Fascinating Life Sciences

Christian Foth
Oliver W. M. Rauhut
Editors

The Evolution of Feathers

From Their Origin to the Present

EXTRAS ONLINE

Springer

Fascinating Life Sciences

This interdisciplinary series brings together the most essential and captivating topics in the life sciences. They range from the plant sciences to zoology, from the microbiome to macrobiome, and from basic biology to biotechnology. The series not only highlights fascinating research; it also discusses major challenges associated with the life sciences and related disciplines and outlines future research directions. Individual volumes provide in-depth information, are richly illustrated with photographs, illustrations, and maps, and feature suggestions for further reading or glossaries where appropriate.

Interested researchers in all areas of the life sciences, as well as biology enthusiasts, will find the series' interdisciplinary focus and highly readable volumes especially appealing.

More information about this series at http://www.springer.com/series/15408

Christian Foth • Oliver W. M. Rauhut
Editors

The Evolution of Feathers

From Their Origin to the Present

Springer

Editors
Christian Foth
Department of Geosciences
University of Fribourg
Fribourg, Switzerland

Oliver W. M. Rauhut
Department for Earth and Environmental Sciences
Ludwig-Maximilians-Universität,
Palaeontology and Geobiology,
GeoBioCenter
München, Germany

ISSN 2509-6745 ISSN 2509-6753 (electronic)
Fascinating Life Sciences
ISBN 978-3-030-27222-7 ISBN 978-3-030-27223-4 (eBook)
https://doi.org/10.1007/978-3-030-27223-4

© Springer Nature Switzerland AG 2020
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG.
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Preface

Birds, the last living dinosaurs, have fascinated humans since ancient times, primarily due to their ability to fly and their colourful appearance. Both characteristics are closely related to their unique epidermal integument, the feather, which represents the morphologically most complex and diverse skin derivate within vertebrates. Due to their high diversity in shape that varies between different body regions, feathers can fulfil a large number of biological roles, including flight, body insulation, display and sensory function. But how did this aberrant integumentary structure evolve, and what was its initial biological role?

With the discovery of the famous Urvogel *Archaeopteryx* in the lithographic limestones of southern Germany just two years after the publication of the Darwin's seminal book *The Origin of Species*, it became evident that the presence of modern feather types, including flight feathers, extended back to at least the Upper Jurassic, preceding the origin of toothless beaks, clawless hands with fused fingers or a strongly reduced tail. For decades, it was considered to be common sense that the origin of feathers was primarily driven by the evolution of flight, using *Archaeopteryx* as key witness from the fossil record. Since the description of *Sinosauropteryx* from the Early Cretaceous of China in 1998, numerous new discoveries of non-avian dinosaurs covered with various types of feathers have challenged this idea fundamentally and led to new evolutionary scenarios for the origin of feathers, their changing functional significance and a new understanding of dinosaurs in general. This book is devoted to the origin and evolution of feathers and highlights the crucial impact of palaeontology on this field of research, documenting the successive increase of morphological complexity along the line towards modern birds.

However, this book would not have been possible without the help of many colleagues and friends who need to be acknowledged. First, we thank Verena Penning for inviting us to edit a book on the evolution of feather. Lars Körner and Rajeswari Balachandran are thanked for their patience and editorial support during the production of this book. We further thank all authors for their contributions as well as Richard Butler, Tom Holtz, Jingmai O'Connor, Michael Pittman and Randall Widelitz for their careful reviews. Finally, the

senior editor, Christian Foth, would like to thank Ragnar Kinzelbach and Stefan Richter for their contemplative mentoring during his studies at the University of Rostock, when he started exploring the fascinating world of feathers.

Fribourg, Switzerland Christian Foth
München, Germany Oliver W. M. Rauhut

Contents

Introduction to the Morphology, Development, and Ecology of Feathers

1

Christian Foth

1.1 Introduction

Feathers are a characteristic of modern birds that differentiate them from all other extant non-avian reptiles. The origin of feathers goes back deep into the Mesozoic, preceding the origin of flight (Norell and Xu 2005; Xu and Guo 2009; Rauhut et al. 2012), and early protofeathers 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 morphologically the 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.

1.2 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 pteryla. The calamus contains two openings, the distally located inferior umbilicus and the proximal 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

---

C. Foth (✉)
Department of Geosciences, University of Fribourg, Fribourg, Switzerland

C. Foth, O. W. M. Rauhut (eds.), *The Evolution of Feathers*, Fascinating Life Sciences,
https://doi.org/10.1007/978-3-030-27223-4_1

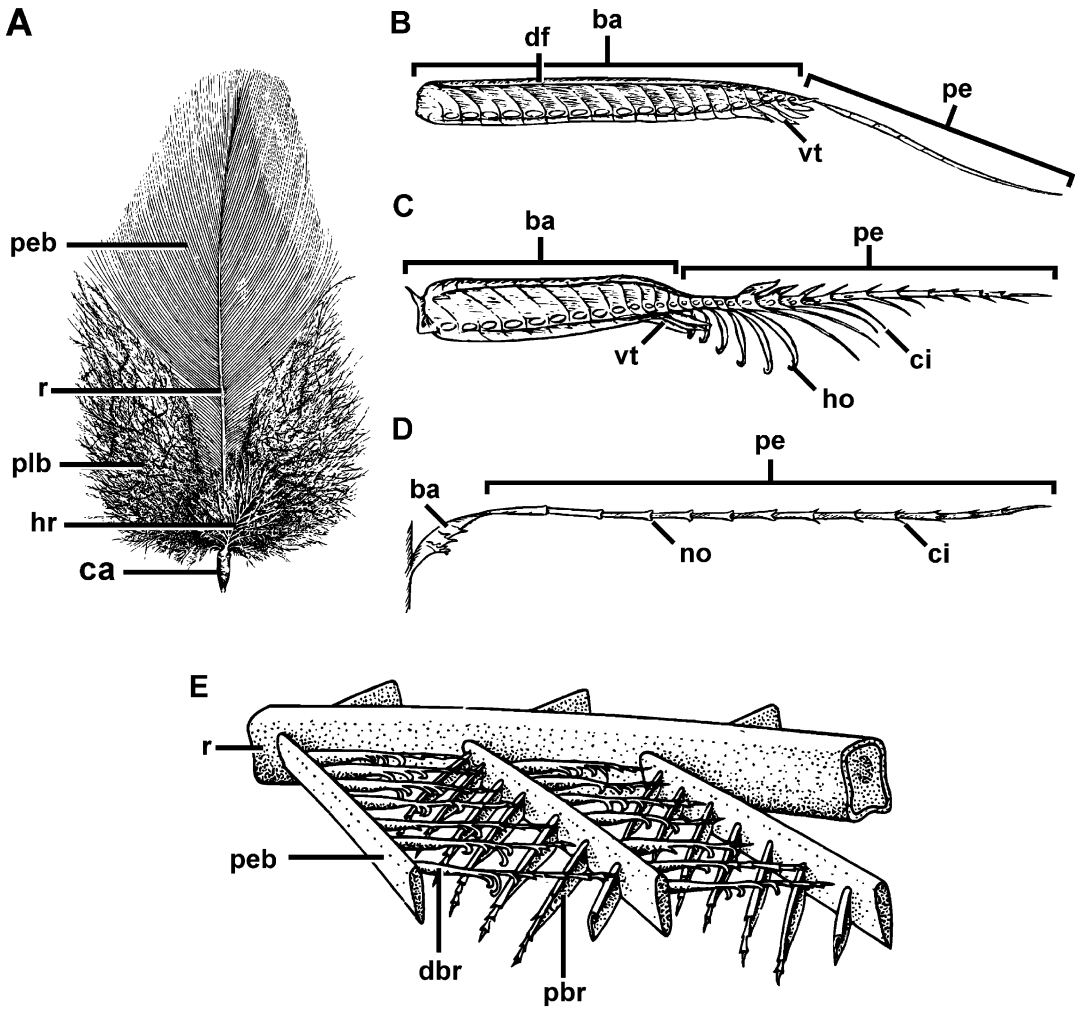

Fig. 1.1 Overview of feather morphology. (**a**) Pennaceous body feather. (**b**) Distal barbule of pennaceous feather. (**c**) Proximal barbule of a pennaceous feather. (**d**) Plumulaceous barbule. (**e**) Detail of a pennaceous feather vane. *ba* basal cells, *ca* calamus, *ci* cilia, *dbr* distal 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)

morphogenesis (see below). With the exception of filoplumes and bristle feathers, the calamus of feathers is not associated with any neurons.

The 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 reach several hundreds. 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).

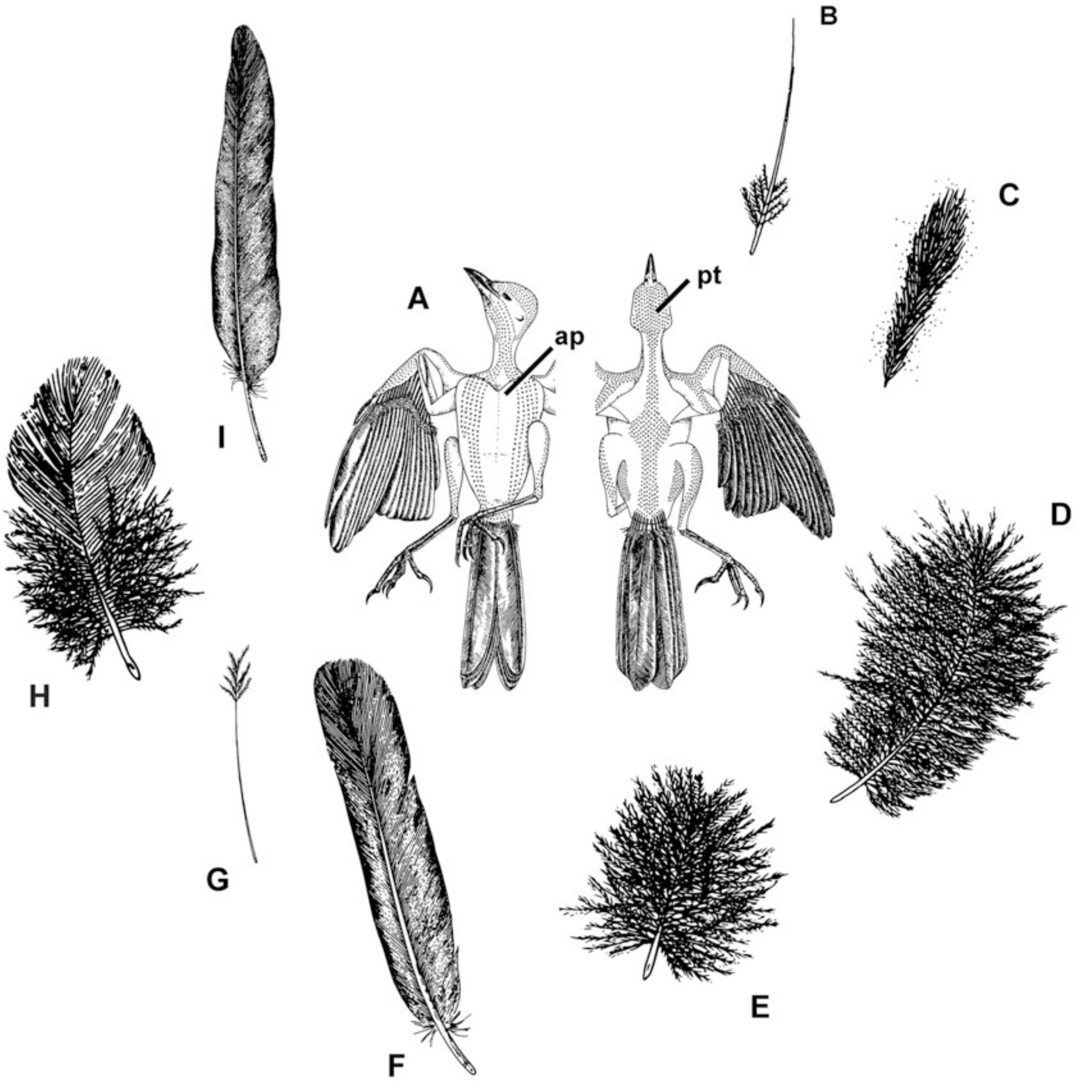

Fig. 1.2 Distribution of feather and main feather types. (**a**) Distribution of pterylae (pt) and apteria (ap) in the common blackbird (*Turdus merula*) (modified after Bergmann 1987). (**b**) Bristle feather. (**c**) Powder down. (**d**) Semiplume. (**e**) Down feather. (**f**) Rectrices. (**g**) Filoplume. (**h**) Pennaceous body feather. (**i**) Primary remiges. (**b**, **c**) modified after Chatterjee (1997)

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 is 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 2011). Feathers furthermore contain α-keratin, which is primarily expressed in the feather sheath (Prin and Dhouailly 2004, see below).

In addition to being morphologically complex, 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 have a dark brown to black color and are synthesized in rod-like eumelanosomes, while the latter are 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 the beginning of keratinization, 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 noniridescent colors. Iridescent structural colors are primarily produced in the feather barbules, in which melanosomes are densely packed in multiple, parallelly 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 results 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 et al. 2015). Iridescent structural colors can also be produced in barbs and rhachides by parallel organization of keratin layers or fibers in the cortex (Vigneron et al. 2006; D'Alba et al. 2011).

In contrast, noniridescent 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).

1.3 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 are usually 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 also function as toxic storage organs, allowing repetitive excretion due to molting (Reichholf 1996; Metcheva et al. 2006; Dumbacher et al. 2009).

1.3.1 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. 1.2e). In adult birds, down feathers usually contain 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).

1.3.2 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 nonspecialized (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 (Figs. 1.1a and 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, nonspecialized 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 (Busching 2005; Bachmann et al. 2007). In distal primaries and proximal rectrices, the outer vanes are significantly narrower than the inner vane, which is caused 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 (Busching 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; McGowan 1989; Livezey 2003).

1.3.3 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 nonspecialized 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 play 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 is derived from cells that surround the developing barbules during development and is later shed onto neighboring feathers (Lucas and Stettenheim 1972).

1.4 Feather Development

The embryonic development of feathers starts with the formation of feather tracks in particular body regions, 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 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 stage, 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 expresses signal molecules, which play an important role in the morphogenesis of the epidermis (Yu et al. 2002). During

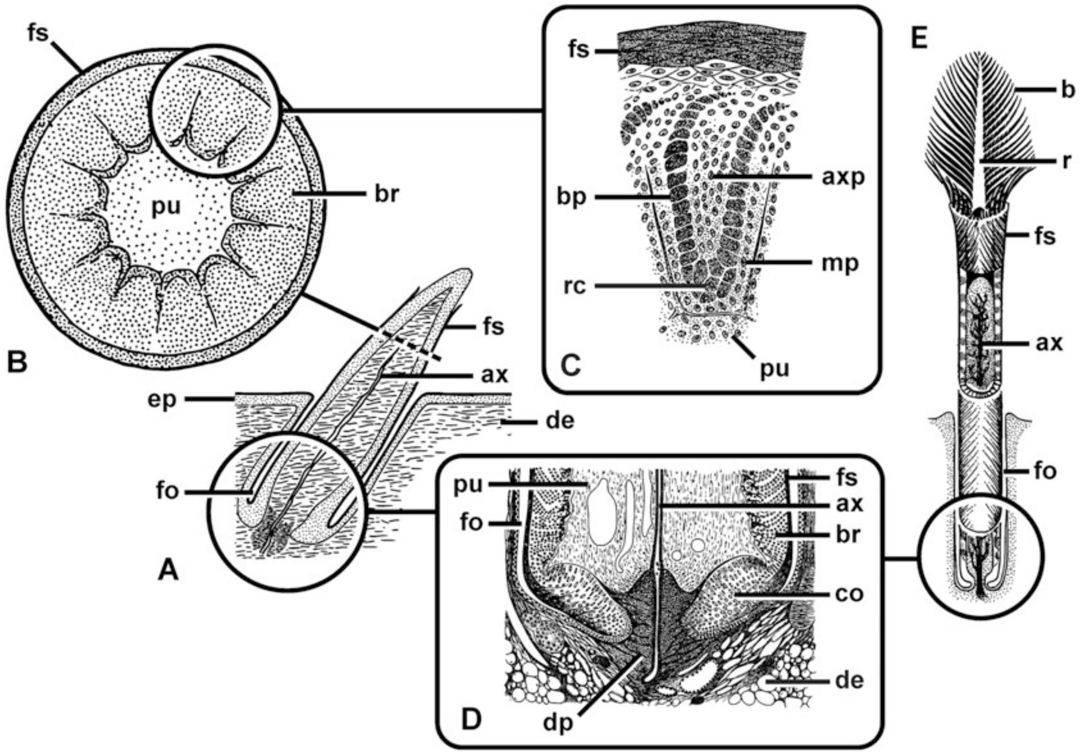

Fig. 1.3 Development of feathers. (**a**) Feather bud anlage during embryonic development. (**b**) Cross section through the feather bud. (**c**) Detail of a barb ridge in cross section. (**d**) Longitudinal section through the feather follicle and the collar. (**e**) Anlage of a molted feather. *ax* 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)

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 second 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 2003) 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 2003).

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 a 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 an 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 grows 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; Wohlauer 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, comes into contact with the dermal musculature (see above) allowing the movement of the final 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 throughout 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.

1.5 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 in 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).

Acknowledgments I thank Walter Joyce (University of Fribourg) for proofreading this chapter. The review was supported by the Swiss National Science Foundation grant PZ00P2_174040.

References

Aparicio JM, Bonal R, Cordero PJ (2003) Evolution of the structure of tail feathers: implications for the theory of sexual selection. Evolution 57:397–405

Bachmann T, Klän S, Baumgartner W, Klaas M, Schröder W, Wagner H (2007) Morphometric characterisation of wing feathers of the barn owl *Tyto alba* pratincola and the pigeon *Columba livia*. Front Zool 4:23

Barrett PM, Evans DC, Campione NE (2015) Evolution of dinosaur epidermal structures. Biol Lett 11:20150229

Bartels T (2003) Variations in the morphology, distribution, and arrangement of feathers in domesticated birds. J Exp Zool (Mol Dev Evol) 298B:91–108

Bergmann H-H (1987) Die Biologie des Vogels. AULA, Wiesbaden

Bleiweiss R (1987) Development and evolution of avian racket plumes: fine structure and serial homology of the wire. J Morphol 194:23–39

Brinkmann A (1958) Die Morphologie der Schmuckfeder von *Aix galericulata* L. Rev Suisse Zool 65:485–608

Burckhardt D (1954) Beitrag zur embryonalen Pterylose einiger Nesthocker. Rev Suisse Zool 61:551–655

Busching W-D (2005) Einführung in die Gefieder- und Rupfungskunde. AULA, Wiebelsheim

Chandler AC (1916) A study of the structure of feathers, with reference to their taxonomic significance. Univ Calif Publ Zool 13:243–446

Chatterjee S (1997) The rise of birds: 225 million years of evolution. The John Hopkins University Press, Baltimore

Chuong C, Edelman GM (1985) Expression of cell-adhesion molecules in embryonic induction. I. Morphogenesis of nestling feathers. J Cell Biol 101:1009–1026

D'Alba L, Saranathan V, Clarke JA, Vinther J, Prum RO, Shawkey MD (2011) Colour-producing ß-keratin nanofibres in blue penguin (*Eudyptula minor*) feathers. Biol Lett 7:543–546

Darwin CR (1871) The descent of man, and selection in relation to sex, vol 2. John Murray, London

Davies HR (1889) Die Entwicklung der Feder und ihre Beziehungen zu anderen Integumentgebilden. Morphol Jahrb 15:560–645

Desselberger H (1930) Ueber das Lipochrom der Vogelfeder. J Ornithol 78:328–376

Doucet SM, Shawkey MD, Hill GE, Montgomerie R (2006) Iridescent plumage in satin bowerbirds: structure, mechanisms and nanostructural predictors of individual variation in colour. J Exp Biol 209:380–390

Dove CL (1997) Quantification of microscopic feather characters used in the identification of the North American plovers. Condor 99:47–57

Duerden JE (1913) Experiments with ostriches. XXII. The development of the feather, showing absence of cruelty in clipping and quilling. Agric J Union of South Africa 6:648–661

Dumbacher JP, Menon GK, Daly JW (2009) Skin as a toxin storage organ in the endemic new Guinean genus *Pitohui*. Auk 126:520–530

Eliason CM, Shawkey MD (2012) A photonic heterostructure produces diverse iridescent colours in duck wing patches. J R Soc Interface 9:2279–2289

Eliason CM, Bitton P-P, Shawkey MD (2013) How hollow melanosomes affect iridescent colour production in birds. Proc R Soc B 280:20131505

Ewart JC (1921) The nestling feathers of the mallard, with observations on the composition, origin, and history of feathers. Proc Zool Soc London 1921:609–642

Exner S (1895) Ueber die elektrischen Eigenschaften der Haare und Federn. Pflugers Arch 61:427–449

Exner S (1896) Ueber die elektrischen Eigenschaften der Haare und Federn. Pflugers Arch 63:305–316

Feo TJ, Prum RO (2014) Theoretical morphology and development of flight feather vane asymmetry with experimental tests in parrots. J Exp Zool (Mol Dev Evol) 322B:240–255

Foth C (2009) Die Morphologie des Erstlingsgefieders ausgewählter Vogeltaxa unter Berücksichtigung der Phylogenie. University of Rostock, Germany

Foth C (2011) The morphology of neoptile feathers: ancestral state reconstruction and its phylogenetic implications. J Morphol 272:387–403

Godefroit P, Sinitsa SM, Dhouailly D, Bolotsky YL, Sizov AV, McNamara ME, Benton MJ, Spagna P (2014) A Jurassic ornithischian dinosaur from Siberia with both feathers and scales. Science 345:451–455

Greenwold MJ, Sawyer RH (2011) Linking the molecular evolution of avian beta (β) keratins to the evolution of feathers. J Exp Zool (Mol Dev Evol) 316:609–616

Gregg K, Wilton SD, Parry DAD, Rogers GE (1984) A comparison of genomic coding sequences for feather and scale keratins: structural and evolutionary implications. EMBO J 3:175–178

Haake AR, König G, Sawyer RH (1984) Avian feather development: relationships between morphogenesis and keratinization. Dev Biol 106:406–413

Harris MP, Fallon JF, Prum RO (2002) Shh-Bmp2 signaling module and the evolutionary origin and diversification of feathers. J Exp Zool (Mol Dev Evol) 294:160–176

Hopp TP, Orsen MJ (2004) Dinosaur brooding behavior and the origin of flight feathers. In: Currie PJ, Koppelhus EB, Shugur MA, Wright JL (eds) Feathered dragons. Indiana University Press, Bloomington, pp 234–250

Hosker A (1936) Studies on the epidermal structures of birds. Philos Trans R Soc Lond Ser B 226:143–188

Hudon J (2005) Considerations in the conservation of feathers and hair, particularly their pigments. In: Brunn M, Burns JA (eds) Fur trade legacy. The preservation of organic materials. Canadian Association for Conservation of Cultural Property, Ottawa, pp 127–147

Lillie FR, Wang H (1941) Physiology of development of the feather. V. Experimental morphogenesis. Physiol Zoöl 14:103–133

Livezey BC (2003) Evolution of flightlessness in rails (Gruiformes: Rallidae): phylogenetic, ecomorphological, and ontogenetic perspectives. Ornithol Monogr 53:1–654

Lucas AM, Stettenheim PR (1972) Avian anatomy. Integument, Part I and II. U.S. Government Printing Office, Washington, DC

Lüdicke M (1974) Radioaktive Markierungsversuche an Federn von *Casuarius casuarius*. J Ornithol 115:348–364

Mason CW (1923) Structural colors in feathers. II. J Phys Chem 27:401–447

McGowan C (1989) Feather structure in flightless birds and its bearing on the question of the origin of feathers. J Zool (Lond) 218:537–547

Metcheva R, Yurukova L, Teodorova S, Nikolova E (2006) The penguin feathers as bioindicator of Antarctica environmental state. Sci Total Environ 362:259–265

Mickoleit G (2004) Phylogenetische Systematik der Wirbeltiere. Verlag Dr. Friedrich Pfeil, München

Norberg RÅ (1985) Function of vane asymmetry and shaft curvature in bird flight feathers; inferences on flight ability of *Archaeopteryx*. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds) The beginnings of birds. Freunde des Jura-Museums, Eichstätt, pp 303–318

Norell MA, Xu X (2005) Feathered dinosaurs. Annu Rev Earth Planet Sci 33:277–299

Prin F, Dhouailly D (2004) How and when the regional competence of chick epidermis is established: feathers vs. scutate and reticualte scales, a problem en route to a solution. Int J Dev Biol 48:137–148

Prum RO (1999) Development and evolutionary origin of feathers. J Exp Zool (Mol Dev Evol) 285:291–306

Prum RO (2005) Evolution of the morphological innovations of feathers. J Exp Zool (Mol Dev Evol) 304B:570–579

Prum RO, Brush AH (2002) The evolutionary origin and diversification of feathers. Q Rev Biol 77:261–295

Prum RO, Dyck J (2003) A hierarchical model of plumage: morphology, development, and evolution. J Exp Zool (Mol Dev Evol) 298B:73–90

Prum RO, Williamson S (2001) Theory of the growth and evolution of feather shape. J Exp Zool (Mol Dev Evol) 291:30–57

Prum RO, Williamson S (2002) Reaction-diffusion models of within-feather pigmentation patterning. Proc R Soc Lond B 269:781–792

Rauhut OWM, Foth C, Tischlinger H, Norell MA (2012) Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the late Jurassic of Germany. Proc Natl Acad Sci U S A 109:11746–11751

Reichholf JH (1996) Die Feder, die Mauser und der Ursprung der Vögel. Archaeopteryx 14:27–38

Rensch B (1925) Untersuchungen zur Phylogenese der Schillerstruktur. J Ornithol 73:127–147

Sawyer RH, Salvatore BA, Potylicky T-TF, French JO, Glenn TC, Knapp LW (2003) Origin of feathers: feather Beta (β) keratins are expressed in discrete epidermal cell populations of embryonic scutate scales. J Exp Zool (Mol Dev Evol) 295B:12–24

Sawyer RH, Rogers L, Washington LD, Glenn TC, Knapp LW (2005) Evolutionary origin of the feather epidermis. Dev Dyn 232:256–267

Schaub S (1912) Die Nestdunen der Vögel und ihre Bedeutung für die Phylogenie der Feder. Verh Naturforsch Ges Basel 23:131–182

Shawkey MD, Hill GE (2006) Significance of a basal melanin layer to production of non-iridescent structural plumage color: evidence from an amelanotic Steller's jay (*Cyanocitta stelleri*). J Exp Biol 209:1245–1250

Shawkey MD, Hauber ME, Estep LK, Hill GE (2006) Evolutionary transitions and mechanisms of matte and iridescent plumage coloration in grackles and allies (Icteridae). J R Soc Interface 3:777–786

Shawkey MD, D'Alba L, Xiao M, Schutte M, Buchholz R (2015) Ontogeny of an iridescent nanostructure composed of hollow melanosomes. J Morphol 276:378–384

Sick H (1937) Morphologisch-funktionelle Untersuchung über die Feinstruktur der Vogelfeder. J Ornithol 85:206–372

Starck D (1982) Vergleichende Anatomie der Wirbeltier auf evolutionsbiologischer Grundlage. Bd. 3: Organe des aktiven Bewegungsapparates, der Koordination, der Umweltbeziehung, des Stoffwechsels und der Fortplanzung. Springer, Berlin

Stavenga DG, Leertouwe HL, Marshall NJ, Osorio D (2011) Dramatic colour changes in a bird of paradise caused by uniquely structured breast feather barbules. Proc R Soc B 278:2098–2104

Storch V, Welsch U (1997) Systematische Zoologie. Spektrum Akademischer Verlag, Heidelberg

Thomas ALR (1997) On the tails of birds – what are the aerodynamic functions of birds' tails, with their incredible diversity of form? Bioscience 47:216–225

Vigneron JP, Lousse V, Colomer J-F, Rassart M, Louette M (2006) Complex optical structure in the ribbon-like feathers of the African open-bill stork. Proc SPIE 6320:632014

Völker O (1938) Porphyrin in Vogelfedern. J Ornithol 86:436–456

Watson GE (1963) The mechanism of feather replacement during natural molt. Auk 80:486–495

Wetherbee DK (1957) Natal plumages and downy pteryloses of passerine birds of North America. Bull Am Mus Nat Hist 113:339–436

Wohlauer E (1901) Die Entwicklung des Embryonalgefieders von *Eudyptes chrysocome*. Z Morphol Anthropol 4:149–178

Xu X, Guo Y (2009) The origin and early evolution of feathers: insights from recent paleontological and neontological data. Vertebrata PalAsiatica 47:311–329

Yu M, Wu P, Widelitz RB, Chuong C (2002) The morphogenesis of feathers. Nature 420:308–312

Yu M, Yue Z, Wu P, Wu D, Mayer J-A, Medina M, Widelitz RB, Jiang T, Chuong C (2004) The developmental biology of feather follicles. Int J Dev Biol 48:181–191

Zi J, Yu X, Li Y, Hu X, Xu C, Wang X, Liu X, Fu R (2003) Coloration strategies in peacock feathers. Proc Natl Acad Sci U S A 100:12576–12578

Molecular and Cellular Mechanisms of Feather Development Provide a Basis for the Diverse Evolution of Feather Forms

2

Gee-Way Lin, Ang Li, and Cheng-Ming Chuong

2.1 Diversification of Feather Morphology in Evolution

2.1.1 The Structure of Extant Feathers

Feathers are a skin-associated appendage composed of a matrix of intracellular keratin in the external body parts of birds and feathered dinosaurs. The center of a typical contour feather from modern birds is composed of a hollow shaft (calamus) at the proximal end and a rigid shaft (rachis) in the distal part. The primary branches along the rachis are the barbs. The secondary branches along the main shaft of a barb (ramus) are the barbules. Barbules away from the base of the feather are referred as distal barbules, whereas those toward the base of the feather are referred as proximal barbules. A barbule is a stalk of single cells, beginning with squarish cells at the base and ending with a series of elongated distal cells. The elongated cells of distal barbules differentiate laterally to form hooklets attaching to the groove of adjacent proximal barbules. Thus, the interlocked barbs on each side of the rachis form the vane of feathers (Fig. 2.1a).

2.1.2 Diverse Morphology of Feathers

The diverse morphology of feathers is a consequence of microstructural variations in the rachis, rami, and barbules. From filamentous bristles to sail-shaped remiges, a large spectrum of branching patterns can be found not only among different species of modern Aves, but also at different body regions of one individual bird, which usually serve different functions. For example, the radially or bilaterally symmetric plumulaceous feathers distributed in the breast and belly region mainly help to maintain the body temperature (Fig. 2.1b, b′), whereas the bilaterally symmetric pennaceous feathers covering most parts of the trunk determine the body contour (Fig. 2.1c). The bilaterally asymmetric

---

G.-W. Lin
Department of Pathology, University of Southern California, Los Angeles, CA, USA

Department of Biochemistry and Molecular Cell Biology, School of Medicine, College of Medicine, Taipei Medical University, Taipei, Taiwan

A. Li
Department of Pathology, University of Southern California, Los Angeles, CA, USA

Department of Kinesiology, University of Texas at Arlington, Arlington, TX, USA

C.-M. Chuong (✉)
Department of Pathology, University of Southern California, Los Angeles, CA, USA

Research Center for Developmental Biology and Regenerative Medicine, National Taiwan University, Taipei, Taiwan
e-mail: cmchuong@med.usc.edu

C. Foth, O. W. M. Rauhut (eds.), *The Evolution of Feathers*, Fascinating Life Sciences,
https://doi.org/10.1007/978-3-030-27223-4_2

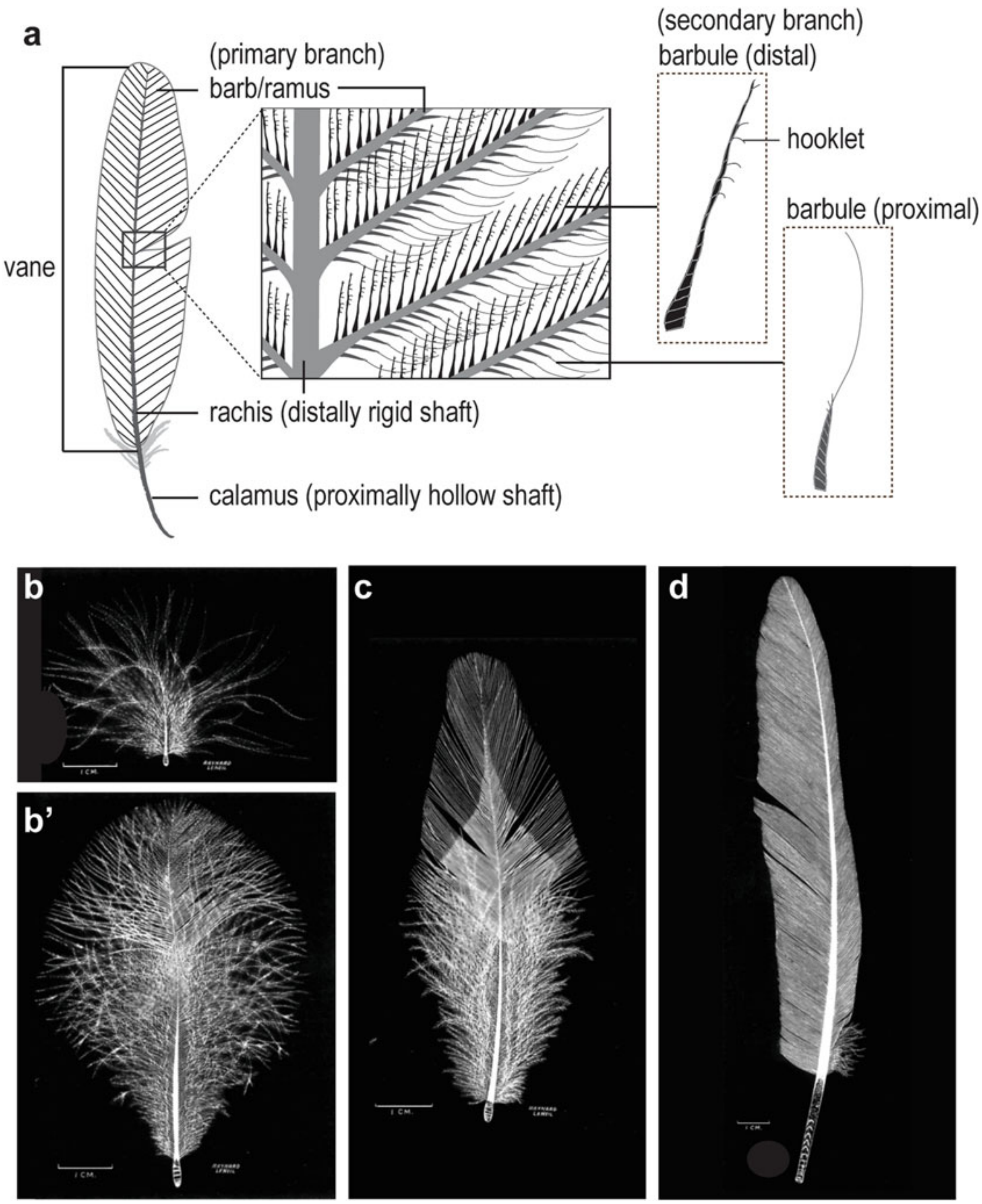

Fig. 2.1 The structure and diverse morphology of feathers: (**a**) hierarchical structure of a feather, (**b**, **b**′) radial symmetric downy feathers from the ventral and lateral sides, (**c**) bilateral symmetric feather from the dorsal trunk, (**d**) bilateral asymmetric feather from the wing (**b**–**d** are modified from Lucas and Stettenheim 1972)

feathers in the wing allow aerodynamic flight (Fig. 2.1d). Therefore, feathers are considered to be the most complex integumentary structure and are used as a model to study how evolutionary novelties in vertebrate skin appendages emerge (Prum 1999; Chuong et al. 2003).

2.1.3 The Evolution and Development of Feathers

Where feathers came from, how feathers evolved, and how modern feather architectures were achieved have long been debated. The appearance of feathers had defined the appearance of birds before fossil records on feathered dinosaurs were found (Brush 1996). Key events in the evolution of feathers had been reconstructed by linkages of the extant structures of feathers and the developmental process. According to analysis of this kind of linkage, a five-staged feather evolution-development (evo-devo) model was proposed by Prum (1999). In this model, the evolution of a feather follicle is characterized by the presence of a cylindrical, unbranched collar (stage I); the inner layer of the collar then periodically differentiates into barb ridges along a horizontal plane (stage II). Later on, the plane of a barb ridge formation becomes oblique, allowing the emergence of new barbs from one side of the collar (barb generative zone, or BGZ) and the fusion of barbs into rachis at the other side. This results in the helical displacement of barb ridges as they grow (stage III). The next step is the further differentiation of barbule plates into structurally distinct distal and proximal barbules (stage IV), accompanied by lateral displacement or duplication of the BGZ (stage V). These innovations produce the bilaterally asymmetric remiges and after-feathers (Prum 1999; Prum and Williamson 2001; Prum and Brush 2002).

Recent paleontological and neontological studies on feathers and feather-like integumentary structures associated with non-avian and avian theropods have greatly improved our understanding of the origin and early evolution of feathers (Xu 2006; Xu and Guo 2009; Xu et al. 2014). It seems that the five-staged feather evo-devo model is still adopted, even though an intermediate morphotype of the avian feather has been identified from amber (Xing et al. 2016). However, the most developmental criteria for modern feathers are not applicable to fossil records (Xu and Guo 2009). In non-avian dinosaurs, eight morphotypes of feathers have been identified, but they could not be interpreted using extant feather morphogenesis (Xu and Guo 2009). This suggests that the early evolution of feathers would have been more complicated than the morphogenic processes of extant feathers have predicted.

The morphogenic processes of modern feathers start during embryogenesis in conjunction with other skin-associated appendages such as scales and glands (Chang et al. 2009). The inner layer of skin, called the dermis, serves as a center of signaling to induce stratification and further periotic patterning in the outer layer, known as the epidermis (Chuong et al. 2000). The molecular and cellular mechanisms involved in the early stages of developing feathers (before the formation of cylindrical filaments) are conserved in a variety of feathers. In contrast, the emergence of evolutionary novelties—such as branching, stem cell niche formation, and the establishment of anterior-posterior (A-P), proximal-distal (P-D), and medial-lateral (M-L) axes—occur relatively late in development (Fig. 2.2) (Widelitz et al. 2003; Xu et al. 2014). In other words, more morphogenetic processes are gradually added in development to make the feather structure more complex. To date, the evo-devo model proposed by Prum in 1999 is generally consistent with newly discovered molecular and cellular mechanisms of feather morphogenesis. Several key mechanisms are illustrated in Figs. 2.2, 2.3, 2.4, 2.5, 2.6, and 2.7.

2.2 Development of Feathers During Embryogenesis

2.2.1 Tract Field Formation

The morphogenetic processes of feathers start from macro-patterning. Even though the mechanism of the macro-patterning is not well understood, regional specificity, such as different feather tracts and scales in the bird's skin, is quite obvious (Fig. 2.3a) (Gill 1994). On the cellular level, the distinct skin regions are closely associated with the accumulation of dermis underlying the epidermis. For example, a region with relatively dense dermis becomes a competent tract field to form feathers (Wessells 1965). Molecular signals derived from the dorsal neural tube, such as Wnt-1, trigger the formation of feather tracts that are characterized by dense dermis (Olivera-Martinez et al. 2001). After that, the neural cell adhesion molecule (NCAM) and nuclear-enriched β-catenin are observed in the epithelium of the feather tract

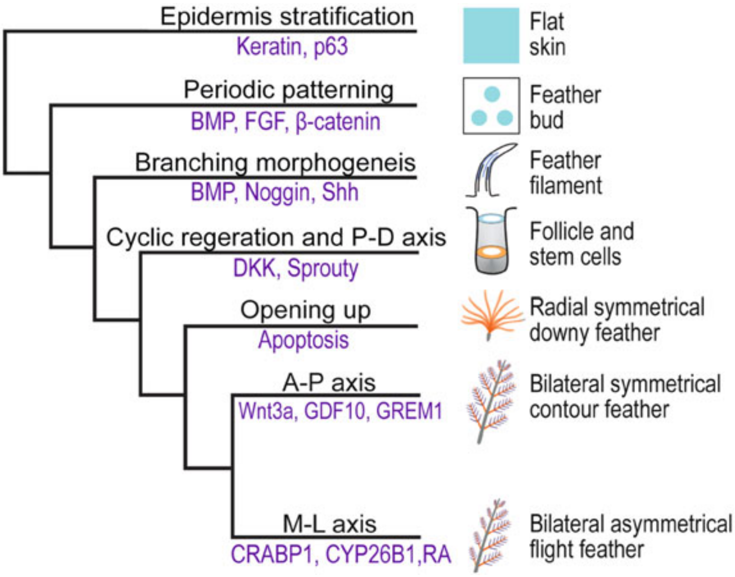

Fig. 2.2 Stepwise evolution of feathers (modified from Xu et al. 2014)

fields (Jiang et al. 1999). Ectopic feather tracts can also be induced by bone morphogenetic protein 2 (BMP2), which up-regulates exogenous expression of cDermo-1 (Twist 2) and then leads to the formation of dense dermis (Fig. 2.3b) (Hornik et al. 2005; Scaal et al. 2002).

2.2.2 Feather Bud Induction

Following the formation of feather tracts, micro-patterning takes place within the homogenous tract field to demarcate bud and interbud regions. This periodic patterning can be generated by reaction diffusion (R-D) and interactions of molecules that promote [activators: fibroblast growth factors (FGFs)] and suppress (inhibitors: BMPs) feather bud formation (Fig. 2.3c) (Widelitz et al. 1996; Jung et al. 1998; Noramly and Morgan 1998). During the micro-patterning processing of bud induction, several genes identified as restrictive expression patterns in the bud domain (e.g., Wnt-7a, β-catenin) or interbud domains (e.g., GREM1 and Wnt-11) define the boundaries between neighboring feather buds (Noramly et al. 1999; Ohyama et al. 2001; Chang et al. 2004a).

2.2.3 Establishment of the A-P Axis and Elongation Along the P-D Axis

After the formation of feather bud boundaries, further specification of bud and interbud regions occurs through the de novo activation of certain molecular pathways within specific regions. For example, sonic hedgehog (Shh) is preferentially expressed in the bud region and induces dermal condensation, whereas collagen I is preferentially expressed in the interbud (Ting-Berreth and Chuong 1996; Atit et al. 2003). In summary, these genes expressed de novo are involved in intra-bud morphogenesis, including bud axis specification, growth, and differentiation. At the early stage, feather placodes are radially symmetric. Then, due to the de novo expression of Notch ligand (Delta-1, Serrate-1) and Notch-1 on the posterior and central region of the outgrowing feather bud, an A-P molecular asymmetry emerges (Fig. 2.3d), after which the symmetric short buds will develop into asymmetric elongated buds (Chen et al. 1997). The outgrowth of feather buds proceeds along the posterior direction on the body, accompanied by increased cell

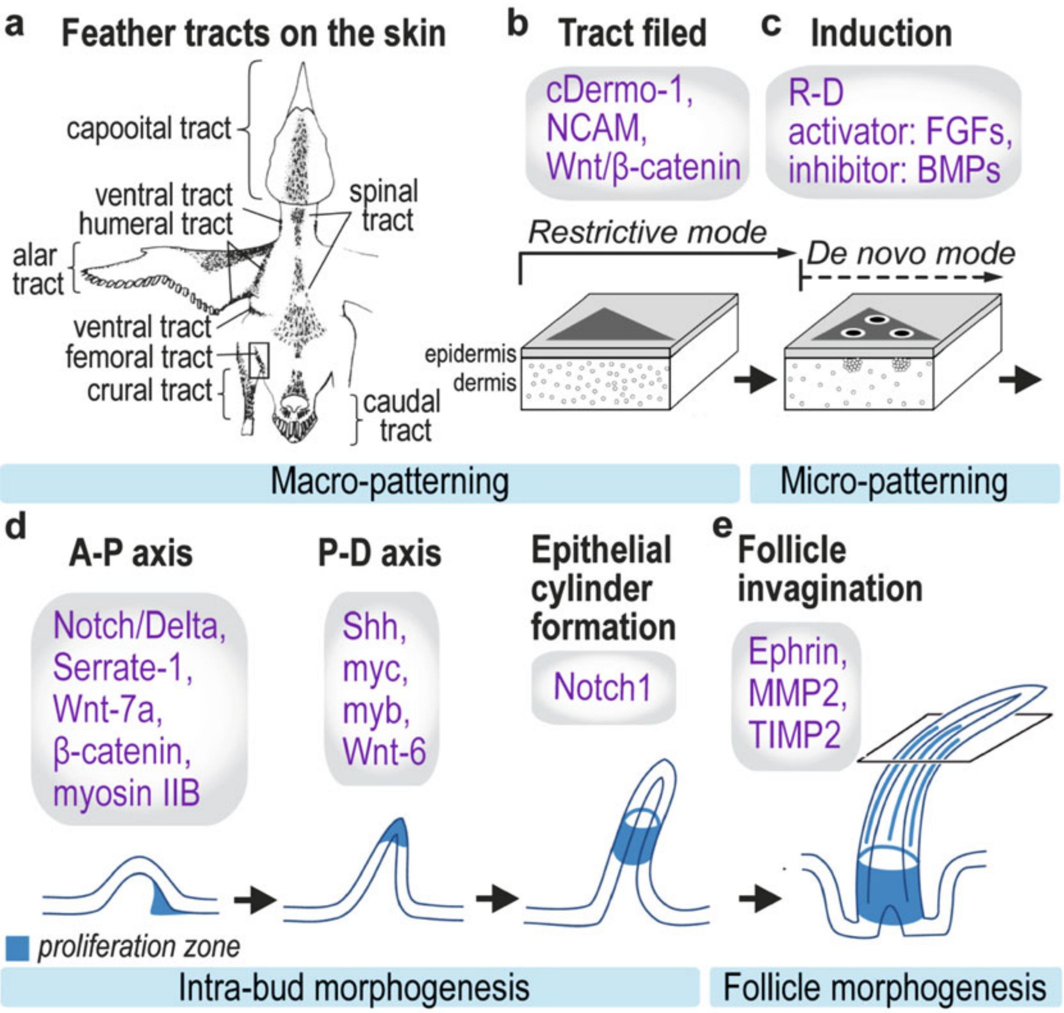

Fig. 2.3 Development of feather follicles during embryogenesis [modified from Gill 1994 (**a**), Chuong et al. 2000 (**b**, **c**), Chen et al. 2015 (**d**, **e**)]

proliferation at the posterior bud epithelium and polarized dermal cell rearrangement (Fig. 2.3d) (Chodankar et al. 2003; Li et al. 2013).

Wnt-7a is initially restrictively expressed at the boundary of feather buds. Later, the asymmetrical expression of Wnt-7a in the posterior-distal bud epidermis becomes an inducer of A-P asymmetry and the elongation of buds along the P-D axis (Widelitz et al. 1999). Wnt-7a induces β-catenin nuclear translocation, which activates non-muscle myosin IIB (NM IIB) and Serrate-1 (Notch ligand) expression. NM IIB enhances cell motility to enable polarized movements, while a positive feedback loop between Wnt and Notch signaling, as well as the lateral inhibition of Serrate-1 and Notch-1, help establish and maintain the spatial configuration of cell rearrangement zones. This ensures the elongation of feathers in a robust manner (Li et al. 2013). In the anterior half of feather buds, Msx-1 and -2 are asymmetrically localized and involved in bud growth and differentiation (Noveen et al. 1995). During feather bud elongation, the localized cell proliferative zone in the epithelium shifts from the posterior to the distal bud end and mediates the expansion of the feather epithelium to adapt to