TAXONOMIC STATUS OF THE SPECIMENS OF *ARCHAEOPTERYX*

PHIL SENTER and JAMES H. ROBINS, Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115, U.S.A.

Archaeopteryx 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 *Archaeopteryx* is of great interest.

To date, seven described fossil skeletons have been assigned to the genus *Archaeopteryx*. In order of increasing size, these are JM 2257 (the "Eichstätt 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, *Archaeopteryx 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 *Archaeopteryx* 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; **HMN**, 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 *Archaeopteryx*, using BIOMstat 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, femur, pubis, ischium, tibia, and pedal digit III) versus femoral length in *Archaeopteryx* (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, $R^2 \geq 0.95$ ($P < 0.03$) (Table 1). For tibial length $\times$ femoral length, $R^2 = 0.94$ ($P = 0.006$). For tail length $\times$ femoral length, $R^2 = 0.93$ ($P = 0.034$). 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 *Archaeopteryx*. 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 *Archaeopteryx*.

The results of all the other element length regressions have high R^2 values, and are consistent with interpretation of proportional differences within *Archaeopteryx* as allometric effects within the growth series of a single taxon. Therefore, for these elements, proportional differences between *Archaeopteryx* 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 sterna in *Archaeopteryx* 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 sterna 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 *Archaeopteryx* 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 gastralial 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 gastralial 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-
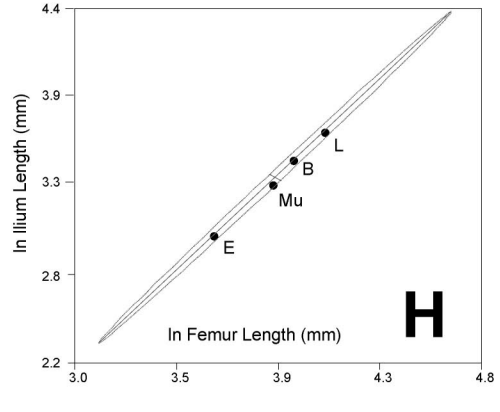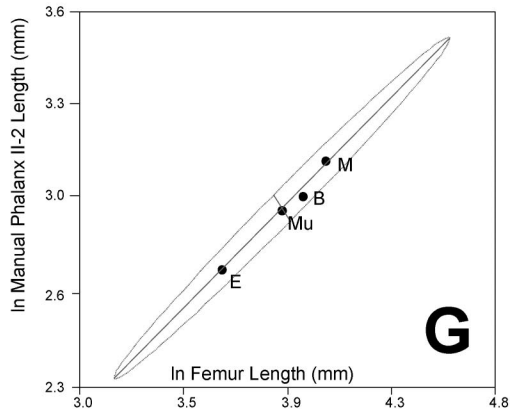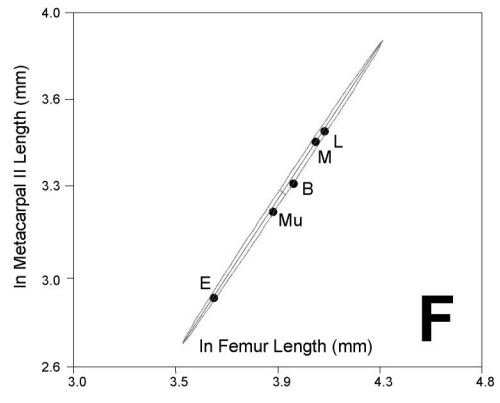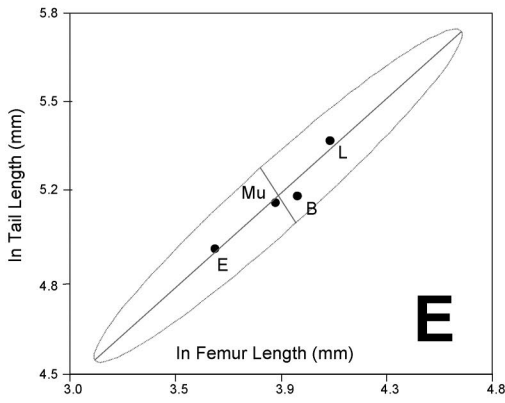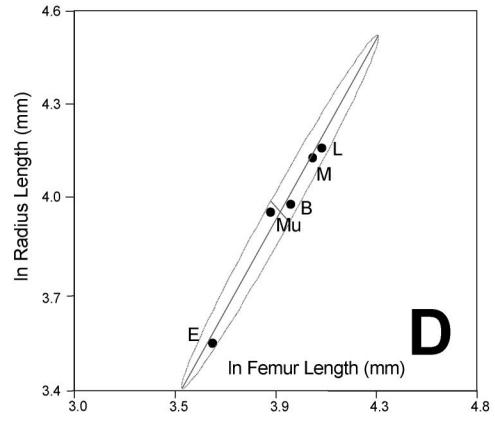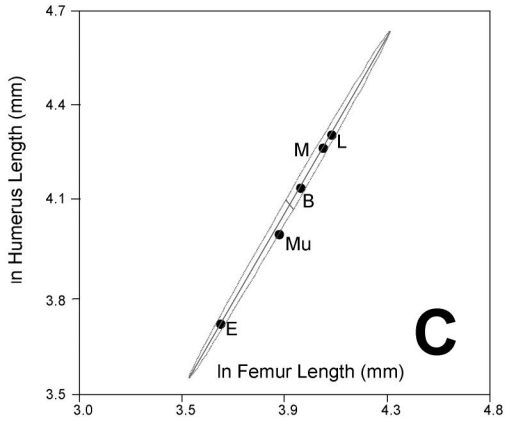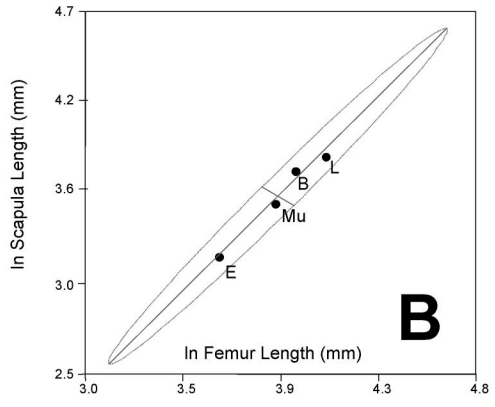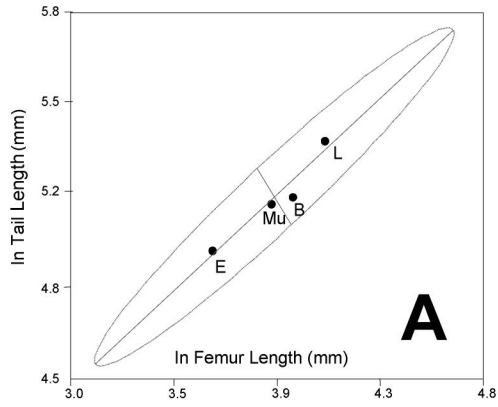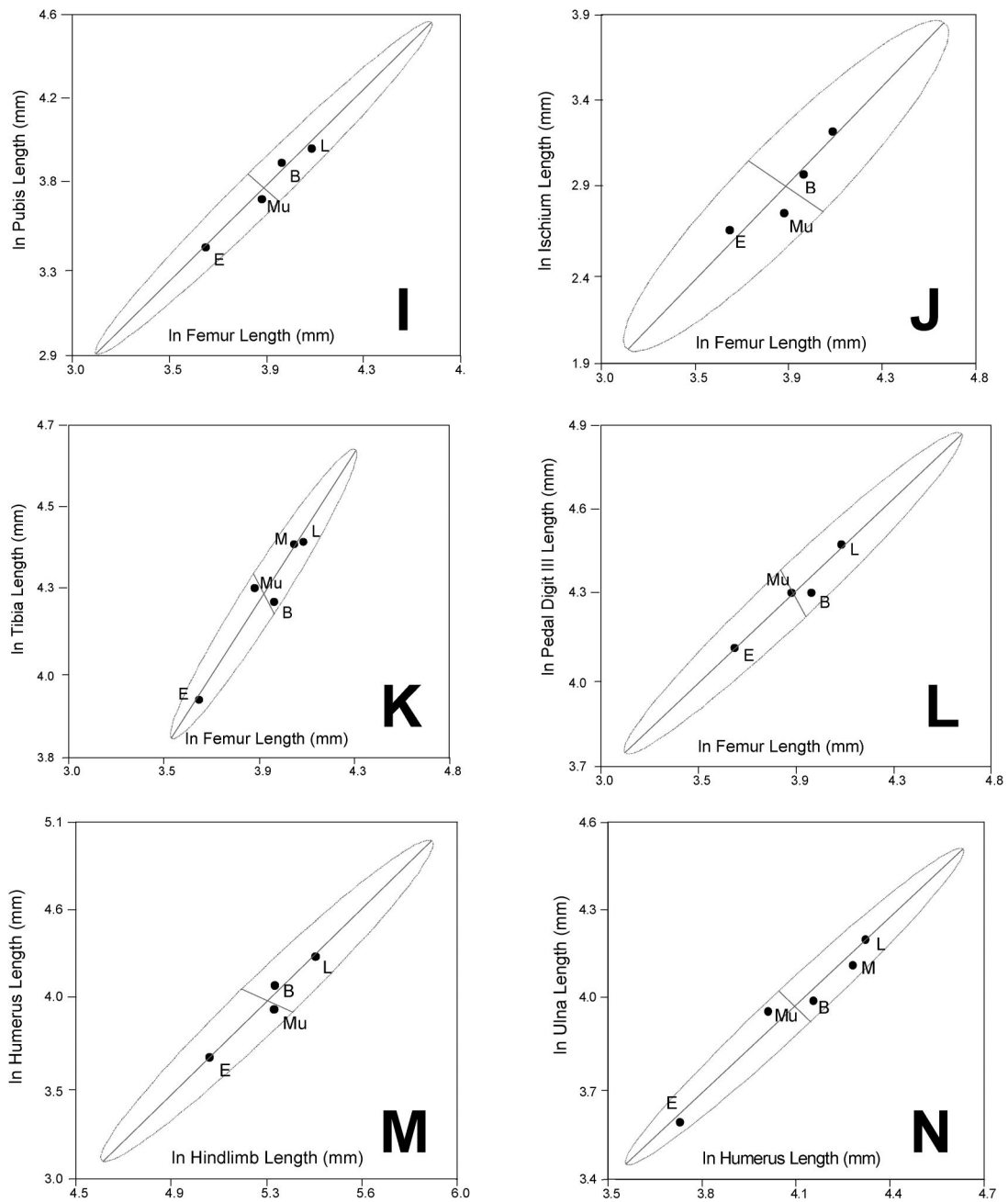
FIGURE 1.   Major-axis regressions of log-transformed element lengths of five *Archaeopteryx* skeletons, with 95% confidence ellipses. **A**, Tail × femur; **B**, scapula × femur; **C**, humerus × femur; **D**, radius × femur **E**, ulna × femur; **F**, metacarpal II × femur; **G**, manual phalanx II-2 × femur; **H**, ilium × femur; **I**, pubis × femur; **J**, ischium × femur; **K**, tibia × femur; **L**, pedal digit III × femur **M**, hindlimb × humerus; **N**, ulna × humerus. **Abbreviations**: **B**, Berlin specimen (HMN 1880/81); **E**, Eichstätt specimen (JM 2257); **L**, London specimen (BMNH 37001); **M**, Maxberg specimen; **Mu**, Munich specimen (BSP 1999 I 50).

TABLE 1.   Major axis regression results for natural log-transformed element lengths in *Archaeopteryx*.

Elements $Y_1 \times Y_2$	Correlation		Major axis parameters		Minor axis parameters	
	R^2	p	Intercept	Slope	Intercept	Slope
Tail × femur	0.93	0.034	2.19	0.76	10.26	−1.32
Scapula × femur	0.98	0.01	−1.50	1.31	6.56	−0.76
Humerus × femur	0.99	<0.001	−0.71	1.23	7.29	−0.82
Radius × femur	0.98	0.002	−1.00	1.27	7.06	−0.79
Ulna × femur	0.98	0.001	−0.76	1.21	7.22	−0.83
Metacarpal II × femur	0.99	<0.001	−2.01	1.35	6.19	−0.74
Manual phalanx II-2 × femur	0.98	0.008	−0.21	0.81	7.71	−1.24
Ilium × femur	0.99	0.001	−1.76	1.32	6.31	−0.76
Pubis × femur	0.97	0.016	−0.38	1.06	7.40	−0.94
Ischium × femur	0.86	0.074	−1.87	1.23	6.08	−0.81
Tibia × femur	0.94	0.006	0.77	0.88	8.67	−1.13
Pedal digit III × femur	0.95	0.024	1.52	0.72	9.73	−1.39
Humerus × hindlimb	0.95	0.025	−3.62	1.46	7.65	−0.68
Ulna × humerus	0.96	0.003	−0.05	0.98	8.14	−1.02

gree of disarticulation in these two specimens (Owen, 1864; Heller, 1959) and by the fact that broad, flat skeletal elements are more susceptible to aquatic transport than are skulls or cylindrical elements such as limb bones (Voorhies, 1969). The high degree of articulation in the Berlin specimen seems, at first, to cast doubt upon postmortem transport as an explanation for this specimen's lack of a sternum. However, some postmortem transport did occur in the pectoral region of this specimen, as is evident from its missing furcula. The lack of sterna in the larger 4 specimens of *Archaeopteryx* can therefore be plausibly explained by slab breakage and postmortem transport. Because of this, sternal preservation in BSP 1999 I 50 is insufficient evidence to taxonomically separate the others.

Elzanowski (2002) recognizes three species of *Archeopteryx*, separating HMN 1880/81 as *A. siemensii* and BSP 1999 I 50 as *A. bavarica*. Characters cited in support of this separation are (1) differences in length of ulna relative to humerus, (2) differences in length of tibia relative to femur, (3) lack of pedal flexor tubercles in HMN 1880/81 and BSP 1999 I 50 versus their presence in BMNH 37001 (the holotype of *A. lithographica*), (4) lack of the iliofemoralis internus fossa on the ilium of HMN 1880/81 and BSP 1999 I 50 versus its presence in BMNH 37001, (5) lack of the anteroventral process on the anterior iliac blade of HMN 1880/81 and BSP 1999 I 50 versus its presence in BMNH 37001, and (6) dental differences. However, none of these differences is sufficient for taxonomic separation of HMN 1880/81 or BSP 1999 I 50. Our regressions show that the first and second characters can be interpreted as allometric effects (ulna × humerus: $R^2 = 0.96$, $P = 0.003$; tibia × femur: $R^2 = 0.93$, $P = 0.006$). In neither case is BSP 1999 I 50 an outlier with respect to the other specimens (Fig. 1K, N). Personal examination by one of us (P.S.) of BMNH 37001 and casts of HMN 1880/81 and BSP 1999 I 50 reveals the presence of pedal flexor tubercles in all three specimens. The presence in BMNH 37001 of iliac markings that are absent in the two smaller specimens can be accounted for by the tendency of bony markings to increase in prominence with age in vertebrates.

Dental differences between the specimens of *Archaeopteryx* have been cited as evidence of taxonomic diversity within *Archaeopteryx*. The teeth of the two smallest specimens, JM 2257 and BSP 1999 I 50, are more recurved and more laterally compressed than those of the larger specimens HMN 1880/81 and BMNH 37001 (Wellnhofer, 1972; Howgate, 1984; Elzanowski and Wellnhofer, 1996). These differences are cited in support of separation of JM 2257 as *A. recurva* (Howgate, 1984) and of BSP 1999 I 50 as *A. bavarica* (Elzanowski, 2002). However, these dental differences can be attributed to ontogeny, as ontogenetic reduction in dental recurvature (especially in posterior teeth) and ontogenetic decrease in lateral compression of teeth are known in theropods. The former is known in *Coelophysis bauri* (pers. obs. by P.S. of AMNH 2742, AMNH 7241, and MCZ 4327) and *Tyrannosaurus rex* (pers. obs. by P.S. of AMNH 5027, BHI 4100, BHI 3033, and TMP cast of CMNH 7541), the latter in Tyrannosauridae (Carr, 1996).

As Elzanowski (2001) correctly notes, allometric coefficients may be similar in closely related species. Our results therefore do not demonstrate that the six *Archaeopteryx* specimens are conspecific. However, our re-

sults do demonstrate that if the specimens are allospecific, then the evidence lies in characters other than the proportional differences that have been cited to date. We therefore recommend that the six specimens be treated as conspecific until evidence to the contrary comes to light.

CONCLUSIONS

The proportional and dental differences between the six described specimens of *Archaeopteryx* can be accounted for by ontogenetic effects. We therefore recommend that all 6 specimens be referred to *Archaeopteryx lithographica* von Meyer 1861, and that *Archaeopteryx recurva* Howgate 1984 and *Archaeopteryx bavarica* Wellnhofer 1993 be considered junior synonyms of *Archaeopteryx lithographica* von Meyer 1861.

LITERATURE CITED

Bonnan, M. F. 2000. The presence of a calcaneum in a diplodocid sauropod. Jornal of Vertebrate Paleontology 20:217–323.

Bryant, H. N., and A. P. Russell. 1993. The occurrence of clavicles within Dinosauria: implications for the homology of the avian furcula and the utility of negative evidence. Journal of Vertebrate Paleontology 13:171–184.

Carr, T. D. 1996. Cranial osteology and craniofacial ontogeny in Tyrannosauridae (Dinosauria: Theropoda) from the Dinosaur Park Formation (Judith River Group, Upper Cretaceous: Campanian) of Alberta. M.S. thesis, University of Toronto, 358 pp.

Chiappe, L. M., S. Ji, Q. Ji, and M. A. Norell. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. Bulletin of the American Museum of Natural History 242:1–89.

Elzanowski, A. 2001. A new genus and species for the largest specimen of *Archaeopteryx*. Acta Palaeontologica Polonica 46:519–532.

——— 2002. Archaeopterygidae (Upper Jurassic of Germany); pp. 129–159 *in* L. M. Chiappe and L. W. Witmer (eds.), Mesozoic Birds: Above the Heads of Dinosaurs. The University of California Press, Berkeley.

———, and P. Wellnhofer. 1996. Cranial morphology in *Archaeopteryx*. Journal of Vertebrate Paleontology 16:81–94.

Heller, F. 1959. Ein dritter *Archaeopteryx*-Fund aus den Solnhofener Plattenkalken von Longenaltheim/Mfr. Erlanger Geologische Abhandlungen 31:1–25.

Hou, L., L. D. Martin, Z. Zhou, and A. Feduccia. 1996. Early adaptive

radiation of birds: evidence from fossils from northeastern China. Science 274:1164–1167.

Houck, M. A., J. A. Gauthier, and R. E. Strauss. 1990. Allometric scaling in the earliest fossil bird, *Archaeopteryx lithographica*. Science 247:195–198.

Howgate, M. E. 1984. The teeth of *Archaeopteryx* and a reinterpretation of the Eichstätt specimen. Zoological Journal of the Linnean Society 82:159–175.

Makovicky, P. J., and P. J. Currie. 1998. The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications. Journal of Vertebrate Paleontology 18:143–149.

Norell, M. A., P. Makovicky, and J. M. Clark. 1997. A *Velociraptor* wishbone. Nature 389:447.

Ostrom, J. H. 1970. *Archaeopteryx*: notice of a ''new'' specimen. Science 170:537–538.

Owen, R. 1864. On the *Archaeopteryx* of von Meyer, with a description of the fossil remains of a long-tailed species, from the Lithographic Stone of Solenhofen. Philosophical Transactions of the Royal Society of London 153:33–47.

Rohlf, F. J., and D. E. Slice. 1996. BIOMstat for Windows, Verson 3.2. Applied Biostatistics, Inc., Setauket, New York.

Voorhies, M. R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. University of Wyoming Contributions to Geology, Special Paper 1:1–69.

Wellnhofer, P. 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. Palaeontographica Abteilung A 147:169–216.

——— 1992. A new specimen of *Archaeopteryx* from the Solnhofen Limestone; pp. 3–23 *in* Papers in Avian Paleontology, Honoring Pierce Brodkorb. Natural History Museum of Los Angeles County, Los Angeles.

——— 1993. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofen Schichten. Archaeopteryx 11:1–47.