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LOCOMOTOR MODULES AND THE EVOLUTION OF AVIAN FLIGHT

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Abstract.—The evolution of avian flight can be interpreted by analyzing the sequence of modifications of the primitive tetrapod locomotor system through time. Herein, we introduce the term “locomotor module” to identify anatomical subregions of the musculoskeletal system that are highly integrated and act as functional units during locomotion. The first tetrapods, which employed lateral undulations of the entire body and appendages, had one large locomotor module. Basal dinosaurs and theropods were bipedal and possessed a smaller locomotor module consisting of the hind limb and tail. Bird flight evolved as the superimposition of a second (aerial) locomotor capability onto the ancestral (terrestrial) theropod body plan. Although the origin of the wing module was the primary innovation, alterations in the terrestrial system were also significant. We propose that the primitive theropod locomotor module was functionally and anatomically subdivided into separate pelvic and caudal locomotor modules. This decoupling freed the tail to attain a new and intimate affiliation with the forelimb during flight, a configuration unique to birds. Thus, the evolution of flight can be viewed as the origin and novel association of locomotor modules. Differential elaboration of these modules in various lineages has produced the diverse locomotor abilities of modern birds.

Key words.—Avian evolution, bird flight, locomotion.

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Investigations into the origin of avian flight have been performed at several levels. At one end of the spectrum, specific structures such as feathers and claws have been the subject of detailed analysis (Feduccia and Tardoff 1979; Yalden 1985; Feduccia 1993). The avian wing represents a somewhat higher level of organization. It has been the focus of a substantial body of paleontological research (e.g., contributions in Hecht et al. 1985) and recent functional investigations (Dial et al. 1987, 1988, 1991; Jenkins et al. 1988; Goslow et al. 1989; Biewener et al. 1992; Dial 1992a,b; Dial and Biewener 1993; Meyers 1993; Tobalske and Dial 1994). Still larger scale interpretations have employed aerodynamic modeling, often in concert with ecological inferences, to delineate probable intermediate stages in the transition from nonflying to flying forms (Caple et al. 1983; Balda et al. 1985; Norberg 1985; Rayner 1985, 1991; Tarsitano 1985; Pennycuik 1986). This uppermost level is exemplified by the controversy between the “ground-up” or “cursorial” scenario and the “trees-down” or “arboreal” scenario (e.g., Bock 1986; Ostrom 1986).

Herein, we explore the evolution of avian flight at an intermediate level of analysis—that of the entire locomotor system. Particular emphasis is given to the hind limb and tail, which have received much less attention than the wings. We employ the well-supported hypothesis that birds are derived theropod dinosaurs specialized for flight (e.g., Gauthier 1986). Using this phylogeny (Fig. 1) and functional analyses of living birds and crocodylians, we trace the transformation of skeletal characters and their significance for locomotion through theropod evolution. Our hope is that this approach will yield insight into how a second, aerial locomotor capability became superimposed onto an exclusively terrestrial theropod body plan.

Towards this end, we designate portions of the body as “locomotor modules.” Locomotor modules are anatomical

subregions of the musculoskeletal system that are highly integrated and act as functional units during locomotion. For example, early tetrapods probably used coupled undulatory movements of the axial skeleton and all four limbs during walking and running (Figs. 2A, 5A). These forms and many living salamanders, which retain much of this primitive organization (Edwards 1977; Frolich and Biewener 1992), have a single locomotor module. Novel locomotor repertoires could originate by the decoupling of such an association of parts. The liberation of primitively linked components could permit the individual specialization of each part and new associations between parts (Young 1938; Lauder 1981, 1989; Lauder and Liem 1989).

The origin of avian flight is an example of this evolutionary mechanism. Specifically, we propose that basal theropods had a single, terrestrial locomotor module composed of the hind limb and tail (Fig. 2B). In contrast, we identify three locomotor modules in extant volant birds: wing, tail, and hind limb (Fig. 2C). At this level of analysis, the origin of flight can be viewed as a shift from one to three locomotor modules. In the following sections, we present evidence used to trace the fate of locomotor modules through theropod phylogeny and the origin of birds.

RESULTS AND DISCUSSION

Basal Theropods

The oldest and most basal theropods, such as *Eoraptor*, *Herrerasaurus*, and the ceratosaurs (e.g., *Coelophysus*, *Syntarsus*, *Dilophosaurus*), have relatively short, raptorial forelimbs (Welles 1984; Gauthier 1986; Colbert 1989; Sereno 1993; Sereno et al. 1993). It is generally agreed that these appendages were not used for terrestrial progression, an interpretation supported by fossil trackways. Obligatory bipedalism in theropods represents a reduction in the primitive tetrapod locomotor module. The forelimbs decoupled from the posterior part of the body and became specialized as appendages for prey capture and manipulation.

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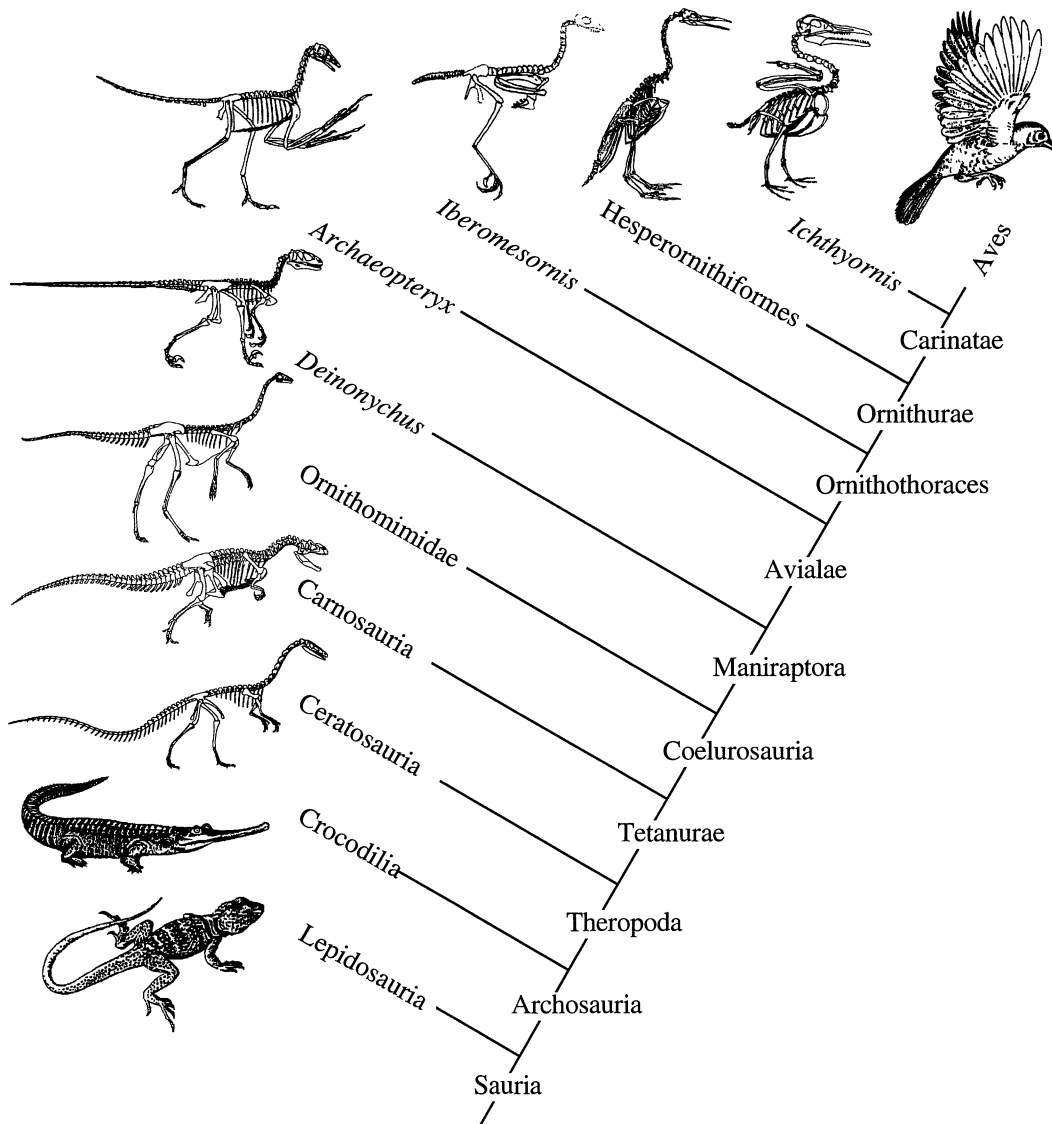


FIG. 1. Cladogram depicting the relationships of select taxa of Sauria. Representative theropods figured from lower left to upper right: *Coelophysis*, *Allosaurus*, *Struthiomimus*, *Deinonychus*, *Archaeopteryx*, *Iberomesornis*, *Hesperornis*, *Ichthyornis*, and a modern passerine. Skeletons modified from Carroll 1988 except *Allosaurus*, after Paul 1987, and *Iberomesornis*, after Sanz and Bonaparte 1992; living saurians from Carr 1963. Cladogram simplified from Gauthier 1986 and Chiappe 1995.

We suggest that basal theropods had a single locomotor module consisting of the hind limbs and tail (Fig. 2B). The tail skeleton, although not often complete, is always composed of a relatively large number of caudal vertebrae (Figs. 3A–B, 6). Early theropods typically have 40–50 segments in a tail that makes up about half of total body length (Welles 1983; Colbert 1989; Gatesy 1990; Novas 1993). Vertebral morphology indicates the presence of ample caudal musculature and a smooth transition from the trunk to a large-diameter tail base. The epaxial musculature ran continuously down the neck, trunk, sacrum, and tail.

One role of the tail in these animals appears to have been to counterbalance the front of the body about the hip joint (Fig. 3D). Although the tail tapers distally, the caudal musculoskeleton must have been a substantial fraction of body mass in basal theropods. In living limbed saurians such as

crocodilians, lizards, and the tuatara, the tail serves another important role during locomotion. Musculature running from the tail to the femur (caudofemoralis) has been shown to be the primary mechanism of limb retraction in walking alligators (Fig. 3C, Gatesy 1990, 1994); lepidosaurs are thought to employ this muscle as well (Snyder 1954; Russell and Bauer 1992). Skeletal evidence supports the presence of a well-developed caudofemoral retraction system in basal theropods, which probably used this primitive mechanism of limb movement during walking and running (Gatesy 1990). Thus, the tail served as an origination site for a major locomotor muscle and was intimately tied to the hind limb (Fig. 3D).

Modern Birds

The tails of extant birds are morphologically distinct from those of basal theropods (Figs. 4A–B). The externally visible

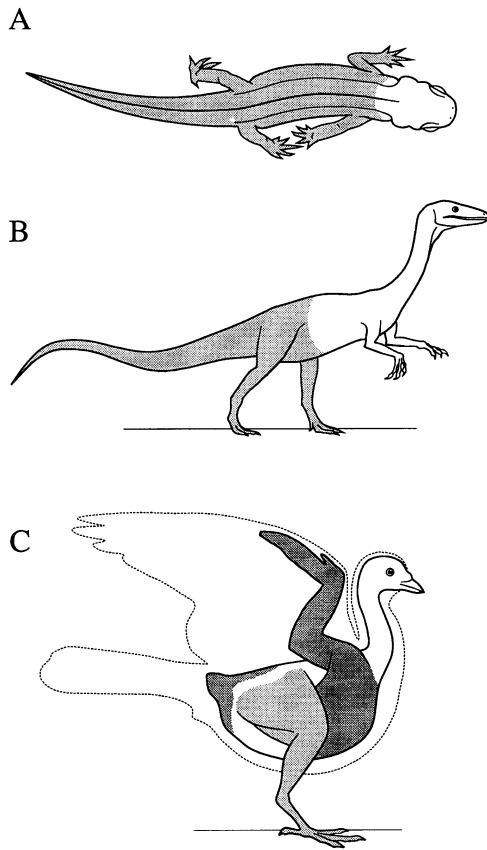


FIG. 2. The evolution of locomotor modules and birds. A. In primitive tetrapods the body axis and all four limbs acted as an integrated unit during terrestrial locomotion. This single locomotor module (shading) is still present in forms such as salamanders. B. Basal dinosaurs and theropods were obligate bipeds. The hind limb and tail comprised a single, reduced locomotor module (shading). C. Birds possess three locomotor modules. During the evolution of birds the forelimb regained locomotor function as a wing. The tail decoupled from the hind limb to specialize in control of the rectrices. The novel allegiance of the pectoral and caudal modules formed the avian flight apparatus (dark shading). The independent hind limb remains as the remnant of the primitive terrestrial module (shading).

“tail” of most extant birds is composed primarily of the main caudal flight feathers or rectrices. The underlying tail musculoskeleton, known as the uropygium, is extremely short. In pigeons the tail skeleton is composed of five or six caudal vertebrae and a bladeliike pygostyle. On each side of the pygostyle lie the rectricial bulbs, specialized fibroadipose structures that encase the roots of the twelve rectrices (Baumel 1988). Capping each bulb is a striated muscle, the bulbi rectricium. Six pairs of muscles connect the rectrices, bulbs, and caudal vertebrae to the pelvis, synsacrum, femur, and vent (Baumel 1988; Gatesy and Dial 1993). In contrast to the condition in basal theropods, the epaxial musculature is not continuous down the dorsal surface of the body. There is a distinct hiatus (up to four spinal segments in the pigeon) in the epaxial musculature of the trunk and the tail (Fig. 4B).

The highly derived tails of modern birds are also functionally distinct from those of other theropods. The tail plays a minor role during terrestrial locomotion in the pigeon (Ga-

tesy and Dial 1993). Unlike the long, muscular tail of basal theropods, the tail of modern birds is ineffective at counterbalancing the front of the body about the hip joint. Consequently, the body's center of mass is located well in front of the acetabulum (Alexander 1983; Manion 1984). Caudofemoral musculature, linking the tail and femur, is reduced relative to other saurians and completely absent in some birds (George and Berger 1966). In contrast to basal theropods, birds use the hamstring muscles to retract the limb (Gatesy 1990, 1994). The primitive caudofemoral system, when present, is no longer functionally significant. During flight, caudal muscles are active bilaterally with each wingbeat (Gatesy and Dial 1993). The rectricial bulbs form a specialized mechanism for tail fanning (Baumel 1988; Gatesy and Dial 1993, in press). Other caudal muscles function to hold and move the adjustable tail fan to direct lift for control and maneuverability (Fig. 4C).

Like the majority of living birds, pigeons are capable of two major forms of progression: locomotion on a substrate (e.g., walking) and locomotion in the air. It has been suggested that the disparate locomotor abilities of birds are produced by two relatively independent locomotor systems, the wings for flying and the legs for walking or running (Ostrom 1979, 1986; Pennycuik 1986; Butler 1991). Evidence for such a segregation can be found in the patterns of muscle activity of a pigeon moving from terrestrial to aerial locomotion (Fig. 5B; Gatesy and Dial 1993). During walking, activity is restricted primarily to the striding legs; wing muscles and most tail muscles are inactive. Muscles from all regions of the body are strongly active during the terrestrial-aerial transition. Wing and tail movements in the first wingbeat combine with the thrusting legs to launch the bird upward during liftoff. Once airborne, wing and tail muscle activity dominates. Hind limb muscles show some activity to stabilize the legs in flight, but this is minor compared with terrestrial use. Prior to landing, wing and leg muscles are coactive in preparation for ground contact.

Thus, in the pigeon, and presumably other birds, particular parts of the body are used almost exclusively during specific locomotor behaviors. Unique among living vertebrates, birds exhibit a specialized neuromuscular integration of the forelimbs and tail to coordinate the pectoral and caudal flight surfaces during aerial locomotion. However, the flight system is almost completely idle during walking. Similarly, the legs function terrestrially but play only a minor role at best when airborne. This is quite unlike the situation in bats, where the hind and forelimbs are both actively involved in aerial and substrate-based locomotion. The independence of wings and legs in pterosaurs continues to be debated (Padian 1983, 1991; Wellnhofer 1988; Bennett 1990; Unwin and Bakhurina 1994).

Evolution of Theropod Flight

We propose that the wings, hind limbs, and tail of modern flying birds qualify as three distinct locomotor modules (Fig. 2C). Clearly, the inception of the forelimb module was essential to the origin of avian flight. It has been suggested that the evolution of wings in theropods was fostered by the earlier appearance of bipedalism, which released the forelimbs from

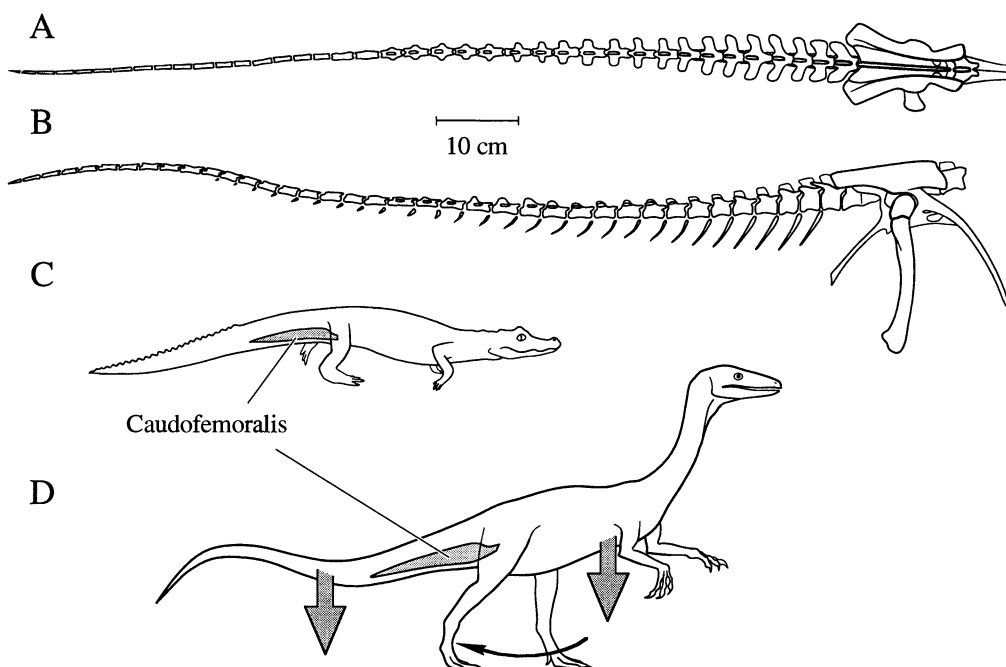


FIG. 3. A. Dorsal and B. right lateral views of the caudal skeleton of an early ceratosaurian theropod, *Syntarsus*. Note the long, robust tail composed of numerous caudal vertebrae and its size relative to the pelvic girdle. C. In living crocodylians substantial caudofemoral musculature connects the tail base and femur. This muscle is the primary retractor of the hind limb. D. In basal theropods the tail served two major roles during locomotion. A large caudofemoralis likely functioned to retract the hind limb (arrow). The tail also served to counterbalance the anterior half of the body about the hip joint (shaded arrows). *Syntarsus* skeleton modified from Paul 1987.

the constraints of terrestrial progression (Ostrom 1979). What has not been recognized are the modifications that took place in the rest of the locomotor system. We hypothesize that the tail became structurally and functionally decoupled from the hind limb and trunk, leading to the formation of independent caudal and hind limb locomotor modules. Once decoupled, the emancipated tail module formed a unique functional association with the forelimb module to create the flight system present in birds today. The tail was released from its functional connection to the hind limb and freed to specialize in control of the caudal flight surface. The hind limb, with a new retraction mechanism, remains as the primary form of terrestrial progression. The transition between the single locomotor module of basal theropods and the three modules of modern flying birds can be viewed as three steps: (1) formation of the pectoral module, (2) liberation of the hind limb and caudal modules, and (3) novel allegiance of the wing and tail to form the flight apparatus.

Pectoral Module.—The substantial literature on the evolution of the avian wing is too voluminous to summarize here. For our purposes, it is most important to ascertain when the predatory forelimbs of theropods returned to locomotor function. *Archaeopteryx*, widely recognized as the oldest and most primitive known bird, had a forelimb skeleton quite similar to that of other Maniraptorans (sensu Gauthier 1986, Fig. 1). Several lines of evidence suggest that *Archaeopteryx* could fly actively (e.g., Feduccia and Tardoff 1979). Analyses of manual and pedal unguals indicate a claw morphology for climbing trees (Yalden 1985; Feduccia 1993). However, with the current limited fossil material, discerning whether the forelimbs were used in arboreal climbing before, during, or

after the evolution of a wing is not possible; arboreal abilities and a wing both appear for the first time in *Archaeopteryx*. In the theropod lineage that gave rise to birds, the forelimbs returned to locomotor use, albeit in innovative ways, after a period of nonlocomotor function. This in itself represents the origin of the pectoral module. Major transformations of forelimb morphology (enlarged sternum, triosseal canal, fusion of the manus, reduction of claws, etc.) must be viewed as refinements, rather than prerequisites, for flight.

Tail Module.—Whereas the pectoral module appears first in *Archaeopteryx*, evidence for a breakup of the basal theropod module is found before the origin of flight (Gatesy 1990, 1994). Thus, although the tail shortened dramatically within early birds, a purely aerodynamic explanation is not sufficient. Reduction in tail size is first seen in coelurosaurs such as ornithomimids and dromaeosaurs (Gauthier 1986; Gatesy 1990, 1994), which have tails of smaller diameter and fewer segments (Fig. 6). The diminution of this major body part affected the location of the center of mass and how the body balanced about the hip joint. Concurrently, skeletal indicators of caudofemoral muscle development are consistent with a reduction in size and functional importance of this primitive limb retractor (Gatesy 1990).

Whereas the functional implications of tail size can be elucidated, the adaptive significance of caudal reduction in terrestrial coelurosaurs is less clear. One possibility is an increased speed and agility stemming from two related factors. First, theropods with shorter, lighter tails might have benefited simply from a lower body mass. Second, a narrower, more mobile tail base may have led to a greater use of tail movement. Ostrom (1976) postulated that in *Deinonychus* the

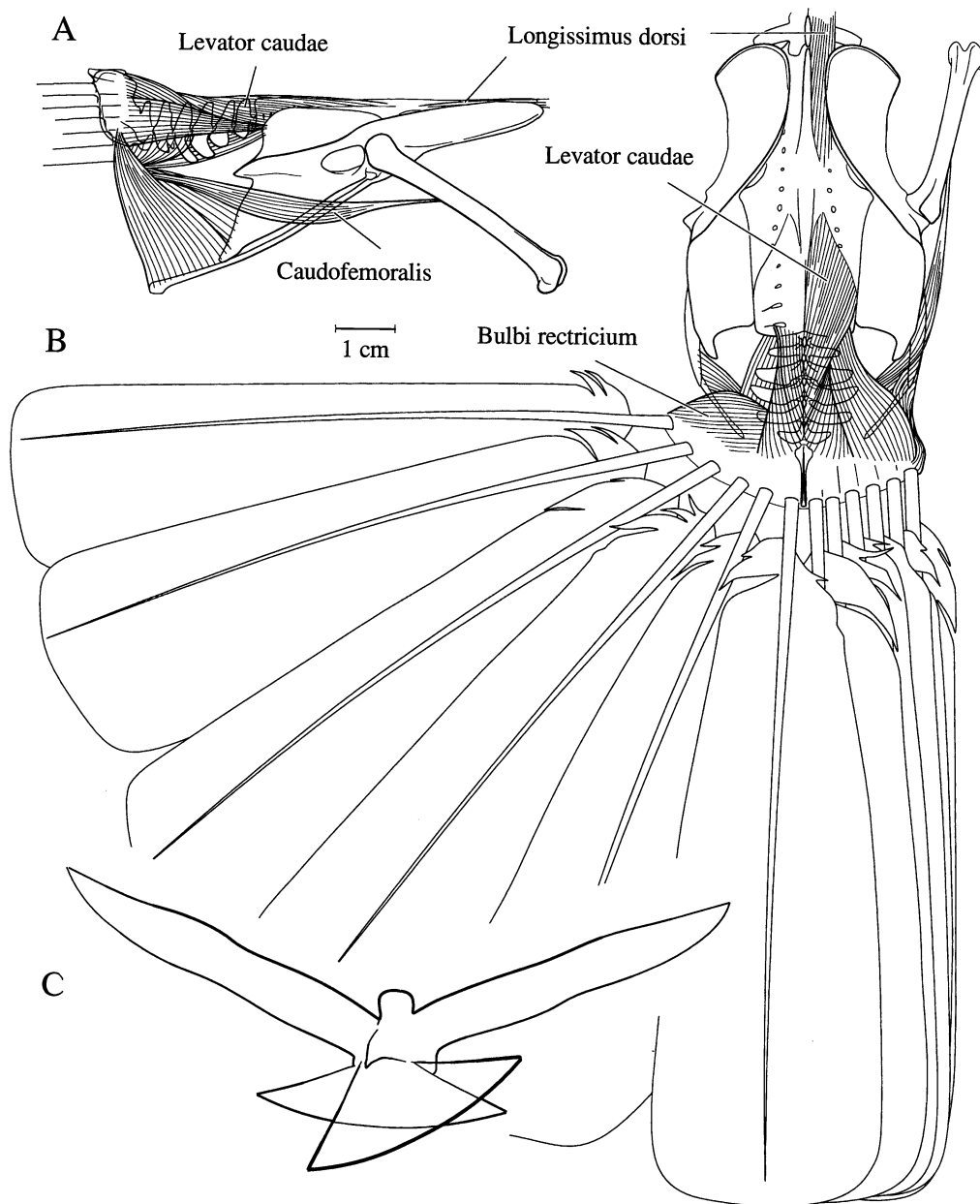


FIG. 4. Anatomy of the caudal region of the pigeon, *Columba livia*. A. Right lateral and B. dorsal views of pelvis and tail. Caudal muscles are transparent to show the caudal vertebrae and pygostyle. The caudal skeleton, although minute relative to the pelvis, supports the 12 rectrices, which form the large tail fan. C. During flight the size and orientation of the tail fan can be changed to produce lift of varying magnitude and direction.

distally stiffened tail could have been used as a dynamic stabilizer during acrobatic maneuvers. However, the tail's ability to stabilize would be compromised if a caudofemoral retraction system was necessary to power the hind limb (especially in hind limb predators such as *Deinonychus*). If the tail took on this new role in coelurosaurs, an incipient form of the hamstring hind limb retraction mechanism found in modern birds may have been evolving as well. This alternative system, powered by muscles originating from the pelvis rather than the tail base, helped decouple the caudal appendage. Such a maneuverable tail may have been preadapted

for its novel aerodynamic role in protobirds (Gatesy 1990, 1994).

The tail of *Archaeopteryx* has 20–23 caudal vertebrae, about half that of basal theropods, but still much longer than in extant birds (Fig. 6). Although the early radiation of birds is still poorly known, forms such as *Sinornis* (Serenio and Rao 1992) and *Iberomesornis* (Sanz and Bonaparte 1992) had much shorter tail skeletons with a pygostyle. Thus, as with the wing, subsequent evolution of the caudal module included refinements for tail fanning (Gatesy and Dial, in press) and improved control.

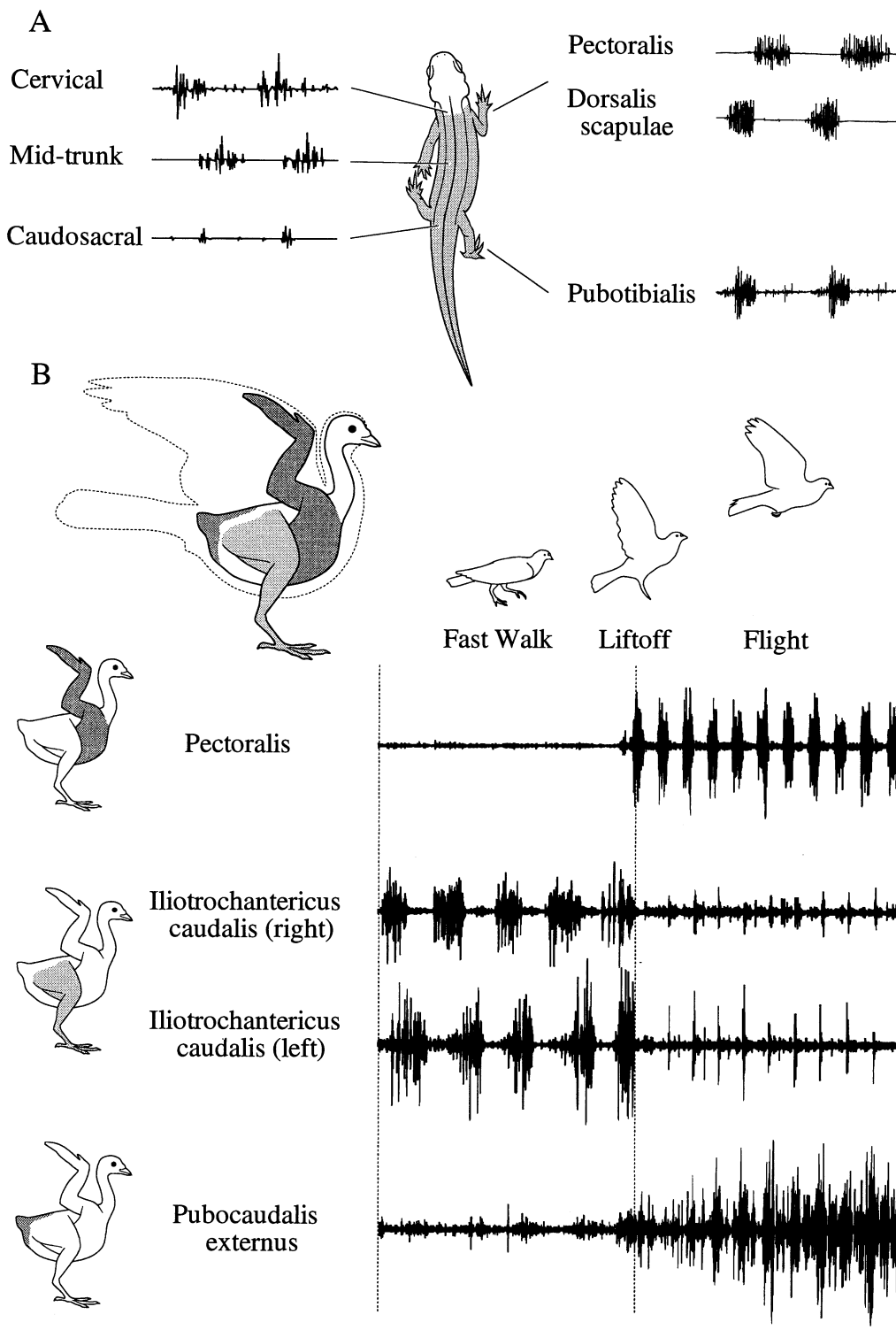


FIG. 5. Muscle activity in a salamander and the pigeon, *Columba livia*. A. Like basal tetrapods, salamanders have a single locomotor module composed of the body axis and all appendages. Axial, forelimb, and hind limb muscles are active simultaneously during terrestrial locomotion. B. The pigeon has three separate locomotor modules. During walking the pelvic module is active. Upon liftoff, the pectoral and caudal modules function as the flight apparatus. Salamander EMGs modified after Szekely et al. 1969, Mangun et al. 1986, and Frolich and Biewener 1992. Pigeon EMGs after Gatesy and Dial 1993.

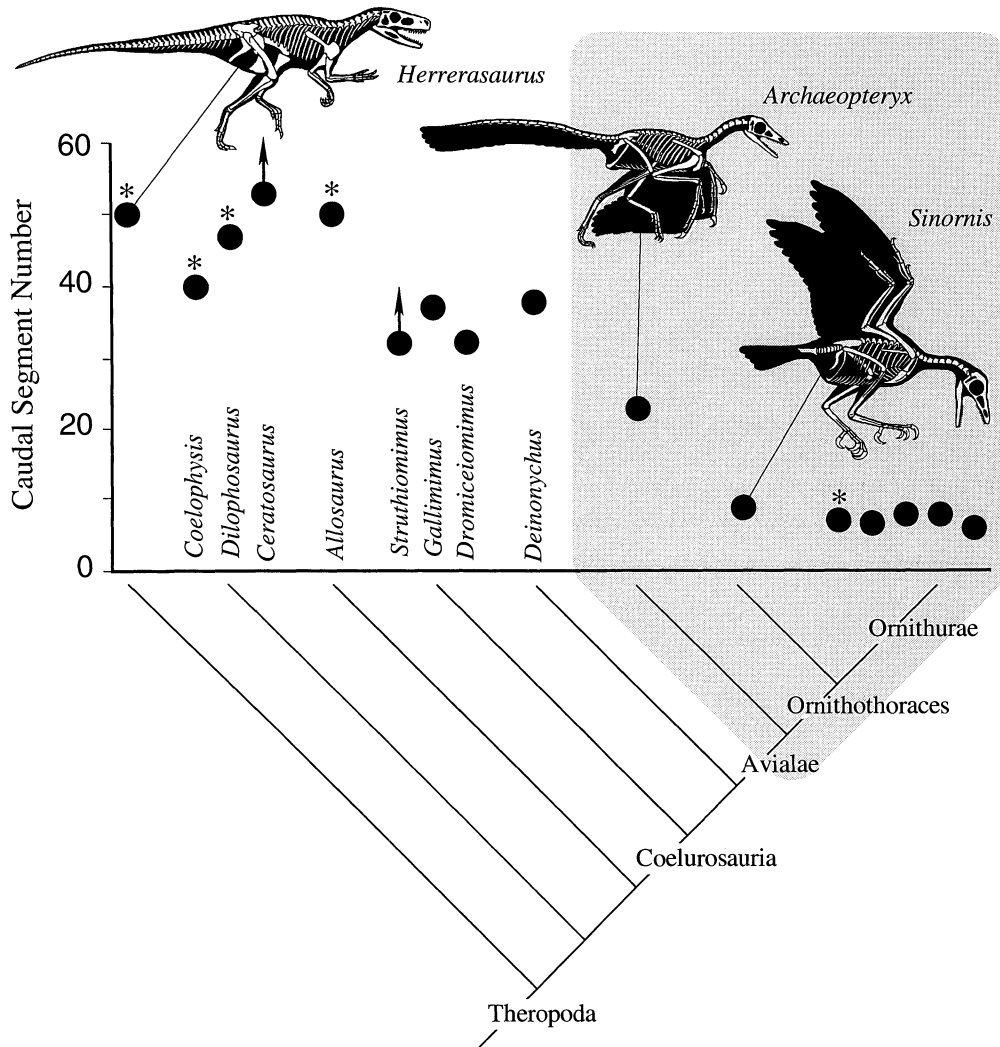


FIG. 6. Plot of caudal segment number through theropod phylogeny. Note the reduction in tail size in coelurosaurs relative to basal theropods such as *Herrerasaurus*. *Archaeopteryx* has fewer caudal segments, but a much longer tail than in Ornithothoraces, which have a pygostyle. Arrows indicate an actual number of caudal segments greater than those preserved. Asterisks designate estimates of total segment number. The shaded region highlights Avialae, the theropod subclade with three locomotor modules and flight. Ornithurine genera from left to right are: *Ichthyornis*, *Columba*, *Apteryx*, *Diomedea*, and *Chordeiles*. Only postsacral caudals are counted as functional tail vertebrae; the pygostyle is treated as a single segment. Cladogram simplified from Gauthier 1986 and Chiappe 1995. Vertebral data from Gatesy 1990, Sereno and Rao 1992, and Novas 1993.

Wing-Tail Allegiance.—Although the tail is not essential for flight in many modern birds, it was undoubtedly a critical component of the flight system at its inception. Bipedalism with fully adducted hind limbs precluded the pelvic appendages from supporting a significant flight surface. Winged forelimbs alone, however, would have been highly unstable, particularly in pitching. The evolution of a caudal flight surface solved this problem. Additional lift from the tail increased stability and shifted the protobird's center of lift posteriorly (Peters and Gutmann 1985). Thus, the caudal module was of critical significance in the early stages of flight, prior to the evolution of refined wing control (Maynard Smith 1952). Only after subsequent functional improvement were the wings able to appropriate the tail's role in lift production (Schaller 1985). Modern birds tolerate

instability and benefit from increased maneuverability (Maynard Smith 1952).

In Early Cretaceous birds such as *Sinornis* and *Iberomesornis*, wing modifications indicative of advanced flight function are accompanied by a shortened tail skeleton and pygostyle (Sanz and Bonaparte 1992; Sereno and Rao 1992). The pelvic limb, however, retains many primitive features. Thus, the fossil record of early bird evolution supports the coevolution of the wings and tail for flight (Chiappe 1991, 1995; Sanz and Bonaparte 1992). This mosaic pattern of locomotor evolution is in accordance with our hypothesis of closely linked wing and tail modules. The anomalous morphology of *Mononykus* (Perle et al. 1993, 1994), a presumably flightless Cretaceous bird, may represent a secondary elongation of the tail skeleton, but

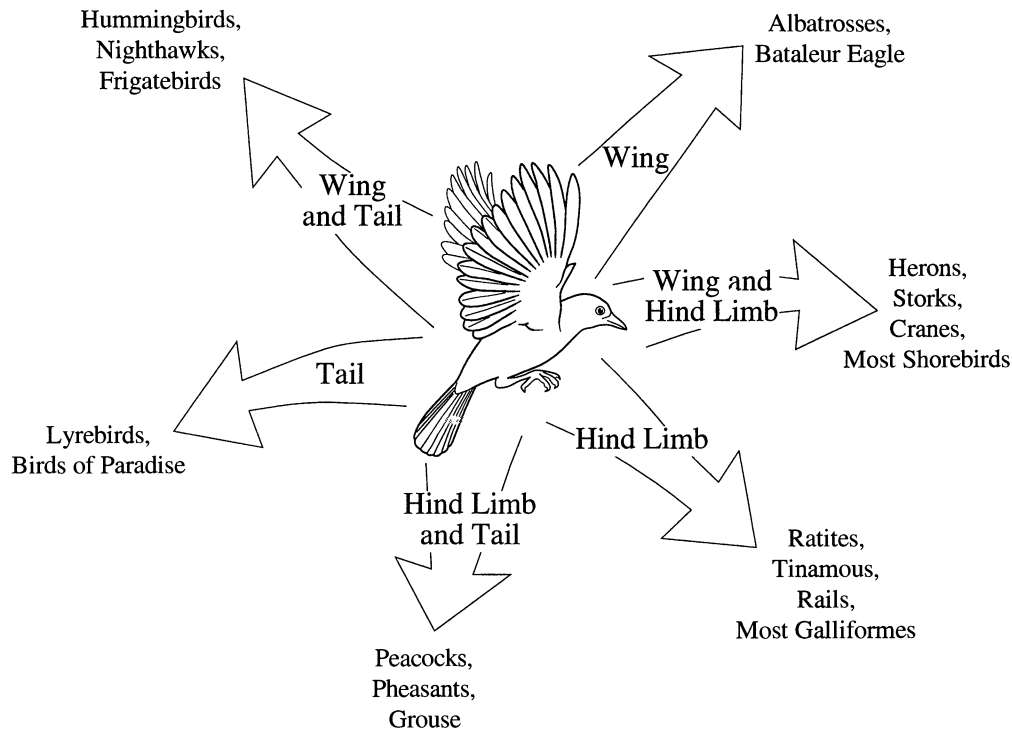


FIG. 7. Birds as mosaics of locomotor modules. Major categories of avian locomotor diversity are the result of the differential elaboration and utilization of wing, tail and hind limb modules. Examples of taxa for which one or two modules have been emphasized are shown. Most passerines occupy a central position in which all modules are moderately developed.

further analysis of this and other Mesozoic theropods is required.

Birds as Mosaics of Locomotor Modules

We propose that avian taxa can be viewed as a composite of three discrete locomotor modules, which are differentially elaborated according to specializations in lifestyle (Fig. 7). For example, the locomotor system will be distinctively organized in species that are highly aerobic, agile, and maneuverable fliers. Specifically, these birds should exhibit reduction in the size of their hind limb module, as this would be excess baggage during flight. This condition is observed in the masters of aerial fliers, the hummingbirds and swifts, for which the ordinal name, Apodiformes, reflects the conspicuous reduction of their hind limb module.

Conversely, taxa that have committed to an exclusively or primarily terrestrial lifestyle should deemphasize their flight apparatus and accentuate their hind limb module. The extreme of this condition is observed in ratites, in which the tail and forelimb modules have been reduced to being either vestigial or are employed as ornaments in breeding displays. Other species that have followed a similar evolutionary path, but that have not abandoned flight, are the tinamous, galliformes and rails. Although still retaining the ability to fly, these groups and others like them have deemphasized the use of their flight modules with a concomitant investment in hind limb locomotion. Most species of birds can be placed somewhere on this aerial to terrestrial continuum.

Considering a completely different medium, many avian species have committed to a primarily aquatic lifestyle. Aerial

locomotion requires use of the wings, just as terrestrial locomotion requires use of the hind limbs. Birds locomoting in water, however, had no such restriction. Two alternatives, either the pectoral or the pelvic module, were available as the primary source of thrust production. Penguins, for example, use the pectoral module for underwater propulsion. The Galápagos cormorant and the extinct Hesperornithiformes are also flightless but employ the hind limb module in their foot-propelled locomotion. Between such extremes are species that move in both air and water, but these can still be divided into wing-propelled (auklets, murrets, and diving petrels) or foot-propelled divers (loons, grebes, and diving ducks).

The caudal module is the least constrained of the three avian locomotor modules. In modern birds the tail is often considered an "auxiliary" flight structure (Pennycuik 1975). We hypothesize that the tail was critical to the origin and early evolution of flight but became less restricted following the perfection of a modern wingbeat cycle and wing control. Many species with large, powerful tails take advantage of the tail module to improve aerial coordination (e.g., accipters, Harris hawks, hummingbirds, swallows, frigatebirds, etc.). Birds that have deemphasized the tail module primarily rely on wing control in open habitats (swifts) or are not highly maneuverable fliers (rails, ducks, and many galliformes). In some taxa, the caudal module has been co-opted for nonlocomotor function during sexual display (e.g., peacocks and birds of paradise).

As some of the previous examples illustrate, the elaboration of one module may require a concomitant reduction in

other modules. Adjacent locomotor modules, in particular, can never be completely independent because they share structures at their common border. For example, the pelvis is at the critical intersection between the hind limb and tail locomotor modules and should be interesting to study in birds exhibiting specialized ecologies. Our preliminary study of avian diversity (Gatesy and Dial 1991, 1992) reveals that pelvic shape is closely related to locomotor ability and flight style. Pelvic morphology may be the result of a compromise between the potentially conflicting demands of tail and leg use. Other such relationships should become apparent when birds and other vertebrates are viewed from a modular perspective.

CONCLUSIONS

In conclusion, we propose that the modular nature of the avian locomotor system offers birds a wide array of evolutionary "options" (Fig. 7). Although these are by no means entirely independent, avian locomotor diversity can be viewed as the differential elaboration of these modules. The dramatic consequences of these options are best appreciated by comparing birds with other theropods that did not evolve flight. The relatively conservative body plan of nonavian theropods was accompanied by low locomotor diversity. Although nonavian theropods reached incredibly large sizes, they were all terrestrial bipeds. For example, we have no evidence that theropods other than birds ever became aquatic, drastically reduced their hind limbs or developed elongate, storklike legs during their 140-million-yr history. Clearly, the origin of flight opened up new habitats and feeding opportunities, but the significance of modular flexibility must also be considered when interpreting the success and radiation of birds.

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