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## Functional Microanatomy of the Feather-Bearing Integument: Implications for the Evolution of Birds and Avian Flight<sup>1</sup>

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**SYNOPSIS.** A selective regime favoring a streamlining of body contours and surfaces is proposed as having been instrumental in driving the morphological and functional transformations of an unfeathered reptilian integument into a feather-bearing avian one. This hypothesis is consistent with a new, structurally and functionally coherent analysis of the microanatomy of the avian feather-bearing integument as a complex, integrated organ system that includes an intricate, hydraulic skeleto-muscular apparatus of the feathers, a dermo-subcutaneous muscle system of the integument, and a subcutaneous hydraulic skeletal system formed by fat bodies. Key elements of the evidence supporting the new hypothesis are (1) the presence of depressor feather muscles that are not needed as antagonists for the erector feather muscles, but can counteract external forces, such as air currents; (2) the fact that the highly intricate feather-bearing integument represents a machinery to move feathers or to stabilize them against external forces; (3) the crucial role of the coat of feathers in streamlining the body contours and surfaces of birds; (4) the aerodynamic role of feathers as pressure and turbulence sensors and as controllable temporary turbulators; and (5) the critical role that a streamlined body plays in avian flight and is likely to have played in the evolutionary transformations from ecologically and locomotorily versatile quadrupedal reptiles to volant bipedal birds without passing through parachuting or gliding stages. These transformations are likely to have occurred more than once. The ancestral birds were probably small, arboreal, hopping, and using flap-bounding, or intermittent bounding, flight.

### INTRODUCTION

Birds have traditionally been identified as such by the presence of feathers, and feathers, therefore, have been the diagnostic character *par excellence* of birds (*e.g.*, Padian, 1998; Dyck, 1985; Gibbons, 1998; Ji *et al.*, 1998). Diagnostic features are needed to classify organisms and taxa in clearly identifiable and delimited groups, and classification is the necessary foundation for comparative studies and evolutionary biology. But if the objective is to reconstruct the history of the evolution of birds from their reptilian ancestors, then it is necessary to go beyond the identification of diagnostic features and to use a comparative anatomical approach that seeks to trace the gradual course of morphological and functional

transformations of structures and organisms across the taxonomic boundaries established by classification (see also Homberger, 2000; Maderson and Homberger, 2000). Such an approach will be used in our study to elucidate the evolutionary transformation of an unfeathered reptilian integument into a feather-bearing avian one.

The reconstruction of the evolutionary history of structures and organisms is achievable because the processes responsible for evolutionary change are known in principle. These processes involve the appearance of structural and functional innovations (*i.e.*, variations) through modifications of the genetic information and developmental processes, as well as the concomitant appearance and action of a selective regime that is compelling enough to overcome stabilizing selection. A successful reconstruction of the evolutionary history has to be biologically realistic and coherent, has to be explicit about its underlying assump-

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tions and inferences, and has to generate hypotheses that can be tested.

The present attempt at reconstructing the evolutionary history of feathers, birds and avian flight is organized in five main sections: (1) a new, structurally and functionally coherent analysis of the feather-bearing integument; (2) a reconstruction of a model of early birds and early stages of avian flight; (3) inferences from data on the anatomy and biology of reptiles about the probable reptilian antecedents of avian structures and their functional and ecological roles; (4) inferences from data on the anatomy and biology of mammals on the structural and functional uniqueness of the avian integument and avian flight; and (5) a new scenario of the probable gradual evolutionary transformations from an unfeathered reptilian organism to a feather-bearing avian organism.

#### PREMISES

Before trying to reconstruct the evolutionary history of feathers, several basic premises need to be considered. First, feathers occur in a great variety of shapes, structures, and functions not only among the various taxa but also within single individuals, and the various types of feathers, except filoplumes, are not sharply defined but intergrade into one another (Hempel, 1931; Lucas and Stettenheim, 1972; Stettenheim, 2000). The avian integument as a whole is even further diversified as rhamphothecae, claws, diverse types of scales, and various other integumentary structures (see also Stettenheim, 2000). Such a regionally diversified morphology of the integument, however, is characteristic of all vertebrates and reflects locally specific interactions between the various body parts and the environment (see also Walker and Homberger, 1992). It is, therefore, biologically realistic to assume that the avian integument had the capacity to grow a variety of feather types already at its very inception, even though previous authors have assumed that the originally appearing feathers were of a single type (see, *e.g.*, Lucas and Stettenheim, 1972; Brush, 2000).

Second, feathers, in particular contour feathers, are relatively large accessory

structures that require a skeleto-muscular apparatus capable of moving and stabilizing them. Therefore, any scenario that reconstructs the evolutionary history of feathers must deal with the entire integument and its subcutaneous structures. Previous authors did not do this, despite the availability of many classic studies on the morphology of the avian integument (for reviews, see Moser, 1906; Greschik, 1915; Lange, 1931; Osborne, 1968; Lucas and Stettenheim, 1972; de Silva, 1995; de Silva and Homberger, 2001).

Third, fossil integumentary material is notoriously incomplete, except with respect to dermal sclerifications therein. Some of the best preserved examples of fossil reptilian skin stem from the epidermis of dinosaurs, which show flat to conical, tuberculate, non-imbricating scales (*e.g.*, Czerkas, 1997; Chiappe, 1998; Chiappe *et al.*, 1998). In contrast, the structural details of the skin of fossils with feathers have not been preserved (Czerkas, 1997). Because the functionally relevant structure of integumentary soft tissues associated with feathers are unlikely to be fossilized, any attempt to reconstruct the evolutionary history of feathers from a scaled integument must rely on studies of extant vertebrates, in which all the relevant morphological, functional and biological features of the integument can be examined. Hypotheses about the functional, ecological and evolutionary significance of the avian integument and its parts can be tested through natural experiments in which the comparisons need not be restricted to taxa that are genealogically closely related (see also Gould, 1976; Bock, 1986; Homberger, 1999a, 2000).

#### FUNCTIONAL MORPHOLOGY OF THE FEATHER-BEARING INTEGUMENT

In the following, a new, structurally and functionally coherent description of the morphology of the feather-bearing integument is presented as a basis for fresh hypotheses on the evolutionary origin of feathers. The feather-bearing integument is defined here as the part of the integument that is covered by a coat of feathers and includes both the feather tracts (*i.e.*, ptery-lae) and the apteria without contour feath-

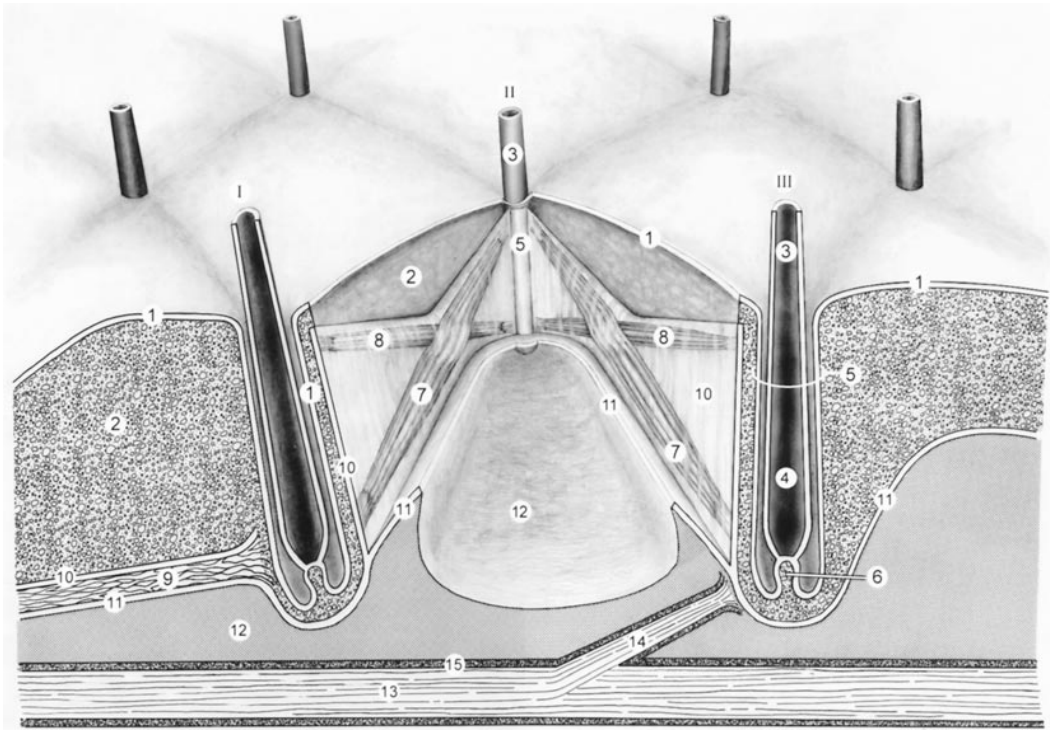


FIG. 1. Diagrammatic transverse section through the feather-bearing integument of *Meleagris gallopavo* at about mid-length of the neck. The view is towards caudal of the bird, the left side of the figure is towards dorsal of the bird, and the right side of the figure is towards ventral of the bird. A wedge of tissue, comprising the epidermis, dermis, elastic membrane, and a superficial portion of the *Fascia superficialis*, was removed from the center of the section to reveal the obliquely arranged feather muscles. 1 epidermis, 2 dermis; 3 rachis of a feather (cut), 4 calamus of a feather, 5 feather follicle, 6 feather papilla, 7 smooth erector feather muscle, 8 smooth depressor feather muscle, 9 smooth apterial muscle, 10 elastic epimysium of the apterial and feather muscles, 11 *Lamina elastica*, 12 *Fascia superficialis*, 13 striated subcutaneous muscle (*M. constrictor colli*), 14 *Pars penna* of the striated subcutaneous muscle, 15 collagenous epimysium of the striated subcutaneous muscles, I-III numbered feathers.

ers. More detailed descriptions and comprehensive reviews of the literature can be found in de Silva (1995) and de Silva and Homberger (2001). Specialized integumentary structures (*e.g.*, scales, claws, etc.) are not considered here (but see Homberger and Brush, 1986).

#### Morphological description

The epidermis, the most superficial layer of the skin (*Cutis*), is characteristically thin, flexible, smooth, and its cells contain  $\alpha$ -keratin (Fig. 1).

The dermis, and in particular its *Stratum superficiale* with its densely arranged collagenous fibers, underlies and supports the epidermis. The *Stratum superficiale* intergrades with the deeper *Stratum profundum*,

which consists mostly of less densely arranged collagenous fibers. Where it underlies feather tracts, the *Stratum profundum* is interlarded with fat tissue roughly in proportion to the size and density of the feather follicles that are embedded in the dermis.

Feather follicles, in which feathers grow and are anchored, are formed by the epidermis and part of the dermal *Stratum superficiale* (Fig. 1). Their bases invaginate and sit atop dermal papillae of connective tissue with blood vessels and nerve fibers. The epidermis covering a dermal papilla is the germinative tissue that produces a feather.

The feather muscles are part of the smooth dermal musculature underlying the dermis. They interconnect and move folli-

cles of contour feathers by attaching to adjacent feather follicles (Fig. 1). Their function is determined by the particular location of their attachments along the lengths of the feather follicles. Among the various types of feather muscles, the erector and depressor muscles are always present and are the only ones that are considered in our present study. These muscles attach in pairs to feather follicles and are generally oriented diagonally to the longitudinal and transverse axes of the body and its parts. Hence, they interconnect feather follicles in such a manner that they form parallelograms of which each angle is marked by a feather follicle (Fig. 1). For example, a pair of erector muscles (*Mm. erectores*) run from the neck of one feather follicle (II in Fig. 1) to the bases of two cranio-laterally adjacent feather follicles (I and III in Fig. 1), and a pair of depressor muscles (*Mm. depressores*) run from the base of one feather follicle (II in Fig. 1) to the necks of two cranio-laterally adjacent feather follicles (I and III in Fig. 1). In doing so, the erector and depressor muscles cross each other midway between two adjacent feather follicles.

Where the smooth dermal musculature underlies apteria, it forms apterial muscles (*Mm. apteriales*), which consist of sheets of parallel fiber bundles of varying length, thickness, and density (Figs. 1 and 2A). The fiber bundles consist of alternating muscular and tendinous segments and are anchored to feather follicles along the periphery of feather tracts. They are generally oriented perpendicularly to the length of the feather tracts to which they are anchored (Fig. 2A).

An elastic membrane (*Lamina elastica*) envelops all dermal muscles as an elastic epimysium and also spans the parallelograms that are framed by feather muscles. Thus, the elastic membrane, together with the enclosed dermal muscles, forms a continuous layer, also called musculo-elastic layer, and separates the cutis from the underlying *Fascia superficialis* (Fig. 1).

The *Fascia superficialis* is a subcutaneous layer of connective tissue of varying thickness and variably interlarded with fat tissue. It is especially thick in the thoracic region and under feather tracts that bear

large contour feathers. In certain areas of the body, clearly circumscribed superficial fat bodies (*Corpora adiposa superficialia*) are anchored to its underside. Their fat tissue is sandwiched between two layers of a distinct deep lamina of the *Fascia superficialis* (Figs. 3A and 4).

The subcutaneous, or constrictor, layer *sensu stricto* underlies the *Fascia superficialis* and forms a continuous sheet that consists of connective tissue (*i.e.*, *Fascia subcutanea s. constrictor*) and interposed sheets of striated subcutaneous muscles (*e.g.*, *M. constrictor*, *Mm. subcutanei*) (Figs. 2B and 4). These subcutaneous muscles do not attach to any bony skeletal elements. The cranial half of the *M. constrictor colli* and *M. subcutaneous dorsalis* connect only to the *Fascia subcutanea*. The other subcutaneous muscles form slips with indirect attachments to feather follicles (as *Partes pennarum*) or to the overlying *Fascia superficialis* (as *Partes fasciales*), where the *Fascia superficialis* is fused or tightly connected to the dermis (Figs. 1, 2B, 3A, and 4). In certain areas of the body, clearly circumscribed subcutaneous fat bodies (*Corpora adiposa subcutanea*) are sandwiched between two laminae of the *Fascia subcutanea* (Figs. 3A, B, and 4).

#### *Theoretical mechanical analysis*

For explanatory purposes, the feather-bearing avian integument can be subdivided conceptually into three functional components, namely (1) a hydraulic skeleto-muscular apparatus of the feathers, (2) a dermo-subcutaneous muscular system of the integument, and (3) a subcutaneous hydraulic skeletal system formed by fat bodies.

The first functional component, the **hydraulic skeleto-muscular apparatus of the feathers**, is restricted to the feather tracts and comprises the *Cutis* and the *Fascia superficialis* (Fig. 5). In the resting position, the feather follicles are oriented obliquely within the cutis and generally point caudally (Fig. 5A). The feather muscles are relaxed, and the elastic membrane and *Fascia superficialis* are not under compression or tension. When the erector muscles contract, each feather follicle is subjected to a force couple, and the center of

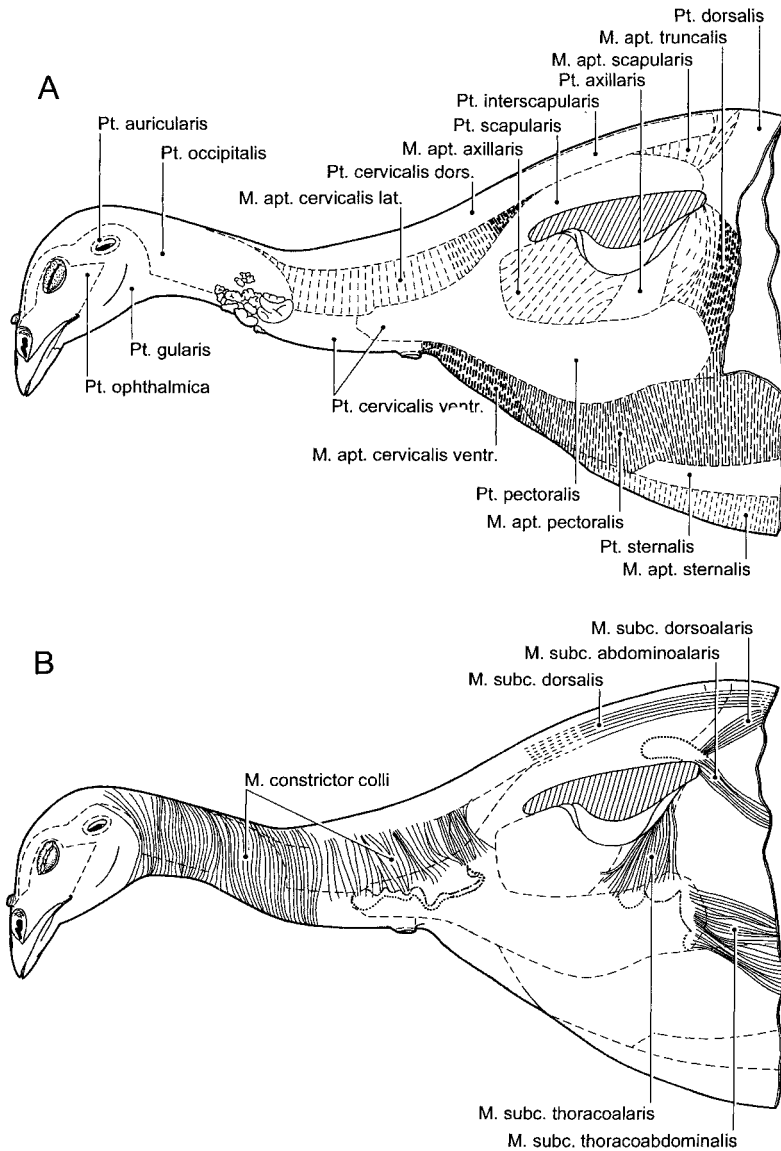


FIG. 2. Diagrammatic lateral views of the head, neck, and thorax of *Meleagris gallopavo*. A: Pterylosis and apterial muscles. The orientation, thickness, and density of the apterial muscles, which bear the names of the apteria they underlie, are indicated schematically. Abbreviations: M.apt. *Musculus apterialis*, Pt. Pteryla. B: Subcutaneous muscles. Dash-dotted lines indicate the extent of their *Partes pennarum*, dotted lines indicate the extent of their *Partes fasciales*. Abbreviations: M.subc. *Musculus subcutaneus*.

rotation of each feather follicle lies at mid-height between the attachments of the feather muscles (Fig. 5B). As the feather follicles are rotated into a more vertical position, their bases dig into the underlying *Fascia superficialis* and create compression points. Fat tissue, however, acts as a non-

compressible hydraulic tissue; it maintains its volume by bulging between the compression points created by the feather follicles and the rhomboid frame created by the feather muscles. This bulging of the *Fascia superficialis* stretches the elastic membrane and fills the spaces between the

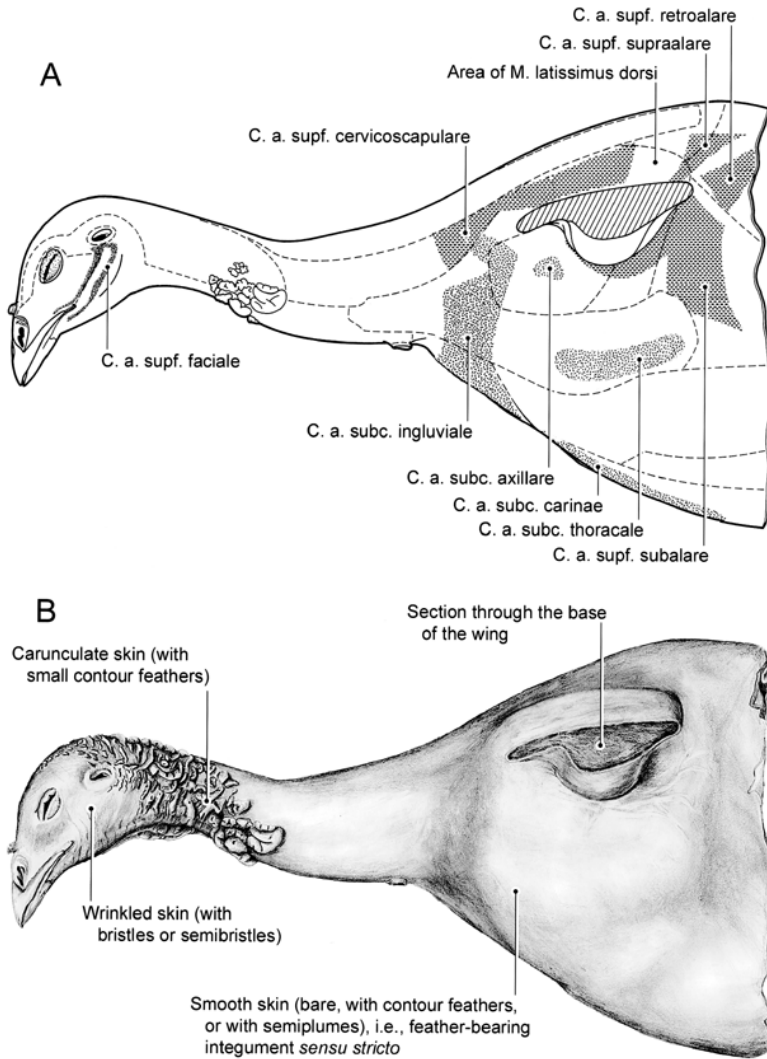


FIG. 3. Diagrammatic lateral views of the head, neck, and thorax of *Meleagris gallopavo*. A: Fat bodies. Abbreviations: C.a.supf. *Corpus adiposum superficiale* (superficial fat body), C.a. subc. *Corpus adiposum subcutaneum* (subcutaneous fat body). B: Contours of the body surface and major types of skin. The feathers have been omitted from the drawing.

feather follicles, which enlarge in proportion with the upward rotation of the feather follicles (Fig. 5B). When the erector muscles relax, the compression points on the fascial fat tissue are released, and the resilience of the stretched elastic membrane compresses and flattens the bulges of the *Fascia superficialis*. As the *Fascia superficialis* returns to its resting configuration, the feather follicles are rotated into a more horizontal position as a result of the re-

duced volume of fat tissue between them (Fig. 5A).

The active raising of feathers through the action of the erector feather muscles allows access to the epidermis for cleaning and removal of parasites (*e.g.*, Osborne, 1968; Brooke and Birkhead, 1991), regulates the amount of air trapped within the coat of feathers to control the body temperature (Bergmann, 1987; Porter *et al.*, 2000), and moves feathers for visual signaling (Morris,

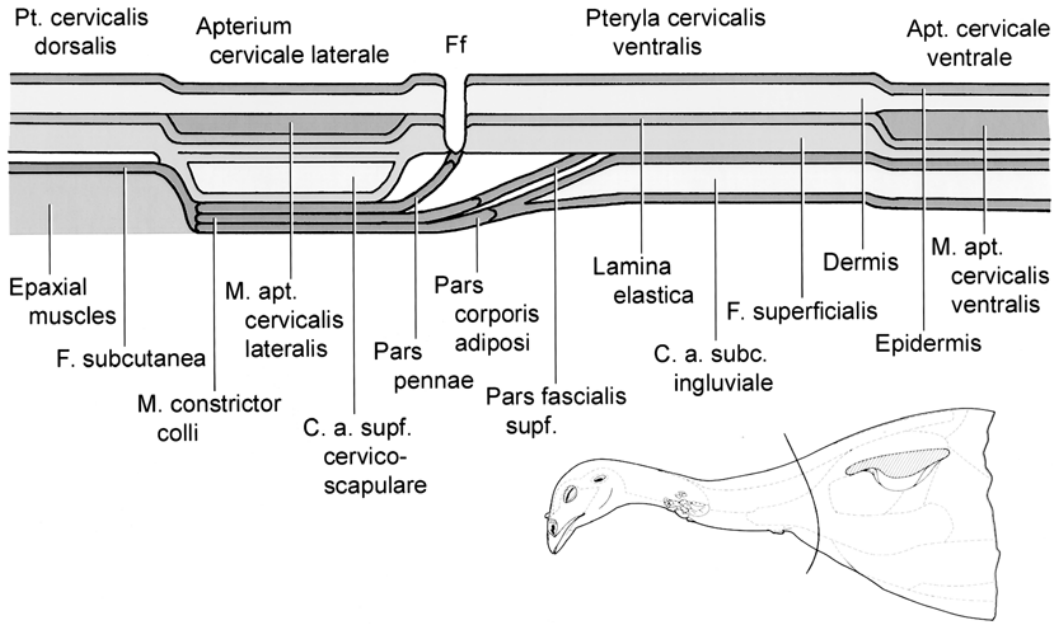


FIG. 4. Diagrammatic transverse section through the integument at the base of the neck of *Meleagris gallopavo*. The level of the section is indicated on the diagram of the lateral view of the turkey. Only one of the many feather follicles in the pterylae is drawn. Note the different construction of the superficial and subcutaneous fat bodies, as well as the different attachments of the three parts of the *M. constrictor*. Abbreviations: C.a. *Corpus adiposum*, F. *Fascia*, Ff *Feather follicle with removed feather*, M. *Musculus*, P. *Pars*.

1956; Osborne 1968; Brooke and Birkhead, 1991). Even though the return of feathers to their resting position is driven mostly by passive forces of elastic recoil (see also Moser, 1906, p. 195), the depressor muscles are always present and usually thicker than the erector muscles (see also Stettenheim *et al.*, 1963; Osborne, 1968). The generally observed sleeking of the feather coat in preparation for take-off or as a fright reaction (*e.g.*, Petry, 1951; Marler, 1956; Morris, 1956, Osborne, 1968), however, does not seem to warrant depressor muscles that are more powerful than erector muscles. Although muscles, in general, are responsible for moving structural elements relative to one another within an organism, they may also play a crucial role in enabling structures to counteract external forces. The depressor muscles of feathers appear to be of this type and serve to counteract air currents that tend to lift feathers and rotate them into a more vertical position (Fig. 5C). This role may require more force than that of raising feathers and explains the gener-

ally greater thickness (*i.e.*, number of muscle fibers) of the depressor feather muscles.

The second functional component of the feather-bearing integument, the **dermo-subcutaneous muscular system of the integument**, consists of the smooth apterial muscles (Fig. 2A) and the striated subcutaneous muscles (Fig. 2B). The apterial muscles counteract the horizontal force components of feather muscles that tend to pull the peripheral feather follicles of a feather tract towards the center of the feather tract. However, apterial muscles are constrained by their arrangement between two adjacent feather tracks, so that their action is restricted to expanding two neighboring feather tracts and shrinking the apterium between them (Fig. 2A).

Subcutaneous muscles are less constrained in their orientation and can adjust the position of peripheral feather follicles in those directions that cannot be accomplished by apterial muscles (Fig. 2B). For example, the caudal part of the *M. constrictor colli* supplements the relatively weak



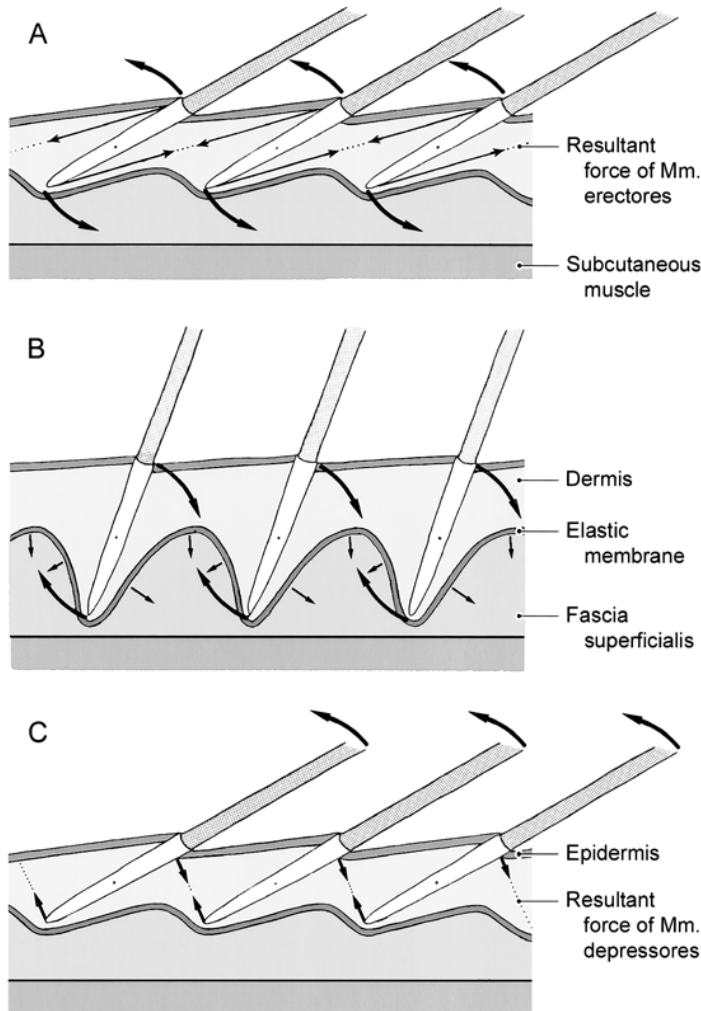


FIG. 5. Two-dimensional model of the movement of feathers. Cranial is to the left of the diagram, caudal to the right. A: Feathers in resting position being raised by contracting erector muscles. B: Raised feathers being returned to their resting position by the resilience of the stretched elastic membrane. C: Feathers being stabilized against lifting external forces by contracting depressor feather muscles.

portion of the *M. apt. cervicalis lateralis*; the *M. subc. thoracoalaris* complements the actions of the neighboring *M. apt. axillaris* and *M. apt. truncalis*; and the *M. subc. dorsalis* and *M. subc. dorsoalaris* generate forces that are oriented perpendicularly to those exerted by the apterial muscles. Thus, the dermal and subcutaneous muscles, despite being separated by the *Fascia superficialis*, create an integrated muscular system in which each muscle performs a specific role in ensuring the proper positioning and configuration of feather tracts on the

surface of the moving body. This role is necessary for the proper functioning of the hydraulic skeleto-muscular apparatus of the feathers.

The third functional component of the feather-bearing integument, the **subcutaneous hydraulic skeletal system**, comprises the fat bodies of both the *Fascia superficialis* and *Fascia subcutanea* (Figs. 3A and 4). The superficial fat bodies are entities that are typically located in depressions or adjacent to bulging structures on the surface of the body (Figs. 2B and 3A, B).

Their being anchored to the underside of the *Fascia superficialis* ensures that the *Fascia superficialis* can maintain its integrity as an even, continuous tissue sheet and fulfill its crucial functions as part of the hydraulic skeleto-muscular apparatus of the feathers. For example, the cervicoscapular superficial fat body lies in the trough between the vertebral and shoulder musculature and is bounded caudally by the transversely oriented skeletal *M. latissimus dorsi*; the supraalar superficial fat body fills the space between the *M. latissimus dorsi* and the *M. subc. dorsoalaris*; the large subalar superficial fat body flanks the *M. subc. abdominoalaris* and lies in the depression of the axillary region ventral and caudal to the attachment of the wing to the trunk; the facial superficial fat body flanks both sides of the prominent jugal bar.

The subcutaneous fat bodies, in contrast, are built directly into the *Fascia subcutanea* as local thickenings to fill depressions on the surface of the body musculature or to cushion prominent structures (Figs. 3A, B and 4). For example, the ingluvial subcutaneous fat body overlies the ventral side of the base of the neck where it pads the abrupt transition between the narrow base of the neck and the broad thorax when the crop is empty, or serves as a hydraulic cushion between the skin and the thin crop wall when the crop is filled; and the axillary and thoracic subcutaneous fat bodies are situated in slight depressions on the surface of the pectoral musculature (Fig. 3A, B). Thus, all fat bodies of both fasciae, despite their different structure, are located strategically to even out depressions under the *Fascia superficialis* so that the hydraulic skeleto-muscular apparatus of the feathers is supported by an even surface without abrupt elevations and depressions. This ensures an even orientation of the feathers and a smooth surface of the coat of feathers.

In conclusion, all cutaneous and subcutaneous structural elements of the feather-bearing integument are integral parts of a single coherent biomechanical machinery that is responsible for stabilizing and moving feathers and for integrating them into the overall body construction of a bird. This biomechanical machinery must have

evolved in conjunction with the evolutionary development of feathers through modification of structural elements that were already present in the integument of reptilian ancestors of birds. The sprouting of feathers on the surface of the skin without a machinery to control and regulate their positions is unlikely to have been selectively advantageous for a reptilian organism (*cf.* Parkes, 1966; but see also Regal, 1975, p. 48). Feathers are also unlikely to have evolved as individual structures and must have evolved as a coat of feathers from their very inception, because their supporting skeleto-muscular apparatus cannot function as isolated units. For the same reasons, feathers could also not have originated in isolated rows of flight feathers along the edges of the forelimbs and tail of reptilian ancestors of birds, as was variously suggested (*e.g.*, von Huene, 1914; Steiner, 1916, 1918; Nopsca, 1923; Heilmann, 1927; Blaszyk, 1935; Böker, 1935; Savile, 1956, 1962; Parkes, 1966; Martin, 1983a; Pennycuick, 1986; Feduccia, 1993; but *cf.* Regal, 1975).

#### DISCUSSION AND COMPARISONS WITH AVIAN MODELS

##### *The integument of birds: Biological roles of feathers, and streamlining effect*

The coat of feathers of extant birds serves many functions, yet, already at its very inception in the ancestors of birds, one particular function is likely to have affected the selective regime acting on the organism and prevented feathers from becoming victims of stabilizing selective processes, while other functions were side-effects that prevented the novel structure from being maladaptive or opened up new evolutionary windows. In order to reconstruct the nature of the primary selective regime under which feathers originated and were selectively advantageous, the structure and function of the feather-bearing integument needs to be scrutinized for evidence of its primary biological role. For example, feathers have been surmised to have evolved under a selective regime favoring thermoinsulation, protection from solar radiation, display and intraspecific communication, camouflage,

water-repellency, excretion of sulfurous amino acids; and aerial locomotion. The various hypotheses have been reviewed by Heilmann (1927), Blaszyk (1935), Tucker (1938), Lucas and Stettenheim (1972), Regal (1975), Dyck (1985), Bock (1986), Feduccia (1996), and Padian and Chiappe (1998) among many others.

Although it has long been recognized that the smooth surface of the coat of feathers may reduce friction drag during flight (Hempel, 1931; Blaszyk, 1935; Petry, 1951; Parkes, 1966; Tarsitano, 1985; Pennycuik *et al.*, 1996), that the coat of feathers is responsible for the fusiform and streamlined body contours of birds and reduces resistance during flight or underwater swimming (Nitzsch, 1867; Böker, 1935; Savile, 1962; Rüppell, 1977; Nachtigall and Bilo, 1980; Bühler, 1990; Parker, 1994; Attenborough, 1998; Greij, 1998), and that a streamlined body is part of the adaptations for avian flight or underwater swimming (Nitzsch, 1867; Lorenz, 1933; Morris, 1965; Osborne, 1968; Pennycuik, 1975; Parker, 1994; Tucker, 1990a; Pennycuik *et al.*, 1996; Greij, 1998; Nachtigall, 1998), the role of streamlined body contours and surfaces has not been considered previously for hypotheses concerning the primary selective value of feathers for the evolutionary origin of birds. Tarsitano (1985) considered streamlining to be of advantage only to cursorial animals and rejected its value in the origin of avian flight.

When dealing with the streamlining effect of feathers, it is necessary to distinguish two separate, though related, aspects. The first concerns streamlining to even out abrupt disruptions of the smoothly curving body outlines so that the resulting fusiform body encounters the least resistance during travel through air or water. The coat of feathers transforms the avian body, with its globular to oval trunk, relatively long thin neck, and bulbous thighs, into a fusiform shape (see, *e.g.*, Bergmann, 1987, p. 111). The evolution of a coat of feathers is an ingenious approach towards achieving fusiform body contours without adding considerable weight in form of fat, which represents a handicap to air-borne organisms (see, *e.g.*, Parker, 1994; Jehl, 1997). Even

though fat tissue is an integral part of the hydraulic skeleto-muscular apparatus of the feathers and of the subcutaneous hydraulic skeletal system, the amount of fat needed for this purpose represents a fraction of the amount of subcutaneous fat that would be needed by itself to streamline an unfeathered body. Streamlining with fat alone would also reduce the mobility and flexibility of the neck, which could be acceptable for penguins, but not for volant and terrestrial birds. The evolution of a pointed beak with an overall conical shape and the concomitant loss of teeth in birds is probably also a function of a selective regime favoring a streamlined body, even though it was made possible in the first place by the special type of the hyoid suspension apparatus in birds (see Homberger, 1999a).

A fusiform body shape is especially significant for the reduction of drag in small birds because of their relatively larger surface area, and small birds are, indeed, generally more completely fusiform than larger ones (see also Lorenz, 1933; Pennycuik *et al.*, 1996). Thus, the selective pressure towards a fusiform body shape is bound to be greater for small birds than for large ones, so that it is likely that the characteristic fusiform body shape of birds originated in a small ancestor. A smaller size is also more forgiving of an imperfect flight apparatus (*e.g.*, Pennycuik, 1986; Spedding and Lissaman, 1998). Also Maurer (1998a, b) argued, on ecological grounds, that birds must have evolved from a small ancestor. In contrast, Hou *et al.* (1999) and Sereno (1999) proposed, on the basis of presently known fossils, that the evolutionary history of birds included a period of miniaturization after *Archaeopteryx*. That may be so; however, in light of the functional and selective correlations between a fusiform body and small body size in birds, it seems likely that the avian ancestor was already small, and that *Archaeopteryx* represents a side branch of birds tending already towards greater size.

The second aspect of streamlining concerns the maintaining of an even body surface to avoid turbulence beyond the boundary layer and to minimize drag. Again, two aspects need to be distinguished: (1) The

surface texture of the feather coat, and (2) the mechanical property of the feather coat itself.

First, the surface of the feather coat is not completely smooth, but textured at least by the longitudinal ribbing created by the individual raches of the feathers, which project slightly above the surface of the vanes. This ribbing is likely to reduce drag in a manner analogous to that of the ribbing of scales in fast-swimming sharks (see Reif, 1985*a, b*; Ball, 1999). This ribbing effect also explains why already the appearance of the earliest precursors of feathers, possibly as conical scales or pin-feather-like projections, could have been selectively advantageous in reducing drag. Furthermore, the ribbed surface texture of the feather coat may explain why Nachtigall (1998) observed that a bird model with glued-on feathers creates less drag in a wind tunnel than a bird model with a completely smooth surface.

Second, the elasticity of the individual feathers provides the feather coat with the necessary elasticity to act as a turbulence dampening device (see also Böker, 1935, p. 105; Nachtigall, 1977, 1982; Starck, 1979, p. 629; Nachtigall and Bilo, 1980). Increasing turbulence tends to raise feathers and, thereby, to increase the thickness of the feather coat (see also Norberg, 1990; Brown and Fedde, 1993). This configurational change, by increasing the speed of air flow across the surface of the feather coat, decreases turbulence and delays a detachment of the air flow from the body surface. The integrity and smoothness of the surface of the feather coat is maintained by the natural curvature of the contour feathers, which ensures that the tips of the raised feathers remain in direct contact with the outer surface of the feathers behind them despite the greater distance between them.

As already suspected for some time for the feather musculature (*e.g.*, Petry, 1951; Marler, 1956; Morris, 1956; Osborne, 1968; Nachtigall and Bilo, 1980; Pennycuick *et al.*, 1988), the depressor feather muscles play an important role during flight. They counteract the lifting forces of air currents on contour feathers and, thereby, prevent the tips of feathers from being raised above

the surface of the rest of the feather coat and from creating turbulence and drag. It is the lack of active depressor feather muscles and neural feedback in frozen bird specimens, which explains the counterintuitive observations by Pennycuick *et al.* (1988) and Tucker (1990*a, b*) that feathers can create significant drag that can be reduced by glueing the feathers down.

Under certain circumstances, such as during landing, individual feathers, however, are raised above the surface of the rest of the feather coat and serve as temporary turbulators, thereby creating turbulence in the boundary layer and preventing the detachment of the air flow from the body surface (Nachtigall, 1977; Stork *et al.*, 1977; Starck, 1979; Norberg, 1990). In these situations, the depressor feather muscles are likely to ensure that only individual feathers are lifted instead of several feathers together, which would create excessive turbulence and drag.

At the same moment in evolution as a coat of feathers emerged and became advantageous in streamlining the body contours, other inherent properties of the feather coat became effective. Foremost among these side-effects was the capacity for thermoregulation, which made homoio-endothermy possible, and the capacity for storing pigments in the feathers, which made camouflage and complex visual communication possible. Both roles are not dependent on feathers, since they are already present in reptiles and, therefore, are unlikely to have been the primary selected role of a feather coat. Other inherent properties of the feather coat, such as water-repellency, prevented the plumage from being maladaptive. Acoustic communication (Stresemann, 1934, pp. 628–633; Prum, 1998), water transport (Cade and Maclean, 1967), and chemical defense (Dumbacher and Pruett-Jones, 1996) are specialized roles, which are found only in particular avian taxa and must have evolved secondarily under particular selective circumstances.

#### *The integument of birds: The cutaneous nervous system*

For the integument to be able to react appropriately to the ever-changing and un-

predictable air currents during flight, a feedback mechanism through an intricate nervous network with sensory receptors and motoric innervation is necessary (see also Dorward, 1970; Schwartzkopf, 1973; Bennett, 1974; Gewecke and Woike, 1978; Spearman and Hardy, 1985; Hörster, 1990*a, b*; Brown and Fedde, 1993). Not only are the feather muscles richly innervated (Ostmann *et al.*, 1963; Tetzlaff *et al.*, 1965; Jenkinson and Blackburn, 1968; Lucas and Stettenheim, 1972; Bennett, 1974), but the sensory apparatus of the skin, especially near the follicles of contour feathers, is especially rich and diverse (Wodzicki, 1929; Dreyfuss, 1937; Schartau, 1938; Stammer, 1961; Winkelmann and Myers, 1961; Cobb and Bennett, 1970; Dorward, 1970; Lucas and Stettenheim, 1972; Schwartzkopf, 1973; Bennett, 1974; Necker, 1985; Brown and Fedde, 1993). Furthermore, there are more touch corpuscles in the skin of birds than in that of mammals (Dorward, 1970), and the touch receptors of birds are smaller than those of reptiles (Schartau, 1938), thereby allowing a more differentiated gathering of sensory information per unit of skin area. The density of touch receptors is significantly higher in the feather-bearing skin of volant birds, as compared to that of flightless ones, and in that of wild birds, as compared to that of domesticated ones (Stammer, 1961), which suggests that the rich sensory innervation of the avian skin is causally related to the demands of flight.

Various experiments (Gewecke and Woike, 1978; Necker, 1985; Hörster, 1990*a, b*; Brown and Fedde, 1993) suggest that the movements of contour feathers create the stimuli that are received and transmitted by the various receptors and filiform feathers, and collected and processed in the spinal cord and cerebellum. Because the number of the sensory neurons of the cutaneous sensory nerves in the grey matter of the periphery of the dorsal horn of the spinal cord is enlarged in birds and arranged in two fundamentally different patterns depending on the various avian orders and families (Woodbury, 1998), it is likely that the elaboration of the cutaneous nervous system in connection with the trend towards powered

flight occurred at least twice, if not more often, in birds.

#### *Locomotion of birds*

Even though avian flight is characteristic of birds and differs fundamentally from the flight forms of other vertebrates and invertebrates, it is far from uniform. In order to be able to identify a realistic and appropriate model for the incipient flight of ancestral birds, it is necessary to determine which type of avian flight is most dependent on a spindle-shaped, small body with a smooth, streamlined surface.

The initial thrust for take-off in birds is derived from the hindlegs (*e.g.*, Lorenz, 1933; Böker, 1935; Kipp, 1950; Marler, 1956; Turback, 1993; Earls, 1997). The movements of the hindlegs during take-off are very similar to those during hopping, which is typical for arboreal passerines, as well as parrots and woodpeckers, and is considered to be primitive for birds and an adaptation to arboreal conditions (Böker, 1924, 1927, 1935; Daanje, 1951; Marler, 1956; Rietschel, 1985). It is during take-off that streamlined body contours are crucial for providing the full benefit of the initial thrust by the hindlegs. Actually, the postural similarity between leaping birds, reptiles and mammals at take-off is striking with respect to the adducted forelimbs, swept-back hindlimbs, and stretched-out body (see Bels and Theys, 1989; Hamrick, 1995; Turback, 1993).

A fusiform avian body with adducted wings generates lift at smaller angles of incidence than a non-fusiform one (Csicsáky, 1977). The trajectory of such a "body lift-glide" has a slightly, though significantly, extended range, flattened trajectory, and reduced sinking speed compared to a glide with only drag and no lift (Csicsáky, 1977). A streamlined body, therefore, confers a selective advantage to an airborne organism and is likely to have done so at the evolutionary reptilian-avian transition. A "body-gliding" phase is also represented by the passive phase of flap-bounding flight, a type of intermittent flight that is characteristic of small, arboreal birds, such as forest-adapted passerines, smaller woodpeckers, and certain parrots (see Lorenz,

1933; Kipp, 1950; Csicsáky, 1977; Rayner, 1985, 1988; Norberg, 1990; Tobalske, 1995, 1996; Tobalske and Dial, 1994, 1996; Tobalske *et al.*, 1997). In comparison to continuously flapping and flap-gliding flight, flap-bounding flight minimizes profile drag and has generally been interpreted as an adaptation to save energy. However, given that a streamlined body is especially effective for hopping, jumping, and flap-bounding flight, and given that these three modes of locomotion represent stages in a continuum of sauropsid locomotory modes, it appears more likely that flap-bounding flight may be more similar to, if not even retained from, the primitive flight type of early birds than the other flight types with their greater profile drag created by the extended wings.

Hence, birds that are small, move over the ground and among branches of trees by hopping, and use flap-bounding flight may be appropriate models to study the origins of avian flight, even though birds with this combination of characteristics, such as certain passerines, are generally considered "highly derived." However, no taxon can justifiably be said to be derived, or primitive, in its entirety, because each taxon consists of a mosaic of primitive and derived characters. It is, thus, conceivable that the phylogenetic line leading to the passerines may have acquired certain derived characters, while retaining certain primitive features, such as the arrangement of the sensory neurons in the spinal cord (Woodbury, 1998), the tight hyoid suspension (Homburger, 1999a), and several adaptations for incipient flight proposed in our study.

#### COMPARISONS WITH REPTILIAN MODELS

At first view, reptiles and birds are so different from each other, that it is difficult to visualize an evolutionary transformation from one into the other. To be able to do so, nevertheless, the functional morphology and biology of reptiles need to be scrutinized for structures and behaviors that can serve as models for those that were likely to have been present in an ancestor of birds and from which avian structures and behaviors could have evolved.

#### *Integument of reptiles*

Relatively little work exists on the anatomy of the reptilian integument, but the available data suggest that the integument of reptiles differs only by degrees, instead of fundamentally, from that of birds. Therefore, an evolutionary reorganization of a reptilian to an avian configuration of the integument might have been less drastic than what has previously been assumed.

For example, dermal muscles, which move imbricated scales relative to one another, and subcutaneous muscles, which move the skin relative to underlying body structures, have been documented for snakes and lizards (Buffa, 1905; Lange, 1931; Wiedemann, 1932; Lissmann, 1950; Auffenberg, 1962; Gans, 1962, 1974; Voris and Jayne, 1976). In snakes, dermal muscles abduct the free edges of scales, and it is the resilience of the connective tissue, not the force of antagonistic muscles, which returns scales to their resting position (Wiedemann, 1932). Although reptiles, in general, have little dermal and subcutaneous fat (Spearman, 1982; unpublished personal observations), presumably structural fat tissue serving as a hydrostatic skeleton supports individual scales (Schmidt, 1912; Lange, 1931; unpublished personal observations), fills spaces between superficial skeletal muscles of alligators to maintain streamlined body contours (unpublished personal observations), or serves as shock absorber (Russell, 1979). Elastic connective tissue at the dermis-subcutis interface was found by Hoffmann (1890) and Lange (1931). Scales, and a dermal and subcutaneous framework of connective tissue fibers, are arranged along diagonal rows relative to the longitudinal and transverse axes of the body (Rathke, 1866; Steiner, 1916, 1918; Frolich, 1997; unpublished personal observations). Finally, the skin of reptiles is highly innervated and supplied with numerous specialized touch receptors that closely resemble those of birds (Keibel, 1896; Schartau, 1936, 1938; von Düring, 1973; Necker, 1974; von Düring and Miller, 1979; Hörster, 1990a; Jackson *et al.*, 1996).

In conclusion, the reptilian integument contains structural elements that could have

served as antecedents to the more specialized structures that are characteristic of the avian integument, and the reptilian integumentary structures are assembled in an array that resembles the organization of the avian integument in certain aspects. Feathers are, however, unlikely to have appeared in a reptilian ancestor that possessed a skin with non-imbricating, tuberculate scales. Such a skin, like that of alligators, is devoid of dermal muscles (Regal, 1975; unpublished personal observations). Since dinosaurs appear to have had a skin with tuberculate, non-imbricating scales (*e.g.*, Czerkas, 1997; Chiappe, 1998; Chiappe *et al.*, 1998), they are unlikely to have sported a coat of feathers (*cf.* Padian and Chiappe, 1998; Fishman 1999).

#### *Locomotion of reptiles*

The lizard locomotory apparatus appears to be a generalized system that allows quadrupedal and bipedal locomotion, gliding, climbing, swimming, as well as ballistic leaping and hopping, though in varying degrees and proportions depending on the species and the particular environmental conditions (Snyder, 1962; Neill, 1971; Losos and Irschik, 1996). Furthermore, there seems to be no strict separation between terrestrial and arboreal life (Neill, 1971). Running up trees and bushes is a common behavior of disturbed lizards on the ground (Neill, 1971) and is likely to fall under a very strong selective regime for smaller reptiles seeking shelter from larger predators (see also Neill, 1971; Bock, 1986). Three of the various reptilian locomotory modes have received special attention as possible precursors of avian flight: Gliding, bipedal running, and leaping or jumping.

Observations on gliding lizards (Tweedie, 1950, 1960; Oliver, 1951; Schiøtz and Volsør, 1959; Heyer and Pongsapipatana, 1970; Marcellini and Keefer, 1976; Russell, 1979; Garland and Losos, 1994) indicate that a certain degree of gliding aerial transport is possible even without specialized structures serving as air foils. Furthermore, gliding lizards do not show a tendency towards evolving streamlined body contours, probably because these would be counterproductive to effective gliding as it reduces

the necessary drag. Thus, within the framework of our new data, gliding lizard-like reptiles do not provide useful models for an ancestor of birds.

Observations on quadrupedal lizards that are capable of bipedal locomotion indicate that bipedality is a function of speed, as the hindlimbs provides the thrust for both locomotory modes (Böker, 1935; du Brul, 1962; Snyder, 1962; Neill, 1971; Reilly and Delancey, 1997). The selective regime controlling bipedality, however, seems not to have favored streamlined body contours, probably because the raising of the trunk during bipedal running automatically exposes a large drag-generating surface that cannot be obviated by a streamlined or fusiform body. Thus, given our new data, bipedality is unlikely to have been the specialized locomotory mode of an ancestor of birds.

The little we know about the mechanism of leaping or jumping in lizards (see Böker, 1935; Neill, 1971; Bels and Theys, 1989; Bels *et al.*, 1992; Garland and Losos, 1994; Losos and Irschik, 1996) indicates that lizards assume streamlined body contours through an elongated pointed snout, forelimbs held closely to the trunk, and swept-back hind limbs when they push themselves off with their hind legs at take-off. This streamlining provides the full benefit of the initial forward thrust during take-off. Because streamlined body contours are already part of the selective regime controlling leaping and jumping, this mode of locomotion appears to be a heuristically useful model as an antecedent of avian locomotion for which streamlined body contours represent a crucial adaptation. Although for different reasons than ours, leaping and jumping lizard-like reptiles have repeatedly been considered as models for ancestors with incipient avian locomotion (see Steiner, 1916, 1918; Böker, 1924, 1927, 1935; Neill, 1971; Stephan, 1974).

In conclusion, the consideration of motorically and ecologically versatile reptiles as models for the ancestors of birds liberates the contemporary controversy about avian origins from the mental straight-jacket of viewing the question of avian origins in rigid terms of being *either* terrestrial-bi-

pedal *or* arboreal-quadrupedal, and of having to have passed through a gliding stage. Small, lizard-like, motorically and ecologically versatile reptiles may have served as a reservoir for the evolution of various specialized modes of aerial transport, such as gliding and parachuting to slow descent on the one hand, or leaping and jumping to lengthen the distance covered on the other hand (see also Abel, 1911; Steiner, 1918; Böker, 1924, 1935; Neill, 1971; Stephan, 1974; Bock, 1986; Pennyquick, 1986; p. 88). The latter is likely to have been the departure point towards avian flight (see also Böker, 1935; Neill, 1971), but it is unlikely that a patagium was acquired as part of the adaptations leading to avian flight. A patagium is incompatible with the needed mobility of motorically and ecologically versatile lizard-like reptiles, and it would have precluded the functional independence of the fore and hind limbs, which is characteristic of avian locomotion (Steiner, 1916, 1918; Böker, 1935; but cf. Pennyquick 1986, p. 88).

#### COMPARISONS WITH MAMMALIAN MODELS

Since ample evidence exists that birds and mammals have evolved independently from different reptilian ancestors, comparisons between the two classes serve as natural experiments to test functional hypotheses that were proposed on the basis of functional-morphological data (see also Homberger, 1999*a*, 2000).

#### *Integument of mammals*

The structural differences between the avian and mammalian integuments underscore the uniqueness of the avian integument. The integument of mammals is structurally less complex than and quite different from that of birds (see, *e.g.*, Bargmann, 1977). In particular, the smooth dermal musculature consists only of hair erectors, the *Mm. arrectores pilorum*. The resilience of the dermis acts as their antagonist. The absence of dermal depressor muscles suggests that these may not be needed for, or would not be effective in, counteracting the ruffling effects of air currents on fur. Subcutaneous muscles (*e.g.*, facial muscles) are only rarely present, and their arrangement

has no functional relationship to that of the dermal muscles. The sensory innervation of the skin is considerable, but touch receptors in form of specialized corpuscles are much less numerous than in the skin of reptiles and birds (Dorward, 1970), which indicates that the integument of mammals is a less actively dynamic machinery than that of birds.

#### *Mammalian locomotion*

The observations on aerial locomotion of certain gliding mammals underscore the importance of streamlining as a means of maximizing the initial thrust of a leap or jump, as is the case in leaping lizard-like reptiles and small birds at take-off, as well as the importance of a breaking device for landing after a forceful leap through the air.

Hair can play an aerodynamic role in certain leaping arboreal primates. The caudal extension of elongated matted hair on the arms of certain lemurs (*Propithecus*) (von Huene, 1914; Stephan, 1974; Feduccia, 1993) and the cloak of long hair along the sides of the trunks of *Colobus* monkeys (Morbeck, 1979) serve as passively deployed breaking devices during the landing phase of a leap.

None of the terrestrial mammals that travel through the air are fusiform or streamlined. But recent evidence suggests that at take-off, gliding mammals leap with tucked-in forelimbs to minimize drag and get the full benefit of the initial thrust, while they extend their forelegs and expand their skin folds only after their initial propulsion (compare Hamrick, 1995; and Gould and McKay, 1998, pp. 56 and 62).

#### PREVIOUS SCENARIOS CONCERNING THE EVOLUTION OF FEATHERS

It is not feasible, within the framework of this paper, to provide a comprehensive review of the voluminous literature concerning the evolutionary origin of birds, which extends far beyond the contemporary dichotomic controversy concerning the question whether birds originated from terrestrial-bipedal dinosaurs or arboreal-quadrupedal archosaurs. Even a cursory survey of the literature reveals, however, that practically all earlier scenarios postulate trans-



formations from an originally quadrupedal terrestrial reptilian vertebrate to a bipedal, volant bird and are permutations of various plausible hypotheses concerning individual steps of morphological, functional and ecological transformations. At this point, only a few, selected hypotheses that might appear to contradict our new scenario will be discussed.

The many earlier, non-aerodynamic hypotheses concerning the primary biological role of a coat of feathers are not consistent with our new analysis of the feather-bearing integument. Although Regal (1975) stressed the crucial role that dermal muscles may have played in moving elongated scales or feathers to regulate the body temperature or to handle solar radiation, a hydraulic skeleto-muscular apparatus possessing only erector muscles, comparable to that of imbricated scales of reptiles or mammalian hair, would have been adequate for this task. Similarly, feathers used for visual signaling could also be moved without depressor muscles. The fact, that the hydraulic skeleto-muscular apparatus of feathers uniquely possesses depressor muscles indicates that it is designed to control external forces acting on feathers.

The earlier hypotheses that assumed that the primary role of feathers was related to flight, also assumed implicitly that flight feathers (*i.e.*, remiges and rectrices) evolved prior to a body-covering coat of feathers (*e.g.*, Steiner, 1916, 1918; Heilmann, 1927; Blaszyk, 1935; Böker, 1935; Savile, 1956, 1962; Parkes, 1966; Martin, 1983a; Pennycuik, 1986; Feduccia, 1993). Body contour and flight feathers share several structural and biomechanical features that enable them to resist forces and pressures from underneath (Steiner, 1916, 1918; Blaszyk, 1935; Tucker, 1938; Lucas and Stettenheim, 1972, pp. 239–261; Vogel, 1998). These features were considered highly adaptive for flight feathers, but of no use to body contour feathers by Steiner (1916, 1918) and Blaszyk (1935), who inferred that body contour feathers must have evolved from flight feathers. However, considering our new conceptualization of the avian integument, the structural and biomechanical properties of the body contour feathers

must be reinterpreted as part of the original role of the coat of feathers in maintaining streamlined body contours and surface. Thus, the contour feathers were preadapted to the mechanical demands that would arise when some of them became elongated and eventually modified into flight feathers. In other words, remiges and rectrices evolved through modification of contour feathers (see also Dyck, 1999).

Several authors (*e.g.*, Martin, 1983a, b, 1991; Peters, 1985; Bock, 1986; Peters and Ji, 1999) have mentioned the conceptual difficulties of an evolutionary derivation of bipedal volant birds from an arboreal ancestor because bipedality would presumably preclude the climbing of trees. This conceptual difficulty is exacerbated if avian flight is postulated to have evolved through a gliding stage, which leads to an inevitable loss of height and makes climbing a necessity. In reality, however, bipedality, arboreality, and a capacity for climbing are not mutually exclusive: Lizards that can run bipedally on the ground, often also climb up trees and bushes (Neill, 1971), and various types of birds are able to climb. As a matter of fact, even specialized tree-climbing birds, such as nut-hatches, tree-climbers, woodpeckers, and some parrots, cannot be recognized as such by their skeletal features alone, but only by an ensemble of behavioral, integumentary and skeleto-muscular specializations. For example, the Gymnogene (*Polyboroides radiatus*) (see Newman, 1971) and the Streaked Shearwater (*Calonectris leucomelas*) (see Attenborough, 1998) would not have been suspected of being able to climb trees unless they had been observed actually doing so.

With few exceptions (*e.g.*, Böker, 1924, 1927, 1935; Padian, 1985; Caple *et al.*, 1983), scenarios describing the evolution of avian flight comprise a gliding stage. For a gliding vertebrate, however, there is no selective advantage to acquire streamlined body contours and surfaces. And for a bipedal vertebrate there would be no selective advantage to start to spread its forelimbs while running. Such a motion, which is a necessary first step towards flapping flight, would be counterproductive by increasing drag and unnecessary for a voluntary re-

duction of speed which can be achieved by reducing the force and frequency of the movements of the driving hindlimbs.

OUTLINE OF A NEW SCENARIO FOR THE  
EVOLUTION OF BIRDS, FEATHERS, AND  
AVIAN FLIGHT

1. The evolutionary line towards birds starts with a small, lizard-like, unfeathered reptile with imbricated scales, dermo-subcutaneous musculature, dermal fat supporting at least some scales, subcutaneous fat bodies filling spaces between skeletal muscles, and a well-developed cutaneous sensory innervation. This reptile is ecologically and locomotorily versatile, being able to move quadrupedally as well as bipedally on the ground and in trees, to climb, and to leap. Its pelvic limbs serve as motor to thrust the body forward during locomotion.

2. Arboreality provides protection from larger predators and selectively favors a capacity to leap farther and farther between branches and even between trees. The small, lizard-like reptile does this by propelling itself ballistically from a branch with its hindlegs and by assuming streamlined body contours by adducting its forelimbs. When nearing its landing place, it extends its forelimbs to grab a holding or footing.

3. The appearance of projecting scales or pin-feather-like projections on the surface of the skin through changes in genetic and developmental processes creates a ribbed surface and is selectively advantageous because it reduces drag during leaps.

4. The subsequent modification of the initial integumentary projections into a coat of feathers through changes in genetic and developmental processes is selectively advantageous because it supports the streamlining of the body contours and, thereby, promotes "body lift-gliding," which extends the distance traveled through the air, flattens the trajectory, and reduces the sinking speed. The spreading of the forelimbs near the end of the trajectory breaks the landing speed by increasing profile drag. The role of the dermo-subcutaneous musculature and the cutaneous sensory and motoric peripheral nervous system and feedback mecha-

nisms gain in importance as they ensure a smooth body surface and control drag.

5. Even slight elongations of feathers along the caudal surfaces of the forelimbs and along the sides of the tail improve the role of the forelimbs and tail in breaking the landing. Because all feathers are equipped with dermal muscles and at least some of them with subcutaneous muscles as well, these incipient remiges and rectrices can be folded together or spread apart appropriately during "body lift-gliding" or landing, respectively.

6. When the remiges and rectrices have become long enough to serve as effective air foils for effective breaking and adjusting maneuvers during landing, they can also be used to provide thrust during the "body lift-glide" phase through individual flapping movements and, thereby, to extend the distance covered. Imperfections in the design of the thrust-generating wing movements are not catastrophic because of the small size of the ancestral feather-bearing bird.

7. The role of the forelimbs as thrust-generators gradually becomes more important relative to that as landing gears, and this trend is accompanied by morphological modifications, such as a reduction of the number and independence of fingers, and a stabilization of the shoulder joint and girdle. Claws on the remaining fingers are retained primarily to assist in landing. The hindlimbs retain their original roles in providing the initial thrust for the trajectory while gradually taking on the additional role as the main landing gear. The functional and motoric-nervous separation of the forelimbs and hindlimbs is thereby initiated. *Archaeopteryx* was probably situated at this stage of the evolutionary path towards avian flight.

8. The next stage towards avian flight involves a gradual increase in the maneuverability of flight (see Groebels, 1929; Maynard Smith, 1952; Dawkins, 1998). One major step in this direction is the acquisition of a carina on the sternum, which allows forceful asymmetrical movements of the wings and, thereby, a more maneuverable and accurate flight (Rietschel, 1985; Peters and Ji, 1999). With this innovation, a consistent and secure landing on

the hindlegs is achievable and permits a further gradual specialization of the forelimbs for active and maneuverable flight and a concomitant further reduction of the free fingers and finger claws. The increased flight maneuverability requires a further development of the nervous system, leading to a special spatial arrangement of the increased number of sensory neurons in the spinal cord. The demands of maneuverable flight also favor the modification of a tooth-bearing reptilian snout into a pointed edentulous avian beak to maximize streamlining. It is probable that a gradual increase in flight maneuverability with a concomitant increased complexity of the cutaneous nervous system, as well a trend towards an edentulous beak, occurred several times independently during the early stages of avian evolution.

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