



## CHAPTER 9

# THE “WALKING EAGLE” *WETMOREGYPS DAGGETTI* MILLER: A SCALED-UP VERSION OF THE SAVANNA HAWK (*BUTEOGALLUS MERIDIONALIS*)

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**ABSTRACT.**—The so-called “walking eagle,” currently known as *Wetmoregyps daggetti* from the Pleistocene of southern California and northern Mexico, is practically identical in morphology and proportion to the living Savanna Hawk (*Buteogallus meridionalis*) but ~40% larger. It should therefore be known as *Buteogallus daggetti*, new combination. Its habits were perhaps like those of a Savanna Hawk in that it was capable of taking much larger prey, given that the weight of *B. daggetti* may have exceeded that of the modern Secretarybird (*Sagittarius serpentarius*), and it may have occupied a similar niche. Any connection between its extinction and the disappearance of the North American mammalian megafauna is dubious at best. *Received 27 November 2006, accepted 5 February 2007.*

**RESUMEN.**—*Wetmoregyps daggetti*, encontrado en el Pleistoceno en el sur de California y norte de México, es prácticamente idéntico en morfología y en proporciones al gavilán pita venado *Buteogallus meridionalis*, aunque un 40% más grande. Por lo tanto, debe considerarse como *Buteogallus daggetti*. Probablemente, sus hábitos eran muy similares a los del gavilán pita venado, siendo capaz de capturar grandes presas. Su tamaño excede al del secretario (*Sagittarius serpentarius*), pudiendo ocupar un nicho similar. Cualquier conexión entre la extinción de *Wetmoregyps daggetti* y la desaparición de la megafauna de mamíferos en Norte America es, cuando menos, dudosa

IN THE COURSE of investigating the relationships of several species of large fossil raptors from Cuba with William Suárez, I borrowed skeletons of the two living species of “eagles” of the genus *Harpyhaliaeetus*, which are extremely rare in collections. Taking the opportunity to study their relationships in turn, we collaborated with Stephen Parry and also included in our comparisons some of the large species of Accipitridae described from the Pleistocene of Rancho La Brea, California. We eventually realized that we could identify a previously unrecognized radiation of raptors, all of which could be accommodated in the genus *Buteogallus*. Three of the living species of *Buteogallus*, all differing in skeletal proportions, appeared to have nearly identical counterparts, either living or fossil, that were scaled up more than 30–40% in size, so that they have been regarded as

“eagles.” Each of these instances will be treated separately, beginning here with the fossil species now known as *Wetmoregyps daggetti*.

That species was described originally by Miller (1915) as *Morphnus daggetti*, on the basis of a very long, slender tarsometatarsus that Miller regarded as having belonged to a “walking eagle.” Three additional tarsometatarsi and an incomplete tibiotarsus were assigned to the species a few years later (Miller 1925). Miller (1928, 1931) identified fragmentary tarsometatarsi from the Carpinteria asphalt deposits as this species. In re-evaluating its affinities, he had “no hesitation in placing the Pleistocene bird nearer to *Urubitinga* [= *Buteogallus*] than to *Morphnus*,” while noting the “strong superficial resemblance of the Daggett Eagle to...weak-footed and small-mouthed raptors,” such as *B. urubitinga* or *Caracara* spp. (Miller 1928:255). Nevertheless, probably influenced by its great size, he created for it a new genus, *Wetmoregyps*, though the allusion to vultures in the name

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(Greek, *gyps* = vulture), as we shall see, was misleading. It continued to be known as *W. daggetti* up to the present.

Apart from referring a coracoid, and tentatively some phalanges, Howard (1932:15) could "add almost nothing to the knowledge of this species," and she gave no measurements. She later mentioned two additional individuals of *W. daggetti* from Rancho La Brea but did not indicate which elements had come to light (Howard 1936). The geographical range of the species was extended >2,100 km to the southeast with the discovery of two coracoids and a tarsometatarsus in San Josecito Cave, Nuevo León, Mexico (Miller 1943).

Miller's (1928:255) diagnosis of *W. daggetti* was as follows:

Size equal to, or greater than, *Aquila*; tarsus extremely elongate; papilla of tibialis anticus placed high up on the shaft, resulting in a ratio of power arm over weight arm of approximately 12.5 per cent; superficial resemblance to *Urubitinga urubitinga*, but less excavated on the antero-proximal face and with trochleae more nearly of equal size and elevation.

Additional points of divergence from *U. urubitinga* include the following: (1) Inner cotyla exceeds the outer to a greater degree; (2) sagittal diameter of head greater in relation to transverse diameter; (3) outer hypotarsal ridge lower but broader; (4) scar of the distal rudiment of metatarsal 1 shorter and placed centrad from the inner profile of the bone; distal foramen placed lower down.

Howard (1932) found that fragmentary remains of *W. daggetti* were difficult to discern from like elements of the fossil eagle then known as "*Morphnus*" *woodwardi*, which is understandable because, as it turns out, *M. woodwardi* is another member of the buteogalline radiation referred to above (S. Olson unpubl. data).

Miller and Howard thus came very close to discerning the true relationships of the "Daggett Eagle," and had they extended their comparisons, they doubtless would have noted the extreme similarity between *W. daggetti* and the living Savanna Hawk (*Buteogallus meridionalis*; formerly placed in the monotypic genus *Heterospizias*). Howard (1932) had borrowed a skeleton of *B. meridionalis* and included its measurements in her monograph, but she evidently did not notice its similarity to *W. daggetti*.

#### SYSTEMATICS

##### Family Accipitridae

##### Genus *Buteogallus* Lesson, 1830

Synonym. *Wetmoregyps* Miller, 1928: 255; type-species by original designation *Morphnus daggetti* Miller, **new synonymy**.

##### *Buteogallus daggetti* Miller (1915), **new combination**

*Morphnus daggetti* Miller, 1915:179; 1925:97.

*Wetmoregyps daggetti*: Miller, 1928:255.

*Referred material examined*.—Complete left tarsometatarsus LACM K3159; left tibiotarsus lacking proximal articulation LACM 79744.

*Comparative skeletal material examined (all USNM)*.—*Buteogallus meridionalis* 32968, 319439, 319440, 347849, 560138, 622379, 630248; *B. urubitinga* 343972, 345786; *Sagittarius serpentarius* 621021, 621022.

*Comparisons*.—Once the comparison is made between *B. daggetti* and *B. meridionalis* (Figs. 1–3 and Table 1), there is little left to be said. Apart from size, the tarsometatarsi are practically identical. The size of *B. daggetti* is ~40% greater than the average size of *B. meridionalis*. Considering that the mass of the larger bird would have been more than triple that of the smaller, the lack of more purely size-related differences between them is remarkable. The individual of *B. meridionalis* with the largest skeleton examined in the series weighed 1,050 g, whereas *B. daggetti* likely exceeded 3,000 g (see below). The greatest proportional difference is in the width of the shaft of the tibiotarsus, which is 49% larger in *B. daggetti*, versus 38–41% in the other width measurements.

The only noticeable qualitative difference is the protuberance in *B. daggetti* on the lateral surface of the proximal end, in the area identified by Baumel et al. (1979, their fig. 14A,C) as the *sulcus musculo fibularis longus* and *impressio ligamentum collateralis lateralis*. This protuberance is not observed in *B. meridionalis*. The tarsometatarsus of *B. daggetti* agrees with that of *B. meridionalis* and differs from that of *B. urubitinga* in being longer and more gracile, with a shorter medial hypotarsal crest (shortness of this crest is characteristic of all the buteogallines) and in having a larger and more distally situated distal foramen (as noted by Miller 1928). There are certainly no differences that could be considered of



FIG. 1. Left tarsometatarsi of *Buteogallus* in anterior view: (A) *B. urubitinga* USNM 345786, (B) *B. meridionalis* USNM 630248, (C) *B. daggetti* LACM K3159, and (D) *B. meridionalis* USNM 630248. (A) and (B) are enlarged to the same size as (C). Scale = 2 cm for (C) and (D).



FIG. 2. Left tarsometatarsi of *Buteogallus* in posterior view: (A) *B. urubitinga* USNM 345786, (B) *B. meridionalis* USNM 630248, (C) *B. daggetti* LACM K3159, and (D) *B. meridionalis* USNM 630248. (A) and (B) are enlarged to the same size as (C). Scale = 2 cm for (C) and (D).

TABLE 1. Mean measurements (mm) (range in parentheses) of Savanna Hawk (*B. meridionalis*;  $n = 7$ ) compared with those of *Buteogallus daggetti*. Measurements of the referred tarsometatarsus examined are essentially identical to those given by Miller (1915) for the holotype of *B. daggetti*; those for the tibiotarsus are from LACM J9744.

|   | <i>B. meridionalis</i> | <i>B. daggetti</i> |
|---|------------------------|--------------------|
| <b>Tarsometatarsus</b>                                      |                        |                    |
| Length  | 106.6 (101.5–115.1)    | 167.0              |
| Proximal width  | 12.6 (12.0–13.4)       | 20.8               |
| Least shaft width   | 5.4 (4.9–6.0)          | 9.1                |
| Distal width  | 14.2 (13.3–15.2)       | 22.8               |
| <b>Tibiotarsus</b>  |                        |                    |
| Length from distal end of fibular crest to external condyle | 87.4 (83.4–92.6)       | 142.6              |
| Least shaft width below fibular insertion                   | 6.6 (6.0–7.1)          | 13.0               |
| Distal width  | 12.5 (11.8–13.1)       | 21.4               |



FIG. 3. Left tibiotarsi in anterior view: (A) *Buteogallus urubitinga* USNM 345786, (B) *B. meridionalis* USNM 630248, (C) *B. daggetti* LACM K3159, and (D) *B. meridionalis* USNM 630248. (A) and (B) are enlarged to the same size as (C). Scale = 2 cm for (C) and (D).

generic value, so *Wetmoregyps* must now be subsumed in *Buteogallus* when that genus includes *Heterospizias*.

DISCUSSION

*Buteogallus daggetti* was a rare bird even at Rancho La Brea and has not yet been recorded outside of southern California and northern Mexico. We may infer something of its probable habits by studying the habits of its most similar living relative, *B. meridionalis*. As its name implies, the Savanna Hawk inhabits open grasslands or savannas with scattered trees or

shrubs. It may hunt from a perch but also forages on the ground, especially at the edges of advancing fires (Ferguson-Lees and Christie 2001). Prey is diverse, including mammals, reptiles, amphibians, and arthropods. During the wet season in the llanos of Venezuela, it feeds largely on crabs (Mader 1982).

The long, slender legs of *B. daggetti* indicate a significant terrestrial component in its behavior, similar to that of *B. meridionalis*, as Miller (1915) correctly inferred at the outset. Likewise, it also must have been an inhabitant of open country. Steadman et al. (1994:580) determined that grassland species made up a "very strong component" of the fossil avifauna of San Josecito Cave, though they did not infer habitat preferences for most of the extinct species, including *B. daggetti*. The puzzling report that Miller had later concluded "that *Wetmoregyps daggetti* was a forest inhabiting species rather than a walking eagle as previously considered" (Storer 1931:177) turned out to be based on some spurious and somewhat circular reasoning. Because *Wetmoregyps* was more abundant in the much less numerous fossil material at Carpinteria than at Rancho La Brea, and because the environment at Rancho La Brea was believed to have been open, Miller (1931:369) concluded that the environment at Carpinteria must have been different so that "*Wetmoregyps* was a sylvan form." This assumption was based on only five bones of *Wetmoregyps* from Carpinteria, and Miller did not say how many individuals were represented. For a rare species, chance alone could produce 5 bones among a total of 1,000 at one site and 5 among 100,000 at another.

Miller (1928:255) was more accurate in characterizing the species as "weak-footed," so that one may visualize *B. daggetti* as a New World analog of the Old World Secretarybirds (*S. serpentarius*), which today are confined to Africa but which also inhabited Europe during the Tertiary (Mourer-Chauviré and Cheneval 1983). The two species of *Pelargopappus* in Europe had proportionately shorter tarsometatarsi than *Sagittarius*. Extrapolating from distal width, the length of the tarsometatarsus of the smaller of the two European species (*P. schlosseri*) would have been 168 mm, which is essentially the same as that of *B. daggetti*. Least diameter of the shaft of the tibiotarsus is a good indicator of body mass (Campbell and Marcus 1992). In captive specimens of male and female Secretarybirds weighing 2,685 and

3,330 g, respectively (USNM 621022, 621021), the least diameter of the shaft of the tibiotarsus was 31 mm, whereas in the specimen of *B. daggetti*, it was 35 mm. This indicates that this species was at least as hefty as a modern Secretarybird and, therefore, could well have occupied a similar niche. This is not unlike the situation in which the open country of North America produced felids convergently similar to Old World cheetahs (Van Valkenburgh et al. 1990).

Secretarybirds (*Sagittarius*), like Savanna Hawks, feed on diverse prey items but are best known for their predilection for snakes. *Buteogallus daggetti* may have had somewhat similar habits and would certainly have been capable of subduing much larger snakes than *B. meridionalis*. There appears to be no reason for considering that *B. daggetti* was anything other than an incidental scavenger, if that, contrary to the speculation of Steadman and Martin (1984). Thus, it is unlikely that the extinction of *B. daggetti* can be directly related to the extinction of the North American mammalian megafauna, unless some of the extinct mammals were responsible for the existence of suitable open habitats for the raptor.

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#### LITERATURE CITED

- BAUMEL, J., A. S. KING, A. M. LUCAS, J. E. BREAZILE, AND H. E. EVANS, EDs. 1979. *Nomina Anatomica Avium: An Annotated Anatomical Dictionary of Birds*. Academic Press, London.
- CAMPBELL, K. E., JR., AND L. MARCUS. 1992. The relationships of hindlimb bone dimensions to body weight in birds. Pages 395–412 in
- Papers in Avian Paleontology Honoring Pierce Brodkorb (K. E. Campbell, Jr., Ed.). Natural History Museum of Los Angeles County, Science Series no. 36.
- FERGUSON-LEES, J., AND D. A. CHRISTIE. 2001. *Raptors of the World*. Christopher Helm, London.
- HOWARD, H. 1932. Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea. Carnegie Institution of Washington Publication 429: 1–82.
- HOWARD, H. 1936. Further studies upon the birds of the Pleistocene of Rancho La Brea. *Condor* 38:32–36.
- MADER, W. J. 1982. Ecology and breeding habits of the Savanna Hawk in the llanos of Venezuela. *Condor* 84:261–271.
- MILLER, L. 1915. A walking eagle from Rancho La Brea. *Condor* 17:179–181.
- MILLER, L. 1925. The birds of Rancho La Brea. Carnegie Institution of Washington Publication 349:63–106.
- MILLER, L. 1928. Generic re-assignment of *Morphnus daggetti*. *Condor* 30:255–256.
- MILLER, L. 1931. Pleistocene birds from the Carpinteria asphalt of California. University of California Publications Bulletin of the Department of Geological Sciences 20:361–374.
- MILLER, L. 1943. The Pleistocene birds of San Josecito Cavern, Mexico. University of California Publications in Zoology 47:143–168.
- MOURER-CHAUVIRÉ, C., AND J. CHENEVAL. 1983. Les Sagittariidae fossiles (Aves, Accipitiformes) de l'Oligocene des Phosphorites du Quercy et du Miocene Inférieur de Saint-Gerand-le-Puy. *Geobios* 13:803–811.
- STEADMAN, D. W., AND P. S. MARTIN. 1984. Extinction of birds in the late Pleistocene of North America. Pages 466–477 in *Quaternary Extinctions. A Prehistoric Revolution* (P. S. Martin and R. G. Klein, Eds.). University of Arizona Press, Tucson.
- STEADMAN, D. W., J. ARROYO-CABRALES, E. JOHNSON, AND A. F. GUZMAN. 1994. New information on the late Pleistocene birds from San Josecito Cave, Nuevo León, Mexico. *Condor* 96: 577–589.
- STORER, T. I. 1931. Sixth Annual Meeting [Cooper Ornithological Society]. *Condor* 33:177–179.
- VAN VALKENBURGH, B., F. GRADY, AND B. KURTÉN. 1990. The Plio-Pleistocene cheetah-like cat *Miracinonyx inexpectatus* of North America. *Journal of Vertebrate Paleontology* 10:434–454.