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12. Because of the finite horizontal resolution of the model and the effects of spectral truncation, the complex mountain topography of the western United States was represented as a broad ridge with a maximum elevation of ~3 km. Because its central axis parallels the Rocky Mountains, we will refer to this feature by that name.
13. Although no observed soil moisture data are used for comparison, the correspondence between the distribution of dry climates in the M experiment and the observed distribution is evident when the climate classification system developed by Köppen is used. In this scheme monthly mean temperature and precipitation are used to determine a climatic classification designed to correspond to the prevailing vegetation. This scheme is described in detail by H. H. Lamb [in *Climate: Present, Past and Future* (Methuen, London, 1972), pp. 509–514]. On the basis of this system, the distribution of desert and steppe climates (Köppen's category B) from the M experiment is quite similar to that observed in the mid-latitude Northern Hemisphere; this similarity implies that the model's simulation of temperature and precipitation is realistic.
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Allometric Scaling in the Earliest Fossil Bird, *Archaeopteryx lithographica*

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Archaeopteryx is almost universally considered a primitive bird. Debate persists, however, about the taxonomic assignment of the six skeletal fossils. Allometric scaling of osteological data shows that all specimens are consistent with a single growth series. The absence of certain bone fusions suggests that no specimen is full-grown. Allometric patterns, as compared to growth gradients of other dinosaurs, extant ectotherms, and extant endotherms, suggest that _Archaeopteryx_ was likely a homeothermic endotherm with rapid growth and precocial abilities for running and flying. Multivariate allometric models offer a significant potential for interpreting ontogenetic patterns and phylogenetic trends in the fossil record.

Archaeopteryx REPRESENTS A RARE transitional form in the fossil record (*1, 2*). During the past 130 years of scrutiny and sustained controversy, the six described specimens have been variously parceled among six different genera and nine different species (*3*). The most recent taxonomic revision occurred in 1985 (*4*) and the most recent disclosure of a new specimen in 1988 (*5*).

Contention about the status of these specimens has persisted because of the inconsistencies in relative sizes and proportions and the lack of unambiguous diagnostic characters (*6*). Because previous attempts have not resolved the taxonomic issues, we reexamined the variability among the specimens with an exponential allometric (growth-series) model. The allometric model is useful in interpreting growth patterns among developmental stages within a taxon (*7, 8*), and divergent growth patterns can distinguish multiple taxa (*9*). Growth patterns differ among taxa either because the relative growth rates (allometries) of individual characters differ or because the timing (heterochrony) of structural development differs. The most divergent allometric (or heterochronic) variables can contribute to the evolutionary separation of closely related taxa within a phylogeny (*9*).

To apply an allometric growth model as an alternative hypothesis against which to test patterns of phylogenetic change (*10*), we first needed to determine whether the specimens represented elements of a consistent progression, differing only in absolute size (age). Nine major skeletal components, and available dimensions for maxillary and premaxillary teeth, were examined as simple functions of femur length, a commonly used index of body size in birds. All linear regressions resulted in high correlation coefficients, consistent with a single series (Fig. 1).

Skeletal fusions, an independent qualitative line of evidence, also support the interpretation of ontogenetic stages. All full-grown coelurosaurs (*11*) are known to have had a variety of skeletal fusions that were complete in full-grown adults (*12*). Even though a substantial size range exists among the six *Archaeopteryx* specimens (the largest being twice the size of the smallest), no specimen had a full complement of these age-related fusions. The smallest specimen (Eichstätt) had no such fusions. The limited extent of skeletal fusions suggests that none of the specimens was full-grown.

Growth and the development of flight feathers are frequently correlated in extant birds. A full complement of wing and tail feathers existed in the Eichstätt specimen, despite its small size. This might suggest that the Eichstätt specimen was a full-grown member of sympatric (but smaller) species, but this is not a necessary conclusion. Some megapodes have a full complement of flight feathers and are fully homeothermic immediately upon hatching (*13*), and most volant precocial birds can fly short distances within the first week of post-hatching development (*14*). Thus, the development of feathers in the smallest specimen is not incompatible with a single-species growth series. Further, it is consistent with a hypothesis that precocial flight and thermoregulation are ancestral for living birds.

The parsimonious conclusion is that all six fossils are consistent with a single size-series and that none of the specimens were fully grown (*15*). Therefore it is appropriate to use an allometric growth model to examine changes in skeletal proportions that accompany differences in size. The growth dynamics of *Archaeopteryx* can then be compared with related theropod lineages in terms of ancestral affinities and context with extant taxa. Such comparative allometric ap-

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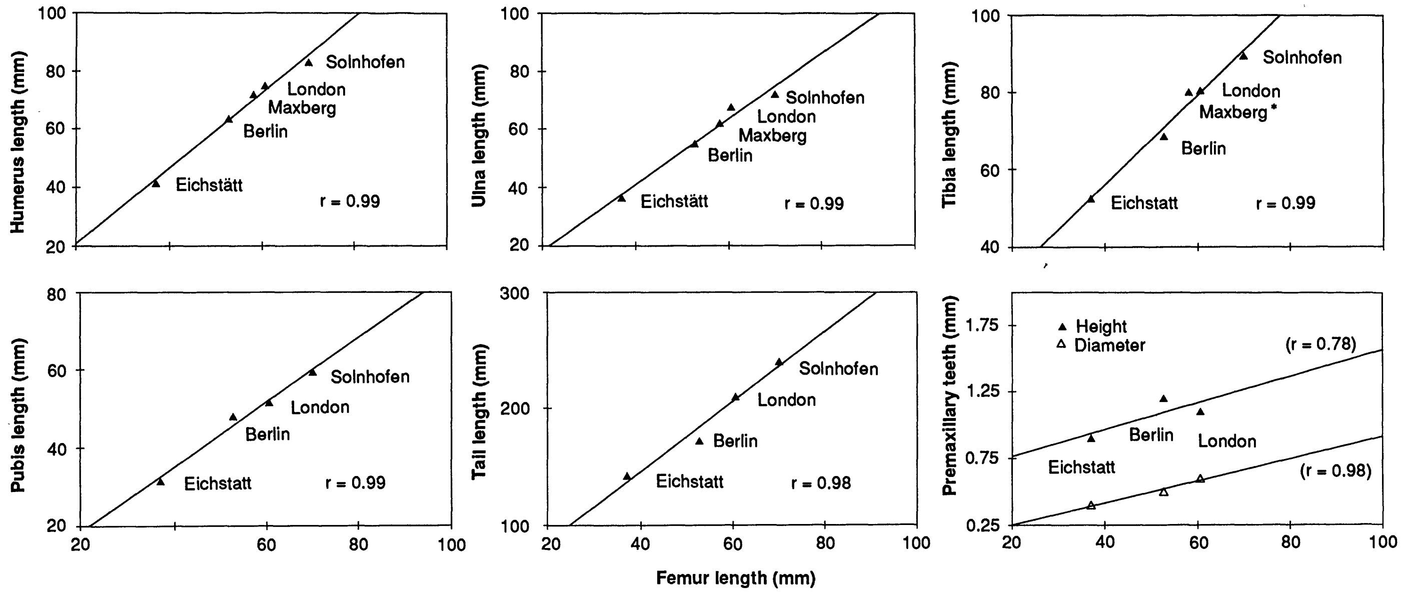

Fig. 1. The allometric coefficients (relative growth rates) for skeletal elements and premaxillary teeth of *Archaeopteryx*, scaled with respect to femur length (bivariate allometries, α_b). The five skeletal comparisons were chosen to include representation from both of the limbs and the pelvis. The four skeletal plots not shown also had high correlation coefficients: radius ($r = 0.98$), illium (0.95), ischium (0.93), and Digit III (0.99). Premaxillary tooth dimensions (*5*) scaled with femur length, as did maxillary height ($r = 0.90$) and diameter (0.98) which are not shown. Variance in premaxillary tooth height may be due to erosion because these teeth encounter all food entering the mouth and are the most vulnerable to mechanical damage during food acquisition. The asterisk indicates approximate measurement.

proaches have been recognized as conceptually important in systematics, evolutionary biology, and functional morphology (*16, 17*).

Multivariate allometries were examined among 135 characters of *Archaeopteryx* (*18*) by major-axis regression, a robust estimation procedure. The analysis revealed that 98% of the total variance among characters can be explained by variation in general size (*19*), a finding that is also consistent with a single growth series (*20*).

In living vertebrates, the size-dependent scaling of bones typically deviates from isometry (in other words, constant proportions). Concerning differences among bird species, Callison and Quimby (*8*) cogently stated that "little big birds just do not look like big little birds." For instance, among cursorial birds, adults of the larger species have larger distal femur widths relative to length than do smaller species (*21*).

Multivariate growth allometries of the limbs in *Archaeopteryx* (Fig. 2) indicate that lengthening of the long bones of the wing during development was disproportional both to the leg and to general size. Moreover, the wing lengthened proximodistally with a uniform pattern of positive allometry along the primary limb axis through manual digit **II**. The radius-ulna complex contributed most to wing extension. As in other saurischian dinosaurs (*11*), the second digit was the longest in *Archaeopteryx*. Similar patterns of growth characterize even the earliest coelurosaurs (*11*), which are distinguished from other theropods by their long forelimbs and large hands (*6*). The coelurosaurian-like allometric relations are further expressed during the ontogeny of extant birds, in which "[sustained] flight has apparently required the length of the wing bones to scale at a substantially greater rate of increase, relative to increasing body mass, than has that of the leg bones" (*22*).

Compared to ornithurine birds, *Archaeopteryx* retained ancestral dinosaurian allometries in the long bones of its hindlimb. The femur became relatively longer ($\alpha_m = 1.09$) with an increase in body size, but the limb decreased proximodistally (for example, tibia, $\alpha_m = 0.92$; Mt **II**, $\alpha_m = 0.77$) and became relatively shorter in total length. Similar relations among hindlimb components appear common among most cursorial nonavian dinosaurs (*6*). In larger forms, such as *Allosaurus*, the femur was relatively longer than the tibia. Smaller theropod dinosaurs such as *Compsognathus* had a femur relatively shorter than the tibia.

Metatarsal **I-II** of the foot of *Archaeopteryx* (including the reversed hallux) also became relatively shorter with growth. Thus perching would have been more difficult as size increased, making the possibility of the adult being a "perching bird" even more unlikely than previously thought (*23*).

Carrier and Leon (*24*) have recently established that, in California gulls, negative allometry in long bone thickness may characterize rapidly growing species that require the early use of limbs during development. Avian wing bones are negatively allometric in diameter, becoming relatively thinner with increased size (for example, humerus: $\alpha_b = 0.80$) (*22*). Flight mechanics requires that wing bones become exceptionally longer and thinner to accommodate flexion and arching during flight. Rapid growth and negative midshaft allometries of long bones are a general pattern common to extant endotherms (*17, 22, 24*).

In cases in which the legs function in locomotion or support soon after hatching (in other words, encounter early stress), the long bones initially have an increasing midshaft diameter. Carrier and Leon (*24*) conclude from fracture tests that the wider midshaft diameter compensates for reduced strength in developing tissues. During growth, the bone tissue strengthens and the diameter of the bone narrows. This trade off between strength and width results in a bone being able to withstand a constant amount of strain (relative to mass) throughout development. The Eichstätt specimen had a relatively thicker midshaft femoral diameter ($\alpha_b = 0.089$) than the larger specimens (for example, $\alpha_b = 0.067$ for Berlin), which is consistent with the hypothesis concerning early locomotion in extant birds.

Similar contrasts of growth allometries can be made with extant ectotherms. In ectotherms, however, femoral and humeral width scale either isometrically or positively (often highly so) with size (7). Thus, the long bones of ectotherms become relatively thicker with age, not thinner as in homeothermic endotherms. Femora and humeri from an early sauropodomorph (*Massospondylus*) and an early theropod (*Syntarsus*) showed such an ectothermic pattern of growth (*25*).

In addition, the presence of fibrolamellar bone in subterminal ontogenetic stages of medium to large dinosaurs indicates a capacity for sustained rapid growth, suggesting a higher metabolic rate than that observed in any extant ectotherm of equivalent size (*26*). Although fibrolamellar bone appears to be ancestral in dinosaurs, only some dinosaurs show negative allometry in the change of midshaft diameters of long bones during ontogeny. In fact, the only dinosaurs known to display the full suite of "endothermic" features, including a thermocoel of feathers, is that group of theropods to which *Archaeopteryx* and later birds belong.

Partial skulls are preserved from only two *Archaeopteryx* specimens, and most bony elements are not represented well enough for more than cursory consideration of allometric relations (Fig. 2). The skull of *Archaeopteryx* appears to have shortened and deepened relative to increasing size. This pattern is consistent with what is known about carnivorous archosaurs (*6*). Skull reduction can be accounted for by the significant relative shortening of the beak and lower jaw ($\alpha_m = 0.20$). Through ontogeny, *Archaeopteryx* gained a significantly deeper orbit ($\alpha_m = 1.63$) and a smaller antorbital fenestra. These features typically distinguish smaller theropod dinosaurs (for example, *Syntarsus*) from larger ones (for example, *Tyrannosaurus*) (*6*).

In the axial skeleton, there is a complex series of growth gradients (*27*). However, examined as functional units, the cervical section increased in relative length ($\alpha_m = 1.47$) with increasing size. This is similar to the condition in other long-necked saurischian dinosaurs, in which the first five cervical vertebrae were usually isometric but more posterior cervicals and the first trunk vertebrae were highly positively allometric.

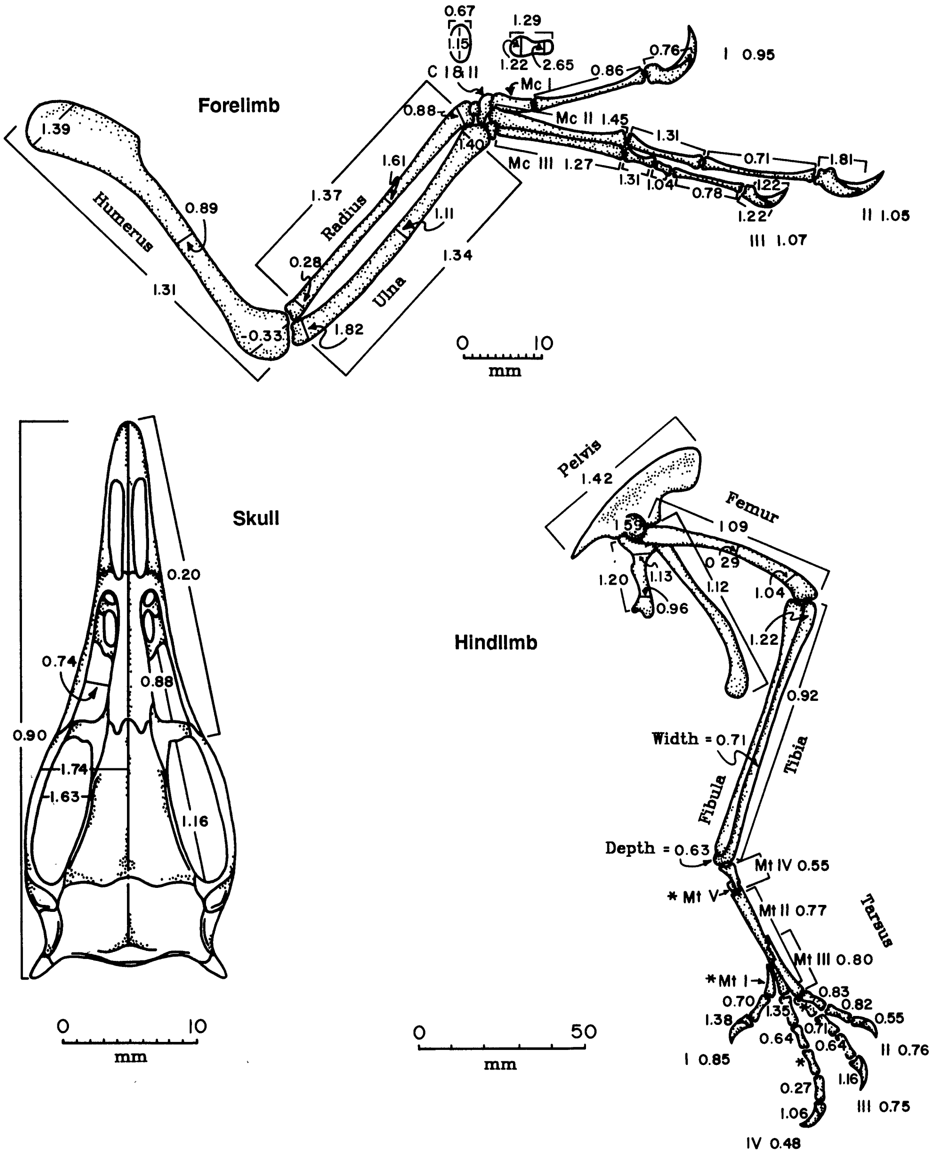

Fig. 2. Multivariate allometric coefficients of limb and skull elements of *Archaeopteryx*. Forelimb and hindlimb elements are represented by lateral projections, and the skull by a dorsal projection. Unmeasurable or damaged elements are indicated by an asterisk. Digits were analyzed as units and by segment.

The thoracic portion of the axial skeleton was approximately isometric ($\alpha_m = 1.02$) in *Archaeopteryx*. The sacrum increased in relative length ($\alpha_m = 1.60$) while the tail length was relatively reduced ($\alpha_m = 0.80$). This pattern appears to be general to all stiff-tailed, tetanurine theropods. The proximal caudal elements were negatively allometric, whereas the distal elements were positively allometric. Such a reduction in proximal vertebral length, in conjunction with the presence of smaller, free elements at the base of the tail, would have provided increased tail maneuverability with growth.

The sacrum of *Archaeopteryx* was typical of theropod saurischians. Its five vertebrae were highly positively allometric, indicating that sacral support for the ilium (and associated pelvic musculature) increased with size. As in other theropod dinosaurs, the ilium in *Archaeopteryx* was highly positively allometric, and the acetabulum enlarged with increasing size. The pubis and ischium also lengthened with size. The latter grew relatively faster than the former, a condition that was also present in ornithomimids (*25*) and may have been general in early coelurosaurs.

We conclude that the six specimens of *Archaeopteryx* represent a subadult size series of primitive birds that were probably homeothermic endotherms capable of precocial ambulation and flight. Multivariate allometric models, as applied to *Archaeopteryx*, offer a significant potential for interpreting ontogenetic patterns and phylogenetic trends from the fossil record. The methods are generally applicable to all taxonomic levels, are especially valuable when applied to the skeletal fossil record, and can suggest functional dynamics invoked during growth and through evolutionary time.

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12. P. Wellnhofer, *Palaeontogr. Abt. A Palaeozool. Stratigr.* **147**, 169 (1974); J. H. Ostrom, *Biol. J. Linn. Soc.* **8**, 91 (1976); see also (*6*). Retained subadult characteristics of coelurosaurs: free cervical ribs, separate sacral vertebrae, and an unfused scapulocoracoid. Most extant birds have a ball-and-socket joint between the scapula and coracoid which never fuses. The scapula and coracoid fuse when growth ceases in extant ratites which (like *Archaeopteryx*, *Hesperornis*, and other dinosaurs) do not have such a joint. The subadult status may also account for the lack of an ossified sternum [G. DeBeer, *Archaeopteryx lithographica*, British Museum (Natural History), London (1954)]. Sternal ossification appears late in the development of extant birds and other full-grown theropods, this condition pre-dates the origin of birds (*6*).
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19. Multivariate allometric coefficients (α_m) are with respect to general size [F. L. Bookstein, *Syst. Zool.* **38**, 173 (1989)]. General size was estimated as the major axis, equivalent to the first eigenvector of the covariance matrix. Allometries (α_m) were estimated as growth rates of characters with respect to general size, scaled to a mean of one = isometry. All measurements were log-transformed to ensure homoscedasticity and to linearize allometric scaling effects [P. Jolicoeur, *Biometrics* **19**, 497 (1963)].
20. The conclusion of a single growth trajectory is parsimonious and consistent with the data. In the absence of diagnostic characters for *Archaeopteryx*, however, we cannot exclude heterochrony via hypermorphosis or progenesis (identical growth trajectories, differing only in adult size), which can occur in closely related taxa (for example, species flocks).
21. If *Archaeopteryx* contained more than one taxon, larger specimens might have had relatively larger distal femora. They do not (Eichstätt: $\alpha_m = 0.12$; Berlin: $\alpha_m = 0.10$; and London: $\alpha_m = 0.12$).
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28. We thank P. Wellnhofer for his encouragement and for sharing his manuscript on the new Solnhofen specimen. We thank D. Carrier for his unpublished manuscript. B. Calder, D. Carrier, C. Vleck, and D. Vleck critically edited the manuscript. Supported by NSF grants BSR 83-07711 to M.A.H., BSR-87-09455 to J.A.G., and BSR 83-07719 to R.E.S.

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Global Climate Change and Intensification of Coastal Ocean Upwelling

ANDREW BAKUN

A mechanism exists whereby global greenhouse warming could, by intensifying the alongshore wind stress on the ocean surface, lead to acceleration of coastal upwelling. Evidence from several different regions suggests that the major coastal upwelling systems of the world have been growing in upwelling intensity as greenhouse gases have accumulated in the earth's atmosphere. Thus the cool foggy summer conditions that typify the coastlands of northern California and other similar upwelling regions might, under global warming, become even more pronounced. Effects of enhanced upwelling on the marine ecosystem are uncertain but potentially dramatic.

THE COASTAL OCEAN OFF THE WESTERN United States is a classic wind-driven coastal upwelling system (*1*, *2*). During the warmer seasons of the year, strong northerly and northwesterly winds induce offshore transport of surface waters. Upwelling of cool, nutrient-enriched water from depth (Fig. 1) balances the resulting loss of surface water near the coast and infuses essential plant nutrients to the surface layers of the ocean. Rich phytoplankton growth supports an abundant trophic pyramid, including valuable fishery resources and important seabird and marine mammal populations (*3*). Cooling and stabilization of the onshore air flow by contact with the upwelled surface waters leads to the cool summer climate of the adjacent coastlands (*4*). Similar upwelling systems occur in the other major subtropical eastern ocean boundary regions; examples are the Canary current system off the Iberian Peninsula and northwestern Africa, the Benguela current system off southwestern Africa, and the Peru current system off western South America. Upwelling in all of these regions tends to be highly seasonal in temperate latitudes, where it peaks in the spring-summer, but tends toward year-round continuity in the more tropical portions (*1*).

The vigorous alongshore wind that drives coastal upwelling in these systems is maintained in part by a strong atmospheric pressure gradient between a thermal low-pressure cell that develops over the heated land mass and the higher barometric pressure over the cooler ocean (*5*). Because of the large-scale atmospheric subsidence occurring in the eastern limbs of the subtropical gyres, and also because of the stabilized, dehumidified onshore air flow, the areas of these coastlands inland of the direct influence of coastal stratus and fog are characterized during the upwelling seasons by dry Mediterranean-type (or desert) climates and clear atmospheric conditions (*4*). The clear conditions lead to strong daytime heating by short-wave solar radiation, particularly in interior valleys such as the Central Valley of California, and rapid nighttime, long-wave radiative cooling.

Recent decades have seen a substantial build-up of CO_2 and other greenhouse gases in the earth's atmosphere (*6*). Resulting inhibition of nighttime cooling and enhancement of daytime heating should lead to intensification of the continental thermal lows adjacent to upwelling regions. This intensification would be reflected in increased onshore-offshore atmospheric pressure gradients, intensified alongshore winds, and accelerated coastal upwelling circulations (Fig. 1). As a positive feedback, the cooling of the ocean surface that results might locally intensify the low-altitude barometric highs at the oceanic sides of the onshore-offshore pressure gradients.

No routine observations of actual rate of upwelling are available. Accordingly, a coastal upwelling index based on an estimate

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