A new genus and species for the largest specimen of *Archaeopteryx*

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The Solnhofen (Sixth) specimen of *Archaeopteryx* is assigned to *Wellnhoferia grandis* gen. et sp. n. on the basis of qualitative, size-independent autapomorphies. *Wellnhoferia* differs from *Archaeopteryx* in a short tail with the estimated number of 16–17 caudals; a nearly symmetric pattern of pedal rays II–IV with metatarsals II and IV of equal length and digit IV substantially shorter than in *Archaeopteryx*; and the number of four (instead of five) phalanges of pedal digit IV, which most probably results from a phylogenetic reduction rather than individual variation. A combination of large size and details of the pelvic limb suggests a locomotor specialization different from that of *Archaeopteryx*.

Key words: *Archaeopteryx*, *Wellnhoferia*, birds, Aves, Jurassic, Solnhofen.

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Introduction

The vicissitudes of the taxonomic treatment of the Archaeopterygidae have led to the prevailing skepticism as to the possibility of establishing species differences between the seven studied specimens: London (1st), Berlin (2nd), Third ('Maxberg', lost from a private collection), Haarlem (4th), Eichstätt (5th), Solnhofen (6th), and Munich (7th). Separate species have been erected for the London, Berlin, and Eichstätt specimens (Stephan 1987), but none of them has been widely accepted and the name *Archaeopteryx lithographica* has been broadly applied to the 1st through 6th specimens (Wellnhofer 1992). However, a new species, *Archaeopteryx bavarica*, has been erected for the Munich (7th) specimen (Wellnhofer 1993), which is tentatively accepted here as evidence of species-level differentiation within the genus *Archaeopteryx*.

Paradoxically, the Solnhofen (6th) specimen, which is the largest and, as it turns out, the most distinct among the major (fairly complete) archaeopterygid specimens, is the only one that has not yet been classified into a separate species. This specimen, of

Table 1. Meristic and qualitative differences between the archaeopterygid specimens.

	Eichstätt	Munich	Berlin	Haarlem	Third	London	Solnhofen
Caudal vertebrae	22	21	22	?	?	23	16–17 est.
Pedal digit IV phalanges	5	5	5	?	?	5?	4
Manual digit III ph. 1/ph. 2 art.	movable	movable	movable	?	?	?	partly fused
Scapulocoracoid articulation	loose	loose	tight	?	?	tight	loose

unknown origin in terms of exact horizon and locality, was identified as another *Archaeopteryx* specimen and assigned to *Archaeopteryx lithographica* (Wellnhofer 1988a,1988b,1992). Wellnhofer reported close similarities in the tooth structure and limb proportions between the Solnhofen and London specimens but also noted and illustrated two striking differences: an aberrant phalangeal formula of the pes, which has been interpreted as a pathology (see also Ostrom 1992) and the absence of fusion between the scapula and coracoid, which has been left uninterpreted. A conservative taxonomic treatment of the Solnhofen specimen is justified in part by the context of its discovery and in part by its poor preservation, which has been made even worse through the unprofessional handling by its former private owner.

The postcranial part of the Solnhofen specimen is nearly complete, but most of the skull is gone. The vertebral column, girdles, and proximal limb segments are heavily damaged by crushing and breaking against one another. In addition, most long bones (including the tibiae and manual unguals) are collapsed, which makes the comparisons of their diameters to those of other specimens impossible. Not collapsed are only metacarpal III (in part), manual digit I phalanx 1, digit II phalanx 2, digit III phalanx 3, pubis, the right fibula, metatarsal I, metatarsal II (proximal half), pedal digit I phalanx 1, and pedal digit III phalanx 3.

The Solnhofen specimen was initially misidentified as *Compsognathus* and kept in a private collection before being identified as another *Archaeopteryx* specimen (Wellnhofer 1988a, 1988b). Apparently as a result of this particular historic context, Wellnhofer stressed the many detailed similarities to *Archaeopteryx*, especially to the London specimen, and downplayed a few differences he noted (four phalanges in the fourth toe and unfused scapula and coracoid).

However, detailed comparisons demonstrate that the Solnhofen specimen shows pronounced differences from the *Archaeopteryx* specimens in meristic and qualitative characters (Table 1) as well as proportions (Tables 2–6), and that there is no reason to treat these differences as cases of individual variation. Therefore, the Solnhofen specimen is here transferred to a new species, which is classified into a new genus because of evidence for species-level differences among the specimens that remain in the genus *Archaeopteryx* (Wellnhofer 1993).

Systematic paleontology

Class Aves Linnaeus, 1758

Family Archaeopterygidae Huxley, 1872

Genus *Wellnhoferia* gen. n.

Type species: *Wellnhoferia grandis* sp. n.

Fig. 1. *Wellnhoferia grandis* gen. et sp. n., the holotype Solnhofen (6th) specimen. The arrow points to the shortened and narrowed terminal caudal vertebrae (followed by a mistakenly painted extension of the tail). Scale bar 10 cm.

Derivation of the name: In honor of Dr. Peter Wellnhofer, Chief Curator Emeritus, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.

Diagnosis. — As for the species.

Wellnhoferia grandis sp. n.

Fig. 1.

Archaeopteryx lithographica: Wellnhofer 1988a: figs. 1, 2.
Archaeopteryx lithographica: Wellnhofer 1988b: pls. 1–8.
Archaeopteryx lithographica: Wellnhofer 1992: figs. 1, 2.
Archaeopteryx sp.: Ostrom 1992: fig. 2B.

Table 2. Minimum depth (dorsoventral diameter) to length ratios (in %) of manual (M) and pedal (P) phalanges measurable in the Solnhofen and other specimens of the Archaeopterygidae. The measurements are listed in Appendices 1 and 2.

Specimen	MI/1	MII/2	PI/1	PIII/3	PIV/4
Eichstätt	5.84	6.9	12.7	11.4	14.3
Munich	5.75	6.1	18.3	13.1	–
Berlin	6.0	6.2	–	12.8	15.1
Haarlem	8.2	–	–	–	–
London	–	–	21.1	–	20.0
Solnhofen	8.4	8.9	15.0	18.1	25.3

Holotype: Solnhofen (6th) specimen (Wellnhofer 1988a, 1988b, 1992) housed at the Bürgermeister-Müller-Museum, Solnhofen (Bavaria, Germany).

Type horizon: unknown (probably Upper Solnhofen Lithographic Limestone), Late Jurassic (probably Malm zeta 2b, lower Lower Tithonian).

Type locality: unknown (in all probability Altmühl Valley, Bavaria, Germany).

Derivation of the name: Latin *grandis* large.

Material. — Only the holotype specimen including the nearly complete postcranial skeleton and the incomplete skull.

Diagnosis. — Large archaeopterygid species that differs from *Archaeopteryx* species in having manual digit I with the ungual of approximately one third the length of the basal phalanx; pedal digit IV short (less than 80% the length of digit III) and composed of only four phalanges including a long ungual (the longest of all phalanges) with the flexor tubercle widely separated from the ungual base; and a short tail with the estimated number of 16–17 caudals.

Description. — See Wellnhofer (1988a, b, 1992).

Comparisons. — The differences between *Archaeopteryx* and *Wellnhoferia* are most evident in the autopodials and tail, probably because these parts are better preserved than the skull, girdles, and proximal limb segments, which largely defy detailed comparions with other specimens.

The scapula and coracoid are clearly separate in the Solnhofen (the largest), Munich, and Eichstätt (the smallest) specimens, but firmly connected in the Berlin and London (second largest) specimens. This variation is clearly independent of size and thus more likely to reflect taxonomy than ontogeny. The backward slant of the pubis in the Solnhofen specimen is estimated as 128° (Wellnhofer 1988b, 1992), which is more than 110° approximated for the remaining specimens including the Third (Wellnhofer 1985, 1993).

In the manus, the relative depths of the only two phalanges that are measurable in this respect in the Solnhofen specimen and the only one in the Haarlem specimen are much higher than in the remaining archaeopterygid specimens, which do not reveal a positive allometry of this dimension (Table 2). Manual digit III phalanges 1 and 2 are immovably connected in the Solnhofen specimen by what appears to be a convoluted suture (Wellnhofer 1988b: fig. 5.4, 1992: fig. 10B) and suggests a partial fusion, which also occurs in the oviraptorids, e.g., *Ingenia* (H. Osmólska personal communication).

Table 3. Inter- and intradigital proportions of the manus in the Archaeopterygidae (digits in Roman, phalanges in Arabic numerals). In parentheses are ratios based on at least one approximate measurement. The measurements are listed in Appendix 1.

Specimen	All digits I + II + III=100%	Digit I 1 + 2 = 100%	Digit II 1 + 2 + 3 = 100%	Digit III 1 + 2 + 3 + 4 = 100%
Eichstätt	27.3 + 43.5 + 29.2	68.8 + 31.2	–[1]	(23.3 + 10.2 + 44.2 + 23.3)
Berlin	27.2 + 44.0 + 28.8	66.2 + 33.8	(31.9 + 40.5 + 27.6)	20.8 + 13.0 + 40.1 + 26.1
Third	–	–	(34 + 39 + 27)[2]	–
Haarlem	–	70.6 + 29.4[3]	–	–
Solnhofen	26.5 + 43.6 + 29.9	75.1 + 24.9	29.7+42.2+28.1	19.0+14.7+42.2+24.1

[1] The ungual is not measurable.
[2] Heller (1959).
[3] Ostrom (1972).

Table 4. Metatarsal ratios (in %) in the Archaeopterygidae. The measurements are listed in Appendix 2.

Specimen	II+III+IV =100%	III/II	III/IV
Eichstätt	33.0+35.2+31.8	106.7	110.6
Munich	–	–	109.5
Berlin	–	105.7	–
Third	31.9+35.3+32.8	110.5	107.7
London	–	110.0	–
Solnhofen	33.2+33.6+33.2	105.6	105.6

The ginglymoid articulation between these phalanges is poorly developed in other specimens as well, but they are clearly separate and disarticulated in the Berlin specimen. A photograph of the Third specimen suggests the presence of two separate phalanges (Heller 1959: fig. 9) but its describer remarked upon their 'insufficient preservation' and curiously failed to provide their lengths although he did so for phalanx 3. Manual digit III phalanges 1 and 2 are not preserved in the Haarlem specimen. The ungual of manual digit I is strikingly short, approximately one third the length of the basal phalanx. It is much shorter than in three other specimens and no allometric trend toward its shortening is evident (Table 3).

Most differences between *Wellnhoferia* and unquestionable *Archaeopteryx* specimens are found in the foot, although the preservation of feet makes them difficult to compare because the feet of most specimens are exposed in side views. The only exceptions are the right foot of the Solnhofen specimen, which shows its ventral aspect, and the only preserved foot of the Third specimen, which probably shows its dorsal aspect. The three main metatarsals (II, III, and IV) seem to be proximally fused in the Solnhofen specimen (although its peculiar limonite encrustation may have obscured the sutures) and this fusion may indeed be more advanced than in other archaeopterygid specimens except for the Third specimen, which shows evidence of the proximal fusion (Heller 1959). Metatarsal II has been reported to be longer, that is, to have the trochlea more distal than metatarsal IV in the Eichstätt specimen (Wellnhofer 1974), but its trochlea is more proximal in the Third (pers. obs. on Heller's X-ray photograph) and probably Haarlem (Ostrom 1972) specimens. Metatarsal trochleae II and

Table 5. Inter- and intradigital proportions of the pes in the Archaeopterygidae (digits in Roman, phalanges in Arabic numerals). In parentheses are ratios based on at least one approximate measurement. The measurements are listed in Appendix 2.

Specimen	All digits[1] I + II + III + IV = 100%	Digit I 1 + 2 = 100%	Digit II[2] 1 + 2 = 100%	Digit III[2] 1 + 2 + 3 = 100%	Digit IV 1 + 2 + 3 + 4 + 5 = 100%
Eichstätt	8.6 + 21.9 + 37.4 + 32.1	61.0 + 39.0	50.4 + 49.6	37.5 + 33.3 + 29.2	–[4]
Munich	(9.6 + 17.7 + 37.5 + 35.2)	57.7 + 42.3	–[3]	39.0 + 30.7 + 30.3	(24.5 + 18.3 + 16.8 + 21.4 + 19.0)
Berlin	7.3 + 21.3 + 37.6 + 33.8	49.3 + 50.7	53.9 + 46.1	35.8 + 33.6 + 30.6	22.7 + 21.0 + 15.9 + 18.4 + 22.0
Third	–	–	(48.7 + 51.3)	–	–
London	–	56.4 + 43.6	50.0 + 50.0	38.3 + 33.1 + 28.6	–
Solnhofen	11.1 + 24.6 + 36.2 + 28.1	(52.9 + 47.1)	49.0 + 51.0	38.0 + 32.8 + 29.2	(24.6 + 20.9 + abs. + 23.4 + 31.0)

[1] Without the unguals.

[2] Without the unguals, which are not measurable in the Solnhofen specimen.

[3] Phalanx 2 not measurable.

[4] Phalanx 5 (ungual) not measurable.

IV are level in the Solnhofen specimen (Table 4), conveying a remarkable symmetry to the tarsometatarsus of *Wellnhoferia*.

Pedal digit IV in the Solnhofen specimen has only four instead of five phalanges. The length and number of phalanges of pedal digit IV are unknown in the Third and Haarlem specimens. De Beer's (1954) claim of four phalanges in digit IV of the London specimen has never been credible (Ostrom 1972) and calls for a verification (Ostrom 1992). A single preserved foot of the London specimen is exposed in medial view and digit IV lies under digit III, which apparently made it impossible to define the ends of phalanges except for the ungual, which is the only phalanx of digit IV that de Beer measured. Whatever its number of phalanges, digit IV in the London specimen is close in length to digit III and thus much longer than digit II (de Beer 1954: pl. II), as in the other unquestionable *Archaeopteryx*. In contrast, in *Wellnhoferia* digit IV is close in length to digit II (Fig. 2).

There are at least two reasons to believe that the aberrant phalangeal formula 2-3-4-4 of the Solnhofen specimen is another taxonomic difference from *Archaeopteryx* rather than a case of intraspecific variation (*contra* Wellnhofer 1992, *contra* Ostrom 1992). First, very little variation, either inter- or intraspecific, in the number of phalanges is known to occur in extant birds and only the Pteroclidae and Caprimulgidae have the exceptional formula 2-3-4-4 (Forbes 1882). Some species of hawks (Accipitridae) have the two basal phalanges of the digit II fused and in one species, the Black-collared hawk (*Busarellus nigricollis*), these two phalanges are fused in the majority of specimens, but remain unfused in some individuals (Olson 1982), which may be the only recorded case of intraspecific variation in the number of phalanges among birds in the wild. Second, there is strong evidence that the number of phalanges in the Solnhofen specimen results from a reduction of one phalanx rather than the fusion of two. The only three non-ungual phalanges of pedal digit IV

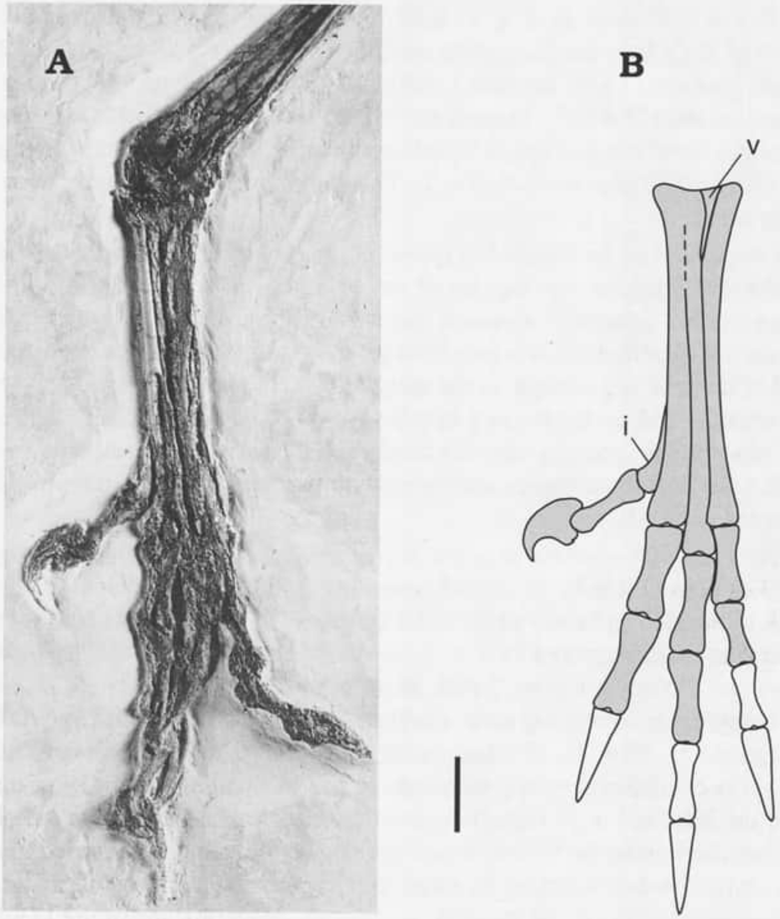

Fig. 2. *Wellnhoferia grandis* gen. et sp. n., the holotype Solnhofen (6th) specimen, foot skeleton. The right foot in plantar (caudal) view and its semidiagrammatic reconstruction. Note the short digit I ungual (with a partly displaced horny sheath) and the digit IV ungual with a separate flexor tubercle and very weak ventral curvature. The ventral outlines of phalanges II/3, III/3, III/4, and the two terminal phalanges of digit IV (all left white) are unknown as are the exact lengths of unguals II and III. Also unclear are the exact proximal outlines of metatarsals II-IV and the resting position of the hallux. Scale bar 10 mm.

in the Solnhofen specimen have comparable relative lengths to phalanges 1, 2, and 4 in the specimens with the usual phalangeal formula (Table 5) and clearly none of them arose by fusion (that is, the lack of separation in the embryo) of two well-developed phalanges. Exclusive of the long ungual, digit IV of the Solnhofen specimen is by 15% shorter than in *Archaeopteryx* (Table 5). This indicates that most likely reduced in the *Wellnhoferia* lineage was the third phalanx, which in *Archaeopteryx* is the shortest and its relative length amounts to approximately 16–17% of the total digit length (Table 5).

The outer toe (digit IV) of the Solnhofen specimen is relatively shorter and its inner toe (digit II) is relatively longer than in *Archaeopteryx* (Table 5). In conjunction with the symmetry of tarsometatarsus, this makes the entire pattern of the three main pedal rays (II–IV) of *Wellnhoferia* (Fig. 2) more symmetrical than in *Archaeopteryx*. The elongation of digit II in the Solnhofen specimen correlates with its phalanx 2 being longer than phalanx 1 (with the ratio 51/49) and the Third specimen reveals an essentially identical ratio (Table 5). In contrast, in the London and Eichstätt specimens the two phalanges are of equal or nearly equal length, and in the Berlin specimen phalanx 2 is much shorter than phalanx 1 (Table 5). This variation is inconsistent with a single allometric trend.

Pedal ungual IV of the Solnhofen specimen, as preserved in its right foot (Fig. 2), differs substantially from the unguals of the other toes as well as those of the other specimens (with a possible exception for the Third specimen, in which the pedal unguals are not identifiable). It is much longer than in *Archaeopteryx* and approaches one third of the total digit length as the longest of all phalanges (Table 5). It is nearly straight ventrally and has the flexor tubercle widely separated from the ungual base. In contrast, other archaeopterygid unguals have ventral curvatures at least equal to and or greater than the dorsal curvatures and their flexor tubercles are not differentiated from the expanded ungual bases.

The bony tail of *Wellnhoferia* is much shorter than that of *Archaeopteryx*, which has 21–23 caudals (Table 1). In the Solnhofen specimen, the caudal series is truncated at a break in the slab and ends with caudal vertebra 15, which is broken, incomplete, and thiner than caudal vertebra 14 (Fig. 1; see also Wellnhofer 1988b: fig. 5). Both vertebrae (14 and 15) are much, by 5 mm, shorter than caudal vertebra 13. In *Archaeopteryx* a comparable shortening occurs only at the end of the bony tail and affects terminal vertebrae 21–22 or 22–23 (Wellnhofer 1974: table 6.2, Wellnhofer 1993: fig. 10, table 9/1). The condition of caudal vertebrae 14 and 15 in the Solnhofen specimen indicates that the bony tail of *Wellnhoferia* may have originally extended at the most for another two diminutive vertebrae, which gives the maximum estimate of 17 caudal vertebrae, which is 4–6 vertebrae less than in *Archaeopteryx*.

The fragmentary Third and Haarlem specimens, which are very close in size (Appendices 1 and 2), are likely to pose problems for any taxonomic revision of the Archaeopterygidae. The Third and Solnhofen specimens show at least one similarity, that is, pedal digit II with phalanx 1 shorter than phalanx 2 (Table 5) and the proximal fusion of their metatarsals II–IV may have possibly been more pronounced than in other specimens. Unfortunately, the most diagnostic character states including pedal formula, length of the tail, and the condition of scapulocoracoid articulation are unknown in either of the two fragmentary specimens (Table 1).

A cladistic analysis is required to determine the mutual relationships of *Archaeopteryx* and *Wellnhoferia*, but their intramembral proportions (Table 6) and several detailed similarities suggest a close relationship. Both *Archaeopteryx* and *Wellnhoferia* have a sigmoid premaxillo-maxillary suture, share identical scapulae (Wellnhofer 1988a), and their pelvic girdles reveal detailed similarities in the shape of the pubic apron and the intermediate process of the ischium (although the angular positions of the pubis may vary). The dentition of the Solnhofen specimen is very similar to that of the London specimen: at least three out of four premaxillary teeth show a waist at the mid-height of the crown, and at least one maxillary tooth has the crown rounded in the basal part and distinctly recurved in the apical part.

Table 6. Intramembral ratios (%) in the Archaeopterygidae (ordered from smallest to largest specimen). In parentheses are ratios based on at least one approximate measurement. The measurements are listed in Appendices 1 and 2.

Specimen	Hu + Ul + McII = 100%	Hu/Ul	Fe + Ti + MtIII = 100%	Fe/Ti	MtIII/DigIII[3]
Eichstätt	43.3 + 38.1 + 18.6	113.7	30.8 + 44.1 + 25.1	69.8	125.8
Munich	(41.4 + 39.8 + 18.8)	(103.8)	(29.3 + 45.1 + 25.6)	(65.0)	146.2
Berlin	42.8 + 38.2 + 19.0	112.1	(32.6 + 44.3 + 23.1)	73.5	(138.1)
Third	–[1]	–[1]	32.3 + 44.3 + 23.4	73.0	
London	42.5 + 38.0 + 19.5	111.9	(32.6 + 43.9 + 23.5)	(74.4)	132.5
Solnhofen	–[2]	(112.2)	(32.4 + 44.6 + 23.0)	(72.8)	(131.9)

[1] Heller's (1959) figures for the forearm bones are probably inaccurate (see Table 1).

[2] Metacarpal II is not measurable.

[3] Non-ungual phalanges only.

Discussion. — A direct body mass estimate of the Solnhofen specimen cannot be calculated from the circumferences of major weight-bearing long bones, which are crushed. However, the linear dimensions of the Solnhofen specimen average 1.1 times those the London specimen (Appendices 1 and 2), which translates to 600–622 g body mass assuming 451–468 g for the London specimen (Elżanowski in press). Because of its large size, some characters of the Solnhofen specimen, such as the fusion of digit II phalanges 1 and 2 may possibly be size-dependent. However, most of the differences from *Archaeopteryx*, including the character states used in the diagnosis, as well as the loose scapulocoracoid articulation, great depth of manual phalanges, especially those of manual digit II (Table 2), and the long pedal digit II phalanx 2 (Table 5) are clearly independent of size and thus substantiate a taxonomic separation of the Solnhofen specimen.

Houck *et al.* (1990) concluded that the six then known specimens (including the holotype of *Wellnhoferia*) represent a single species (*A. lithographica*), because their allometric scaling is consistent with a single growth series and some osteological features suggest that none of them is fully grown. It is true that even after the adjustments of some incorrect measurements and the inclusion of the Munich specimen, some 98% of metric trait variation is size-dependent and thus can be fitted within a single allometric curve (Elżanowski & Paśko in preparation). However, allometric scaling alone cannot differentiate between ontogenetic allometry in a real growth series and static allometry in a set of closely related species because allometric coefficients may be maintained among closely related species (see e.g., Gould 1971 and references therein). Therefore, the conclusion reached by Houck *et al.* (1990) hinges on their interpretation of the archaeopterygid skeleton as being subadult by the standards of nonavian theropods (coelurosaurs). However, the assumption that primitive birds were reaching the same ossification stage as their theropod ancestors is highly questionable. The origin of birds was accompanied by a substantial reduction of size and avian flight may have originated as a juvenile defense adaptation (Elżanowski 2001), which makes some involvement of paedomorphosis in the origin of birds a likely possibility. Accordingly, in the ratites the pectoral girdle is peramorphic and reaches a stage comparable to that of adult coelurosaurs (Elżanowski 1988), which suggests paedomorphosis at some earlier stage of avian evolution.

Despite a great size difference between the smallest (Eichstätt) and the largest (London) specimen of *Archaeopteryx*, not a single unequivocally age-related difference could be determined among the five first described specimens (Howgate 1985). The regression of the tibia/femur length ratio on body size is consistent with the interpretation of archaeopterygid specimens as fully grown individuals (Callison & Quimby 1984) and the faint impressions of the right wing and tail feathers in the smallest (Eichstätt) specimen do not reveal any difference from the plumage of larger specimens (Wellnhofer 1974). Houck *et al.* (1990) list (in a footnote) free cervical ribs, separate sacral vertebrae, unfused scapulocoracoid, and the lack of ossified sternum as evidence for the juvenile to subadult age of the archaeopterygid specimens. In fact, (1) the cervical ribs are known to be free only in the Eichstätt Munich and Berlin specimens but not preserved in the large specimens. If the cervical ribs were free in the large specimens, as Houck *et al.* (1990) tacitly assume, it would be more likely a paedomorphic character of the Archaeopterygidae than a juvenile character of all known specimens, both small and large. (2) The boundaries between the centra of sacral vertebrae remain distinct in both the archaeopterygids and many coelurosaurs but even in the smallest (Eichstätt) specimen the five sacral vertebrae are coossified (Wellnhofer 1974) and no more independent than in nonavian theropods. (3) The scapula and coracoid are firmly connected in the Berlin, London, and Third but not in the Eichstätt, Munich and Solnhofen specimens, which shows that the condition of scapulocoracoid articulation does not correlate with size and makes the single growth series interpretation untenable because the Solnhofen specimen is the largest of all known archaeopterygid specimens. (4) The absence of the bony sternum in most archaeopterygid specimens is probably a preservation artifact, as the sternum is first to be lost from a decaying avian cadaver (Bickart 1984), and its interpretation as a juvenile character has been invalidated by the discovery of the bony sternum in the Munich specimen (Wellnhofer 1993).

Wellnhoferia may have differed from *Archaeopteryx* in the locomotor adaptations. The foot of *Wellnhoferia* is more symmetrical (Fig. 2), which suggests a more cursorial adaptation than in *Archaeopteryx* (Coombs 1978), and the more backward pubic orientation may possibly be correlated with more cursorial habits.

However, the unique shape of pedal ungual IV remains to be interpreted. The forelimb to hindlimb ratio (1.02) is essentially the same as in the London specimen (1.00), which may suggest a higher wing loading (unless *Wellnhoferia* had relatively longer flight feathers), heavier flight, and an even more difficult takeoff than in *Archaeopteryx*. Also, a short tail suggests the aerodynamics of flight to be different from that of *Archaeopteryx*.

None of the differences between *Archaeopteryx* and *Wellnhoferia* are as dramatic as some of those once proposed to taxonomically distinguish between the London and Berlin (Petronievics 1927) and between the Eichstätt and all other specimens (Howgate 1985). Claiming exaggerated differences marred previous attempts to subdivide *Archaeopteryx* (Nopcsa 1925), demonstrating the necessity of a careful taphonomic analysis prior to taxonomic or functional comparisons. Ruben *et al.*'s (1997) speculations about the mechanisms of pulmonary ventilation being different in *Archaeopteryx* and the theropods, which are based on a reconstruction that heavily exaggerates the backward slant of the pelvis in *Archaeopteryx*, visualize the possible functional impact of the once claimed differences in position of the pubis (Howgate 1985) if they weren't post mortem deformations, and make them even less likely than 'catching the pelvis in the act of rotation' (Walker 1980) at the very first moment of divergence of birds with the modern avian pelvis.

The existence of more than one archaeopterygid species is not unexpected (Olson 1987; Stephan 1987; Ostrom, 1992; see also Bonde 1996). Well-developed and clearly functional wings of the archaeopterygids suggest a high probability of accidental colonization of nearby land masses and hypothetical islands, which may have been present between the land masses (Olson 1987; Chatterjee 1997). On the other hand, the interchange between populations over vast stretches of water must have been low to nonexistent because of a limited control of flight, which facilitates allopatric speciation.

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Nowy takson dla największego okazu praptaków (Archaeopterygidae)

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Streszczenie

Solnhofeński, czyli szósty okaz praptaków przeniesiony zostaje z *Archaeopteryx lithographica* von Meyer, 1861 do *Wellnhoferia grandis* gen. et sp. n. na podstawie autapomorfii niezależnych od wielkości ciała, w tym cech jakościowych, merystycznych i proporcji. Okaz ten różni sie od okazów *Archaeopteryx* krótszym ogonem o szacunkowej liczbie kręgów 16–17, bardziej symetryczną budową stopy z kośćmi sródstopia II i IV jednakowej długości i palcem IV zbliżonym długością do palca II, a więc znacznie krótszym niż u *Archaeopteryx,* i składającym się z 4 zamiast 5 paliczków. Taka budowa stopy przy stosunkowo dużych rozmiarach ciała sugeruje również nieco inną niż u *Archaeopteryx*, prawdopodobnie bardziej kursorialną, specjalizację lokomotoryczną.

Appendix 1

Revised length measurements of the wing bones in the Archaeopterygidae (in mm). Approximate measurements in parentheses. Left and right elements marked by superscripts.

	Eichstätt	Munich	Berlin	Third[1]	Haarlem[2]	London	Solnhofen
Humerus	41.5^{l}	(55.0)	63.0	(72.0^{r})	n/m	75.0	83.0
Ulna	36.5	53.0	56.2^{l}	$(62.0^{r} + ?)^{3}$	n/m	67.0	(74.0)
Radius	35.0	53.0	54.4	$(63.0^{l})^{3}$	n/m	(63.0)	(74.0)
Metacarp. I	5.2	7.0	(7.0)	(10.0)	10.0	n/m	n/m
Metacarp. II	17.8	25.0	28.0	(33.0)	n/m	34.4	n/m
Metacarp. III	16.5	23.0	24.5^{l}–24.8^{r}	(30.0)	29.4	n/m	n/m
Digit I/ph. 1	15.4	20.0	21.5	n/m	23.3	n/m	28.0
min. depth	0.8^{l}–1.0^{r}	1.15^{r}	1.3	n/m	1.9	n/m	2.4^{l}–2.3^{r}
Digit I/ungual	7.0	10.6	11.0	(12.0)	9.7	n/m	9.3
Digit II/ph. 1	10.1	12.5	15.2^{l}–15.4^{r}	(19.0)	n/m	n/m	19.0
Digit II/ph. 2	14.5	18.0	(19.4)	(22.0)	n/m	n/m	27.0
min. depth	1.0	1.1	1.2^{l}	n/m	n/m	n/m	2.4^{l}
Digit II/ungual	n/m	(9.2)	13.2	(15.0)	n/m	n/m	18.0
Digit III/ph. 1	(4.8)	n/m	6.4	n/m	n/m	n/m	7.9
Digit III/ph. 2	(2.2)	n/m	4.0	n/m	n/m	n/m	6.1
Digit III/ph. 3	9.5	12.0	12.3	(16.0)	n/m	n/m	17.5
Digit III/ungual	5.0	6.5	8.0	n/m	9.0	n/m	10.0

[1] Heller (1959) provided round millimeter values, which are here considered to be approximate.

[2] Ostrom (1972).

[3] Heller (1959) reported 63 mm for the left radius and approximately 62 mm for the right ulna. The figure for ulna is most probably too low as it implies the forearm to be relatively shorter than in any other archaeopterygid specimen and the ulna to be shorter than the radius (unless the wings were asymmetric).The left radius is halved between the two slabs and each fragment ends with a splinter, which makes a precise measurement of the total length extremely difficult and thus the figure is treated here as an approximate value.

Appendix 2

Revised length measurements of the leg bones in the Archaeopterygidae (in mm). Approximate measurements in parentheses. Left and right elements marked by superscripts.

	Eichstätt	Munich	Berlin	Third[1]	London	Solnhofen
Femur	37.0	(46.5)	52.2	(58.0)	(61.0)	(67.0)
Tibiotarsus	$(53.0)^{l}$	$(71.5)^{l}$	71.0	(79.5)	(82.0)[3]	92.0
Fibula	50.5	69.5	tbd	n/m	n/m	82.4
Metatarsale I	n/m	n/m	n/m	n/m	n/m	9.9
Metatarsale II[4]	28.3[5]	n/m	(35.0)	(38.0)	(40.0)	45.0
Metatarsale III[4]	30.2	40.5	(37.0)	(42.0)	44.0	(47.5)
Metatarsale IV[4]	27.3[5]	37.0	n/m	(39.0)	n/m	45.0
Metatarsale V	6.5	(10.0)	n/m	n/m	7.9	10.5
Digit I/ph. 1	5.5^{r}	7.1	5.2^{l}–5.5^{r}	n/m	8.8	11.0
min. depth	0.7	1.3	n/m	n/m	1.86	1.65
Digit I/ungual	3.5	5.2	5.5	n/m	(6.8)	(9.8)
Digit II/ph. 1	$(7.1)^{l}$	(6.0)	8.2	(9.5)	11.0	12.0
Digit II/ph. 2	7.0^{r}	n/m	7.0	(10.0)	11.0	12.5
Digit II/ungual	5.8	7.0^{l}–7.4^{r}	n/m	n/m	(11.0)	n/m
Digit III/ph. 1	9.0	10.8	9.6	(11.0)	12.7	13.7
Digit III/ph. 2	8.0	8.5	9.0	(10.5)	11.0	11.8
Digit III/ph. 3	7.0	8.4	8.2	n/m	(9.5)	10.5
min. depth	0.8	1.1	1.05	n/m	1.9	1.9
Digit III/ungual	5.4^{l}–4.8^{r}	6.8^{l}–7.0^{r}	8.8	n/m	(14.0)	n/m
Digit IV/ph. 1	6.1 (r)	8.0	7.0^{r}	n/m	n/m	10.0
Digit IV/ph. 2	5.0	6.0	6.4^{l}–6.6^{r}	n/m	n/m	8.5
Digit IV/ph. 3	4.6^{l}–4.7^{r}	(5.5)	4.9	n/m	n/m	absent
Digit IV/ph. 4	4.9	n/m	5.6^{l}–5.8^{r}	n/m	n/m	9.5
min. depth	0.6–0.8	0.9	0.9	n/m	n/m	2.4
Digit IV/ungual	n/m	6.2	6.8	n/m	(11.0)	(12.6)

[1] From Heller (1959) except for metatarsals II and IV and pedal phalanges, which were measured on the original Heller's X-ray photograph kindly provided by Prof. J.T. Groiss.

[2] Distal end recrystallized.

[3] A part of the tarsometatarsus including the fused distal tarsals.

[4] These measurements necessitate more scrutiny because of the difficulty in obtaining a precise superposition of bone fragments from the two slabs.