Introduction to the morphology, development, and ecology of feathers

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Introduction

Feathers are one of the key characters of modern birds that differentiate them from all other extant non-avian reptiles. The origin of feathers goes back deep into the Mesozoic, preceeds the origin of flight (Norell and Xu 2005; Xu and Guo 2009; Rauhut et al. 2012), and early protofeather were probably present in the ancestral Tetanurae (Barrett et al. 2015), Dinosauria, or even Ornithodira (Rauhut et al. 2012; Godefroit et al. 2014). Among extant vertebrates, the feathers of modern birds are the morphological most complex integumentary structure (Fig. 1-1) with enormous shape diversity (Fig. 1-2B-I) resulting from a hierarchical organization of repetitive morphological and developmental modules (Prum and Williamson 2001; Prum and Dyck 2003). In this chapter, the morphological ground patterns of modern feathers, their underlying developmental processes, and the biological roles of different feather types are reviewed.

Main morphological organization

The skin of birds is relatively thin compared to non-avian reptiles, but can form different kinds of derivates, including scales (in the tarsal region), glands (uropygial gland), feathers, and other epidermal outgrowths (e.g. the turkey beard, combs) (Lucas and Stettenheim 1972). Except among secondary flightless birds (Busching 2005), the skin of birds is organized in pterylae and apteria (Fig. 1-2A), skin portions that grow feathers or remain naked, respectively (Lucas and Stettenheim 1972). The distribution of pterylae and apteria varies between different bird species (Burckhardt 1954; Wetherbee 1957; Lucas and Stettenheim 1972), but remains constant in every individual throughout its ontogeny after initial formation during embryogenesis (Burckhardt 1954, see below).

Feathers itself contain several morphological units, which vary morphologically between different feather types (see below). The main units are the calamus, barbs, barbules, and the rhachis and hyporhachis (Fig. 1-1A, Lucas and Stettenheim 1972; Prum and Brush 2002). The calamus is the most proximal portion of the feather, tubular in shape, and anchors the feather into the skin in a so-called follicle. The follicle is associated with a complex mesh of muscles, which connects nearby follicles with each other, and thereby allows for a synchronized movement of the feather within each pterylae. The calamus contains two openings, the proximally located inferior umbilicus and the distal superior umbilicus. The calamus is hollow and contains a number of horizontally orientated pulp caps, which represents serial epidermal overgrowths of the dermal pulp (pulpa) that form during morphogenesis (see below). With exception of filoplumes and bristle feathers, the calamus of feathers is not associated with any neurons.

The feather barbs represent the main branching unit of the feathers. Depending on the feather type, they can be stiff or flexible. Barbs are usually serially aligned and proximally fused into a central element, called rhachis, which gives the feather a bilaterally symmetrical organization. The serially aligned barbs form the vane.

Depending on the size of the feather, the number of barbs can be reach several hundred. Along the proximal and distal side of the barbs, feathers possess a second, serially aligned branching structure, the barbules (Fig. 1-1B-E). In their main organization, barbules consist of one to multiple basal cells, which are proximally attached to the barb, and multiple distally located pennulum cells. Based on the feather type, the morphology of the barbules can be highly specialized (see below).

The rhachis is the central element of a feather. It is anteriorly located, and, depending on the feather type, circular to rectangular in cross section. In contrast to the calamus, the rhachis not hollow, but filled with a spongy pith consisting of large, polygonal medullary cells. Although the rhachis and the calamus are both tubular in organization, they are not continuous structures, but separated from each other by the superior umbilicus. On the posterior side of the feather, a second rhachis-like structure can be developed, the hyporhachis. If neither rhachis nor hyporhachis are developed, the feather barbs are radial symmetrically organized and merge into the calamus (Prum and Brush 2002).

Feathers consist of two special forms of the structural protein β-keratin, feather-β-keratin and feather-like-β-keratin, which are significantly shorter in their amino acid sequence length by lacking the characteristic four 13-amino acid repeats present in scale- and claw-β-keratins (Gregg et al. 1984; Greenwold and Sawyer 2010). Feathers furthermore contain α-keratin, which is primarily expressed in the feather sheath (Prin and Dhouailly 2004, see below).

In addition to being morphologically complexity, feathers are often extremely colorful and reflective due to the presence of pigmentation and structural coloration. The main pigments are melanins and carotenoids (Lucas and Stettenheim 1972). Melanin is a heterogenous polymer synthesized through oxidation of the amino acid tyrosine. This process occurs in specific cell organelles, the melanosomes, of specialized pigment cells, the melanocytes, which are produced in the epidermal collar during feather morphogenesis (see below). Here, melanosomes are transferred to the epidermal cells of the intermediate layer and embedded in the keratinized cell membrane (Lucas and Stettenheim 1972; Hudon 2005; Prum and Williamson 2002). The two main types of melanins are eumelanins and phaeomelanins. The former has a dark brown to black color and is synthesized in rod-like eumelanosomes, while the latter is yellow to reddish brown and synthesized in small, round phaeomelanosomes (Hudon 2005). By contrast, carotenoids are highly unsaturated hydrocarbons that are dissolved in fats and organic solvents. They cannot be synthesized by birds themselves, but rather are ingested with the diet and slightly modified. Carotenoids are transported to the feather collar via the blood stream and deposited in the intermediate layer during feather morphogenesis in the form of fat droplets (see below). With begin of keratinisation, the droplets disappear, while the carotenoids are absorbed by the viscous keratin matrix. Carotenoids produce most of the bright red, orange, and yellow colors apparent in birds (Desselberger 1930; Lucas and Stettenheim 1972; Hudon 2005). Further pigments known from recent birds include among others psittacofulvins and porphyrins (Völker 1938; Lucas and Stettenheim 1972; Hudon 2005). Computer simulations indicate that the complexity of feather coloration relies on a reaction-diffusion process distributing pigments during feather morphogenesis (Prum and Williamson 2002).

The structural colors produced in feathers are based on absorption, reflection, and refraction of light along special morphological structures, often in interplay with feather pigments. These structures can produce both iridescent and non-iridescent colors. Iridescent structural colors are primarily produced in the feather barbules, in which melanosomes are densely packed in multiple, parallel-arranged layers on the upper surface of the barbules (Mason 1923; Rensch 1925). Other melanosome arrangement include squares (Zi et al. 2003) or hexagonal arrays (Eliason and Shawkey 2012; Eliason et al. 2013). For the production of iridescent structural colors, the barbules are broadened and rotated by about 90° thereby exposing the broad surface of the barbule (Rensch 1925). The iridescence itself result from thin-film interferences, due to the repeated refraction and reflection of light at the surfaces of the single melanosome layers, which in turn is based on contrasting refractive indices and wave impedances of β-keratin, pigments, and air (Lucas and Stettenheim 1972; Shawkey et al. 2006; Doucet et al. 2006). The melanosomes of these specialized barbules are usually pigmented (Rensch 1925), but in at least seven bird clades hollow melanosomes have evolved independently from each other, creating a whitish shine (Eliason et al. 2013; Shawkey 2015). Iridescent structural colors can also be produced in barbs and rhachides by to parallel organization of keratin layers or fibers in the cortex (Vignerona et al. 2006; D'Alba et al. 2011).

In contrast, non-iridescent structural colors are produced at modified barbs and rhachides. These colors are produced through reflections at keratin-air interfaces between the cortex and the pith (see above). Pigmented melanosomes of the cortex or pith can additionally absorb transmitted light, in contrast to iridescent structural colors, where light is refracted and reflected (Lucas and Stettenheim 1972; Shawkey and Hill 2006).

Feather types and their biological role

The highly variably morphology of feathers is achieved through changes to the absolute growth rate of the feather, the initial number of barb ridges, the location of new barb loci, regions that produce new barb ridges during morphogenesis, within the feather collar, the angle of barb ridges relative to the rhachis ridge, the rate of new barb ridge addition, the barb ridge diameter, and the angle of the barb ramus expansion after emergence from the sheath (Prum and Williamson 2001, Feo and Prum 2014). Nearly all feather shapes are created through modification of these parameters. The main feather types that occur in recent birds are down feathers, semiplumes, pennaceous feathers, bristles feathers, filoplumes, and powder downs. The morphology of these feather types is described below (Fig. 1-2B-I). The different feather types usually are specialized for different biological roles, including body covering, thermoregulation, flight, display and camouflage function, tactile function and plumage maintenance. Despite these morphotype-specific biological roles, feathers like other integumentary structures function also as toxic storage organs, allowing repetitive excretion due to molting (Reichholf 1996; Metcheva et al. 2006; Dumbacher et al. 2009).

Down feathers and semiplumes

Down feathers (or plumes) are primarily used for body heat insulation (thermoregulation) and also function in hatchlings as body covering (Fig. 1-1E). In adult birds, down feathers usually contain of a medium number of long and soft barbs forming open vanes, a short calamus, and a short rhachis and hyporhachis, which are circular in cross section. The barbs contain a high number of plumulaceous barbules, which have a short, twisted proximal basis, and a long, flexible distal pennulum (Fig. 1-1D). The pennulum consists of many elongated cells, whose distal end are expanded to nodes or wear one to four cilia (Lucas and Stettenheim 1972, Dove 1997). Because of their long and flexible morphology, barbs and barbules produce electric repulsive forces due to constant friction, which makes these feathers fluffier and increases their insulatory effect (Exner 1895, 1896). In addition to true down feathers, many birds also possess a second type of insulation feathers, semiplumes, which differ in the development of a prolonged rhachis and calamus (Fig. 1-1D). In contrast, the down feathers of hatchlings, so called neoptile or natal downs, are often characterized by the absence of a rhachis and hyporhachis, leading to radial symmetry. Here, the calamus can be strongly reduced so that the barbs of natal downs are continuous with the distal tips of the barbs of the second feather generation (Schaub 1912; Ewart 1921; Foth 2011).

Pennaceous feathers

Pennaceous feathers possess a medium to high number of serially aligned barbs, which are proximally attached to an elongated rhachis. The barbs are stiffer than in down feathers. Pennaceous feathers possess two main types of barbules, which are developed at a high density along the barbs. The basis of the barbules is long and stiff and contains many short basal cells. The pennulae of the barbules that are located on the distal side of the barb possess short cells with ventral hooks (Fig. 1-1B), while those located on the proximal side of the barb are often non-specialized (Fig. 1-1C). Their basis, however, possesses a ventrally recurved flange on their dorsal edge, although a similar flange can also occur in the distal barbules. As a result, the hooks of the distal barbules can interlock with the basis of the proximal barbules (Fig. 1-1E), as in a zipper, forming a close, planar vane (Lucas and Stettenheim 1972). Beyond this ground pattern, the barbules of pennaceous feathers can be very diverse in shape (Chandler 1916; Sick 1937).

Within different body regions, pennaceous feathers vary in their morphology corresponding to varying biological roles. Pennaceous body feathers (Fig. 1-1A, 1-2H) are used for body covering, protection, thermoregulation, and, depending on their coloration, for display or camouflage (Lucas and Stettenheim 1972; Prum and Brush 2002). Their distal portion possesses open vanes with short, non-specialised barbules along the barbs. In the mid-section the vanes are close showing the typical pennaceous barbule morphology (see above). Proximally, pennaceous body feathers possess also plumulaceous barbs for thermoregulation (see above). Furthermore, these feathers have a long downy hyporhachis and a short calamus.

The pennaceous feathers of the wing are called remiges (Fig. 1-2I), which can be subdivided into primaries attaching the manus, and secondaries attaching the ulna. The remiges are primarily adapted for flight, but fulfil further biological roles, including display (Darwin 1871) and brooding (Hopp and Orsen 2004). The pennaceous feathers of the tail are called rectrices (Fig. 1-2F) and also play a crucial role in flight and display (Thomas 1997; Aparicio et al. 2003). In contrast to body feathers, remiges and rectrices have elongated rhachis with a rectangular cross-section. To fulfil their aerodynamic function, the barbs of remiges and rectrices are stiffer and possess pennaceous barbules (see above) resulting in closed vanes. Proximal downy vanes or a hyporhachis are reduced or absent, while the calamus is elongated and deeply anchored within the skin. Depending on their position within the wing, the remiges vary in symmetry, which relies on the ratio of the width of the inner and outer vane (Bushing 2005; Bachmann et al. 2007). In distal primaries and proximal rectrices, the outer vanes are significantly narrower than the inner vane, which is cause by differences in barb length and barb angle (Bachmann et al. 2007; Feo and Prum 2014), increasing the aerodynamic performance of the feathers (Norberg 1985). The degree of asymmetry, however, can also vary within one feather from distal to proximal (Bushing 2005). In proximal primaries, secondary remiges and distal rectrices the vanes are more equal in width.

A special type of pennaceous feathers are display feathers, which can possess complex color patterns (Prum and Williamson 2002; see above) and can be extremely variable in the size and morphology of the rhachis, barb, and barbule, creating aberrant morphologies (Darwin 1871; Brinkmann 1958; Bleiweiss 1987; Bartels 2003; Stavenga et al. 2011). Such feathers are usually developed on the head, breast, wing and tail region, where they can be easily recognized visually.

The secondary loss of flight can have a significant effect on the morphology of pennaceous feathers, in particular through a decrease of the barb number and a simplification and reduction of barbules, giving the feathers a more down or bristle-like morphology (Lüdicke 1974; McGowen 1989, Livezey 2003).

Bristles feathers, filoplumes and powder downs

Only two types of feathers are innervated by nervous cells at the base and function as tactile organs. Bristle feathers (Fig. 1-2B) are usually present in the face around the beak and eyes. The rhachis of these feathers is long and stiff. The barbs are short and stiff, and reduced in number. They are sparsely covered with barbules, which are simplified and stiff. The calamus is short (Lucas and Stettenheim 1972). In contrast, filoplumes (Fig. 1-2G) are short and associated with pennaceous feathers, sensing the position of the latter within the plumage. They have a tiny, flexible rhachis, which possesses a small number of short barbs on its distal end. The barbs themselves have short non-specialised barbules. A short calamus is developed at the proximal end (Lucas and Stettenheim 1972).

Powder downs are another type of feather (Fig. 1-2C) that plays an important role in the maintenance of the plumage. Morphologically, this feather type is very similar to ordinary down feathers and semiplumes, but the barbs are less fluffy. These feathers are coated with a fine powder that derived from cells that surround the developing barbules during development and is later shed onto neighbouring feathers (Lucas and Stettenheim 1972).

Feather development

Embryogenesis

The embryogenesis of feathers starts with the formation of feather tracks in particular body region, the pterylae, which usually develop down-like feathers, so called neoptile or natal downs, as first feather generation (Lucas and Stettenheim 1972; Foth 2011). In these areas, the skin forms parallel rows of placodes, which are local thickening of dermis and epidermis (Lucas and Stettenheim 1972; Prum and Brush 2002). The placodes do not develop simultaneously, but show regional specifications, depending on the morphotype of the later feather generation (e.g., pennaceous feather filoplume, etc.; Burckhardt 1954). After a certain developmental stage, placode formation stops so that their number, and thus also the number of potential feathers, remains constant over the remaining lifetime of the animal (Burckhardt 1954). In the next step, each placode develops into to a feather bud with a distally located epidermal growth zone (Fig. 1-3A). The dermal core inside the feather bud forms the pulpa (Fig. 1-3B, D), which supplies the feather bud with nutrients via blood vessels, but additionally transfers pigment cells into the epidermis (Lucas and Stettenheim 1972; Yu et al. 2004). The pulpa also express signal molecules, which play an important role in the morphogenesis of the epidermis (Yu et al. 2002). During growth, the dermal pulpa is produced continuously, but reabsorbed periodically, which goes hand in hand with pulp cap formation by the epidermis (Lucas and Stettenheim 1972).

Within the feather bud, the epidermis starts to differentiate into three main layers: the outer layer, the intermediate layer, and the basal layer. The outer layer is homologous with the 2nd periderm of embryonic bird scales and forms the feather sheath, which protects the inside of the feather germ. The feather sheath formation is characterized by strong α-Keratin expression and subsequent apoptosis (Sawyer et al. 2003, 2005). The basal layer forms the pulp caps and the marginal plates (Fig. 1-3C) that separate the barb ridges (Fig. 1-3B-D) from each other and control the morphogenesis of the intermediate layer (Harris et al. 2002; Prum and Dyck 2005) into barbs, barbules, rachis, and calamus. Finally, the intermediate layer is formed between the outer and basal layer due to cell proliferation, forming the barb ridges through a balloon-like expansion into the basal layer (Prum and Dyke 2005).

Within the barb ridge, cells differentiate into a ramogenic column, central axial plate, and two lateral barbule plates so that the axial plate ends up separating the two barbule plates medially (Fig. 1-3C) before disintegrating at the end of this developmental process (Lucas and Stettenheim 1972). The ramogenic columns form the barbs. The barbule plates contain a single row of cells and differentiate into simplified plumulaceous barbules (Lucas and Stettenheim 1972). Here, the innermost cells of the barbule plate become the base and fuse to the ramogenic column, while the more peripheral cells become the elongate distal cells of the pennulum (Lucas and Stettenheim 1972). The process ends with the apoptosis of the cells of the marginal plate and axial plate and the keratinization of the cells of the barb ramus and barbule plate. After keratinization, the remaining cells die as well (Lucas and Stettenheim 1972; Haake et al. 1984; Yu et al. 2002). As written above, barb ridges formation initially starts at the distal end of the feather bud and then moves in proximal direction (Lucas and Stettenheim 1972). This process goes hand in hand with the delocation of the growth zone to the base of the feather bud, forming the ring-shaped collar. At this point feather embryogenesis can form two different morphologies. The first morphology results from an early stop of barb ridge morphogenesis, resulting in a radially symmetric arrangement. Follicle formation is initiated, while calamus formation is often suppressed and the barbs are held together proximally by the feather sheath. When the second feather generation is formed during the first molting process (see below), the barbs of the first feather generation are continuously connected to the distal barbs of the second generation (Schaub 1912, Foth 2009, 2011). Alternatively, the barb ridges "move" during the proximal delocation of the growth zone in anterior direction, anteriorly fuse with each other at their proximal end, and form the rhachis ridge. Thus, natal feathers gain a bilaterally symmetric arrangement of the barb ridges. In contrast to later feather generations, the initial number of barb ridges remains and no new barb ridges are formed. As a result, when barb ridge formation is finished the calamus formation is initiated by a stop of differentiation processes in the intermediate layer. As with the barbs, calamus formation, and thereby feather morphogenesis, ends with keratinization and final apoptosis (Lucas and Stettenheim 1972).

During embryogenesis the feather bud growth out, but simultaneously sinks into the skin, forming a follicle (Fig. 1-3A, D, E). The timing of the process is variable between different body regions, but also between species. In *Anas platyrhynchos*, *Anser anser* (both Anseriformes), *Columba livia* (Columbiformes), and *Eudyptes chrysocome* (Sphenisciformes), follicle formation starts after barb ridge formation (Davies 1889; Wohlhauer 1901; Hosker 1936). By contrast, in *Struthio camelus* (Struthioformes) the follicle is formed before barb ridge formation (Duerden 1913), while in *Gallus gallus* (Galliformes), follicle formation can happen before, after or simultaneously with barb ridge formation (Hosker 1936, Lucas and Stettenheim 1972, Chuong and Edelman 1985). Independent from the timing of this process, the collar is finally placed under the skin and divided into two zones (Fig. 1-3D): a proliferation zone and the ramogenic zone (Lucas and Stettenheim 1972). Due to follicle formation the outer follicle wall, which surrounds the calamus, got into contact with the dermal musculature (see above) allowing the movement of the feather.

Feather embryogenesis can be further varied through placement of the germ under the skin before barb ridge formation is initiated. In this case, all developmental processes rest until hatching. This process can happen regionally or across the entire body so that the chick appears to be partially or fully naked at hatching, as is the case in Coraciiformes, Cuculiformes, Piciformes, and various Passeriformes. Depending on the species, the hatchling develops an ontogenetically delayed neoptile plumage or skips this process entirely forming the second feather generation immediately (Burckhardt 1954).

After the initial development, feather morphogenesis is periodically repeated throughout ontogeny, a process called molting. As part of this cycle, the old feather generation is shed (ecdysis) and the new feather generation is then formed (endysis) (Fig. 1-3E, Watson 1963, Lucas and Stettenheim 1972). In contrast to embryogenesis, the development of later feather generations is initiated in the collar at the base of the follicle, in which the latter can produce different feather types through lifetime. However, barb ridge, barbule, rhachis, calamus, and feather sheath formation are basically similar to the embryogenic developmental process described above (except for follicle formation), but can produce very different morphologies of the barbules, barbs, rhachides, or calami by modifying the molecular pathways, which control the developmental processes.

Summary

The huge morphological variability of recent feathers strongly relies on the modularity of repetitive morphological structures and their underlying developmental processes, in which small changes to various parameters during morphogenesis (due to changes in the molecular pathway) can have a significant impact on the final shape of the feather (Prum and Williamson 2001). The basis of this modularity, however, relies on the ring-shaped collar, which allows the growth of tube-like epidermal structures, which can be transformed into tuft and plane-like structures due to modular cell differentiation and apoptosis processes (Prum and Brush 2002; Prum 2005). Thus, the key innovation related to the origin of feathers was likely the evolution of a follicle with an internal, ring-shaped collar resulting from the secondary invagination of a tubular epidermal outgrowth (Prum 1999, Prum and Brush 2002).

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Figures legends

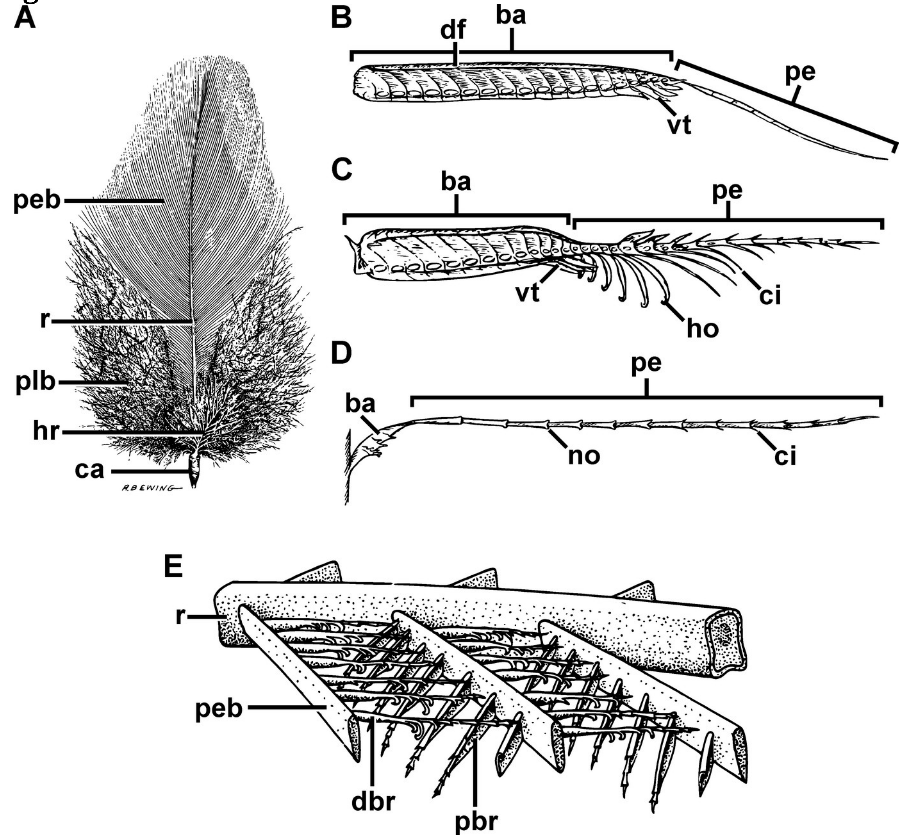

Fig. 1.1 Overview of feather morphology. A Pennaceous body feather. B Distal barbule of pennaceous feather. C Proximal barbule of a pennaceous feather. D Plumulaceous barbules. E Detail of a pennaceous feather vane. ba basal cells, ca calamus, ci cilia, dbr distal barbules, df dorsal flange, ho ventral hooks, hr hyporhachis, no nodes, pbr proximal barbules, pe pennulum, peb pennaceous barbs, plb plumulaceous barbs, r rhachis, vt ventral tooth. A modified after Lucas and Stettenheim (1972), B-D modified after Chandler (1916), E modified after Storch and Welsch (1997).

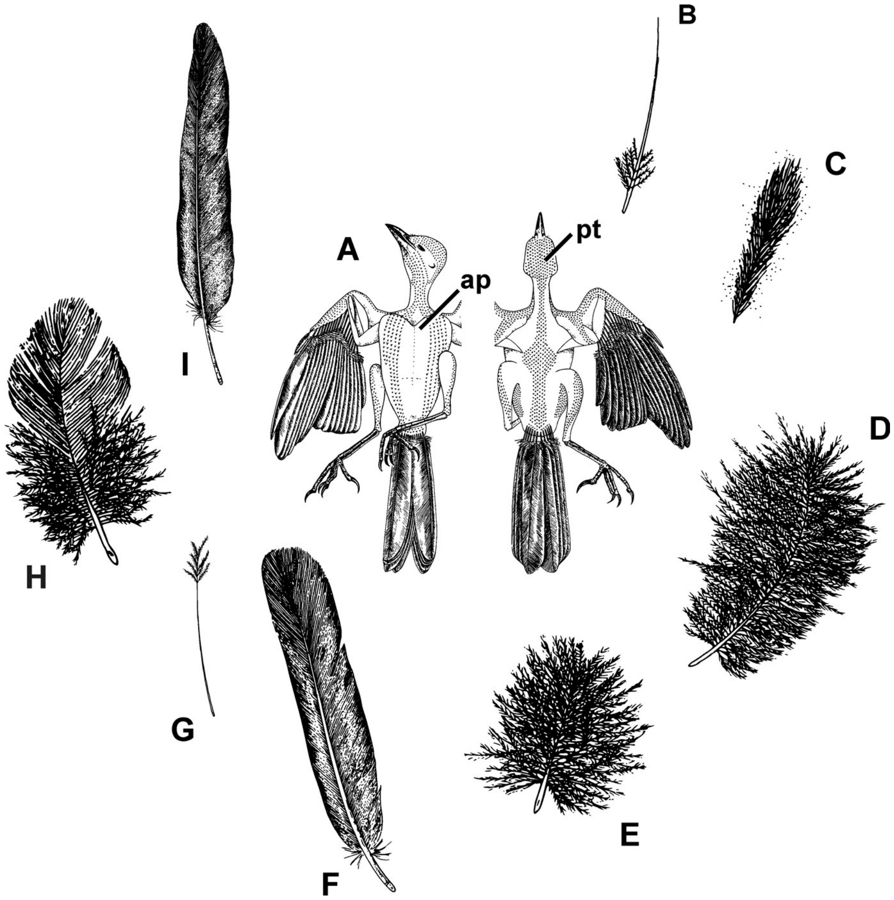

Fig. 1.2 Distribution of feather and main feather types. A Distribution of pterylae (pt) and apteria (ap) in the common blackbird (Turdus merula) (modified after Bergmann 1987). B Bristle feather. C Powder down. D Semiplume. E Down feather. F Rectrices. G Filoplume. H Pennaceous body feather. I Primary remiges. B-C modified after Chatterjee (1997).

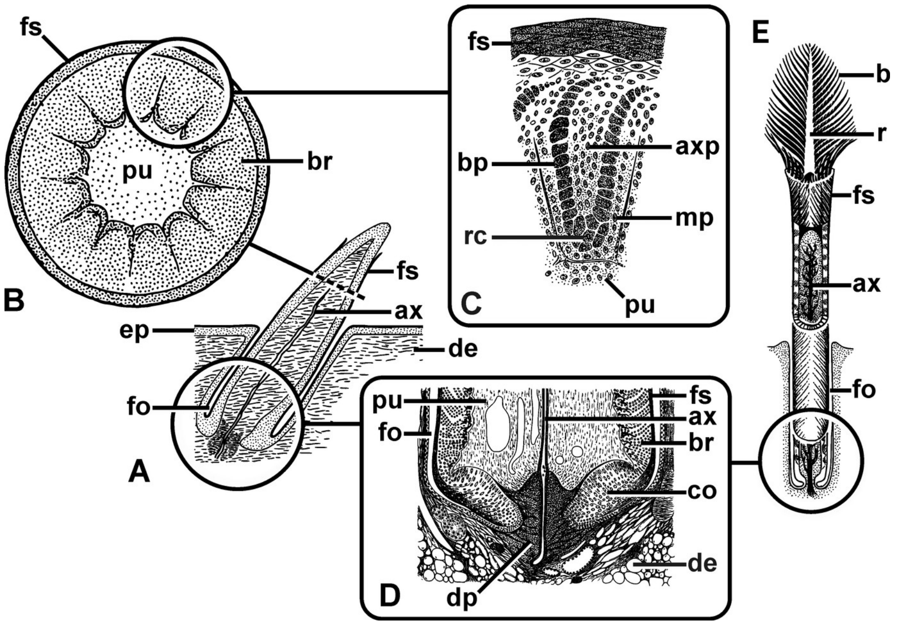

Fig. 1.3 Development of feathers. A Feather bud anlage during the embryonic development. B Cross section through the feather bud. C Detail of a barb ridge in cross section. D Longitudinal section through the feather follicle and the collar. E Anlage of a moulted feather. ax axial artery, axp axial plate, b barbs, bp barbule plate, br barb ridges, co collar, de dermis, dp dermal papilla, ep epidermis, fo follicle, fs feather sheath, mp marginal plate, pu pulp, r rhachis, rc ramogenic column. A, E modified after Starck (1982), B-C modified after Mickoleit (2004), D modified after Lillie and Wang (1941).