture is dynamic resulting in the building of compartments and the modification of the spatial arrangement of DNA sequences, especially their association with nuclear pores. The accessibility of genes is highly regulated by this architecture having immediate consequences on gene expression (Schneider and Grosschedl 2007).

10.7 Cell Division and Chromosome Movements are Orchestrated by Proteins

The maintenance of order throughout the untold number of cell divisions, is the result of inherent mechanisms that correct errors and direct with precision the movement of organelles.

If the chromosomes move in an improper way during cell division, the cell resorts to mechanisms that correct this disturbance. For accurate segregation of chromosomes, microtubule fibers must attach to centromeres, which are directed to opposite poles of the mitotic apparatus. The enzyme Aurora kinase ensures that the chromosome attaches properly to the spindle fibers. If this enzyme is inhibited, chromosomes fail to orient in the correct way (Lampson et al. 2004). Hence, the cell produces specific enzymes that ensure that chromosomes move orderly (Fig. 10.4(1)).

Human cancer could be much more frequent than it actually happens to be. Since birth, the renewal of the cell population in our body is prone to errors that could lead to many cancers. In humans, as many as 10^{11} cells die in each

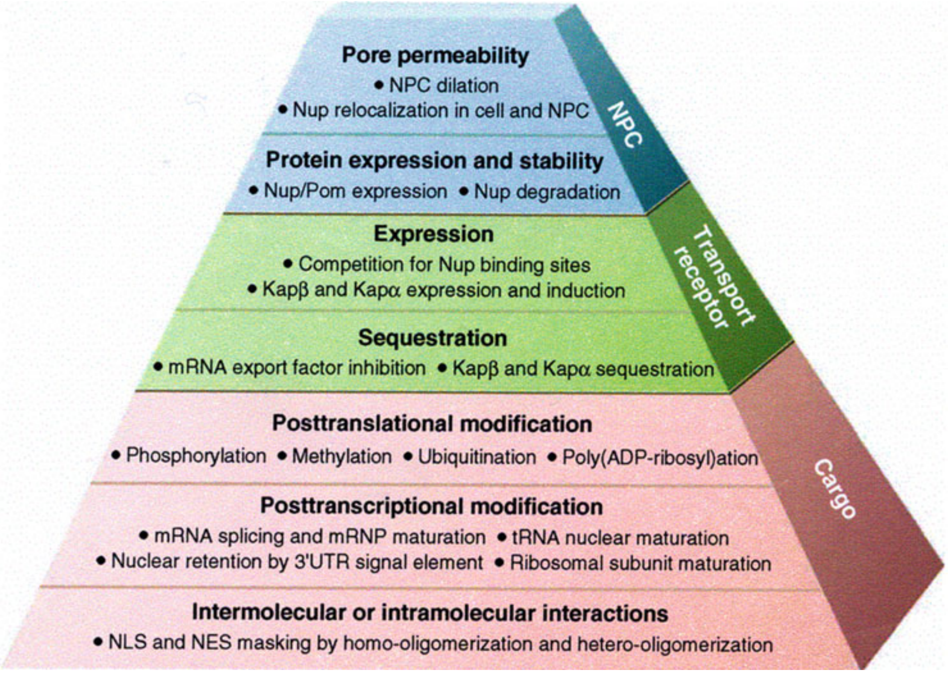

Fig. 10.3 Nucleocytoplasmic transport of macromolecules is regulated at three levels: pore permeability, transport receptors, and individual cargoes (*blue*, *green* and *red* sections of the pyramid). The pyramid shows the hierarchy of levels used to regulate nucleocytoplasmic transport, with control at higher levels (*right side*) having broader impacts on trafficking. Each level is controlled by multiple mechanisms. *NPC* nuclear pore complex, *Nup* elements that contribute to the nuclear pore architecture, *Poms* pore membrane proteins, *Kap beta* and *Kap alfa* transport receptors, *mRNA* messenger RNA, *tRNA* transfer RNA, *NLS* nuclear import sequences, *NES* nuclear export sequences

adult, each day, and are replaced by other cells (Gilbert 2000). What an opportunity for total confusion.

One of the reasons why this does not happen "is that normal cells can somehow perceive and arrest aberrant cycles of cell division that are triggered by cancer-promoting (oncogenic) stimuli" (Venkitaraman 2005). Early cancer lesions result in aberrations in DNA replication. This event triggers the activation of a cellular DNA-damage response (DDR) which arrests cell proliferation or causes cell death inhibiting cancer development (Gorgoulis et al. 2005; Bartkova et al. 2005) (Fig. 10.4(2)).

Recently, three independent groups of researchers concentrated on elucidating the orchestration of cell division that leads to correct segregation of newly replicated chromosomes in yeast and human cells.

The *chromosomal passenger complex* is the main actor in a process where several proteins are involved. It is called "passenger" because it changes its location. Initially it is found on chromosome arms at the beginning of cell division, but later concentrates at the inner part of the centromere—the region that leads the chromosomes during their movements. This complex consists of four proteins the most important being *Aurora B* and *Survinin*.

Aurora B phosphorylates *histone H3* which is regularly associated with the chromosomal DNA. This occurs with the intervention of another protein *Haspin*. As a result the chromosomal passenger complex gets located at centromeres allowing the correct movement of chromosomes to opposite poles and an ensuing normal cell division (Wang et al. 2010; Kelly et al. 2010; Yamagishi et al. 2010).

10.8 The Unexpected Regular Arrangement of Chromosomes in the Sperm

For a long time an unanswered question in cell research was whether chromosomes were arranged randomly in sperm or whether they occupied specific positions.

Modern methods of chromosome painting combine fluorescent light microscopy with *in situ* hybridization, to mark repeated or unique DNA sequences, whose position on the chromosomes is known. This procedure gives each chromosome of the complement a different colour allowing to identify them with accuracy during cell division or in the heads of sperm.

Monotremes are unique among mammals in laying eggs. Their large sperm heads are suitable for a study of chromosome arrangement along the length of the sperm.

All species of monotremes share a karyotype comprising six large chromosome pairs and a number of small chromosomes that cannot be easily identified due to their size. Watson et al. (1996) used chromosome painting, accompanied by radioactive *in situ* hybridization, to map

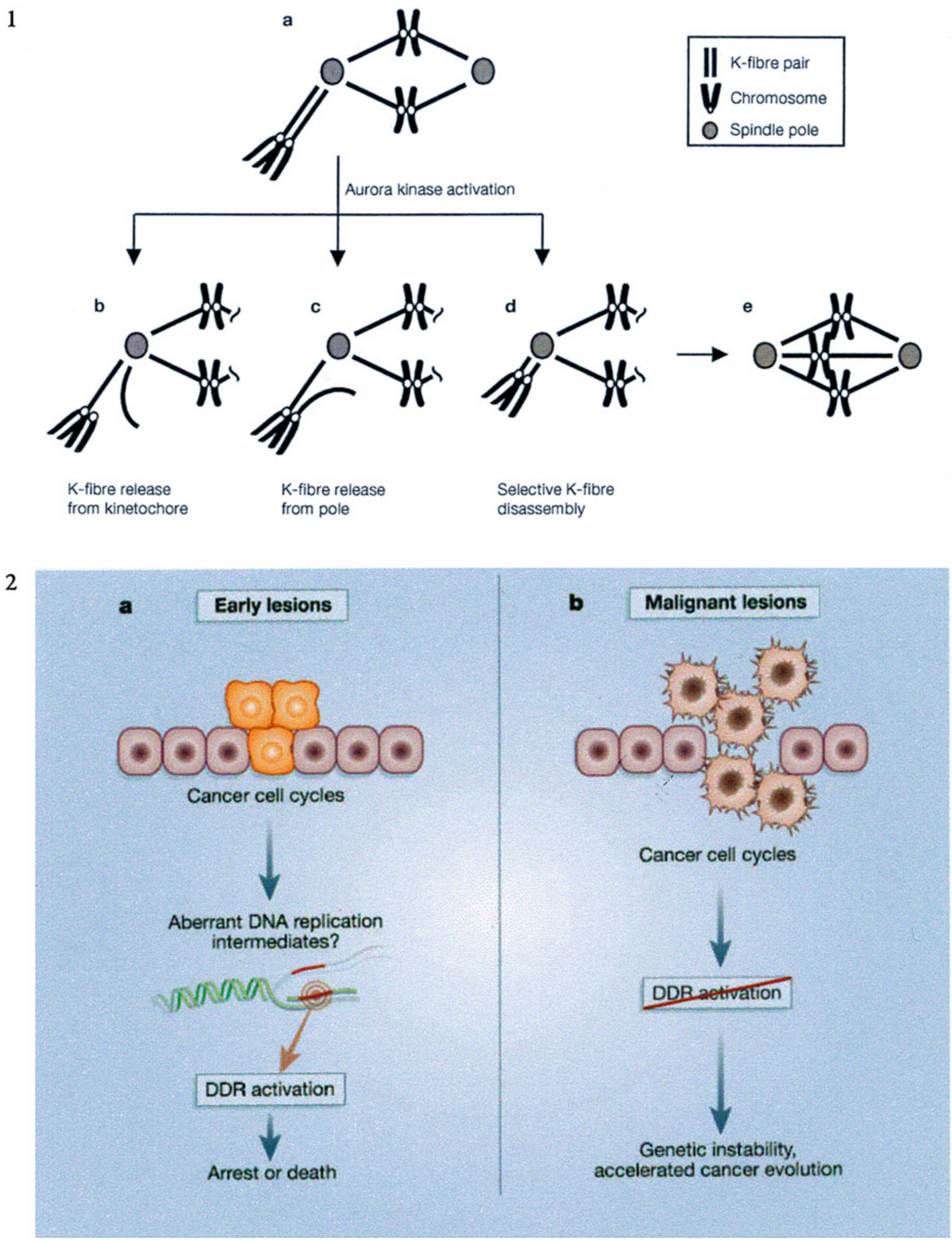

Fig. 10.4 **(1) Mechanisms which correct chromosome mal-orientations during cell division**. Each chromosome becomes divided into two chromatids which will move in opposite directions to daughter cells. These chromatids may be prone to errors in spindle attachment during their separation at cell division. Activation of the enzyme *Aurora* kinase is considered to be responsible for ensuring accurate segregation. If the two chromatids happen to be maloriented being connected to the same pole by kinetochore or centromere (K) fibres, these are disrupted by *Aurora* kinase activation which ensures a stepwise perfect orientation. (**a**) Both chromatids happened to be erroneously attached to the same pole by fibres. (**b**) K-fibre is released from the centromere. (**c**) K-fibre is released from pole. (**d**) Selective K-fibre disassembly. (**e**) Finally the chromatids are aligned with the others ensuring a correct separation. **(2) Sensing and stopping wayward cell divisions**. (**a**) In early cancerous lesions, cell-divisions driven by oncogenic stimuli, result in aberrations in DNA replication. This triggers the activation of the cellular DNA-damage response (DDR). The mechanism arrests cell proliferation or causes cell death. (**b**). On the contrary the progression of malignancy may be accompanied by DDR inactivation which would accelerate cancer evolution and tumor growth

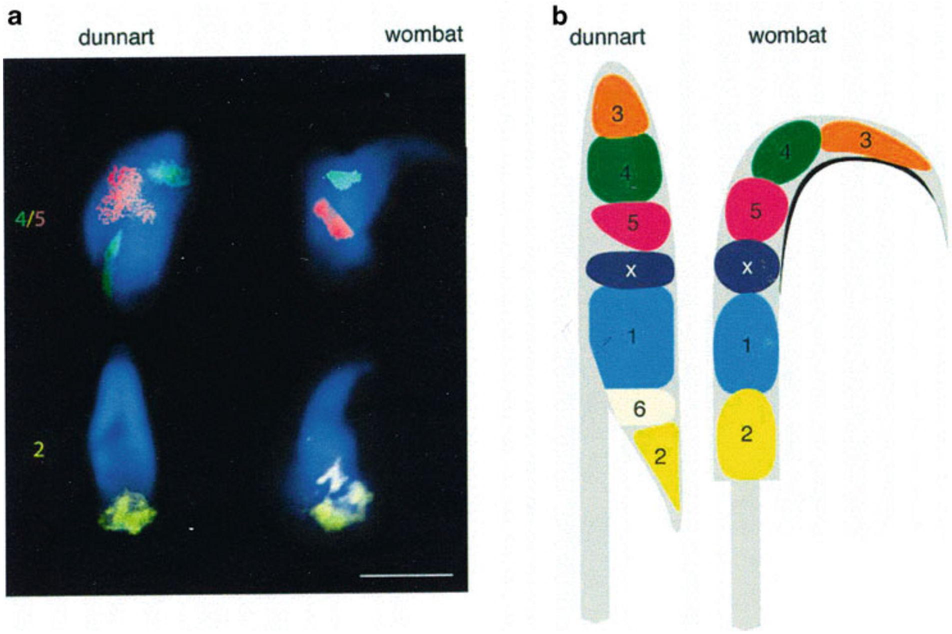

Fig. 10.5 **Ordered position of chromosomes in marsupial sperm.** (**a**) Homology of position is seen by double and single chromosome painting with probes to chromosome 4 (*green*), 5 (*pink*) and 2 (*yellow*) in dunnart and wombat sperm. (**b**) Comparison of the positions of homologous chromosomes in the arrow-shaped dunnart and the hook-shaped wombat sperm nuclei. Wombat chromosome 6 could not be satisfactorily detected. Bar represents 5 μm

specific genes and conserved DNA sequences. They found that the arrangement of the chromosome ends in sperm was "strikingly nonrandom." Chromosomes were arranged tandemly and in a defined order in the sperm nucleus. More astounding was that the order of the chromosomes was preserved in species separated by millions of years of evolution. Using the same chromosome painting technology Greaves et al. (2003) found that the position of homologous chromosomes was conserved in sperm of two marsupial species that diverged 50–60 million years ago—the dunnart and the wombat. The wombat belongs to a different marsupial order from the dunnart but its chromosome set is virtually identical. The order of chromosomes was absolutely conserved in both species (Fig. 10.5). Chromosomes 3, 4 and 5 were located in the anterior region of the sperm head. Chromosomes 1 and 2 lay in the posterior region, the X chromosome being located between the anterior and posterior groups. The chromosome order in both species was 3-4-5-X-1-(6)-2. Chromosome 6 could be identified with accuracy only in the dunnart.

A similar study in bird sperm confronted difficulties, due to the presence of many minute chromosomes that produced a blurry picture, but the authors could conclude that microchromosomes tended to lie in the centre of the sperm and macrochromosomes toward the extremities (Greaves et al. 2003). In humans and other primates, chromosomes 18 and 19, as well as the X, occupy conserved positions in the cell nucleus of these species (Tanabe et al. 2002).

When molecular probes were used that allowed the exact identification of single chromosomes, their ordered arrangement became evident as well as the maintenance of their positions independently of millions of years of evolution.

10.9 Previously Despised MicroRNAs and Proteins Coordinate Embryonic Morphogenesis

The cell's small RNAs were despised. They were too small to produce a protein and as a consequence were considered of no interest. It turns out now that they are among the keys to the order of gene function and that they decide the fate of the messenger RNAs that are stored in the cell. They have been called "short interfering RNAs" and "micro RNAs." Their regulatory role is known as "RNA interference."

The micro RNAs may have a length of 21–22 nucleotides and arise from non-protein coding genes (Carrington and Ambros 2003; Denli and Hannon 2003). They regulate gene expression by binding to complementary messenger RNAs. This is possible because the small RNAs have the same base sequences as their target messengers. This sequence recognition triggers: (1) messenger RNA elimination and (2) the arrest of messenger RNA translation into protein. These events are critical in shaping the road map of the emerging embryo (Matzke and Matzke 2003).

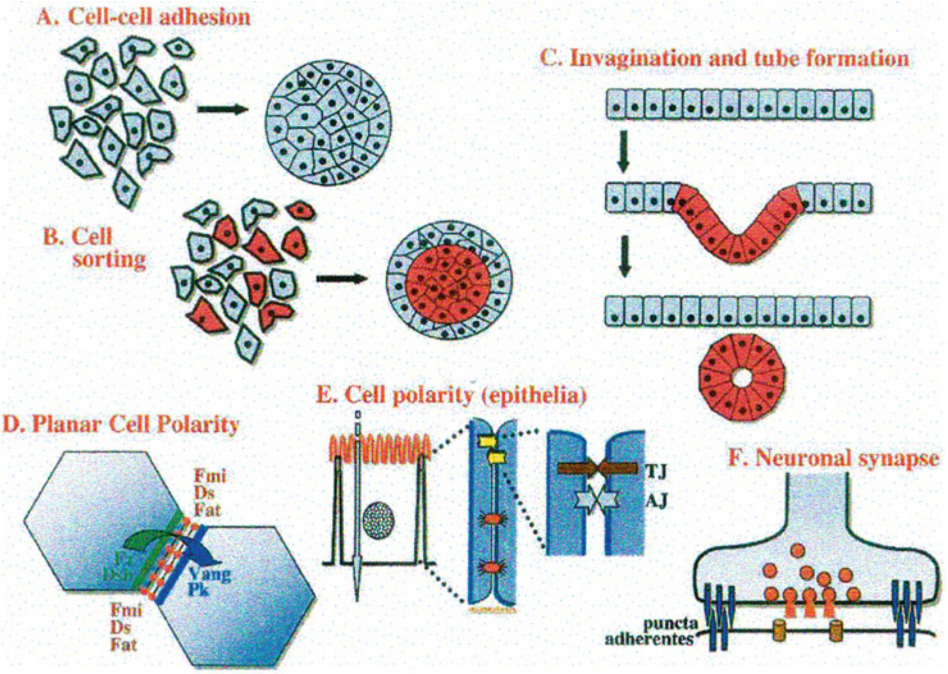

Fig. 10.6 **The diversified roles of cadherins during embryonic development. The dramatic transformations that change an embryo into a newborn were most difficult to explain, because they were so different and so innovative. Suddenly they turn out to be directed by a family of proteins**. The morphogenetic capacity of the cadherins includes: (**A**) Cell-cell adhesion. (**B**) Sorting out of mixed cell populations. (**C**) Coordination of cell movements leading to invagination and tube formation. (**D**) Planar cell polarity. (**E**) Activation of cell polarity in epithelia, such as skin. (**F**) Last but not least, they are implicated in neuronal synapse, a critical event in locating the millions of brain cells in their correct positions. These are crucial transformation steps in the embryo for which before there was no known molecular mechanism

As development progresses drastic morphological changes occur in the embryo which give it its novel shape. The mechanisms that guide these reshapings are now understood. The proteins called cadherins have been found to have a function, not limited to cell adhesion, but which extends to multiple aspects of tissue morphogenesis. These include: cell recognition and sorting out, boundary formation, coordinated cell movements, induction and maintenance of cell polarity. Such diversified activities are carried out by over 100 members of the cadherin family (Halbleib and Nelson 2006) (Fig. 10.6).

10.10 Directed Mutations Advantageous to the Organism are no Longer Disputed

The controversy over directed mutation lasted until 2003 when it was finally realized that it had mainly historical interest. The three previous assumptions that mutations: (1) occur at random, (2) are independent of environment and (3) appear during replication at a constant rate, had to be re-examined (Brisson 2003).

In 1943 Luria and Delbrück planned an experiment to test the occurrence of mutation in bacteria. During World War II, and later on, to think in terms of randomness was in fashion. They submitted cultures of the bacterium *E. coli* to the action of the bacterial virus T1. Most cells died but some survived the infection. Mutations that were resistant to the virus were considered to occur randomly at various times. Their conclusion was cited as the proof of mutation's randomness.

It was not until 1988 that the experiment was repeated, but now looking for the possibility of another type of response from the same bacterium (Cairns et al. 1988). A strain of *E. coli* was found which could not use the sugar lactose as an energy source. When the cells were plated on a medium containing lactose as the only sugar, the number of mutants that arose enabling the bacteria to use the sugar, became suddenly significantly high. The cells responded to the adverse medium by creating mutations in a direction that allowed them to survive. Mutation was not random. Numerous attempts have been made to discover flaws in this experiment, without success and similar results have been obtained with other bacteria (Brown 2007).

Two novel experiments confirm and enlarge *Cairns*' results.

Zhang and Saier (2009) described a new mechanism of directed mutation mediated by the transposon *IS5* in *Escherichia coli*. Transposons are elements capable of

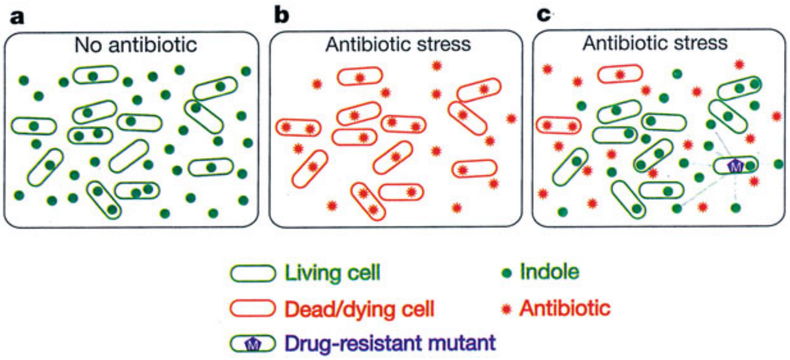

Fig. 10.7 **A population-based antibiotic-resistance mechanism**. A bacterial population is shown. (**a**) In the absence of antibiotic stress, wild-type cells naturally produce indole. (**b**) Under antibiotic stress, wild-type cells stop producing indole and eventually die. (**c**) When a drug-resistant mutant emerges, it is able to produce indole even under antibiotic stress. This indole allows the more vulnerable cells in the population to survive the antibiotic stress, by inducing various antibiotic-tolerance mechanisms, thereby boosting the survival capacity of the population

jumping from one site of a chromosome to another DNA segment activating or inactivating DNA sequences such as operons or single genes, when inserted into appropriate chromosomal loci. Transposon-mediated mutations occur under stress conditions (*e.g.* starvation). In *E. coli* the mutants carrying the *Crp* deletion mutate specifically to glycerol utilization at rates that are enhanced by glycerol. In the absence of *Crp* the promoter can be activated by the transposon *IS5* when this genetic element inserts upstream of the promoter, leading to high-level expression of the activated operon. This insertion event is a genuine example of non-random mutation because transposon intervention is directed to a specific operon and occurs with a tenfold higher frequency when glycerol is present. The result is that it allows benefit to the organism.

Another experiment is equally elucidating.

No one seems to have heard before of “Bacterial Charity” but that is the title of the work of Lee et al. (2010). Population dynamics in *E. coli*, during the development of antibiotic-resistant strains, revealed the following. When the cells faced increasing levels of antibiotics the vast majority of isolates were less resistant than the population as a whole. The few highly resistant mutants improved the survival of the population’s less resistant individuals by producing a signaling molecule generated by actively growing unstressed cells. Indole production by bacteria serves to turn on drug efflux cell pumps and other protective mechanisms. The bacterial altruism was made possible by drug resistant mutations capable of indole production. The result was that a small number of resistant mutants provided protection to other more vulnerable individuals, enhancing the survival capacity of the overall population. As Youk and Oudenaarden (2010) commented, one is dealing with “A charitable deed by a few cells in a bacterial culture” (Fig. 10.7).

10.11 Adaptation in Higher Organisms – One of the Black Boxes of Genetics

The results in bacteria lead us to the problem of adaptation in higher organisms. This subject has not been treated in this work and it was not even mentioned in the preceding pages.

The reason is that on one hand, adaptation in animals and plants was recognized long ago as a most important phenomenon. On the other hand, this subject has been the source of much controversy due to the lack of a mechanism, or mechanisms, responsible for its emergence.

We are in a situation comparable to that of embryonic development, which was a black box before molecular cytogenetics took over the problem. What earlier was inexplicable became understood in terms of gene functions and molecular cascades.

Perrins (2003) expresses the traditional view on this subject when he calls a section of his work: “Adaptations for Swimming.” Many aquatic and semi-aquatic birds have webbed feet in which membranes extend between the toes. These allow better swimming or walking in water. However, other birds that live in wetlands, such as the Painted Snipes (*e.g. Rostratula benghalensis*) have free toes without traces of webbing.

At present it is not known how the occurrence of water in the environment influences the atomic evolution of DNA.

Water molecules are known for their polarity and hydrogen-bonding capabilities. Water diminishes the bonding interactions between other molecules by a factor of 80 (Stryer 1981). This event affects the hydrogen-bonds of DNA during their binding with other molecules—a critical genetic event. Such a situation is of particular significance because the DNA molecule has not a single conformation but can occur in the: *A*, *B*, *Z* and other forms, which are associated with different degrees of water concentration in the medium. These various

DNA conformations lead to different DNA-protein interactions with immediate genetic consequences (Brown 1999).

Adaptation remains a virgin area when it comes to the understanding of the physico-chemical mechanisms that participate in its emergence.

10.12 Order is Never Total – Yet "Errors" are of Particular Configurations Deviating only Slightly from the Initial Canalization

Although not usually mentioned, but most significant, is that when the copying is not an exact replica of the original DNA sequence, not all kinds of alternatives are possible as it would be in a random situation. In the so called "errors," bases are not substituted by all possible kinds of chemicals available in the cell. Usually only bases that have the same chemical formula but differ in the position of one or a few atoms within the molecule, are incorporated during replication. Well-known base analogues are 5-bromouracil and 2-aminopurine which can be easily incorporated into DNA. Thus, there are chemical constraints on the alternatives accepted. The "errors" are only of a particular type and should instead be called alternatives.

Surveying DNA replication Strachan and Read (2000) conclude that "The frequency of individual base substitutions is nonrandom" and also that "The location of base substitutions in coding DNA is nonrandom." This means that even "genetic noise" is not of all possible kinds and as a consequence the original molecular canalization is maintained.

In evolution what counted was the "genetic music" which resulted in variation that maintained the harmony of chromosome organization. This resulted in the emergence of novel organisms that maintained a coherent structure and function.

If order had been too strict or total there would not have been evolution.

10.13 Without Atomic Order Any Molecular Edifice would have Collapsed

One is compelled to realize that it is extreme rigidity which has allowed variation. Without a firm order, functioning as a frame, any modification of structure or function would have led to the collapse of any non-living as well as living molecular edifice. Life would not even have reached the single cell stage.

This evidence is also to be found at the atom level. Before the experiments carried out by the physicist Niels Bohr (1885–1962) the negative electrons were assumed to be spread around the central positive atom nucleus. According to classic physics this system would be unstable and would disintegrate. *Bohr* suggested instead that the electrons moved around the nucleus in fixed concentric orbits, and that the electrons could only adopt multiples of a certain fixed energy value. Radiation was only emitted or absorbed when an electron jumped from one allowed orbit to another. Electrons could not move in all directions and could not occupy positions between the orbits. These constraints were soon confirmed by the study of the spectrum lines in different atoms. Moreover, of the many electrons located in concentric orbits around the atom nucleus it was only those of the outermost shell that determined the properties of each atom, and as a consequence decided its position in the Periodic Table of the Elements.

These two severe restrictions imposed an order that could not be erased and was found to be common to all known atoms (Greenwood and Earnshaw 1989; Masterton and Hurley 1993; Scerri 2007).

Thus, at the dawn of the organization of matter there is this initial rigidity that is perpetuated in every macromolecular configuration.

Even more significant are the recent experiments that reveal that there is an atomic memory. This was demonstrated by showing that atomic systems that lost their ordered state can be induced to recover their initial order. Experiments using coloured dyes in a viscous fluid and employing glycerin placed in a magnetic field led to the conclusion that the samples retained the memory of their initial state (Brewer and Hahn 1984).

Hence, evolution is not primarily based on variation—which has been the main preoccupation of evolutionists—but on the constraints that have led to permanence. The main task that lies ahead, is to combine the study of genetic alternatives, with the discovery of the mechanisms behind this order which is to be searched at the atomic, if not at the electronic level.

Sources of Figures

Fig. 10.1 Fasken, M.B. and Corbett, A.H. 2005. Process or perish: quality control in mRNA biogenesis. Nat. Struct. Mol. Biol. 12: 482–488 (Fig. 1 page 483).

Fig. 10.2 Cakmak, Y.O. 2009. A review of the potential effect of electroacupuncture and moxibustion on cell repair and survival: the role of heat shock proteins. Acupunct. Med. *27*: 183–186 (Fig. 2 page 184).

Fig. 10.3 Terry, L.J. et al. 2007. Crossing the nuclear envelope: hierarchical regulation of nucleocytoplasmic transport. Science *318*: 1412–1416 (Fig. 2 page 1414).

Fig. 10.4 **(1)** Lampson, M.A. et al. 2004. Correcting improper chromosome spindle attachments during cell division. Nat. Cell Biol. *6*: 232–237 (Fig. 4 page 236), **(2)** Venkitaraman, A.R. 2005. Aborting the birth of cancer. Nature *434*: 829–830 (Fig. 1 page 829).

Fig. 10.5 Greaves, I.K. et al. 2003. Conservation of chromosome arrangement and position of the X in mammalian sperm suggests functional significance. Chromosome Research *11*: 503–512 (Fig. 1 page 506).

Fig. 10.6 Halbleib, J.M. and Nelson, W.J. 2006. Cadherines in development: cell adhesion, sorting, and tissue morphogenesis. Genes Dev. *20*: 3199–3214 (Fig. 4 page 3203).

Fig. 10.7 Lee, H.H. et al. 2010. Bacterial charity work leads to population-wide resistance. Nature *467*: 82–85 (Fig. 4 page 84).

A Bird's Plumage is a Stage Curtain Hiding a Molecular Scenario – An Overview

11

11.1 A Closing Remark

Several main subjects were treated in this work:

1. A geometric pattern is present on the avian body which extends to the whole organism in a repetitive way. This is characterized by the same type of circles and parallel lines being evident at most body locations.
2. The geometry turns out to be a molecular process because it is determined by well- defined molecular cascades that direct the feather pigments to their exact locations. The number of components involved in molecular geometry is higher than in Euclidean and non-Euclidean geometries.
3. There is a periodic occurrence of specific organs during animal evolution, due to the presence of similar genes being activated in a punctuated way. Significant for the understanding of bird evolution is the sudden appearance of the wing in restricted groups of invertebrates and vertebrates.
4. Extra organs emerge at different parts of the body. They appear as "ready-made" structures. These are structurally and functionally coherent.
5. A rigid chromosomal and cellular order has its origins at the atomic level and is controlled by a plethora of molecular processes occurring at every level of gene action. The order that is patent in embryonic development and inheritance appears as the direct consequence of this initial order.
6. Extensive genetic research has disclosed that the same genes are responsible for a given type of organ formation in such diverse species as flies, birds and humans, revealing an extreme conservation of gene structure and function. This evidence is complemented by the experimental production of the same organ—such as a leg, wing or an eye—at the most unexpected body positions. The combination of these two types of results elucidates the emergence in birds of the same organ—or the same geometric pattern—at quite different body locations.
7. Moreover, the agreement, between the repetitive distribution of the geometric pattern throughout the avian body and the genetic evidence on the emergence of the same organ at different body locations disclose a unity of body construction. The fact that birds exhibit unique colour traits has made it easier to detect this unity that may extend to other classes as well.
8. The symmetries displayed by living organisms turn out not to be a biological event but go back to the minerals and beyond.
9. Birds and humans have many genes in common. Their behaviour shows similarities that extend from the building of tools to musical display.

The problems raised by the experiments and observations described in this work demanded a particular sequence because they contained novel relationships in which different disciplines had to be intertwined. These were: genetics, molecular biology, anatomy, palaeontology, evolution, physics, chemistry, mineralogy and others. For this reason it may be appropriate to include an overview that condenses the main items treated.

The results described in the following pages will not be accompanied by citations of the literature when these were given in previous *Chapters* of this work. Instead Figures are mentioned, that deal with the statements made. They function as a guidance to the site where the subject is treated in detail and where the references are available.

11.2 The Impact of Novel Technologies on Bird Studies

What makes a bird most attractive is its sparkling colours, surprising patterns and dynamic behaviour. But when one contemplates a bird one hardly sees the animal's skin but mainly a carpet of feathers. They actually are built like a stage curtain which disguises its internal construction. At the same time this plumage displays many guide lines which previously could not be understood and whose molecular significance could not be deciphered. They were considered to be accidental feather traits without immediate relevance.

A. Lima-de-Faria, *Molecular Geometry of Body Pattern in Birds*,
DOI 10.1007/978-3-642-25301-0_11, © Springer-Verlag Berlin Heidelberg 2012

This bird scenario preoccupied ornithologists for two centuries culminating in the accumulation of a most impressive and solid body of information. Their initial approach remained mainly limited to the study of the animal's periphery, its anatomical traits and general behaviour. This had to be so because, so many factors are involved in living processes, that scientific endeavour demands that one starts from what is easiest to approach. Besides, the technology available at a given time is a limiting factor that cannot be easily overcome.

When DNA methods became a general laboratory procedure, ornithologists seized them to better establish phylogenetic relationships among bird families. Mitochondrial and nuclear DNA sequencing, accompanied by DNA–DNA hybridization, allowed to build "phylogenetic trees." In some cases these were correlated to anatomical traits, such as spermatid structure, and to behaviour which included nest building. As the authors realized, the results turned out to be conflicting and led to contradictory hypotheses, reversing in some cases the biogeographic evidence (Xiang et al. 2004; Barker et al. 2004; Johansson and Ericson 2005).

Bird specialists had to await for genetics to give rise to molecular biology, to embark on a new phase of avian studies. It is only now that chromosome research, combined with embryonic development, makes it possible to penetrate into the inner core of a bird, where: DNA, RNA and proteins make their initial and critical decisions and from where an orchestrated plethora of molecules follows paths that finally lead to plumage display and different forms of behaviour. Novel technologies have led to obtain single genes in the test tube and to manipulate them in such a way that the pathways between a fertilized egg and an embryo, a juvenile and an adult can be discerned all the way.

In the present work the initial approach was concentrated on uncovering the molecular processes behind feather pattern and distribution. However, it turned out that most questions concerning: bird origin, evolution, behaviour and cognition could not be separated from the body pattern and its construction because they turned out to have a common denominator—all are reducible to simple gene functions involved in equally simple molecular pathways.

11.3 The Formation of Feathers and the Location of their Pigments are Molecularly Guided

The fertilized egg of a vertebrate, such as that of a bird, could not lead to the formation of another bird, if the ensuing multiple cell divisions were not directed by a severe order. Participating in this canalization are two antithetical processes: one of rapid increase and another of equally rapid decrease in cell numbers. The first results in the formation of new tissues, the second in the permanent removal and destruction of cell groups or whole organs. One is called embryonic development, the other programmed cell death. The road map of development is mainly dictated by microRNAs, and the program of cell death by bioactive lipids such as ceramids. In both cases messenger RNAs and proteins play important roles. The interplay between these two antagonistic actions is to be found all the way into the adult stage (Fig. 2.1).

A feather germ on the skin builds a follicle from which the feather emerges. The growth of feathers, their differentiation and death is determined by two genes: *Sonic hedgehog* and *bone morphogenetic protein 2*.

The actual ramification of feathers in chickens, is due to an antagonistic balance between the modulating factor *noggin* and the *bone morphogenetic protein 4*. This protein promotes rachis formation (main axis) and barb fusion, whereas *noggin* has the contrary effect leading to barb branching. Another, not less important, structural feature, is the occurrence of spaces between these structures, which is the source of the repetitive pattern characteristic of every feather. This feat is achieved by the *sonic hedgehog* gene which participates in the cell death that produces the spacings between successive barbs (Fig. 2.3).

Like teeth and hair, feathers are born and die as a result of internal genetic decisions. If the feathers are removed from the avian body new ones will grow rapidly. Besides, feathers will be shed at specific intervals and be soon replaced by new ones which are not necessarily identical. These cyclic events have been called by ornithologists moulting and regeneration. The rebuilding of feathers is due to the intervention of *sonic hedgehog* and *bone morphogenetic protein 2* (Fig. 2.4).

Many pigments, of which the chemical formulas have been established long ago, are the source of the colours displayed by the avian body. How could their exact location be specified along each feather? How could a grass green band go over to a sky blue patch or a blood red circle, having between them sharp frontiers? How could these features be transmitted to the progeny with equal accuracy? Answers are turning out. Pigments in birds are programmed in what concerns their origin, location and dynamics. Biochromes, like melanin, are produced by specialized cells called melanoblasts. These are specified before they migrate. *Ephrins,* and other molecules, are transmembrane receptors that guide them in their route along the skin. The terminal site of migration that results in the formation of circles, stripes and bands, observed on the plumage, is directed by *spondins* and a group of proteins.

Hence, the patterns that these biochromes build in the feathers in the form of different configurations, are the result of well defined molecular pathways that are internally dictated by DNA sequences and which the birds do not control.

What before were considered "fancy curiosities" turn out to be the result of well-defined molecular cascades.

11.4 The Wing is an Organ that Re-Emerged Periodically in Evolution – Similar Genes were Activated at Unexpected Times

Nothing fascinates more than the wing, yet it has had an apparently unpredictable evolution and during this process its emergence resulted in most different structural solutions.

Invertebrates appeared 600 million years ago. During this long period of evolution only once did the wing arise. The invertebrates were able to diversify into over 25 phyla some of them being much more complex than the insects. Yet the wing became an event solely limited to the insects.

Flight in its original form attained already full capacity. The forests of the Carboniferous were populated by large swarms of the fossil giant dragonfly *Meganeura* with wings 73 cm from tip to tip. Several bird species have smaller wings and most living insects have also smaller wings.

The emergence of the vertebrates did not result in the formation of a wing. The fishes, amphibians and most reptiles could not fly. Suddenly, the flying reptiles, the pterosaurs, conquered the skies 230–195 million years ago. These became extinct during the Cretaceous having no survivors. Between 180 and 135 million years ago the wing re-emerged in the birds. But evolution could not be stopped, and the mammals appeared about 100 million years ago. Again, no wing was in sight. The mammals diversified into 21 orders and 140 families, some so different that they left the land to inhabit the sea, such as the whales. Yet no wing was formed.

Without a previous warning an equally surprising event occurred. Among the land mammals (about 40 million years ago) the bats acquired perfect wings and full flying capacity. Fossils that represent stepwise stages of wing formation have not been found, yet those that exist are well preserved (Fig. 4.1).

Significant is that the complexity of flight is not directly related to evolutionary sequence. There is no indication that the flight of bats is more advanced than that of insects or birds. The environment does not seem either to be a major factor in the emergence of the wing since fishes got it and fly in air—a medium adverse to their own normal habitat (Fig. 4.2).

One of the formidable arguments against the occurrence of the same organ in invertebrates and vertebrates was that the wings in one case had no bones whereas in the other they were part of a well-developed skeleton. It was reasoned that this dissimilarity had to be the result of the action of different genes or other agents. As a result the two types of wings were considered analogous and could not be homologous structures.

The genetic results disposed of this reasoning.

Homeobox genes, discovered in the fruit fly, were found to consist of an array of genes that specified the body plan of the insect. These genes are arranged in the same order along the chromosome as they are expressed along the anteroposterior axis specifying the corresponding body regions (Fig. 7.2). The head and anterior thoracic segments are specified by the *Antennapedia* complex whereas the posterior thoracic and abdominal segments are specified by the *bithorax* complex genes (Fig. 7.3). What was remarkable is that these genes were found to be of general occurrence. They were soon identified in mammals, birds, frogs, squids, plants and humans. In all species they had the same basic function of deciding the plan along the body axis. Moreover they had been preserved nearly intact and continued to occupy the same order along the chromosome's DNA.

It was further demonstrated that these genes were responsible for the development of the wings of flies as well as the wings of birds. Other experiments showed that the development of the human vertebral column, as well as the sequence of flower parts in plants, were also decided by these genes (Fig. 7.1).

Biological structures that seemed to be totally unrelated became, overnight, the product of the same gene complex, that had been preserved for millions of years.

The sudden re-emergence of the wing during evolution at unexpected occasions can now be seen as a periodic event. Its emergence is expected to be decided by the sudden activation of the homeotic genes responsible for its formation. From the experiments in the fruit fly it could be ascertained that these genes can be suppressed or activated as the result of changes in the organism's DNA, producing flies with wings or without wings.

The length of the period at which the wing re-emerges is at present difficult to determine because we are just being confronted with this phenomenon. Since the length of the periods varies already at the chemical level, as is clear from an inspection of the Periodic Table of the Elements, it is not surprising that at the biological level, where the degree of complexity increases, the determination of the length of any period has to await the gathering of more evolutionary information.

Previously the reappearance of similar organs, in different animal groups, had been attributed to what was called convergence. This term, coined many years ago, was defined by Simpson (1980) as follows: "when different lineages of animals are evolving separately but in similar environments and in adaptation to similar ways of life they commonly also become similar in the structure of the functional part involved." As he points out, this phenomenon has been a source of disquiet to biologists. Such interpretations based on the action of the environment were valuable but do not agree with the available data. The punctuated emergence of the wing, the penis, the teeth and prominent feathers, at various body locations, do not show any direct correlation with the environment. However, this does not mean that the environment may not intervene modulating their expression, or may facilitate their emergence in specific situations.

11.5 Extra Wings, Extra Legs and Extra Feathers Appear "Ready-Made" in Birds and Occur at Different Body Locations

The experimental approach went one step further. Following genetic manipulation, combining two genes: *bithorax* and *postbithorax*, normal flies with four wings, instead of two, were produced directly. Insects with four wings exist in nature, such as the butterflies. One was recreating evolution in the laboratory. What was significant is that, contrary to the generally accepted "mechanism" of evolution, these four-winged flies were neither obtained by selection of individuals that originally had rudimentary wings, nor by random gene mutations that led to successive progenies with bigger and better wings. The flies were obtained directly without progressive transformations, appearing with "ready-made" perfect wings. Significant is that the novel wings were formed at another location which turned out to be the same as that of normal wings in butterflies (Fig. 7.2). Ducks and cocks with four legs had been reported long ago but were considered a curiosity without genetic or evolutionary significance (Fig. 5.2).

Different laboratories performed a series of experiments that led to the production of birds with four legs and four wings. When leg grafts were placed in the wing, in chick embryos expressing the gene *Tbx4*, these developed into toe-like digits. Conversely, wing grafts, expressing another gene *Tbx5*, when placed in the leg developed wing-like digits. Both genes specified limb identity and were shown to be linked to the activity of three signaling proteins that are necessary for the next stage of limb patterning. Two of these proteins: *fibroblast growth factor* and *bone morphogenetic protein* establish cell fate determination. Cell determination was changed when the protein *fibroblast growth factor* was combined with the gene *Tbx4*. This was achieved by implanting into the chick embryo beads containing this protein. Depending on the position and timing of the implantation of the beads along the body axis of the bird extra wings or extra legs were formed (Fig. 5.3).

It could not be simpler, a single protein, by changing its position, decided whether a wing or a leg would be formed. In *Drosophila* the genes of the *bithorax complex* removed the legs from the abdominal segments, leaving only three pairs of legs located on the thorax (the normal condition in insects). By inactivating the gene specifying the first abdominal segment eight-legged flies were obtained.

Again these extra organs, had a different body location, were formed "ready-made" being coherently constructed (the skeleton of birds being accompanied by the corresponding muscles) and looking normal in every respect (Figs. 7.2 and 5.3). The identification of the genes, combined with their protein messages, led to the production of a given organ at different locations.

Such a well established mechanism is expected to be equally active in the occurrence of prominent feathers that have been found at different body locations in birds. The long feathers stick out of the tail, head and wing (Fig. 3.11). Pertinent to this question is that the genes responsible for feather growth, differentiation and death have now been identified. They are: *Sonic hedgehog* and *bone morphogenetic protein 2*, which like any other genes, can be suppressed or activated by other DNA sequences leading to the emergence of a given type of feathers or their suppression.

The following features characterize this phenomenon: (1) The number of prominent feathers tends to be two. (2) The location on the tail, head and wing is precise emerging at a specific site or feather number. (3) The prominent feathers on the wing appear only in males and only during the breeding season. (4) The long feathers on the tail appear in species that belong to unrelated families with quite different geographic distribution, habitats and food preferences. (5) Long feathers may be located at four different positions within the same individual: head, lower neck, breast and back. (6) Prominent feathers are not necessarily related to the plumage complexity of the species, they appear in the discrete body of the small horned lark as well as in the sumptuous ornaments of Birds-of-paradise.

We are actually dealing with an event apparently dictated by the activation of genes that lead to the emergence of a given trait at different locations, either within the same individual or in different families which are not necessarily closely related (Fig. 3.7).

11.6 The Absence of Teeth in Birds Ought to have a Genetic Basis – Teeth, Like Feathers, are Continuously Replaced in Most Vertebrates

Millions of years of evolution were at the disposal of the over 25 different phyla of invertebrates. Such a long period would easily allow them to populate their mouth with teeth, where they would have a valuable function. Such an event happened in one particular group. Teeth turned up in the mollusks, such as *Octopus briareus*, where a series of teeth build a radula.

The teeth were also unknown in lower vertebrates. Characteristic of fishes and reptiles is the large number of teeth. To be noted is, that like feathers, they are being replaced throughout life in these animals.

Teeth are constantly being formed deep within the tissues of the jaws growing in size and shape. Moreover, through resorption at their bases they are shed and replaced by a new generation of teeth. The similarity with the life cycle of feathers is impressive. Feathers are being replaced throughout life being constantly formed deep within the skin, changing subsequently their shape and size. Fossil birds, such as the *Archaeopteryx*, had teeth. Later their formation was suppressed in modern birds. The same phenomenon occurred in turtles and in mammals the monotremes and the whalebone whales lost their teeth as adults.

The emergence, as well as the suppression, of teeth is, like that of other organs, under genetic control. In the mouse, a co-ordinated restriction of signaling molecules was found to ensure the correct tooth number, several proteins being responsible for the emergence and suppression of teeth (Fig. 4.5).

11.7 The Near Absence of Penis in Birds has an Evolutionary History Similar to that of the Wing

The penis turns out to have had an equally long and unpredictable evolutionary history. When studied at close range it turns out to have had an emergence and disappearance not much different from that of the wing, in that it comes and goes without previous announcement.

Marine worms (Gnathostomulids) have a penis in the form of a stiffened stylet. Another phylum, the Gastrotrichs, have a penis that allows transfer sperm to another partner. Among the mollusks, the *Busycon* species display a large penis that sits in the frontal part of the body and an equally long penis is found in the sea dweller *Buccinum undatum*.

There is a sudden occurrence of a well developed penis in insects. The dragonflies copulate by means of such an organ following a complex courtship. Among the crustaceans, barnacles (*Balanus*) are known for their long penis. The testes are located in the cephalic region and the penis, upon protrusion, reaches a female distantly located.

In flatworms (Platyhelminthes) this organ is as complex as in mammals. It consists of: (1) a cirrus (the protruding part of the penis), (2) genital atrium, (3) ejaculatory duct, (4) prostate gland, (5) seminal vesicle and (6) vas deferens. Most birds lack a penis but it reappears in a few species (ostrichs) attaining 20 cm.

Just as wings can appear in insects and fishes, numbering 2 or 4, the penis and the vagina can also double in number. Unlike human females, marsupials (like the kangaroos) have a double genital system with two uteri each with its own lateral vagina. This is often matched in the male by a two-lobed penis (Macdonald 2002).

We are faced with a situation in which the penis: (1) Emerged in totally unrelated groups. (2) Its appearance does not seem to be related to a specific environment. (3) Its degree of differentiation is unrelated to animal complexity. (4) It may have different locations within the animal's body. In most respects the evolutionary emergence and disappearance of the penis follows the periodicity pattern of the wing in which gene activation and repression are known to be involved.

11.8 Beak Morphogenesis and its Final Shape are Decided by Modulating Calcium Signals

It could be expected that the circularity present in the body pattern was confined to the plumage where it is so evident. But no, the beak is also a prisoner of this geometry. This organ displays coloured marks that can be as many as seven on a single bill. They tend to be partly circular, start at the base of the beak and extend along its whole length. These marks appear as cross sections of larger circles, that extend from the head at a greater distance from the eye, and that are concretized only on the bill. They seem to be like the end of waves that move beyond the head (Fig. 8.28).

Another type of circularity can be discerned in the beak. A series of bill shapes start with a long downward curvature, that gives the bill the form of a semicircle, then it becomes successively less curved becoming like a straight line. The reverse process leads to an upright curvature approaching a complementary semicircle (Fig. 8.32).

Few bird organs have been the subject of so much evolutionary speculation as the beak. The re-emergence of its most variable shape in different bird families and world locations have been a permanent preoccupation to evolutionists.

The uncovering of the molecular mechanism deciding the three-dimensional shape of a bird's beak, moved this problem to the original level of the beak's organization. Genes were found in the chicken, and in finches, which correlate to beak morphogenesis. Calmodulin is a molecule involved in mediating calcium signaling. It is expressed at higher levels in long and pointed beaks than in most robust beak types. Higher levels of calmodulin led to elongation of the beak providing an explanation for its independent growth along different axes, as confirmed by *in situ* DNA hybridization in chicken cells. Simple atoms such as calcium participate in the tailoring of the shape of beaks (Fig. 5.6).

11.9 Bird Behaviour Depends on Genes and these are not Much Different from those of Humans

Behaviour turns out to be reducible to molecular events in the cell.

The sequencing of the whole DNA contained in the chromosomes of a species is valuable because it furnishes information on gene distribution within chromosomes. Additionally it reveals homologies between the DNA sequences of other species. What it does not convey is knowledge of gene interaction and gene interdependence within a given chromosome or between the chromosomes of the complement.

Since the 1970s it was known that a certain number of genes were common to unrelated species, but these were considered to be a minor portion of the genome. It was then reasoned that the big differences between humans and other animals were due to large number of genes not yet identified.

As has happened many times in biology, it turned out to be other way. The genetic similarities were found to be of the order of 99% when humans were compared with mice (Goldstein 2001; Hudson et al. 2001). Moreover, the number of genes was expected to be higher in more complex organisms, but again, it turned out to be of a similar magnitude.

The sequencing of the chicken genome gave a clear cut answer to these questions. The human genome has about 3.0 billion and the chicken circa 1.2 billion base pairs. But the genome of the frog *Xenopus laevis* is 3.1 billion base pairs which is slightly larger than that of humans. This means that DNA amount is not related to organism complexity.

Alignment of the chicken and human genomes identifies 70 million bases that are supposed to function similarly in both species. The similarities between chicken and human are as high as about 60% when protein coding genes are compared.

The number of genes in humans is now estimated to be of the order of 20,000 (21,787 in Fig. 5.1) and the value, 17,709 genes, has been given for the chicken (Fig. 5.1).

These similarities are striking, when one considers that birds and mammals have diverged 310 million years ago. They also allow to better understand the similarity of behaviour between chimpanzees and birds that has been compared in detail (Fig. 6.1).

The molecular evidence elucidates behaviour in a still more specific way. The genome sequencing of another bird species, the song bird zebra finch, has revealed that singing engages gene regulatory networks in the brain, altering the expression of non-coding RNAs (small RNAs which do not code for proteins), microRNAs, transcription factors and their targets. These results couple musical behaviour with specific molecular events in the brain at the level of the smallest RNAs. Moreover, the acquisition of song experience has also been related to a rapid evolution of genes that participate in this type of behaviour. Other types of molecules influence the avian song. These are hormones whose activity is affected by the function of the enzyme aromatase. Besides, dopamine, a modulatory transmitter in the brain, participates in song development.

High mental ability, like any other body function, does not fall outside molecular mechanisms (Fig. 6.6).

11.10 The Eye Appears as a Master Organ – Eyes can be Formed on Wings and Wings on Eyes

Like the formation of long feathers that occur at different body locations the circular patterns and other geometric figures displayed by the body plumage, are evident not only on the head but on the wing, tail, throat, breast, belly and extend to the beak and legs in a more discreet form. This localized geometry may also occur within the same individual or in different species which are not necessarily closely related. Significant is that the geometric patterns emerge already in the embryo in the form of bands that later extend to other parts of the body (Fig. 7.8).

The most intriguing feature of a bird's geometry is that the circularity of the pattern apparently irradiates from the eye, or a closed location on the brain, and spreads like a wave, reaching every region of a bird's body. One is dealing with a trait appearing not only at different locations but extending to every corner of the body.

It turns out that this feature, like the others, has also a genetic and well defined molecular path.

In the early days of genetics, researchers concentrated from the beginning on the functions of eye genes. This was not an accident. It resulted from the fact that many colour mutants and other eye modifications turned out on the eyes of fruit flies.

Later, the primary importance of eye genes became established by two findings. First, it was discovered that the gene responsible for eye formation had been conserved intact throughout evolution. The *homeobox* gene *eyeless*, in the fruit fly, turned out to have its homologue in mice, called *Small eye* and *Aniridia* in humans. The similarity between these three genes has been confirmed by extensive nucleotide homology.

Second, the obtainment of transgenic flies, as well of other transgenic animals and plants, became a standard procedure in the hands of experienced molecular biologists. The initial use of this experimental procedure led to the production of flies in which eyes were formed on the wings, legs and antennae. The eyes which appear in these most unexpected locations are real eyes because they are identical in structure, as revealed by electron microscopy, and contain functional photoreceptors (Fig. 7.4).

These results are confirmation that the same organ can arise at different body locations, and most significant, this organ turns out to be none but the eye.

Still more impressive is that the use of another gene, *Antennapedia*, leads to the formation of little wings in the eye region. Hence, eyes can be formed on wings and wings can be formed on eyes. These results disclose a unity of body formation which supports the construction of the geometric disk, in which the eye is considered a master organ in the determination of body pattern (Fig. 8.36). Another experiment reinforced the importance of eye genes. The mouse gene *Pax-6* (*Small eye*) was able to induce eyes in the fruit fly. There seems to be no limit to the ordered juggling of organs to different locations within a species and between unrelated species as far removed from each other as a mouse and a fly (Fig. 7.5).

Nothing surprises us any more. It turns out that the wing of a fly and the human fingers are controlled by the same proteins. A direct relation can be established between each region of the wing and each of the five human fingers. Mainly responsible for this patterning is the *Sonic* (*Shh*) *hedgehog* protein (Fig. 7.6). Again, it is this same protein that is involved in avian feather development. *Sonic hedgehog* mediates key interactions between the epithelium and mesenchyme during feather morphogenesis. The unity of body construction extends from flies to birds and to humans, being guided by common genes and similar molecular pathways.

Adding to the unity of body construction is another feature that is of general occurrence in birds and other living organisms. The bilateral symmetry displayed by the avian body is equally a part of its geometry because the two cannot be separated.

What is significant is that symmetries are not an event that arose at the biological level but they can be traced back to the minerals and beyond. Crystals of quartz occur already in a left-handed and right-handed form and this type of symmetry was transmitted intact all the way to the human body (Fig. 9.1). The bilateral symmetry is also present in argirodite crystals and has been preserved throughout evolution to this day. Even before the minerals, elementary particles combined following symmetry principles (Fig. 9.2).

A unitary pattern of organization has been at work since the dawn of matter. It allowed an impressive variation but this could only occur within a rigid basic frame.

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