The life style of *Archaeopteryx* (Aves)

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Abstract. The lack of modern flight adaptations and flight maneuverability makes both ground-up take-off and arboreal foraging of *Archaeopteryx* extremely improbable (even if trees were present in a part of its habitat). A combination of heights-down take-off and ground foraging necessitated a swift terrestrial escape to a launching site and probably climbing elevated objects. *Archaeopteryx* does not show any distinctive cursorial specialization and the leg intramembral ratios suggest a slow-pace to multimode (i.e., using various gaits) forager, similar in behavior to today's tinamous and most galliforms. *Archaeopteryx* was an escape runner, not a cursorial predator. The limbs of *Archaeopteryx* and (non-avian) theropods reveal substantial functional differences, which make their similarities even more likely to be synapomorphic.

Keywords. *Archaeopteryx*. Birds. Paleobiological reconstruction. Flight. Locomotion. Foraging. Jurassic.

Introduction

Starting with Heilmann's (1926) portrayal of *Archaeopteryx* von Meyer 1861 as an arboreal animal, all major paleobiological reconstructions of the urvogel have been biased by their authors' views on the origins of birds and avian flight. Current views on the life style of *Archaeopteryx* are heavily influenced by Ostrom's (1974) known attempt to interpret the most primitive bird as a cursorial forager by arguing for the conservation of function of the limbs across the bird/theropod transition, which is implausible, because the bird/theropod transition entails the emergence of flight as a major locomotor type, which had far-reaching consequences for the action of hind limbs (Jones *et al.*, 2000) as well as forelimbs. Accordingly, the limb skeleton of *Archaeopteryx* differs from that of the Dromaeosauridae (widely believed to be birds' closest known relatives) in the structure of the shoulder girdle including the sternum, conformation of humeral ends, relative length of the forelimb which functioned as a wing, proportions and details of the pelvis, morphology of the femur, and intramembral proportions of the leg. Such differences obviously translate into different relative positions and attachment areas of appendicular muscles in *Archaeopteryx* and theropods and thus cannot be biomechanically neutral. Not unexpectedly, the movements and positions of the theropod leg segments were markedly different from those of modern ground-dwelling birds (Gatesy *et al.*, 1999) and the limb allometry of theropods is closer to the pattern observed in mammals than in birds (Christensen, 1999).

While the scenario of using the wings as insect nets (or fly swatters) met with deserved skepticism, the vision of *Archaeopteryx*'s legs being both raptorial and cursorial has been broadly accepted with the help of Paul's (1988) suggestive representations of *Archaeopteryx* as a miniature *Deinonychus* Ostrom, 1969 with the raptorial second pedal digit. At first glance, the second digit may look similar to that of *Deinonychus* in the Eichstätt specimen, because it is rotated upside down due to a preservational artefact, but other specimens belie the tale of the raptorial foot of *Archaeopteryx* (Elzanowski and Pasko, 1999), which is perpetuated in semipopular literature (Shipman, 1998).

Also important is the size difference between *Archaeopteryx* (0.17-0.47 kg, depending on specimen) and typical (nonavian) theropods, *e.g.*, *Deinonychus* (60-75 kg). Small vertebrates tend to be more versatile in locomotor habits than are large vertebrates and many rodents and lizards are at ease both on the ground and in trees. Lull (1929) called them terrestrio-arboreal forms and noted that their climbing adaptations are not well-marked. If *Deinonychus* was the size of *Archaeopteryx*, it would be difficult to rule out the use of its claws for climbing (Naish, 2000) and baby maniraptorans may have climbed rocks and banks (if not trees), as do young crocodiles.

Conservation of function is a murky subject, poorly addressed in the literature and complicated

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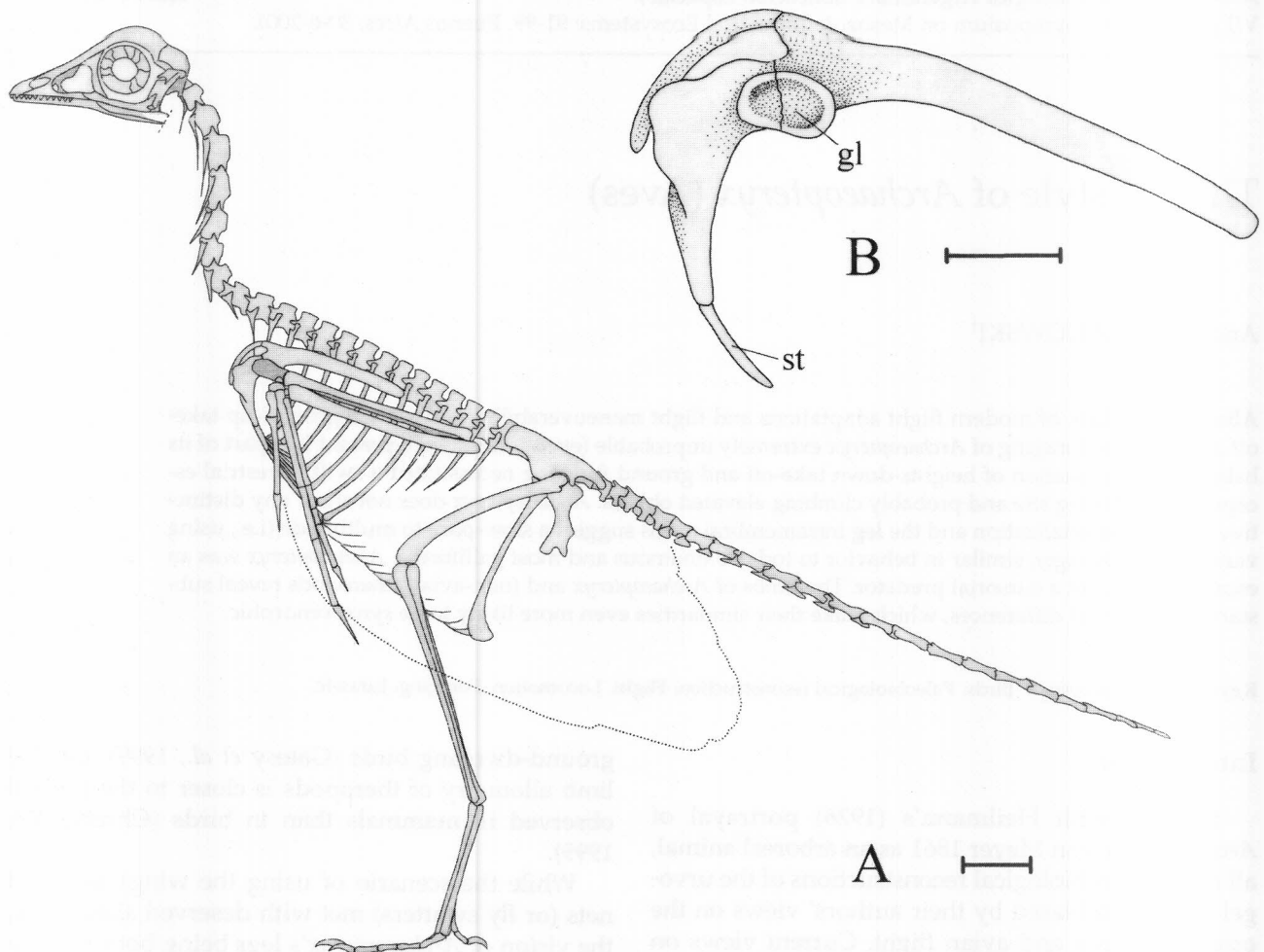
Figure 1. A-B, skeletal reconstructions of *Archaeopteryx*; **A,** the complete skeleton with proportions of the Berlin specimen and pubis oriented as in the Munich specimen. The wing is shown in a hypothetical, maximally folded position involving a distal shift of the radius relative to the ulna (Elzanowski and Pacéko, 1999). **B,** the thoracic girdle with details based on the London specimen. Abbreviations: gl, glenoid; st, bony sternum (which may have been caudally extended by a cartilaginous part). Scale bars equal 10 mm in A and 20 mm in B.

by the notoriously imprecise usage of the term function in biology. There is a laudable tendency to restrict the term function to the action of a structure or the way a structure operates (Lauder, 1999), which is inseparable from the structure itself within "the form-function complex" (Bock and von Wahlert, 1965); and to distinguish thus defined function sensu stricto (which is the meaning adopted henceforth) from the biological role (Bock and von Wahlert, 1965), which is properly assigned to the form-function complex. Conservation of function is equivalent to conservation of the form-function complex and thus implies maintaining the details of adaptation, which seems to be a commonplace between closely related populations and species but becomes less and less common with the increasing divergence of taxa. A case of actual conservation of function is equivalent to the lack of adaptive evolution and thus falls under the heading of evolutionary stasis if it persists over a long stretch of geologic time.

Curiously enough, the conservation of limb func-

tion between *Archaeopteryx* and theropods has been adopted in the context of cladistic reconstruction of bird origins (Gauthier and Padian, 1985; Padian and Chiappe, 1998), although it has little to do with cladistics and, in fact, does not help the purpose of sealing the theropod origins of birds because functional differences between avian and theropod limbs make their similarities more likely to be synapomorphic than do identical or similar functions, which could raise the possibility of homoplasy. While some functional similarities of the limbs of *Archaeopteryx* and theropods are demonstrated by shared biomechanical properties (such as the sweeping movement of the hand driven by the semilunate carpal), no other similarities should be claimed just because of a known cladistic relationship. This relationship is by definition relative and it, does not say anything about the absolute evolutionary distance; thus it is irrelevant for functional predictions. Synapomorphic homology alone may or may not imply a functional similarity. The limb function is determined by the

limb structure, physics of the substrate, size and shape of the entire animal, and the neural control of behavior, which may be responsible for substantial functional differences despite nearly identical morphology (Lauder, 1995). Because of the evident differences in limb anatomy and proportions as well as in the adult body mass and shape, no limb function can be assumed to be conserved between the theropods and *Archaeopteryx*.

Another meaning to conservation of function is a persistent relationship between a form-function complex and a biological role. In the course of phylogeny, the form-function complexes and thus structures are constantly reassigned or co-opted to new biological roles (see, *e.g.*, Raff, 1996) and lose the old ones while still maintaining some similarity. Probably the most important condition for the conservation of a single structure/role relationship is the conservation of other structure/role relationships, because the set of biological roles to fill remains constant within each major type of organisms (such as the tetrapods). The assignment of biological roles to locomotor modes and structures is likely to remain constant, *e.g.*, within uniform genera or families of birds, where species differ in the ways their homologous adaptations work (*i.e.*, in the homologous form-function complexes) rather than in the kind of tasks they perform. In contrast, the emergence of a major organizational type usually entails a redistribution of tasks between form-function complexes and the theropod/bird transition must have been accompanied by the reassignment of biological roles to locomotor modes because of the emergence of a novel locomotor mode (flight), which evolved to fill one of the existing biological roles (probably defense).

Flight

The wings and tail of *Archaeopteryx* are distinctive flight adaptations, which leave no doubt that it could fly. However, considerable differences of opinion persist as to whether and to what extent *Archaeopteryx* was capable of active (= flapping) flight (Vazquez, 1992; Bock and Bühler, 1995; Feduccia, 1999). A scale reconstruction of the skeleton (figure 1.A) reveals that the pectoral girdle is remarkably small and the rib cage below the glenoid very shallow, which limits the mass and fiber length of the wing depressors and thus the arch over which they can operate (Jenkins, 1993). In addition, *Archaeopteryx* lacks the fused carpometacarpus, carpal trochlea, U-shaped ulnare (cuneiform), and polyhedral radial carpal (scapholunar), which are essential for powered flight inasmuch as they help withstand the torsional and shearing stresses of the power stroke (Sy, 1936; Swartz *et al.*, 1992), particularly to counteract

the passive pronation of the manus during the power stroke (Vázquez, 1992), and coordinate the flexion and extension of the forearm and manus (Vázquez, 1994).

The prevailing opinion among experts in flight mechanics is that *Archaeopteryx* was capable of active flight in its simplest form (Norberg, 1985; Rayner, 1991). The wings, as well as the tail (Gatesy and Dial, 1996), lacked the maneuverability used by modern birds for landing, takeoffs, and flight between obstacles (such as tree branches). *Archaeopteryx* was poorly if at all adapted for flight at low speeds, which is biomechanically complex. Flight at low speeds necessitates controlled changes of the pitch of the entire wing relative to the body and of the plane of the manus relative to the wing. It involves upstroke supination and downstroke pronation of the humerus and flicking of the manus from the plane of the wing toward the body in the upstroke to avoid excessive drag (Rayner, 1991). The minimum power speed (at which the least work has to be done) was around 8 m/s for the Berlin specimen (Yalden, 1971b; Rayner, 1985). Some modern birds may have the power output less dependent on flight speed (Dial *et al.*, 1997), but this may have been achieved through the advanced flight adaptations of modern birds and thus may not apply to basal birds.

Takeoff

Since the maximum running speed of the Berlin *Archaeopteryx* is 2 m/s and the stalling speed about 6 m/s (Yalden, 1971a; Rayner, 1985), it could take off either from the heights or run into the wind (Rayner, 1991). *Archaeopteryx* may have or may have not been able to use the wind inasmuch as maneuvering in the wind after takeoff may have surpassed its steering capabilities. But even if some urvögel mastered the wind start, it is extremely improbable that this was their only way to start because the escape tactics of a species that relies on an appropriate wind from an appropriate direction would be terribly ineffective.

None of the recent attempts to show that *Archaeopteryx* was capable of a ground-up take-off were successful. Ruben (1991) assumed that the flight muscle of *Archaeopteryx* made up at least 7% of its body mass (which is testable with a rigorous skeletal reconstruction) and was reptilian in its metabolism and fiber composition (which is untestable) and thus *Archaeopteryx* was capable of anaerobic "burst level" power output of today's lizards and snakes (assumed to be 450 W/kg), which enabled it to a "ground upward takeoff from a standstill". Ruben's power output assumptions were countered by Speakman (1993) and the proposal remains in the crowded limbo of speculations (see also Padian and Chiappe,

1998; Shipman, 1998). Marden (1994) accepted the flight muscle mass to be 7% of the body mass and calculated that a 200 g *Archaeopteryx* with the wings of the Berlin specimen would be just capable of a ground-up take-off assuming the avian anaerobic burst power output (225 W/kg), but realized that the lift/power ratio assigned to *Archaeopteryx* by his regressions is higher than in any living bird and thus unrealistic. In fact, the lift/power ratio of *Archaeopteryx* must have been substantially lower than in modern birds because of the visibly poor anatomical adaptation of the wing for active flight, which cannot be compensated by slightly more generous allowances for the flight muscle mass (contra Shipman, 1998). In addition, the Berlin specimen weighed about 270 g (Elzanowski, in press) and the lift recalculated on the same assumptions would not suffice even for 250 g (Shipman, 1998). Shipman (1998) tried to save the ground-up takeoff by assuming a much higher estimate of the wing area, which is, however, based on a highly inaccurate reconstruction of the *Archaeopteryx* wing, with the forearm and the set of secondaries at least 1.5 times longer than permitted by the wing skeleton (Elzanowski, in press).

Avowedly inspired by a phylogenetic bias toward the cursorial origins of avian flight, Burgers and Chiappe (1999) proposed that avian powered flight originated as a by-product of running and rowing with the wings to generate additional thrust on the ground. Aside from the optimistic assumption that *Archaeopteryx* was well adapted for powered flight, there are at least two fatal flaws in Burgers and Chiappe's model. The generation of additional thrust in running *Archaeopteryx* assumes an extensive rotation of the humerus about its long axis from a heavily hyperpronated to a horizontal flight position. In fact, an extensive rotational movement is impossible in the shoulder joint of *Archaeopteryx*, because both the glenoid and the humeral head are elongated, that is, extended approximately cranio-caudally (figure 1.B).

Burgers and Chiappe's central claim is that flapping the wings to speed up a run generated a "residual" lift that, at a critical speed, enabled *Archaeopteryx* to take off. Even if *Archaeopteryx* were adapted well enough to try it, the increasing lift would result in a loss of traction, which continues to be one of the major difficulties of all cursorial models of the origin of flight (Feduccia, 1999). A simultaneous use of feet and wings for the takeoff in waterbirds, which Burgers and Chiappe cite as an example, does not resolve the loss-of-traction problem, because a starting waterbird holds its feet perpendicular to the water surface and uses them as paddles. In conclusion, the cursorial takeoff of *Archaeopteryx* remains as unlikely as ever.

Foraging

The teeth of *Archaeopteryx* suggest broadly defined insectivory, that is, feeding on small animals, primarily arthropods. *Archaeopteryx* may have foraged in the interior of the German and Bohemian land masses (Wellnhofer, 1995) between mostly bushy to arborescent conifers (mostly araucarias), bennettites, ginkgos and seed ferns; on the shores of pools and streams (Thulborn and Hamley, 1985) inhabited by numerous water insects; as well as on beaches (Viohl, 1985) if launching sites for rapid emergency takeoffs were available nearby. Indeed, since beaches are among the richest feeding grounds and birds are the only small-to-medium-size vertebrates that extensively forage on them (Dyck, 1985), there is a good possibility that avian evolution started in the shore habitat, as suggested by the remarkably early appearance of highly specialized water birds that must have descended from shore foragers
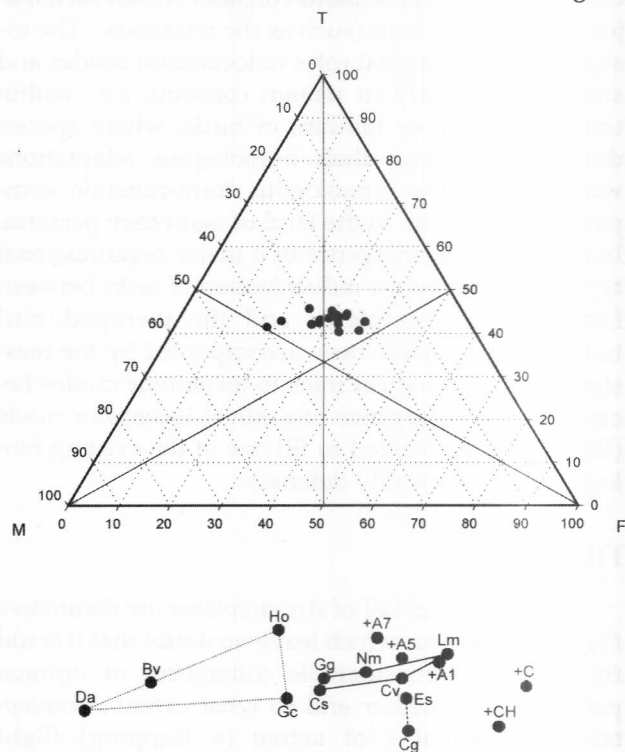

Figure 2. Triple ratios of femur (F) to tibiotarsus (T) to tarsometatarsus (M) in the basal birds (+), cursorial foragers (dotted line), terrestrial multimode foragers (continuous line), arboreal cuckoos (broken line). Each species is represented by a unique combination of the percentage length values for F, T and M (Table 1) on the three corresponding axes of a ternary diagram. The scatter plot is magnified below the ternary diagram. Abbreviations: +A1 *Archaeopteryx lithographica*, +A5 Eichstätt *Archaeopteryx*, +A7 *Archaeopteryx bavarica*, Bv *Burhinus vermiculatus*, +C *Confuciusornis sanctus*, +CH *Changchengornis hengdaoziensis*, Cg *Clamator glandarius*, Cs *Centropus sinensis*, Cv *Colinus virginianus*, Da *Dromas ardeola*, Es *Eudynamys scolopacea*, Gc *Geococcyx californianus*, Gg *Guira guira*, Ho *Haematopus ostralegus*, Lm *Lagopus mutus*, Nm *Nothura maculosa*. See Table 1 for taxonomic assignments.

(Elzanowski, 1983), and the recent paleoecological reconstruction of a basal bird, *Confuciusornis* Hou *et al.* 1995 (Peters and Ji, 1999) suggests a riparian or aquatic habitat. Wellnhofer (1995) argued against the beach habitat of *Archaeopteryx* because of its rarity as a fossil, especially in comparison to the pterosaurs, but the probability of a flying animal's falling into the water is heavily if not primarily dependent upon its use of flight, which was a foraging mode for the pterosaurs but probably only an emergency mode for *Archaeopteryx*.

There are at least two reasons why foraging in trees is extremely unlikely for *Archaeopteryx* even if they were present in its range. First, *Archaeopteryx* was not adapted for the pursuit of small, mobile animals (primarily arthropods) among the branches, because this requires high maneuverability that does not seem possible for a bipedal animal without the maneuverability of wings or, as in some mammals, a prehensile tail (Cartmill, 1985). In fact, only passerines and a few other avian taxa evolved enough maneuverability to forage effectively in trees. Secondly, it does not look like the Solnhofen araucarias harbored much food easily available to unspecialized arboreal insectivorous birds, which today feed, as do some cuckoos, on caterpillars and similar larvae of symphytan hymenopterans. The flighted imagoes of such insects would have been preserved in the rich Solnhofen fauna (Barthel *et al.*, 1990) if they were abundant.

Garner *et al.* (1999) proposed the Pouncing Proavis Model according to which birds evolved from predators that perched and pounced on ground prey and obviously implied this mode of life for *Archaeopteryx*. However, the Pouncing Proavis Model has two major problems. First, a pouncing attack requires a considerable precision of landing and is used today by advanced skillful fliers, such as the owls (Strigiformes), rollers (Coraciiformes), and shrikes (Laniidae), which cannot run and most of them are poor walkers. Second, it is hard to see what would the protobirds, which were clumsy fliers, unable to take off back to the perch, gain by poorly controlled pouncing, climbing back, and waiting again instead of using their strong legs of terrestrial birds to pursue the prey on the ground, and thus "why a cursorial dinosaur became a sit-and-wait ambush predator" (Hedenström, 2000). A feeding adaptation cannot evolve unless it brings energetic gains and this seems extremely unlikely for the initial stages of avian flight no matter what sequence of behavioral adaptations led to its origins. Avian flight is a costly adaptation and its origins involved a high energetic cost of building up in ontogeny and maintaining through life a second, in addition to the strong legs, locomotor apparatus for climbing and flying. In contrast to bats and pterosaurs, flight does not replace but rather functions in addition to terrestrial locomotion (or swimming) in all primitive birds. In the majority of modern birds and the main flight muscles (pectoralis and supracoracoideus) alone make up 15%-25% of the body mass. Such a costly adaptation could have evolved only in response to predation since only survival that leads to reproduction (and, of course, reproduction itself) is maximized at any cost, while other functions are optimized in terms of lowest cost/benefit ratios.

Terrestrial locomotion

Many reconstructions of the terrestrial locomotion in fossil vertebrates are muddled by the notorious imprecision of the term "cursorial" (Stein and Casinos, 1997; Carrano, 1999). With reference to terrestrial birds, it is proposed here to distinguish between escape runners, such as today's tinamous and many galliforms, which run only in emergency to escape a predator, and cursorial foragers, such as some charadriiforms, which run almost constantly in pursuit of food. A cursorial forager has to be so well adapted for running as to make it profitable in terms of energy gains whereas an escape runner does not.

Archaeopteryx has a strong but unspecialized hind limb (figure 1.A) with a full-length fibula and an asymmetrical anisodactyl foot with digit IV much longer than digit II. However, the pes of the Solnhofen specimen (to be classified in a separate genus) is more symmetrical and thus suggests somewhat more cursorial habits. The opposable hallux and laterally compressed pedal claws indicate perching ability (Yalden, 1985, 1997) and the preservation of right foot of the Munich specimen in a grasping position, with the claws of hallux and fourth toe superimposed, support this conclusion (Wellnhofer, 1995). But *Archaeopteryx* was certainly at ease on the ground, as attested by its strong legs, with the tibia longer than the femur, and a slightly elevated, short hallux that did not interfere with terrestrial locomotion. However, not a single feature of *Archaeopteryx* represents the cursorial end of the spectrum of ambulatory adaptations (Carrano, 1999) and modern ground birds seem to have the hind limb, pelvis and vertebral column (especially synsacrum) better adapted for cursorial locomotion than *Archaeopteryx* (Bock, 1986).

Traditionally, the intramembral leg proportions of *Archaeopteryx* have been compared to those of birds that are similar to *Archaeopteryx* in overall shape (body, limbs and tail), such as cuckoos and touracos (Engels, 1938; Brodkorb, 1971), which are arboreal and arboreo-terrestrial foragers (table 1). However, the leg proportions of *Archaeopteryx* show the best

Table 1. Leg intramembral triple ratios of femur (Fe) to tibiotarsus (Ti) to tarsometatarsus (Me) in selected Mesozoic (?) and modern birds representing arboreal (A), multimode terrestrial (T), and cursorial (TC) foragers (ordered by the decreasing femur length). CU Cuculiformes, GA Galliformes (Phasianidae s. l.), SH shorebirds (Charadriiformes), TI Tinamiformes.

Species	Foraging mode[1]	Body mass in grams[2]	Fe + Ti + Me = 100%
✞*Confuciusornis sanctus*	?	?	37.0 + 42.6 + 20.43
✞*Changchengornis hengdaoziensis*	?	?	36.8 + 40.6 + 22.63
Clamator glandarius (CU)	A	138-169	33.0 + 40.3 + 26.7
✞*Archaeopteryx lithographica*	tbd	451-468est.	32.6 + 43.9 + 23.5
Lagopus mutus (GA)	T	422	32.6 + 44.4 + 23.0
Eudynamys scolopacea (CU)	A	238	32.0 + 42.1 + 25.9
Colinus virginianus(GA)	T	178	31.4 + 43.1 + 25.5
Eudromia elegans (TI)	T	660	31.2 + 42.9 + 25.9
✞*Eichstätt Archaeopteryx*	tbd	161-178est.	30.8 + 44.1 + 25.1
Odontophorus guttatus (GA)	T	294-314	30.2 + 42.6 + 27.2
Nothura maculosa (TI)	T	300	29.5 + 43.4 + 27.1
✞*Archaeopteryx bavarica*	tbd	208-225est.	29.3 + 45.1 + 25.6
Centropus sinensis(CU)	T	236-268	28.1 + 42.4 + 29.5
Guira guira (CU)	T	136-168	28.0 + 43.0 + 29.0
Geococcyx californianus (CU)	TC	376	26.8 + 42.0 + 31.2
Haematopus ostralegus (SH)	TC	526	24.6 + 45.6 + 29.8
Burhinus vermiculatus (SH)	TC	320	20.5 + 42.8 + 36.7
Dromas ardeola (SH)	TC	325	18.3 + 41.4 + 40.3

[1]The categorization of Cuculidae based on Payne (1997).
[2]Body mass estimates of Archaeopteryx are derived from the femur diameters using the regression calculated by Campbell and Marcus (1992) and those for extant taxa are from Dunning (1993). 3Median values calculated from Chiappe *et al.* (1999).

match with phasianid galliforms and tinamous (table 1; figure 2), which are typical escape runners and slow-pace to multimode foragers. The phasianid galliforms have been suggested before as ecomorphological analogs of the urvögel (Wellnhofer, 1995). The comparison of leg intramembral ratios amongst birds of comparable size demonstrates that *Archaeopteryx* was anything but a cursorial forager.

Gatesy and Middleton (1997) showed a similarity of leg proportions between *Archaeopteryx* and *Confuciusornis, Sinornis,* and *Cathayornis,* which were once thought to be arboreal. However, these results are based in part on erroneous measurements taken from the literature. In fact, the length ratio of the femur to tibiotarsus to tarsometatarsus based on correct measurements of *Confuciusornis* (Chiappe *et al.,* 1999) is unlike that in *Archaeopteryx* (table 1; figure 2) and suggest a very different function of the leg. The life style of *Confuciusornis* may have been aerial and/or aquatic but does seem to have been arboreal (Peters and Ji, 1999). The correct length measurements for the femur, tibiotarsus, and tarsometatarsus in *Sinornis* are, respectively, 19.0, 25.5, and 14.0 mm (pers. obs.), and their ratio of 32.5+43.6+23.9 = 100% is even closer than reported to that in the much larger London specimen of *Archaeopteryx* (table 1) but different from the ratios in sparrow-sized arboreal passerines (Palmgren, 1937). The length figures used by Gatesy and Middleton (1997) for the femur and tibiotarsus of *Cathayornis yandica* specimen #9769 are correct but that for the tarsometatarsus is at best un-

certain, because the bone cannot be measured with any precision (pers. obs.). The functional meaning is of the similarity in leg proportions between the crow-sized London *Archaeopteryx* on one hand and the sparrow-sized *Sinornis* and only slightly larger *Cathayornis* on the other is heavily obscured by their considerable size differences inasmuch as the similarity of limb proportions in animals from different size categories does not directly imply the similarity of leg function (Alexander, 1997).

The comparisons of leg proportions (table 1; figure 2) agree with what is implied by the combination of ground foraging, inability to take off on the spot, and presence of *Compsognathus* Wagner, 1861 and (unless *Archaeopteryx* was endemic to the Solnhofen area) other theropods, which were threatening at least as competitors and probably also as predators of the young: *Archaeopteryx* most probably was an escape runner (figures 3 and 4), whether it ran to take off to a nearest launching site ("perch"), or less likely but possibly, to leap up and glide (Norberg, 1990) or to take off against the wind (Rayner, 1991). *Archaeopteryx* ran only as far as needed to take off, most probably to launching sites, such as rocks, arborescent bushes, or conifer stem succulents (up to 3 meters tall) or simply use a break in topography, as proposed by Peters (1985). This scenario does not require a habitat replete with launching sites such as cliffs (contra Gauthier and Padian, 1985): in emergency, *Archaeopteryx* was certainly able to use even a single launching "perch" as today's lizards and
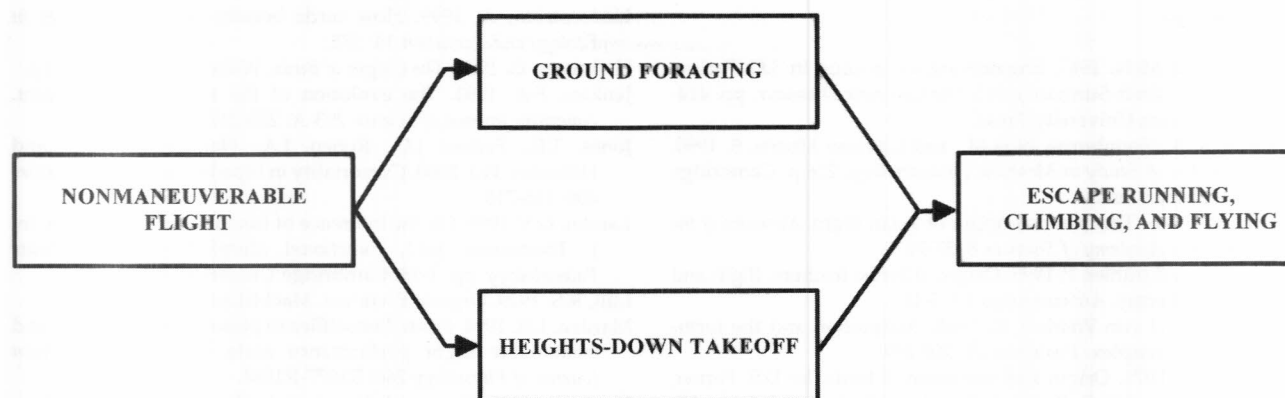
Figure 3. A reconstruction of the main constraints to the locomotion and foraging of *Archaeopteryx* as a bird. Each arrow means "constrained *Archaeopteryx* to".

snakes (with probably lesser cognitive abilities) are able to remember and use their single preferred refuges (Greene, 1994; Stone *et al.*, 2000; Mark Paulissen, pers. comm.).

Running, climbing, and flying were used primarily or exclusively for escape (figure 4), which makes plausible the use of the manual claws for climbing as advocated by Yalden (1985, 1997): if used only occa-

opposed arboreal and cursorial interpretations of *Archaeopteryx*. Ostrom (1974) and his followers are right in part insofar as *Archaeopteryx* was a ground forager and thus predominantly terrestrial, but so are Bock (1986), Bock and Bühler (1995), and Yalden (1985, 1997) insofar as *Archaeopteryx* climbed and used its claws to do it. However, the present paleobiological reconstruction of *Archaeopteryx* clearly
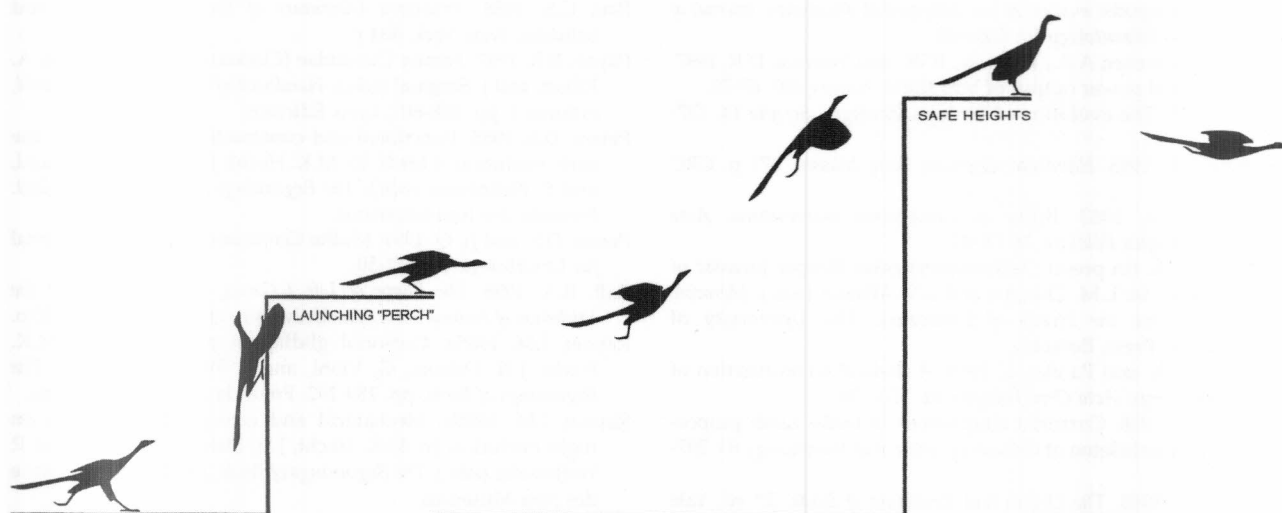

Figure 4. The escape behavior of *Archaeopteryx* as reconstructed from the locomotor adaptations and functional constraints (figure 3). The term "perch" stands for any structural feature of the habitat that enabled *Archaeopteryx* to use of gravity for takeoff. The launching "perch" is not necessarily predator-safe and used only for rapid takeoff.

sionally in emergency, the likely damage to the wing feathers was tolerable because, in terms of Darwinian fitness, if a feature is necessary for survival, it pays to maintain it even if it moderately interferes with other functions.

Conclusion

The present reconstruction of *Archaeopteryx* as a leisurely forager and an escape runner, climber and flier (figures 3 and 4) integrates the two, heretofore

speaks against the cursorial origin of avian flight.

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