

ONTOGENY AND *ARCHAEOPTERYX*

S. CHRISTOPHER BENNETT, Department of Biological Sciences, Fort Hays State University, Hays, KS, 67601-4099, U.S.A.,
cbennett@fhsu.edu

The taxonomy of *Archaeopteryx* has long been controversial even though to date only ten skeletal specimens and one isolated feather have been referred to the genus (Elzanowski, 2002; Wellnhofer and Röper, 2005; Mayr et al. 2005; Mayr et al., 2007). Over the years, some workers have proposed six generic names and ten species names for those specimens, while others have viewed them all as representing a single species, *A. lithographica*. Houck et al. (1990) noted evidence of immaturity in each of the six skeletal specimens then known, and noted that relative maturity increased with absolute size. They presented bivariate scatter plots of length measurement data of various skeletal elements versus femur length, noted high correlation coefficients, found no evidence that the sample included more than one species, and therefore concluded that it was most parsimonious to interpret the six specimens as a growth series of *A. lithographica*. Elzanowski (2001) argued that the large Solnhofen specimen was generically distinct from *Archaeopteryx* and proposed the name *Wellnhoferia grandis* for it. In his subsequent review of the taxonomy of the Archaeopterygidae, Elzanowski (2002) rejected the notion that all or even most of the specimens were immature, dismissed Houck et al.'s (1990) interpretation as untenable, and recognized the London, Berlin, and Munich specimens as three species of *Archaeopteryx* (*A. lithographica*, *A. siemensis*, and *A. bavarica*, respectively) and the Solnhofen specimen as *W. grandis*. Senter and Robins (2003) repeated the analysis of Houck et al. (1990), adding the Munich specimen that had not been available in 1990 and excluding the Solnhofen specimen as *W. grandis*. Again analysis of length measurement data of various skeletal elements versus femur length showed close correlations and failed to provide evidence that more than one species was present. The authors considered the characters that Elzanowski (2002) had used to separate the Berlin, Solnhofen, and Munich specimens from *A. lithographica*, interpreted many of them as ontogenetic characters and rejected them, and concluded that in the absence of evidence to the contrary the six skeletal specimens they analyzed should be viewed as a growth series of *A. lithographica*. Wellnhofer and Röper (2005) described the ninth specimen of *Archaeopteryx*, an isolated right wing skeleton, and interpreted the specimen as immature because the humerus exhibited immature bone grain indicative of incomplete ossification and active growth. They referred the specimen to *A. lithographica*, and viewed all of the known specimens except the Munich specimen (= *A. bavarica*) as forming a growth series of *A. lithographica*. Lastly, Mayr et al. (2007; see also Mayr et al., 2005) described the tenth or Thermopolis specimen of *Archaeopteryx*, a nearly complete articulated skeleton, and rejected the separation of the Solnhofen specimen as *W. grandis* but concluded that there are two species of *Archaeopteryx*: *A. siemensis* consisting of the Berlin, Munich, and Thermopolis specimens, and *A. lithographica* consisting of all other specimens including the large Solnhofen specimen.

Recently, Christiansen (2006) challenged the validity of the statistical methods that Houck et al. (1990) and Senter and Robins (2003) applied to *Archaeopteryx*, as well as the similar methods that I applied to *Rhamphorhynchus* and other Solnhofen pterosaurs (Bennett, 1995, 1996). Christiansen analyzed measurement data from multiple closely-related species of *Larus* and *Panthera*, and compared correlation coefficients of pairs of skeletal elements from samples of single species with correlation coefficients of pairs of skeletal elements from lumped samples of multiple species of the same genus. He noted that the correlation coefficients of data from lumped samples of multiple species of *Larus* or *Panthera* were higher than those of samples of single species of those genera, and based on that he questioned the statistical methods and conclusions about *Archaeopteryx* of Houck et al. (1990) and Senter and Robins (2003), and suggested that the size differences of *Archaeopteryx* specimens might indicate that they were not conspecific. However, Christiansen seems to have misunderstood the way in which Houck et al. (1990), Senter and Robins (2003), and Bennett (1995, 1996) used statistical analyses of measurement data, he seems not to have understood why his samples of individual species had lower correlation coefficients than his lumped samples of multiple species, and he ignored ontogeny so that his samples of *Larus* and *Panthera* are not comparable to the samples of *Archaeopteryx* and *Rhamphorhynchus*. In response to Christiansen's paper, this note presents statistical analyses of a sample of the extant crocodylian *Alligator mississippiensis*, compares the results with the results of the statistical analyses of *Archaeopteryx* and *Rhamphorhynchus*, discusses Christiansen's results and his objections to the statistical analyses of *Archaeopteryx* and *Rhamphorhynchus*, and discusses the importance of ontogeny in evaluating samples of specimens.

Materials and Methods

Measurements of 46 specimens of *Alligator mississippiensis* and 2 specimens of *A. sinensis* were taken from Brochu (1996). Note that I corrected what seems to be a typographical error in that the radius length of UF 35147 is probably 30.7 mm rather than 20.7 mm given that the associated humerus and ulna are 40.9 and 32.1 mm, respectively; however, the change did not affect the analysis significantly other than removing what would have been an outlier on the plot of radius vs. ulna length data. Lengths of skeletal elements of all specimens of *A. mississippiensis* and four subsets of specimens were plotted in bivariate scatter plots, and linear regression equations and correlation coefficients were calculated. The four subsets of specimens were: one selected by arranging the specimens in order of increasing femur length and selecting every fifth specimen so as to produce a subset sample of 10 specimens (Texas Memorial Museum, Austin, [= TMM] m-6804, m-983; Florida Museum of Natural His-