Explanatory History of the Origin of Feathers

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SYNOPSIS. Historical-narrative evolutionary explanations for the origin and further evolution of avian feathers involve two steps. The first phase reconstructs a series of probable morphological changes from a reptilian scale to the primitive feather. The second deduces possible functions and biological roles of the features and feasible selective demands on these features at all stages in its evolution. The best explanation for the evolutionary origin of feathers would be one consistent with historical-narrative evolutionary explanations for the origin and further evolution of other features in the history of birds. Feathers of Recent birds have a number of functions and biological roles, and it is difficult to ascertain which of these functions and roles were involved in feather origin. Two major rival published theories are based on the roles of feathers in insulating the body against heat loss and in providing an aerodynamic surface for flight. However, because of the lack of knowledge about the roles and ecological relationships of protofeathers and of the most primitive feathers, it is not possible to test strongly either of these theories, or others as proposed in this symposium, against objective empirical observations to determine which is falsified or is the most probable. Finally it is argued that test of historical-narrative evolutionary explanations, including classifications and phylogenies, is generally difficult to impossible because of the lack of the necessary objective empirical observations.

INTRODUCTION

Feathers are perhaps the most characteristic feature of birds (Class Aves), being complex epidermal structures that evolved from reptilian scales. When most people think of avian feathers, they envision only typical contour feathers covering the body of birds. But feathers come in a wide variety of forms (Lucas and Stettenheim, 1972; Stettenheim, 2000). In addition to the contour feathers, remiges (wing feathers) and rectrices (tail feathers), there are semiplumes, down feathers of several types, oil gland feathers, powder downs, bristles of several types, semi-bristles, filoplumes, and a large series of specialized and often bizarre courtship plumes. The highly modified courtship plumes found in many species of birds of paradise (Paradiseaeidae) are only one extreme of the diversity of courtship plumes found in birds. The two elongated plumes extending from the head of the King of Saxony Bird of Paradise (Pteridophora alberti) with their series of small plate-like flags attached to one side of the central rachis are perhaps the most modified and bizarre feather found in birds.

A contour feather, as a typical feather, has a complex morphology consisting of a central shaft or rachis to which barbs are attached on two margins to form a vane. The barbs possess two rows of barbules of different types, the proximal and the distal barbules, whose morphology permits them to lock together and thereby maintaining the integrity of the vane. The base of the vane may have a downy portion. The proximal end of the central shaft, or calamus is imbedded in the skin and usually has a set of cutaneous muscles attached to it. The main feather may have an afterfeather (or aftershaft) attached to it, arising from the underside of the feather at the superior umbilicus. Embryological development of feathers is equally complex with the flat, two-dimensional feather growing from a circular base.

The diversity of functions and biological roles of avian feathers is also great. Most people think of feathers serving only for in-
sulation of the body and for flight. However, feathers are also involved in protective coloration, signaling of all types (aggression, species recognition, flashing signals) between conspecific individuals as well as between interspecific individuals, courtship displays of all types, streamlining of the body (Bühler, 1990), cleaning of the plumage (powder from powder downs or powder feathers), waterproofing of the plumage rather than of the body itself, sound production, and apparently chemical defenses (Dumbacher, 1994; Dumbacher and Pruett-Jones, 1996). The last was discovered only within the past decade when toxic chemicals were found to be present in the feathers, as well as other body parts of the bird, and may serve as a chemical defense similar to that present in the skin of many amphibians. Interestingly, these feather toxins are chemically similar to toxins found in amphibian skin (Dumbacher and Pruett-Jones, 1996, p. 137).

Feathers do not exist as isolated structures on the surface of the avian body, but are connected together, along with other structures, to form the plumage. The plumage together with the skin, including a layer of fat, dermal and subdermal cutaneous muscles, ligaments and sense organs (Homberger and de Silva, 2000), forms an interconnected series of separate features—an organ. A complex pattern of feather muscles connects the calami of neighboring feathers. Most likely the structural and functional requirements of those feather muscles have determined the arrangement of the body feathers into rather sharply delimited pterylae (feather tracts) in almost all groups of birds, rather than being spread evenly over the entire surface of the body as in the penguins (Spheniscidae), or almost so as in the ostriches (Struthionidae) and screamers (Amhimidae) (Homberger and de Silva, 2000).

Feathers are, therefore, not isolated features in the avian body, but are part of the complex organ, the integument. Feathers come in a variety of morphologies within a single species, and also vary considerably among species, as can the other features of the integument. Therefore it is not realistic to discuss the evolution of the avian feather independently of the evolution of the avian integument with all of its interconnected features. The evolution of such a complex system as the avian integument must certainly have been a pattern of mosaic evolution (de Beer, 1954) in which the different features of the integument evolved at different times, at different rates, and under the control of diverse selective demands (Bock, 1965, 1972, 1979). Without doubt the selective demands operating during the earlier phases in the evolution of the avian integument are different from those acting on modern birds. And indeed the suite of selective demands acting on the avian integument, including the feathers, differs among the diverse groups of modern birds.

Within a historical-narrative explanation of the evolution of the avian integument from the reptilian integument, one can inquire about the evolution of avian feathers from reptilian scales. Again feathers are not a simple feature, but are composed of a number of different parts which almost certainly had evolved in a pattern of mosaic evolution (Regal, 1975, 1985). Clearly the first question to ask would be about the possible morphology of these structures in the most primitive stages in the evolution of feathers. This is not a simple question because the primitive stage in feather evolution could have been most similar to a flight feather, or to a down feather, or to a contour feather with or without an aftershaft. And it is possible that some diversity already existed in the morphology of the most primitive feathers. The second question to ask would be how the diversity of feather types found in modern birds evolved from this original feather or feathers. Associated with these questions are those on the possible functions and biological roles in all stages in the evolution of the primitive avian feather from the reptilian scale, and in their further evolution into the diverse types of feathers present in modern birds. Moreover it is necessary to speculate about the feasible selective demands acting at all stages during these evolutionary episodes. Reflections on the possible selective demands acting on the evolution of feathers must be coupled with deliberation on the selective demands acting during the evolution of the entire integument.

Lastly, one must realize that any historical-narrative explanation of the evolution of feathers or of the avian integument must
treat these features as a holistic system in which all of the parts interact morphologically and functionally and are, at least, not grossly selectively disadvantageous. Moreover, explanation of the evolution of the avian integument and of feathers must be considered with the evolution of the entire animal in a similar holistic way. Hence, one must be aware not only of the possible functional and adaptive attributions of the evolving integument, including the feathers, but how these changes fit into the evolution of all other features found in the intermediate stages in the evolution of birds from reptiles.

FACTUAL KNOWLEDGE

The factual knowledge available on which we can speculate on the evolution of the avian integument is most scanty. We know much about the morphology, function and biological roles of the skin, including feathers in Recent birds. Further, we know much about the diversity of feather types within and among individual species of Recent birds. We know much about the skin and scales of Recent reptiles. Fossil remains of the skin of reptiles are rare and tell us little to nothing about the morphology of scales in possible avian ancestors among the reptiles. Fossil feathers of birds are equally rare, and most of these are either remiges or rectrices. Contour feathers are known, but fossils of other feather types are either completely unknown or exceedingly rare. To my knowledge, there are no fossil remains of the other features of the avian integument, except for rare finds of the rhamphotheca and podotheca which are of no assistance to the question of the evolution of feathers. The excellent fossil remains of feathers from the several specimens of *Archaeopteryx* are remiges and rectrices. These fossil *Archaeopteryx* feathers show some of the details of feather structure, such as the barbs, very well. But we lack completely fossils of all intermediate stages between reptilian scales and the most primitive feather. Moreover, analysis of the increasing number of known avian fossils from the Mesozoic suggests that *Archaeopteryx* appears to belong to the subclass Ornithurae, together with the “opposite-birds” (the Enantiornithes), which are a side branch to the lineage leading to the known Recent birds (Kurochkin, 1995). Hence the attributes of feathers observed in *Archaeopteryx* may not be of much assistance in considering the evolution of these structures from their reptilian homologues to the feathers found in Modern birds, all of which are members of the subclass Ornithurae.

The complex structure of avian feathers, including all information from fossilized feathers such as those present in *Archaeopteryx*, suggests strongly that feathers evolved only once in the history of the Vertebrata. This conclusion is based on the complicated morphology present in all feathers, as well as their particular and intricate mode of embryological development. Had feathers present in fossil and Recent forms originated more than once in the evolution of tetrapods, one would not expect the entire suite of complex morphological attributes to have evolved in the two or more independent lineages of birds possessing feathers.

Aside from the general consensus that the remiges of *Archaeopteryx* possess the typical asymmetrical vane structure of the flight feathers of Recent birds and that, hence, the remiges of *Archaeopteryx* form an aerodynamic surface of the forelimb of this animal, little to nothing can be said from the fossil record on functions and roles of feathers, especially of the intermediate stages between the reptilian scale and the primitive avian feather. The rectrices of *Archaeopteryx* appear to have a symmetrical or almost symmetrical vane. I would like to note that there appears to be no question that *Archaeopteryx* possessed a definite wing, but the available evidence from this fossil (e.g., size and structure of the coracoids and sternum) does not permit a conclusion that *Archaeopteryx* was an active flapping flier able to propel itself through the air (i.e., gain altitude) with forces generated by flapping of the wings (Bock and Bühler, 1995). The known wing structure, including the morphology of the remiges, of *Archaeopteryx* is completely consistent with the conclusion that this bird was a specialized glider.
EXPLANATIONS FOR FEATHER ORIGIN

THEORIES FOR THE ORIGIN OF FEATHERS

Explicitly stated theories for the origin of avian feathers had their origins toward the close of the 19th century with Pycraft (1894, 1896, 1910) arguing that feathers arose in connection with flight. Heilmann (1926:197–200) concurred with this conclusion and declared that feathers arose as scales elongated along the posterior margin of the forelimbs and hindlimbs and along the lateral edges of the tail to provide a parachute and subsequently an aerodynamic surface for flying. Fürbringer (1888) and Tucker (1938) argued that feathers arose in association with thermoregulation, associated with the evolution of homiothermy.

The flight theory for the origin of feathers was supported in more recent years by Parkes (1966), Feduccia and Tordoff (1979), and Feduccia (1993; 1996). The thermal insulation theory was championed further by Regal (1975, 1985), Bock (1965, 1985, 1986), Bock and Bühler (1995), and Griffiths (1996).

The flight theory argues that primitive feathers were flight feathers that arose as elongated scales along the posterior edge of the forelimb and the lateral margins of the tail in connection with providing a larger surface for these projections of the body in association for parachuting and later for flight which evolved from gliding and developed into active flapping flight. As the scales elongated, they became frayed and this condition developed into the barbed structure of feathers. The feathers then spread over the rest of the body, presumably in connection with the evolution of homiothermy. Some advocates (Parkes, 1966) of the flight theory argued that if feathers had evolved originally in connection with insulation, then the primitive feather would be down-like, and that such a feather would be easily damaged unless protected by an outer layer of contour feathers. But there is little foundation for the claim that primitive feathers had to be similar to present-day avian down to serve as insulation. Most advocates of the flight theory support the conclusion that the evolution of avian flight was down from elevated places, such as trees.

The insulation theory is based on the conclusion that primitive feathers were a type of contour feather. These primitive contour feathers did not have to be good insulators, that is, they could have lacked a downy base as present in the contour feathers of many Recent birds. None of the proponents of the insulation theory argued that the primitive feather was down-like. Regal (1975) emphasized that the insulating properties of elongating scales and primitive feathers did not necessarily have to prevent heat from leaving the animal’s body, but could well have served as sun shades to prevent excessive heat from entering the animal’s body. Once present as a covering on the body of a protobird, contour feathers along the posterior edge of the forelimb and the lateral margins of the tail could have elongated and evolved into flight feathers in response to selective demands associated with parachuting, then gliding, and finally active flight. Most proponents of the insulation theory agree that the evolution of homiothermy predated the evolution of avian flight and that the origin of avian flight was from an elevated site [i.e., tree-down] rather than from the ground-up. Bock (1985) and Bock and Bühler (1995) argue that avian homiothermy could have evolved in connection with birds becoming arboreal for some of their activities for which homiothermy would have been advantageous. They point out that an animal, such as a protobird, could have searched for its food on the ground and used trees for resting, hiding, sleeping and possibly nesting. Hence the features of early birds, such as Archaeopteryx, could exhibit adaptations for both ground-living and tree-dwelling.

Other theories for the origin of feathers have been advocated over the years but have attracted less attention. Thulborn and Hamley (1985) argued that feathers arose as an insulating blanket in juveniles. Further they claimed that primitive birds lived along the shoreline for which the plumage served as a waterproof insulation, and that feathered wings evolved to form a canopy to cast a shadow over an area in the water while searching for fish. This is in analogy to a technique used by a few species of present-day herons (e.g., Black Heron, Hydran-
**Assa ardesiaca: Ardeidae; Hancock and Elliott, 1978.** Dyck (1985) concluded that avian feathers evolved for water repellency. Reichholf (1996) proposed that feathers originated as a sink for the deposit of excess sulphur waste products from the metabolism of certain proteins. Homberger and deSilva (2000) argues that feathers arose to provide a streamlined outer shape of the body in connection with moving efficiently through the air. Subsequently feathers would have acquired biological roles associated with water repellent, heat conservation and finally flight.

**Testing These Theories**

The several theories for the origin of avian feathers, as well as for the origin of the winged forelimb and avian flight, are all historical-narrative explanations (Bock, 1985, 1999). Historical-narrative explanations must be founded on pertinent and well tested nomological-deductive explanations (Bock, 1999, 2000). Historical-narrative explanations must be most carefully presented with their diverse parts in proper chronological order. Moreover a historical-narrative explanation pertains only to the particular phenomenon being examined; they are never general. Hence a well-tested historical-narrative explanation for the origin of flight in birds cannot be applied to the origin of flight in bats or in pterosaurs. It is true that explanations of the origin of flight in these three groups of tetrapods involve nomological-deductive explanations for aerodynamics, but these aerodynamic explanations form part of the essential underlying nomological-deductive explanations for each of the separate historical-narrative explanations for origin of flight in birds, bats and pterosaurs.

The historical-narrative explanations for the origin of feathers, the avian plumage, or avian flight are also evolutionary explanations. As such they depend on a number of additional prerequisites. First the modifications of the features and the organisms must be arranged in a series of realistic evolutionary steps (Bock, 1979) arranged in a proper chronological sequence. The resulting pattern of modifications form a mosaic configuration of evolutionary change (de Beer, 1954). Second, the organisms at every stage in the evolutionary sequence must be functional wholes interacting successfully with selective demands arising from the particular environment of the organisms at each stage in the evolutionary sequence. Third, the sequence of evolutionary steps must be continuous and gradual with no large saltational changes.

It is also necessary to specify the form and detail of the evolutionary historical-narrative explanation that one wishes to advocate. These explanations can vary from those that consider only a series of morphological evolutionary (=phylogenetic) changes from the ancestral group to the descendent group or from the primitive to the advanced stages of a feature to the considerably more difficult explanations dealing with the functional and adaptive bases of these evolutionary modifications. Both types of historical-narrative evolutionary explanations are difficult to test because of the objective empirical observations available for the testing. However for most groups and/or features of living organisms, fossil or Recent, the second type of explanation are generally well beyond the possibilities for objective empirical testing because the needed empirical observations, such as information on the biological roles and the selective demands are not available to the biologist.

Let us consider first the simpler explanation of a series of morphological evolutionary changes in the evolution of avian feathers from reptilian scales. A most realistic series of changes has been outlined by Regal (1975) in which he showed that the original reptilian scales could have first elongated, then subdivide into a series of lateral plates (i.e., protobars) on each side of a central shaft. These protobars developed protohooklets and friction areas (a velcro-like structure). Finally the lateral plates could have subdivided again to form protobarbules. There is still the question of how the original flat scale growing from a linear base evolved into the circular ontogenetic system of feathers which achieve their flattened form only after they have developed fully and emerged from the sheath covering the growing feather. And there is
still the unanswered puzzle of the morphology of the primitive feather—whether it was a simple contour feather with or without a downy base, whether it was a contour feather with an aftershaft, whether it was a downy feather, or whether it was a flight feather. Was the primitive feather waterproof or, better said, water-resisting? Not all feathers in Recent birds are water-shedding or water-resistant. Cormorants (Phalacrocoracidae) and some other members of the Pelecaniformes do not have water-resisting feathers in spite of being water birds. Even though the series of stages from reptilian scales to the avian feather proposed by Regal is reasonable, no empirical evidence exists with which to test it.

The more difficult explanation of the functional properties and the associated selective demands at all stages in the evolutionary origin of the avian feather from reptilian scales is more interesting, but almost impossible to test. One can present a number of realistic explanations of the functional properties and selective demands associated with the evolution of the avian feather, but how can one first test the several individual theories and then chose between rival explanations? I have argued (Bock and Bühler, 1995) that a more convincing explanation for the origin of feathers can be achieved if this explanation is linked with explanations for the evolution of other features, such as arboreal habits, homoiothermy and flight, in the evolution of birds with avian flight more likely evolved from the heights (trees) downwards. Claw structure in Archaeopteryx argued strongly for these animals being arboreal for at least part of their daily life. Taking to trees was more likely for reasons such as hiding, resting and nesting than for obtaining food. Being in trees is cooler than being on the ground. Homoiothermy could have evolved for such purposes as incubating a clutch of eggs in a tree nest. Feathers could have evolved together with the origin of homoiothermy. Feathers could have elongated on the forelimbs and lateral margins of the elongated tail in connection with leaping and parachuting out of trees. Parachuting could have evolved into gliding and finally into active flight. Active flight required a more rapid metabolic rate together with elevated body temperature, and etc. However, as satisfying as this explanation may be to some workers, there is no way to test it against objective empirical observations because we know nothing about the ecological relationships of protobirds or primitive birds at the time feathers originated.

Possibly an equally satisfying explanation could be developed for the origin of feathers as flight structures, but none of the workers who advocate this explanation have presented a sufficiently full explanation linked with explanations for the evolution of other avian features. The usual explanation that scales along the posterior edge of the forelimbs and the lateral margins of the long tail is possible, but it has never been presented together with the evolution of other associated attributes of protobirds. The argument for the evolution of flight feathers as presented by Feduccia (1993, 1996) could apply equally well, and even better, to the elongation of original contour feathers along the forelimbs and tail rather than the elongation of scales as he assumed.

Another difficulty in assessing rival explanations for the origin of feathers and associated features as the wing and flight is the rather easy trap of arguing that a particular evolutionary modification is “easier” or “simpler” than others, and hence would be the correct explanation. Consider the evolution of the feathered avian wing. In all other gliding or flying tetrapods, the aerodynamic surface is a flattening of the body and/or the enlargement of a flap of skin generally associated with the forelimb. Why has an similar simple evolutionary change not taken place in the evolution of an aerodynamic surface in birds. Recent birds have well developed flaps of skin in their wing—the prepatagium along the anterior edge of the wing from the trunk to the wrist and the metapatagium along the posterior edge of the wing from the trunk to the elbow. Such flaps could have been present early in protobirds and could have enlarged to form an aerodynamic surface similar to those present in pterosaurs and bats. One could argue that such a change could have been much simpler than the
elongation of small scales adhering tightly to the skin of protobirds. This argument could also be applied to the elongation of contour feathers to form an aerodynamic surface, except that it is realistic to assume that the contour feathers on the wings of the earliest birds could have had some length and thereby contributed to an initial, unspecialized parachute when early arboreal protobirds descended from trees by leaping. But to argue that the easiest or simplest evolutionary modification to form an aerodynamic surface in tetrapods was the appearance of a flap of skin does not constitute a valid argument for formulating and especially for testing historical evolutionary explanations of the origin of feathers.

**DISCUSSION**

The basic difficulty in proposing full historical-narrative explanations for the origin and further evolution of features in living organisms is that so little information is available for their formulation and especially for their testing. If biologists are fortunate, then a fairly complete series of fossils are known which demonstrate some of the stages in the appearance and further perfection of these features. But such series of fossils are rare for most features, and especially in the earliest stages of their evolutionary modification. Basically what is available in the fossil record are only hard parts—bones and teeth for vertebrates, and shells for mollusks, arthropods and echinoderms. The soft anatomy is lacking except for exceedingly, exceedingly rare fossil finds. For full historical-narrative evolutionary explanations for vertebrates, biologists are faced with formulating functional and adaptive interpretations while having available in fossils only some of the supporting elements of the bony skeleton. (This is equivalent to having only a few nuts, bolts and connecting elements of a complex machine to understand the structure and operation of this machine—clearly insufficient knowledge.) Everything else is lacking, including a knowledge of the cartilaginous ends of the bones, the ligaments binding the skeleton together, the muscles moving the skeletal elements, and etc. In addition, knowledge is totally lacking about the actual environment of the organisms, of the functions and biological roles of the features, and of selection demands arising from the external environment and acting on the organisms. In almost all, if not all, origins and specialization of new features in the evolutionary history of living organisms, these features could have possessed several functions and biological roles during the evolutionary episode and hence could have interacted with several selective demands. And most likely the set of selective demands acting on the “fully evolved” feature, such as those that may be acting on that feature in Recent organisms, are different from those that may have acted when the feature first appeared. I know of no way to ascertain successfully which selective demands were operating on such features when they were appearing and were first becoming more specialized. Hence as much as biologists and the lay public are interested in knowing the details of the appearance and evolution of the diverse and numerous features in living organisms, we must resist the temptation to present definite historical-narrative evolutionary explanations in an authoritative way as well-tested theories, or even worse as facts. This applies to explanations for the evolutionary origin of avian feathers and avian flight. Although I feel that a rather consistent and satisfying explanation can be offered for the insulation theory of the evolutionary origin of avian feathers, this explanation can be offered only as a poorly tested theory and one that probably cannot be tested any better than it has been to date. And the insulation explanation, much as I might prefer it, is no better tested that the flight theory for the origin of feathers, or the sulphur-waste deposition theory or the water resistant theory or the fishing-canopy theory, or any other theory presented in this symposium. We can still present evaluations on which of the rival theories is the most realistic or satisfying, but this does not demonstrate that the most satisfying theory is correct or is even well tested. We can investigate nomological-deductive evolutionary explanations, such as the mechanisms underlying major evolutionary changes. And we can still advocate realistic histori-
cal-narrative evolutionary explanations for the origin and history of individual features and groups. But grave difficulties appear when we are faced with the objective empirical testing of these historical-narrative evolutionary explanations for the appearance and evolution of particular groups of organisms, such as birds and mammals, or of particular features, such as avian feathers or avian flight. We must be careful not to lapse into the excessive speculations that characterized evolutionary biology during the last years of the 19th century and turned so many biologists away from thinking about evolutionary explanations and to consider only strictly functional explanations.

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