**TAXONOMIC STATUS OF THE SPECIMENS OF *ARCHAEOPTERYX***

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*Archaopteryx* is an extremely important taxon to paleontology. Its basal position within Avialae often makes it the epicenter of the debate over bird origins, one of paleontology’s most significant issues. Because of this, any change in the taxonomy of *Archaopteryx* is of great interest.

To date, seven described fossil skeletons have been assigned to the genus *Archaopteryx*. In order of increasing size, these are JM 2257 (the “Eichstädt specimen”), BSP 1999 I 50 (the “Munich specimen”), HMN 1880/81 (the “Berlin specimen”), TM 6928/29 (the “Haarlem specimen”), a specimen that has been lost from a private collection (the “Maxberg specimen”), BMNH 37001 (the “London specimen”), and an unnumbered specimen housed at the Bürgermeister Müller Museum (the “Solnhofen specimen”).

Some authors have cited differences in skeletal proportions between the specimens as evidence that the specimens represent different species (Howgate, 1984; Wellnhofer, 1993; Elzanowski, 2001, 2002). Houck et al. (1990) used major-axis regressions of skeletal element lengths to show that the proportional differences between the specimens could be interpreted as allometric effects within the growth series of a single taxon. They therefore assigned all the specimens to a single species, *Archaopteryx lithographica*. However, their analysis did not include BSP 1999 I 50, which had not yet been discovered. Also, the analysis included the “Solnhofen specimen,” which has since been reassigned to the genus *Wellnhoferia* (Elzanowski 2001), a reassignment with which the present authors agree due to the specimen’s unique pedal and caudal characteristics (Elzanowski, 2001).

In order to test whether differences in skeletal proportions between the remaining six *Archaopteryx* specimens are sufficient to support taxonomic separation of one or more, it has become necessary to run new regressions of element lengths, this time including BSP 1999 I 50 and excluding the “Solnhofen specimen.” This was done by the present authors, and described below.

**Institutional Abbreviations—** AMNH, American Museum of Natural History, New York City, New York; BHI, Black Hills Institute of Geological Research, Hill City, South Dakota; BMNH, Natural History Museum, London, United Kingdom; BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; HNM, Museum für Naturkunde, Berlin, Germany; JM, Jura Museum, Eichstätt, Germany; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts; TM, Teyler Museum, Haarlem, Netherlands; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

**MATERIALS AND METHODS**

Following Houck et al. (1990), we ran major-axis regressions on lengths of bony elements in *Archaopteryx*, using BIOStat 3.2 software (Rohlf and Slice, 1996) (Fig. 1, Table 1). We omitted TM 6928/29, per Houck et al. (1990), because too few of its skeletal elements are preserved for their entire length. We used element lengths given by Wellnhofer (1974, 1993). All data were natural log-transformed to linearize allometric scaling effects. We ran regressions of the lengths of 12 elements (tail, scapula, humerus, radius, ulna, metacarpal II, manual phalanx II-2, ilium, pubis, ischium, tibia, and pedal digit III) versus femoral length in *Archaopteryx* (Fig. 1). These included 9 of the 10 elements used by Houck et al. (1990) in their analysis. We did not use the tenth, premaxillary tooth dimensions, because premaxillae are missing in BSP 1999 I 50. We also ran regressions of hindlimb length versus humeral length and ulnar length versus femoral length.

**RESULTS**

For all but three regressions, $R^2 > 0.95$ ($P < 0.03$) (Table 1). For tibial length $\times$ femoral length, $R^2 = 0.94$ ($P = 0.006$). For tail length $\times$ femoral length, $R^2 = 0.95$ ($P = 0.034$). The only regression for which $R^2 < 0.90$ is ischial length $\times$ femur length ($R^2 = 0.86$, $P = 0.074$).

**DISCUSSION**

The low $R^2$ value for ischial length $\times$ femoral length indicates that this element is more prone to length variation than are other elements in *Archaopteryx*. This may be due to individual or sexual variation, but it is of little concern here, as ischial length has not been cited in support of taxonomic variation within *Archaopteryx*.

The results of all the other element length regressions have high $R^2$ values, and are consistent with interpretation of proportional differences within *Archaopteryx* as allometric effects within the growth series of a single taxon. Therefore, for these elements, proportional differences between *Archaopteryx* specimens are insufficient evidence for taxonomic subdivision of the genus.

Wellnhofer (1993) designated BSP 1999 I 50 the holotype of a new species, *A. bavarica*, on the basis of (1) higher ratio of tibial length to femoral length than in *A. lithographica*, (2) higher ratio of hindlimb length to humeral length than in *A. lithographica*, and (3) ossification of the sternum at a young age in *A. bavarica* but not in *A. lithographica*.

Our regression results show that the first two characters can be interpreted as allometric effects (tibia $\times$ femur; $R^2 = 0.93$, $P = 0.006$; hindlimb $\times$ humerus; $R^2 = 0.95$, $P = 0.025$), and are therefore insufficient evidence for taxonomic separation of BSP 1999 I 50. Furthermore, in neither case is BSP 1999 I 50 an outlier with respect to the other specimens (Fig. 1K, M).

The third character merits more discussion. Wellnhofer (1993) attributed the lack of sternum in *Archaopteryx* specimens larger than BSP 1999 I 50 to a lack of sternal ossification in the larger individuals. Attributing the size differences to age differences, he concluded that the sternum ossified earlier in ontogeny in the population represented by BSP 1999 I 50, than in that represented by the other individuals (Wellnhofer, 1993). This is a reasonable interpretation if the 5 larger specimens lacked sternal ossification in life. However, the premise that the 5 larger specimens lacked ossified sternum in life is based on negative evidence, which must be treated with caution. For example, negative evidence at first led researchers to believe that theropods lacked clavicles (Bryant and Russell, 1993), that diplodocids lacked calcanea (Bonnan, 2000), and that the fossil bird *Confuciusornis sanctus* lacked ossified uncinate processes (Hou et al., 1996). These animals are now known to have possessed these elements (Bryant and Russell, 1993; Norell et al., 1997; Makovicky and Currie, 1998; Chiappe et al., 1999; Bonnan, 2000).

It is plausible that the five larger *Archaopteryx* specimens possessed ossified sterna in life, and that slab breakage or postmortem transport prevented sternal preservation. Slab breakage is the likely culprit in TM 6928/29, in which part of the slab is missing at the anterior end of the gastralia series (Ostrom, 1970), where the sternum would be in an articulated specimen. Incidentally, the absence of a sternum in the one known specimen of *Wellnhoferia* (the “Solnhofen specimen”) may also be due to slab breakage, since part of the slab is missing at the anterior end of the gastralia series in this specimen (Wellnhofer, 1992). Postmortem transport likely removed the sterna of BMNH 37001 and the Maxberg specimen. This explanation is made plausible by the high de-