SIZE AND LOCOMOTION IN TERATORNS (AVES: TERATORNITHIDAE)

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ABSTRACT.—The extinct family Teratornithidae contains the world's largest known flying birds. A new method of determining body weights of extinct birds, based on the size of their tibiotarsi, facilitates the estimation of the wing dimensions of these giant birds. An analysis of the bones of the teratorn wing shows that they closely resemble those of condors, suggesting that teratorns flew in a manner similar to these large New World vultures. The bones of the pelvic girdle and hindlimbs indicate that teratorns were probably agile on the ground, though better adapted for walking and stalking than running. We estimate that the largest teratorn, *Argentavis magnificens,* weighed 80 kg and had a wingspan of 6–8 m. It probably became airborne by spreading its huge wings into the strong, continuous, westerly winds that blew across southern South America before the elevation of the Andes Mountains and, once aloft, flew in the manner of condors. *Received 26 April 1982, accepted 18 October 1982.*

THE extinct avian family Teratornithidae L. Miller 1909 is presently known from four species: *Teratornis merriami* L. Miller 1909, *T. incredibilis* Howard 1952, *Cathartornis gracilis* L. Miller 1910, and *Argentavis magnificens* Campbell and Tonni 1980. The known teratorns ranged from very large to truly gigantic in size, with *A. magnificens* being the largest known flying bird. The single known specimen of *A. magnificens,* an associated partial skeleton from Huayquerian (late Miocene) deposits of Argentina, is nearly 2½ times as large, in linear dimensions, as living condors. *Argentavis magnificens* is also the oldest known teratorn, and, with the exception of an indeterminate specimen from late Pleistocene deposits of southwestern Ecuador (Campbell 1976, Campbell and Tonni 1980), it is the only teratorn known from outside North America.

Interpretations of teratorns have always pictured them as scavengers, flying and feeding in a manner like that of living vultures (Fisher 1945; Howard 1950, 1962a; Stock 1956). When the first species of teratorn, *Teratornis merriami,* was described (Miller 1909), it was placed with the New World vultures in the family Vulturidae (= Cathartidae auct.), probably because of its very elongated, highly vaulted, raptorial-appearing, hooked beak and the close resemblance of its postcranial skeleton to that of condors. These interpretations were reinforced by the recovery of the remains of over 100 individuals of *T. merriami* from the asphalt deposits of Rancho La Brea, California, where remains of raptors and vultures abound (Howard 1962b). It was assumed that the teratorns were entrapped in oil seeps at Rancho La Brea while feeding on carcasses of other trapped animals. Consequently, all reconstructions of teratorns have pictured them as slightly larger versions of condors, usually sitting in a tree waiting for a trapped animal to die or feeding in groups on large carcasses as vultures are wont to do.

As discussed herein, teratorns probably did fly in the manner of condors, but an analysis of the functional morphology of the teratorn skull (Campbell and Tonni 1981) indicates that these birds were not scavengers. The structure of their maxillary rostrum and mandibles and their ability to spread their mandibles proximally, as evidenced by the plane of rotation of their quadrates, indicate that teratorns were predaceous carnivores that consumed their prey whole. They were functionally incapable of feeding by tearing pieces of flesh from carcasses as vultures do. Appropriately sized prey for *Teratornis merriami* would have included frogs, lizards, nestling or fledgling birds, and rodents. With a skull over 55 cm long and 15 cm wide, however, *Argentavis magnificens* was capable of swallowing even hare-sized animals whole.

Although the postcranial skeleton of teratorns always impressed previous workers with

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its similarity to that of condors, major differences were also noted (Miller 1909, 1910; Fisher 1945). A detailed comparative analysis (in progress by KEC) of the bones of *Teratornis merriami* indicates that, while teratorns are related to New World vultures, they may be just as closely related to storks (Ciconiidae). The postcranial skeleton of teratorns displays a mosaic of vulturid, ciconiid, and unique characters. The most striking differences among the three families are found in their skulls, the result of adaptations for very different feeding methods. New inquiries and syntheses of available data (Ligon 1967, Olson 1978, Rea in press) have questioned the traditionally perceived relationships of storks and New World vultures, and an ever-increasing body of evidence is being accumulated that supports the hypothesis of their common origin. The recognition that teratorns are related to both of these groups strengthens this hypothesis.

SIZE

Estimation of body mass and dimensions of extinct animals is often difficult and frustrating. The present work is no exception. Different methods produce different results, and the lack of critical data for modern birds seriously impairs present efforts. Data are particularly sparse for large birds, especially those threatened with extinction, such as condors, the active collection of scientific specimens of which ceased before the importance of such simple information as weight data was recognized.

Greenewalt (1975a) used previously published dimensional data from over 1,400 individual birds to analyze the relationships between (a) live body weight and wing area, (b) wing area and wingspan, and (c) wingspan and aspect ratio. He divided the flying birds (excluding hummingbirds) into three groups: a passeriform model, a shorebird model, and a duck model. Each group differs substantially from the others in wing loading (weight supported per unit wing area) at a given body weight. The New World vultures fall into his "passeriform model," and, because wing loading in teratorns was probably very similar to that in condors (see below), the dimensional relationships observed within New World vultures probably hold for teratorns as well.

Greenewalt expressed the relationship between weight and wing area by the equation

$$W = \alpha_1 \cdot S^{\beta_1}, \qquad (1)$$

where W is weight in g and S is surface area in cm^2. Data were fitted by least squares to the logarithmic form of this and the following equations. The data for the Accipitriformes (= Falconiformes auct.) yielded the following estimation equation:

$$W = 0.05338 \cdot S^{1.275}.$$

Similarly, he suggested a relationship between wing area (S) and wingspan (b, in cm),

$$b = \alpha_2 \cdot S^{\beta_2}. \qquad (2)$$

The values fitted for his passeriform model were:

$$b = 2.221 \cdot S^{0.5313}.$$

The proposed relationship between wingspan (b) and aspect ratio (AR) was:

$$AR = \alpha_3 \cdot b^{\beta_3}. \qquad (3)$$

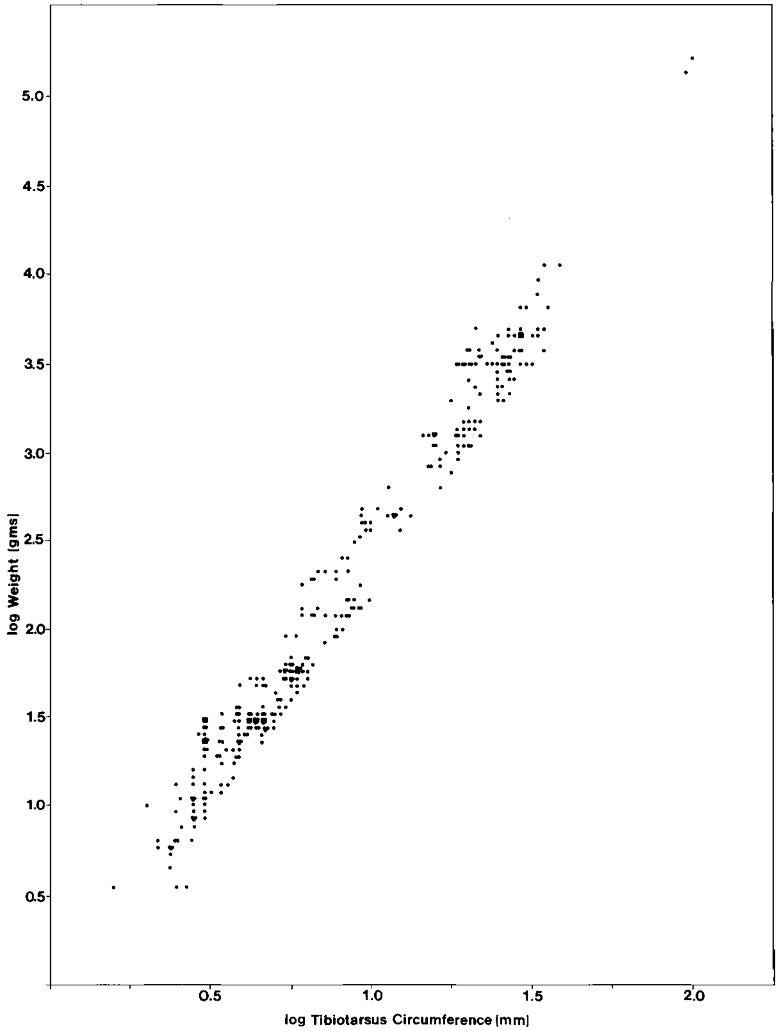
For the passeriform model he obtained the following estimation equation:

$$AR = 4.49 \cdot b^{0.118}.$$

Using this series of equations, each fitted from empirical data, one can predict the wing-surface area, wingspan, and aspect ratio of a fossil bird that conforms to the passeriform model if an accurate figure for its weight can be obtained.

Fisher (1945) was the first to estimate the weight of a teratorn, that of *Teratornis merriami*. He measured the areas of the sternum and synsacrum in the Bald Eagle (*Haliaeetus leucocephalus*) and the California Condor (*Gymnogyps californianus*) and compared those areas with the known weights of the individuals measured in an attempt to determine an index to body weight for birds of different sizes but with similar body build. His estimate for *T. merriami* was "about 50 lbs [23 kg]."

For a bone's dimensions to correlate well with body mass, the bone must function to support the body. In birds, these are the bones of the wing or the leg. Although high correlations between some dimensions of certain wing bones and body weight undoubtedly exist within the numerous morphofunctional groups of birds,



		Mean	St. Dev.	Regression Line	Res. Mean Sq.
N=324	X	.90334	.37234	X=.38272*Y+.06727	.00388
COR=.986	Y	2.1845	.95922	Y=2.5400*X−.10996	.02574

Fig. 1. Computer-generated plot demonstrating the correlation between the live body weight (g) and the least circumference of the tibiotarsus (mm) in birds.

their widely disparate flying abilities preclude any single wing-bone measurement from maintaining a high degree of correlation to body weight throughout the Class Aves. A high correlation, first noted by John Anderson (pers. comm., Anderson et al. 1979), does exist, however, between the least shaft circumference of the leg bones of birds and their live body weights (Fig. 1). Between the logarithm of the least shaft circumference of a bird's tibiotarsus and the logarithm of its live body weight, the correlation coefficient is 0.986 (data from 324 individuals of 19 orders and 45 families, including such disparate taxonomic and morphofunctional groups as penguins, ostriches, falcons, shorebirds, owls, hummingbirds, and passerines). By using the regression equation

$$\log Y = 2.54 \cdot \log X - 0.10996,$$

where Y is live body weight (g) and X is least shaft circumference (mm) of the tibiotarsus (log = common logarithm), we can predict a

TABLE 1. Predicted mean dimensions of *Teratornis merriami*, *Argentavis magnificens*, and *Gymnogyps californianus*; and observed mean dimensions of *G. californianus*.

	Weight (kg)[a]	Wing-surface area (cm^2)[b]	Wingspan (cm)[c]					Aspect ratio[d]
			A	B	C	D	E	
Predicted dimensions								
Teratornis merriami	13.7[e]	17,497	293.8	317.1	398.9	317.0	337.9	8.9
Argentavis magnificens	79.8[f]	69,609	586.0	639.2	830.7	570 ± 10	607 ± 10[g]	9.6
Gymnogyps californianus	10.2[h]	13,915	262.0	282.2	353.2	—	—	8.7
Observed Dimensions								
Gymnogyps californianus	9.5[i]	13,160[k]			274.0[j]			6.0[k]

[a] Predicted from the equation $\log Y = 2.54 \cdot \log X - 0.10996$, where Y is weight (g) and X is least circumference of tibiotarsus (mm).

[b] The predicted surface areas, wingspans, and aspect ratios are based on the predicted mean weights. The surface areas were predicted by use of the equation $W = 0.05338 \cdot S^{1.275}$ of Greenewalt (1975a), where W is weight (g) and S is surface area (cm^2).

[c] The wingspan was predicted using different methods, as follows: A, derived from the theoretically predicted equation for dimensional similarity, $b = \alpha \cdot S^{0.500}$, where b is wingspan (cm), and S is surface area (cm^2), and α is from Greenewalt (1975a), or 2.221; B, derived from the equation $b = \alpha \cdot S^{0.508}$, which predicts the observed wingspan of *G. californianus* from the surface area (13,119.5 cm^2) predicted for that species from its observed weight; C, derived from the equation $b = \alpha \cdot S^{0.5313}$ of Greenewalt (1975a); D, estimated from the ratio "length of humerus : wingspan" of *G. californianus*, or 1:10; E, estimated from the ratio "total wing-bone length : wingspan" of *G. californianus*, or 1:3.3.

[d] Predicted from the equation $AR = 4.49 \cdot b^{0.118}$ of Greenewalt (1975a), where AR is aspect ratio and b is wingspan (cm), using the estimated wingspan from column B.

[e] The value for $\bar{x} - 2s$ is 11.1 kg and that for $\bar{x} + 2s$ is 16.7 kg. The 95% confidence intervals for the values are: $\bar{x}$, (12.5–15.0 kg); $\bar{x} - 2s$, (10.1–12.1 kg); and $\bar{x} + 2s$, (15.2–18.4); $n = 37$.

[f] The 95% confidence interval for the predicted value as representative of an individual is 38.3–166.2 kg; the 95% confidence interval for the predicted value as representative of a population is 70.6–90.2 kg; $n = 1$. Equations for determination of 95% confidence intervals from Simpson et al. (1960).

[g] Calculated by assuming humerus represents 31% of total wing-bone length, as observed for *T. merriami*.

[h] The 95% confidence interval for the predicted value is 9.4–11.1 kg; $n = 3$.

[i] From Koford (1953), with range of 7.7–14.1 kg, $s = 1.8$ kg, and $n = 14$.

[j] From Koford (1953), with range of 250.0–290.0 cm; $n = 33$.

[k] Measured on an LACM mount. The predicted surface area for *G. californianus*, using the equation in b above and based on the mean observed weight, is 13,141 cm^2.

bird's weight with a fair degree of accuracy if we have its tibiotarsus. The details of this relationship are still being pursued, but the important point of concern here is the high degree of correlation throughout the Class Aves. This is significant when working with extinct forms whose means of locomotion are still hypothetical.

The mean least circumference of 37 tibiotarsi of *Teratornis merriami* in the collections of the Natural History Museum of Los Angeles County is 47.0 mm (range, 42.5–49.3, $s = 1.9$), yielding a mean weight for this extinct species of 13.7 kg, with a 95% confidence interval of 12.5–15.0 kg.

The least shaft circumference of the only known tibiotarsus of *Argentavis magnificens* is 94.0 mm, double the mean value of *Teratornis merriami*. The predicted weight is 78.8 kg, with a 95% confidence interval of 36.8–166.2 kg. If the single specimen is treated as the mean of a population, however, the 95% confidence interval for the predicted value becomes 70.5–90.2 kg.

This procedure was applied to the California Condor as a test of its validity. The mean tibiotarsal measurement of three Recent specimens was used in the equation, yielding a predicted mean weight of 10.2 kg, with a 95% confidence interval of 9.4–11.1 kg. These values compare favorably with the mean observed weight of 14 specimens listed by Koford (1953), 9.5 kg (range, 7.7–14.1 kg). The close correspondence between predicted and observed weights for *G. californianus* suggests that the weights predicted for the teratorns are fairly accurate and can be used in the equations of Greenewalt.

Three predicted values for wingspan, resulting from the use of different values for β in equation (2), were derived for each species. The smallest was derived using the value required for dimensional similarity, or $\beta = 0.50$. The largest resulted from using the value of β fitted by Greenewalt (1975a), 0.5313. The intermediate value came from using a value of 0.5078 for β. This value was calculated for *Gymnogyps californianus* by predicting that species' wing-surface area from its observed weight and solving the equation above for β using the predicted wing-surface area, the mean observed wingspan obtained from the data of Koford

(1953), and Greenewalt's fitted value of 2.221 for α. The wingspans predicted by using this value for β most closely agree with the wingspans predicted by using wing bone proportions (see below and Table 1).

Greenewalt's fitted value for β was altered, as opposed to that of α, because, in the case at hand, a change in the fitted value of β of one standard deviation (0.00529) alters the predicted wingspan value by 4.5%, while a corresponding change in α ($s = 0.01688$) alters the predicted wingspan value by only 0.75%. If the data used by Greenewalt had produced an estimation equation with a fitted value of 0.5078 for β, the fitted value for α would undoubtedly have varied slightly from 2.221, but, by ignoring this variation, we believe we introduce only a minor error into the results.

It is clear from this exercise, granting its potential for error, that the value for β in the above equation is closer to that required for dimensional similarity than Greenewalt estimated from the data available to him and that his estimation equation cannot be used to predict the wingspans of large birds. The data he used were heavily weighted toward small- to moderate-sized birds, as are the data presented in Fig. 1. The lack of data on wing-surface area for large birds may have skewed his results, giving too large a fitted value for β. A possible similar effect is noted with the computation of the estimation equation relating log weight to log least tibiotarsus circumference. Removal of data for larger birds gives an equation that underestimates the weights of large birds. In fact, if more data for large birds such as rheas, emus, and cassowaries were available, we believe the predicted weight of *Argentavis magnificens* would be greater than that presented above.

A second way of estimating the wingspan of teratorns uses wing-bone proportions (Table 2). The relative lengths of the different bones of the wing, i.e. the intramembral proportions, vary only slightly from the smallest vulturid, *Coragyps atratus,* to the largest, *Vultur gryphus.* There appears a slight trend with increasing size toward an increase in the length of the ulna relative to the more distal wing bones, but no such trend is apparent for the humeri. These intramembral proportions in *Teratornis merriami* do not differ significantly from those of the vulturid species. This consistency in intramembral proportions disagrees with the findings of Greenewalt (1975b) that ". . . the humerus will become a greater fraction of the wingspan as size increases." It appears, however, that he included in his calculations data from several different morphofunctional groups of birds, which may have given misleading results. Because intramembral proportions do not change significantly in New World vultures of various sizes, the humerus would have to increase in length at a rate faster than the primary feathers for his conclusion to hold for them. Data to support or disprove this hypothesis are unavailable. If the relationship between humerus length and the length of the primary feathers within this morphofunctional group were known, it should be possible to predict the wingspan of an extinct species belonging to this group from the length of its humerus. At present we can only assume that the ratio of primary feather length to wing length within a morphofunctional group is constant.

The ratio "mean humerus length : mean wingspan" for *Gymnogyps californianus* is 1:10, based on four Recent humeri and the mean observed wingspan calculated from the data of Koford (1953). The ratio "mean wing skeleton length : mean wingspan" for the same species is 1:3.3, based on three complete Recent skeletons and the same mean observed wingspan. Wing skeleton length is the sum of the lengths of all the bones of one wing. Wingspans predicted for *Teratornis merriami* from these two ratios (Table 1) are virtually identical to the intermediate value predicted by the two-stage prediction from tibiotarsal circumference to body weight to wingspan, and they are close to the value predicted by dimensional similarity.

The wingspan predicted for *Argentavis magnificens* by the first ratio is uncertain, because the single known humerus of that species is incomplete (Fig. 2). Use of the second ratio to predict the wingspan of *A. magnificens* is tenuous, because the wing-skeleton length for this species is unknown. The percentage of the wing-skeleton length represented by the humerus does not change significantly from *Coragyps atratus* to *Teratornis merriami* (Table 2), where there is an overall size increase of 142%, but we cannot be certain that this relationship will continue to hold when the wing-skeleton length is doubled once again. Nevertheless, the

Table 2. Mean lengths (mm) of the wing bones of the five species of New World vultures, *Teratornis merriami*, and the Wandering Albatross (*Diomedea exulans*) and the mean lengths expressed as a percentage of the mean of the total wing-bone lengths (in parentheses).

	Humerus	Ulna	Carpometacarpus	Digit II, phalanx 1	Digit II, phalanx 2	Mean wing-skeleton length
Coragyps atratus	134.0 (31.8)	155.4 (36.7)	75.6 (17.9)	31.3 (7.4)	26.3 (6.2)	423 (n = 7)
Cathartes aura	143.3 (31.0)	171.8 (37.2)	81.2 (17.6)	35.0 (7.6)	30.6 (6.6)	462 (n = 13)
Sarcoramphus papa	167.4 (31.9)	205.3 (39.2)	88.2 (16.8)	34.3 (6.5)	28.9 (5.5)	524 (n = 5)
Gymnogyps californianus	273.0 (32.7)	315.5 (37.8)	140.0 (16.8)	56.5 (6.8)	48.2 (5.8)	834 (n = 3)
	266.0 (33.1)	308.0 (38.4)	132.0 (16.4)	53.2 (6.6)	43.9 (5.5)	803^{a} (n = 3–8)
Vultur gryphus	280.7 (32.0)	341.0 (38.8)	144.2 (16.4)	61.6 (7.0)	50.9 (5.8)	878 (n = 4)
	280.0 (32.3)	340.6 (39.3)	139.5 (16.1)	57.2 (6.6)	50.1 (5.8)	867^{a} (n = 4)
Teratornis merriami	317.0 (31.0)	421.0 (41.1)	167.0 (16.3)	64.9 (6.3)	54.0 (5.3)	1,024^{a}
Diomedea exulans	405.9 (37.5)	400.5 (37.0)	138.3 (12.9)	67.5 (6.2)	70.1 (6.5)	1,083 (n = 1)

[a] Figures in these lines from Fisher (1945).

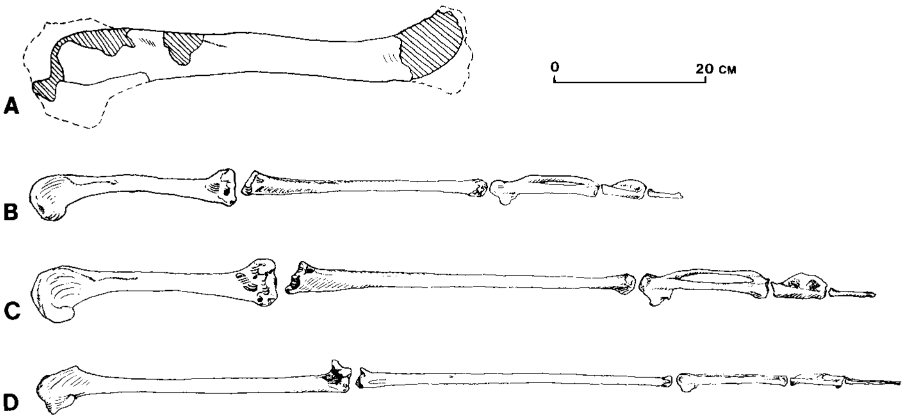


Fig. 2. Wing bones of (A) *Argentavis magnificens* (humerus only); (B) *Gymnogyps californianus;* (C) *Teratornis merriami;* and (D) *Diomedea exulans,* showing general structure, stoutness, and proportions.

wingspans predicted for *A. magnificens* by these two ratios are reasonably close to the smaller of the values calculated from the predicted weight.

The small but almost continuous increase of 4.4% in the proportionate length of the ulna from the smallest vulturid to *Teratornis merriami* must also be considered. If this trend continued in larger forms, then, unless the lengths of the bones distal to the ulna decreased relative to that of the ulna, the wingspan estimates given above would be too small. There is also the question of whether or not the primary feathers increased proportionately with the rest of the wing. If the primaries represented the same percentage of the wing as in *Gymnogyps californianus,* the larger primaries of *Argentavis magnificens* would have been approximately 18–20 cm wide and 140–150 cm long.

The aspect ratio of a bird's wing is given by dividing the wingspan by the mean chord (width) of the wing, which is the same as the square of the wingspan divided by the wing area. Birds with a high aspect ratio fly differently from those with low aspect ratios. Because the aspect ratio of 8.7 given for *Gymnogyps californianus* by Greenewalt's estimation equation (Table 1) is much higher than the observed value of 6, it appears that this formula does not predict the aspect ratios of large birds. The reason for this is probably the lack of large bird data mentioned above in connection with the estimation equation relating wing surface area to wingspan.

There are so few specimens of the two remaining species of teratorns that size estimates are very uncertain. *Teratornis incredibilis* has been estimated as being approximately 40% larger than *T. merriami,* with a wingspan of about 5 m (Howard 1952). This estimate is based on only three fragmentary fossil specimens (a cuneiform, partial beak, and the distal end of a radius) so lacking in diagnostic characters that they may not all represent the same species. *Cathartornis gracilis* is known from only two tarsometatarsi from Rancho La Brea, California. Their length approaches that of the tarsometatarsi of *T. merriami,* but they are approximately one-third narrower, suggesting a lighter body build. These species will be omitted from further discussions.

LOCOMOTION

Adaptations for both aerial and terrestrial locomotion determine a bird's overall morphotype. We think that teratorns flew in a manner very similar to condors, while their terrestrial locomotion was more similar to that of storks and turkeys. The evidence for these interpretations comes from *Teratornis merriami* limb bones from Rancho La Brea.

The largest living birds capable of sustained flight are albatrosses and condors. These two groups use the two different flight strategies, dynamic and up-current soaring, open to very large birds. Beyond a certain size, sustained flapping flight becomes prohibitive because of energy considerations and physical limits of bone and muscle (Tucker 1977). Albatrosses are

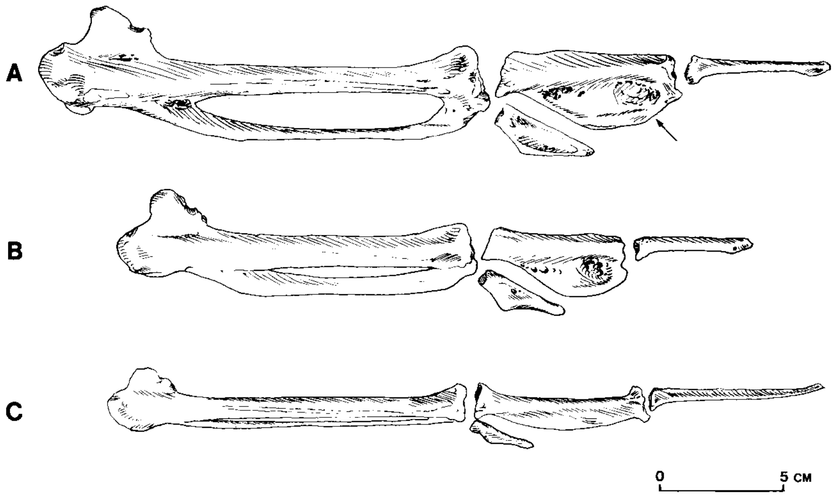


Fig. 3. Terminal right wing bones of (A) *Teratornis merriami;* (B) *Gymnogyps californianus;* and (C) *Diomedea exulans,* showing the difference in structure of these bones between dynamic and upcurrent soarers. Arrow indicates shelf of digit II, phalanx 1, that helps support some of the primary feathers.

dynamic soarers, adapted for nonflapping flight in oceanic regions with strong, continuous, unidirectional winds. They have wings with a low camber (nearly flat), a very high aspect ratio, relatively weak flight musculature, and short, unemarginated primary feathers. The wing bones are very elongated and slender, particularly the more distal bones. The humerus and ulna tend to be of equal length and have straight, relatively flattened leading edges (Fig. 2; Table 2). The largest albatross is the Wandering Albatross (*Diomedea exulans*), which may weigh more than 10 kg and have a wingspan of over 3.4 m.

Condors are up-current soarers, adapted for nonflapping flight over land. They depend for sustained flight upon rising air currents produced by the heating of the earth's surface (thermals), passing storm fronts, or surface winds deflected upward by physiographic features such as ridges or cliffs. They have wings of high camber, a low aspect ratio, flight muscles that are weak (but stronger than those found in the Wandering Albatross), and long, emarginated primary feathers. All of their wing bones are very stout. The humerus is much shorter than the ulna; both are rounded with no tendency toward flattened leading edges, and they are more curved than those of albatrosses. The Andean Condor (*Vultur gryphus*) is slightly larger than the California Condor, occasionally reaching a weight over 15 kg and a wingspan near 3.2 m. No really accurate series of measurements is available for *V. gryphus.*

The role of primary feathers in maintaining flight, which is not the same in dynamic soarers and up-current soarers, is reflected in both the shape of the primaries and the structure of the distal wing bones. Up-current soarers depend upon rising air currents, which are often weak or very localized and may change direction or strength rapidly, as opposed to the continuous strong winds exploited by dynamic soarers. They must be able to react quickly to slight changes in wind direction and strength in order to maximize lift and control for sustained flight. Up-current soarers accomplish this with their large, emarginated primaries, which act as independent airfoils when separated to provide more lift than if they were unemarginated and incapable of independent movement as in dynamic soarers (Oehme 1977). The primary feathers are anchored to and rest upon different portions of the carpometacarpus and carpal phalanges, which increase proportionately in size in forms with larger primaries. Each distal wing joint is flexed or extended as needed, via tendons of the middle wing musculature, to separate or bring together the primaries. The shape of the articular facets and the larger size of the tendon anchorages of the

TABLE 3. Ratios involving the carpometacarpus and digit II, phalanx 1 of the five species of New World vultures, *Teratornis merriami*, and the Wandering Albatross (*Diomedea exulans*).

	Mean wing-skeleton length (mm)	Length of carpometacarpus : wing-skeleton length	Digit II, Phalanx 1 width : length
Coragyps atratus	423 (*n* = 7)	1:5.6	1:2.5
Cathartes aura	462 (*n* = 13)	1:5.7	1:2.5
Sarcoramphus papa	528 (*n* = 2)	1:6.0	1:2.3
Gymnogyps californianus	834 (*n* = 3)	1:6.0	1:2.3
Vultur gryphus	878 (*n* = 4)	1:6.1	1:2.5
Teratornis merriami	1,024[a]	1:6.1	1:2.3
Diomedea exulans	1,083 (*n* = 1)	1:7.8	1:4.9

[a] From Fisher (1945).

distal wing bones of up-current soarers reflect this movement, as opposed to the structure of the albatrosses, where the primaries are held together in an extended position for long periods of time.

A clue to the relative size of primary feathers is the "width : length" ratio of carpal digit II, phalanx I (Table 3). Two or three primaries may anchor to this bone, and the width of the shelf supporting them is a rough indication of their size. This ratio and the shape of the bone (Fig. 3) are very similar among all species of New World vultures and *Teratornis merriami*, but quite different from that of the Wandering Albatross. *Teratornis merriami* probably possessed primary feathers similar in form and function to those of condors. Confirmation comes from the similarities in both relative size and form between the carpometacarpus of *T. merriami* and those of condors. In addition to the intramembral proportions, the general structure of all the wing bones of *T. merriami* is very similar to that of the wing bones of condors. These data suggest that the wings of *T. merriami* looked and functioned like those of condors.

Fisher (1945) thought the flight of *Teratornis merriami* involved more flapping than that of condors, perhaps resembling more the slow, steady flapping observed in herons and pelicans. Our conclusions differ from his for two reasons. First, his estimation of the weight of *T. merriami* was much larger than ours (23 kg vs. 13.7 kg). Because the overall wing-skeleton length of *T. merriami* was not much greater than that of *Gymnogyps californianus*, it was reasonable to assume that more flapping would be necessary to get the bird airborne and that its greater wing loading would reduce its soaring capabilities. The lower weight estimate reduces this problem.

Second, Fisher thought the more distal wing bones of *Teratornis merriami*, especially the carpometacarpus, were relatively weaker than those of condors and incapable of supporting large primaries. The absence of large primaries would have restricted the teratorn's ability to soar. The shafts of metacarpal II and III are relatively smaller in *T. merriami* than in *Gymnogyps californianus*, but the overall width (metacarpal II plus metacarpal III) at the center of the carpometacarpus is proportionately the same (Fig. 3). Fisher also interpreted the areas of muscle origin and insertion on *T. merriami* wing bones to mean that teratorns had a greater development of the proximal wing musculature and relatively reduced distal musculature compared to condors, thus indicating greater power for flapping flight. This may be true, but, as Fisher noted, the power potential of muscles may not be reflected in the size of their origin and insertion, and it is possible that the larger size of the teratorn wings may have resulted in a different physical configuration of the flight

TABLE 4. Ratios of the hindlimb elements of *Gymnogyps californianus*, *Vultur gryphus*, and *Teratornis merriami*. *n*'s refer to values for this study.

	Mean total length (mm) of femur + tibiotarsus + tarsometatarsus	Femur : tibiotarsus : tarsometatarsus	Tarsometatarsus : tibiotarsus
Gymnogyps californianus	480 (464[a]) (n = 3)	1:1.58:0.86	1:1.83
Vultur gryphus	526 (526[a]) (n = 2)	1:1.59:0.88	1:1.87
Teratornis merriami	516[a]	1:1.50:0.91	1:1.64

[a] From Fisher (1945).

muscles than that found in condors. In other words, the larger size of teratorns may have been more important than differences in flight mode in producing the differences in muscle attachments that Fisher observed.

Available wing bones of *Argentavis magnificens* (the humerus and partial ulna, radius, and carpometacarpus) are of similar shape but almost twice the size of those of *Teratornis merriami*. On the ulnar fragment the papillae for the attachment of secondary feathers are almost twice as far apart as those of *T. merriami* (30 mm vs. 15–18 mm), indicating that the secondary feathers were about twice as broad as in *T. merriami*. Large secondary feathers and a properly proportioned carpometacarpus indicate that the wings of *A. magnificens* were fully adapted for flight. This, plus the following leg-bone data, indicates that *A. magnificens* was simply a larger version of the La Brea teratorn morphotype.

The morphology of their leg bones and pelvis suggests that teratorns may have been capable of extended walking and were more agile on the ground than are condors. As with the wing, the lack of articulated specimens of *Teratornis merriami* renders uncertain the exact proportions among the three major leg bones. The mean value for each bone suggests that the leg of *T. merriami* was shorter than that of *Vultur gryphus* and longer than that of *Gymnogyps californianus* (Table 4). The ratios between the femur, tibiotarsus, and tarsometatarsus suggest that, in comparison to condors, teratorns had a slightly shorter tibiotarsus relative to the tarsometatarsus, but this small difference may be an artifact of sampling.

The leg bones of teratorns are very stout and columnar, lack large crests for muscle attachments, and have relatively flat articular surfaces. The longitudinal axis of the tarsometatarsus is more in line with digit II than it is in condors, resulting in greater stability. The metatarsal facet shows that the hallux was positioned farther distally and located closer to the longitudinal axis of the tarsometatarsus than in condors. The toes of *Teratornis merriami* were rather long, as in condors, and their terminal phalanges were long, moderately curved, and blunt at their ends, indicating that the feet were not used for catching or holding prey as in hawks, eagles, and owls. The long toes and the posterior position of the hallux provided greater stability but may have reduced the bird's ability to run.

The pelvis reveals much about how the leg of *Teratornis merriami* functioned. The angle between the long axes of the preacetabular ilium and the postacetabular ilium in *T. merriami* is about 165°, or nearly the same as in the storks (Fig. 4) and other birds that walk a lot searching for food. The same angle in *Gymnogyps californianus* is 155° and in the Golden Eagle (*Aquila chrysaetos*) 140°. The downward tilt of the postacetabular portion of the pelvis is an adaptation for bringing the postacetabular pelvic musculature more nearly parallel to the vector force required to pull the femur backward, as noted by Fisher (1945). This adaptation is generally found only in birds of prey, parrots, and other birds that use their hindlimbs for specialized grasping or predation. The moderate downward tilt of the postacetabular pelvis in condors and other vultures may result from the use of their feet to hold food items while they use their beak to tear off pieces small enough to swallow.

While the depression of the postacetabular pelvis increases the leg's grasping force, it also limits the anteroposterior movement of the leg

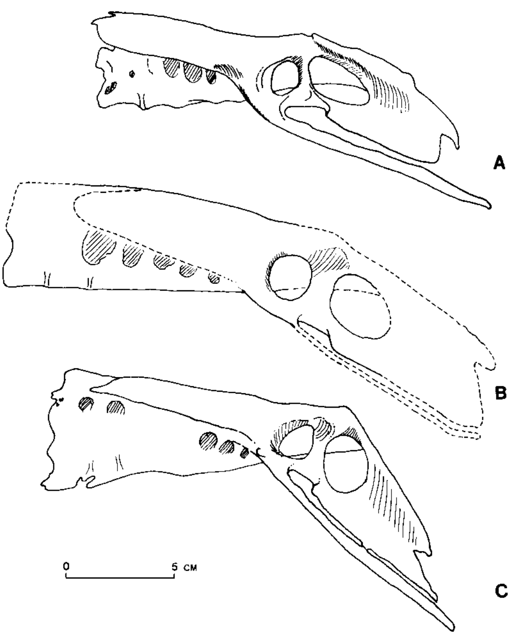


Fig. 4. The pelvis of (A) *Ephippiorhynchus senegalensis*, Saddle-billed Stork; (B) *Teratornis merriami*; and (C) *Gymnogyps californianus*, showing the angle between the preacetabular ilium and the postacetabular ilium. Dashed lines indicate approximate position for edges of bone, which have been eroded from all specimens of *T. merriami*, although most of the pelvis is available.

by shortening the muscles that pull it backward and by physically obstructing posterior movement of the femur. In birds that are specialized for swift terrestrial locomotion, such as ostriches and roadrunners, or those that may walk a lot searching for food, such as storks, herons, and turkeys, the axes of the preacetabular ilium and the postacetabular ilium are virtually parallel.

The general proportions of the pelvis of *Teratornis merriami* are very similar to those of storks, as is the lack of any great depression of the postacetabular ilium. Although nearly the same length, the width of this teratorn's pelvis is about 40% greater than that of a condor. Fisher (1945) incorrectly stated that in *T. merriami* the postacetabular ilium was depressed as in *Gymnogyps californianus* and concluded that terrestrial locomotion in teratorns was probably as awkward as in condors. This is clearly not the case. The features of the pelvis, the stout, columnar nature of the hindlimb bones, and the structure of the phalanges suggest that *T. merriami* did not use its feet for grasping, that its stride was as long as its relatively short legs would permit, that it probably was not a good runner, and that its terrestrial locomotion was not awkward.

The hindlimb of *Argentavis magnificens* is known only from the shafts of a tibiotarsus and a tarsometatarsus, both of which repeat the stout, columnar structure found in *Teratornis merriami*. The position of the metatarsal facet indicates that the hallux was also directed posteriorly in *A. magnificens*. Terrestrial locomotion was probably similar in the two forms.

There has never been any serious doubt that *Teratornis merriami* could fly, although how it took off has been debated. Fisher (1945) considered *T. merriami* more capable of getting airborne by flapping than *Gymnogyps californianus* and thought that it neither required nor was capable of a long run for takeoff. The present, lower weight estimate suggests that the takeoff of *T. merriami* may have been quite like that of condors. Following the procedures outlined above for predicting weight and wingspan, one can predict wing loading for *T. merriami*, although the use of Greenewalt's estimation equation for relating weight to wing-surface area may lead to erroneous results for large birds for the same reason discussed in connection with his other estimation equations. The predicted value is close enough to that of *G. californianus* (Table 5) to suggest that a teratorn could have taken off simply by spreading its wings into the wind, as condors often do. The less restrictive pelvis in *T. merriami* may have increased its running ability sufficiently over that of condors to enable it to become airborne with greater ease. As described above, the available osteological evidence suggests that once airbone, *T. merriami* flew like condors.

It is difficult to conceive that *Argentavis magnificens* became airborne solely by flapping its wings, or without wind assistance. With each wing over 3 m long, the bird would have to be high into the air before it could get in a full wingbeat. With a weight of 80 kg, it is doubtful that *A. magnificens* could jump sufficiently high to give itself enough time to flap its wings and become airborne, even if it were capable of running with a bounding mode in synchrony with flapping, because of the problem of wingbeat frequency: the larger the bird, the lower

TABLE 5. Total weight, wing area, and wing loading for several species of large flying birds.

	Total weight (g)	Wing area (cm)	Wing loading (g/cm^2)
Cygnus olor[a] Mute Swan	11,602	6,808	1.70
Otis tarda[b] Great Bustard	8,950	5,728	1.56
Diomedea exulans[b] Wandering Albatross	8,502	6,206	1.37
Gyps fulvus[b] Griffon Vulture	7,269	10,540	0.69
Leptoptilus crumeniferus[b] Marabou Stork	7,030	8,225	0.86
Branta canadensis[a] Canada Goose	5,662	2,820	2.01
Aquila chrysaetos Golden Eagle	4,664[a] 3,712[b]	6,520 5,382	0.72 0.69
Meleagris gallopavo[a] Turkey	3,897	3,752	1.04
Tetrao urogallus[b] Capercaille	3,361	1,412	2.38
Gymnogyps californianus[c] California Condor	9,500 10,200	13,160 13,915	0.72 0.73
Teratornis merriami[c]	13,700	17,497	0.78
Argentavis magnificens[c]	79,800	69,609	1.15

[a] Data from Poole (1938).
[b] Data from Magnan (1922).
[c] Data from Table 1.

the wing beat frequency (Greenewalt 1962, Goldspink 1977). The reasons for this may lie in the mechanical properties of muscle and tendon tissues, and the ability of these tissues to respond to the forces imposed upon them (Goldspink 1977). Inertia, elasticity, and elastic rebound of the tissues and bones of such large wings must also have presented severe problems for active flapping flight.

The wing loading predicted for *Argentavis magnificens* is less than that of several living species of large flying birds (Table 5). Although the wing loading of *A. magnificens* is greater than that of *Gymnogyps californianus*, it is less than that of *Diomedea exulans*, both of which can become airborne by spreading their wings into the wind. The higher wing-loading value, over that of *Teratornis merriami*, may have made it more difficult for *A. magnificens* to take off, but high wing loading is more advantageous for cross-country soaring (Pennycuick 1972). If *A. magnificens* could not take off without assistance, it either flew only during periods of windy weather or it lived where winds blew constantly. The former seems unlikely, because the bird could become stranded in a food-poor area.

Charts of present global wind patterns show that South America south of approximately 40°S latitude lies within a band of globe-encircling westerly winds. North of this latitude the winds are controlled by high and low pressure systems. North of 31°S, the South Pacific High effectively eliminates the westerlies from the lower levels of the atmosphere throughout the year (Miller 1976). During winter in the southern hemisphere, the strength of the South Pacific High increases, and the westerlies are forced farther southward than during the summer. The height and width of the Andes Mountains north of approximately 30°S are major factors governing the location of the South Pacific High and its effect on the westerlies. North of that latitude, the high altitude of the Andes alone would be sufficient to block the westerlies.

The major orogenic movements leading to the elevation of the Andes Mountains began in the Miocene. Before the elevation of the Andes, and the arrival of the South American continent at its present position on the surface of the earth, the wind patterns across the continent would have differed from those of today. An important difference is that the northward extent of the southern westerlies would not have been limited by the blocking action of the South Pacific High or the Andes, and much more of the continent would have experienced the continual westerly winds. The single specimen of *Argentavis magnificens* was found in late Miocene deposits approximately 37°S, just north of the present limit of the westerlies.

In the regions of Chile dominated by the westerlies, "The wind . . . hardly ever lets up: except for protected interior valleys, calms seldom occur" (Miller 1976: 115). And, as noted by Prohaska (1976: 14) in reference to parts of Argentina under the influence of the westerlies, "In few parts of the world is the climate of the region and its life so determined by a single meteorological element, as is the climate of Patagonia by the constancy and strength of the winds." If similar continual, strong westerly winds were present throughout southern South America until the latter portion of the Tertiary, they would have been more than sufficient to carry *Argentavis magnificens* aloft whenever it spread its huge wings. The evolution of this teratorn to its gigantic proportions was probably directly tied to the presence of these continuous westerly winds.

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