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Considerations on the taxonomy of Late Jurassic Avialae (Theropoda) from the Solnhofen Archipelago

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Abstract

The iconic *Archaeopteryx* still represents the oldest known volant avialan, but its taxonomic history is complex. Several avialan specimens from the Solnhofen Archipelago have been variously assigned to distinct genera, most recently, the Haarlem and Mühlheim specimens. A recent reinterpretation proposed that all these Urvogel specimens belong to *Archaeopteryx*, based on similarities in limb proportions, with observed morphological differences attributed to taphonomic or ontogenetic variation. Here, the taxonomy of the Solnhofen Urvögel is reassessed by comparing limb proportions, conducting specimen-based phylogenetic analyses, reconstructing a forelimb morphospace, and re-evaluating the diagnosis of *Archaeopteryx* and possible morphological differences from the Haarlem and Mühlheim specimens. The phylogenetic analyses recover a monophyletic *Archaeopteryx* that also includes the Maxberg, Ottmann and Steil ("chicken wing"), and Karlsruhe specimens, which have so far only been tentatively referred to this genus, as they do not preserve its diagnostic characters. The Mühlheim specimen is excluded from *Archaeopteryx* and placed more crownward, a result consistent with its distinct position in the forelimb morphospace. The Haarlem specimen is found in various positions at the base of Avialae, indicating that its assignment to *Archaeopteryx* remains unresolved even when key character differences are silenced. Integrating these results with detailed morphological comparisons, it is concluded that the Mühlheim specimen is distinct from *Archaeopteryx*, supporting the validity of *Alcmonavis poeschli*, whereas the Haarlem specimen lacks definitive diagnostic features and is best regarded as Avialae *indet*. Specimens of *Archaeopteryx* probably represent more than a single species, but the results from different analyses are currently contradictory and inconclusive.

Key Words

Avialae, *Archaeopteryx*, Late Jurassic, Solnhofen, taxonomy, phylogeny

Introduction

The iconic Urvogel *Archaeopteryx* still represents the geologically oldest evidence of a feathered theropod dinosaur with volant behavior outside the crown group of birds (Aves L.). Although the plumage of *Archaeopteryx* resembles that of modern birds in great detail (e.g., Wellnhofer 2008, 2009; Foth et al. 2014; Longrich et al. 2020), many osteological traits appear rather ancestral, resembling those of non-avialan theropods (e.g., Ostrom 1976; Mayr 2005, 2007; Wellnhofer 2008, 2009; Rauhut 2014; Rauhut et al. 2018). These include, for instance,

the presence of a prefrontal, an ectopterygoid, and an epipterygoid, as well as the fully closed postorbital bar in the skull and toothed jaws. In other features, such as the structure of the brain (Domínguez Alonso et al. 2004), *Archaeopteryx* shows intermediate morphologies. Discovered just two years after the publication of Darwin's "Origin of Species" (Darwin 1859), the combination of "bird-like" and "reptile-like" features linking these two groups ("missing link") gave this animal its status as an icon of evolution.

Following the discovery of the first fossil in 1861 (von Meyer 1861; now the London specimen), new specimens of *Archaeopteryx* were rather slow to come forward. The second skeletal specimen, now the Berlin specimen, was found almost 25 years after the discovery of the London specimen, probably in 1875 or early 1876 (Tischlinger 2005). The next discovery did not occur until more than 75 years later, in 1951, and the specimen—which came to be known as the Eichstätt specimen—spent another 20 years hidden before it was finally described by Wellnhofer in 1974 (see also Wellnhofer 2008, 2009). In the meantime, yet another specimen had been found in 1956 and was described by Heller (1959). This is the Maxberg specimen, which remained in private hands and could not be found after the passing of its finder and thus remains lost to the present day (see Wellnhofer 2008, 2009). Furthermore, the actual first find of an Urvogel from the "Solnhofen limestones," first reported and misidentified as a pterosaur by von Meyer (1857), was identified as *Archaeopteryx* by Ostrom (1970) and became known as the Haarlem specimen after its repository in the Dutch city of Haarlem.

Since the second half of the 1980s, the pace of discoveries of Urvogel specimens from the Solnhofen Archipelago has increased considerably. Wellnhofer reported the sixth, Solnhofen specimen in 1988 and the seventh, Munich specimen in 1993. The eighth specimen—now the Daiting specimen—was briefly reported by Mäuser in 1997 but was not described in more detail until 2009 (Tischlinger 2009) and was finally designated the holotype of a new species of *Archaeopteryx*, *A. albersdoerferi*, by Kundrát et al. (2019). The next specimens to be reported were the Ottmann and Steil specimen, also known as the "chicken wing" (Wellnhofer and Röper 2005), and the Thermopolis specimen (Mayr et al. 2005). The next decade saw the descriptions of the 11th (Altmühl) specimen in 2014 (Foth et al. 2014), the 12th (Schamhaupten) specimen in 2018 (Rauhut et al. 2018), and the 13th Urvogel specimen (the Mühlheim specimen) in 2019 (Rauhut et al. 2019). Most recently, the 14th (Karlsruhe) specimen and the 15th (Chicago) specimen were reported in 2025 (Foth et al. 2025; O'Connor et al. 2025). Thus, whereas only two specimens were known 100 years after the discovery of the first Jurassic avialan, the last 25 years alone have seen the description of seven new specimens. Consequently, the understanding of these Jurassic avialans from the Solnhofen Archipelago has rapidly increased in recent years.

Despite this wealth of new information, one of the most basic questions about the Jurassic Urvögel of the Solnhofen Archipelago remains debated: how many taxa do these specimens represent?

The taxonomic history of *Archaeopteryx* is complex, and many specimens have been referred to separate species or even genera in the past (e.g., *Griphosaurus* for the London specimen; *Archaeornis* for the Berlin specimen; *Jurapteryx* for the Eichstätt specimen; *Wellnhoferia* for the Solnhofen specimen). This history is best summarized in Wellnhofer (2008, 2009). Since then, however, five new Urvogel specimens have been described (see above), of which the Altmühl, Schamhaupten, Karlsruhe, and Chicago specimens have been assigned to the genus *Archaeopteryx* (Foth et al. 2014, 2025; Rauhut et al. 2018; O'Connor et al. 2025). In addition, the discovery of abundant and diverse avialans from the Late Jurassic of China (see Xu et al. 2016, 2023; Chen et al. 2025, and references therein) raised the question of whether all the Urvogel specimens from the Solnhofen Archipelago truly represented a single lineage or even the same genus. Consequently, the diagnosis of the genus *Archaeopteryx* was updated independently by Rauhut et al. (2018) and Kundrát et al. (2019), whose lists of diagnostic characters are largely in agreement (see Discussion below). The intrageneric taxonomy of *Archaeopteryx*, however, is not yet resolved.

The newly discovered Mühlheim specimen was identified as a new genus and species, named *Alcmonavis poeschli*, and was found to be positioned slightly more crownward in the phylogeny (Rauhut et al. 2019). In addition, Foth and Rauhut (2017) interpreted the Haarlem specimen, originally described as *Pterodactylus crassipes* by von Meyer (1857), as distinct from *Archaeopteryx* but phylogenetically closer to *Anchiornis*. Thus, a new genus name, *Ostromia*, was proposed for the specimen to encompass the species *Ostromia crassipes* (von Meyer, 1857).

The fragmentary nature and strong taphonomic compaction justify doubts regarding the most recent classifications of the Haarlem and Mühlheim specimens as distinct genera by Foth and Rauhut (2017) and Rauhut et al. (2019). Most recently, O'Connor and Marugán-Lobón (2026) argued that the Haarlem and Mühlheim specimens are also referable to *Archaeopteryx*, based on linear regressions between limb elements, a principal component analysis, and anatomical comparisons. They argued that longitudinal furrows along the manual bones and the radius were taphonomic artifacts of compaction, a possibility also discussed by Mulder et al. (2024) and Foth et al. (2025). Other character differences were regarded as ontogenetic, taphonomic, or simply intrageneric variation.

However, the analytical approach of O'Connor and Marugán-Lobón (2026) is not convincing. All the regression analyses are based on the length of the skull and the major long bones of the limbs, including the humerus, ulna, radius, femur, and tibia. Because most of these bones are not preserved or are incomplete in the Haarlem and Mühlheim specimens, the missing values were estimated using stochastic regression imputation (Baraldi and Enders 2010). Although the methodological approach is robust for a certain amount of missing data

in a well-established sample (e.g., Marugán-Lobón and Chiappe 2022), the threshold for missing-data estimation is affected by the size and shape of the dataset, as well as by the distribution of the missing data itself (Strauss et al. 2003; Brown et al. 2012). In the current case, the imputation is based on only two measurements for the Mühlheim specimen and one measurement for the Haarlem specimen, meaning that the comparison of the Mühlheim and Haarlem specimens with the *Archaeopteryx* sample is largely based on simulated data. Even the single value for the tibia in the Haarlem specimen used to simulate the data is an estimate because the bone is missing its distal end. Estimates of the original length provided in the literature range from 75 mm (Wellnhofer 2008, 2009) to 80 mm (Ostrom 1972; Foth and Rauhut 2017; O'Connor and Marugán-Lobón 2026). The impact of this difference has not been tested. Furthermore, because of the data distribution caused by the large amount of missing data, the forelimb–hindlimb ratio—the main difference between *Archaeopteryx* and *Anchiornis* found by O'Connor and Marugán-Lobón (2026)—cannot be assessed confidently for either the Haarlem or the Mühlheim specimen. Even if two related species show similar forelimb proportions, the forelimb–hindlimb ratio does not need to be identical (see, e.g., *Haliaeetus albicilla* vs. *Sagittarius serpentarius* for comparison), as the limb proportions are decoupled from each other in bipedal taxa (e.g., Middleton and Gatesy 2000; Dececchi and Larsson 2013) (see example in Suppl. material 1: fig. S1, table S1). Indeed, for the taxa compared by O'Connor and Marugán-Lobón (2026), *Archaeopteryx* and *Anchiornis*, the proportions within either the forelimbs or the hindlimbs scale equally but not between the forelimbs and hindlimbs (see Discussion). Finally, Foth and Rauhut (2017) found that most differences between the Haarlem and Mühlheim specimens and *Archaeopteryx* occurred in the distal limb elements, which were not taken into account by O'Connor and Marugán-Lobón (2026).

The current study re-evaluates the generic taxonomy of the different Urvogel specimens from the Late Jurassic limestones of southern Germany, with a special focus on the fragmentary Haarlem and Mühlheim specimens. For this purpose, the current study combines a specimen-based phylogeny including all 15 Urvogel specimens, a morphology-based principal coordinate analysis, and a statistical bone-by-bone length comparison of the preserved elements after allometric size correction.

Material and methods

Specimens of *Archaeopteryx*

Because the specimen numbers and names used here for the Solnhofen Urvögel differ somewhat from those applied by O'Connor and Marugán-Lobón (2026), these names are reviewed here to avoid confusion (Table 1). The naming of the specimens follows that established by Wellnhofer (2008, 2009) and Rauhut et al. (2019). Thus, the ninth specimen, for which the name Bürgermeister-Müller specimen was used by O'Connor and Marugán-Lobón (2026), is the Ottmann and Steil specimen, also informally known as the "chicken wing." For the 11th and 12th specimens, the names Altmühl and Schamhaupten specimens are used, respectively, following Rauhut et al. (2019). Following the suggestion to use numbers for Urvogel specimens from the Solnhofen Archipelago in general, regardless of whether they can be referred to *Archaeopteryx* with

Table 1. Overview of all known Urvogel specimens and their taxonomic referral. BMMS, Bürgermeister-Müller-Museum, Solnhofen, Germany; BMNH, British Museum of Natural History, London, UK; DNWK, Datenbank National Wertvollen Kulturgutes; EMK, Evolution Museum Knuthenborg, Denmark; FMNH, Field Museum of Natural History, Chicago, USA; JM, Juramuseum Eichstätt, Germany; MB, Museum für Naturkunde, Berlin, Germany; WDC, Wyoming Dinosaur Center, Thermopolis, USA; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns–Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; TM, Teylers Museum Haarlem, the Netherlands; NA, not available.

No.	Specimen name	Specimen no.	Taxonomic identification
1	London specimen	BMNH 37001	*Archaeopteryx lithographica* (neotype of type species)
2	Berlin specimen	MB.Av.101	*Archaeopteryx* sp.
3	Maxberg specimen (lost)	NA	cf. *Archaeopteryx* sp.
4	Haarlem specimen	TM 6928, 6929	Avialae indet.
5	Eichstätt specimen	JM 2257	*Archaeopteryx* sp.
6	Solnhofen specimen	BMMS 500	*Archaeopteryx* sp.
7	Munich specimen	SNSB-BSPG 1999 I 50	*Archaeopteryx* sp.
8	Daiting specimen	EMK002	*Archaeopteryx* sp.
9	Ottmann and Steil specimen ('Chicken wing')	NA	cf. *Archaeopteryx* sp.
10	Thermopolis specimen	WDC-CSG-100	*Archaeopteryx* sp.
11	Altmühl specimen	DNWK 2923	*Archaeopteryx* sp.
12	Schamhaupten specimen	DNWK 02924	*Archaeopteryx* sp.
13	Mühlheim specimen	SNSB-BSPG 2017 I 133	*Alcmonavis poeschli*
14	Karlsruhe specimen	SMNK-PAL 10000	cf. *Archaeopteryx* sp.
15	Chicago specimen	FMNH PA 830	*Archaeopteryx* sp.

certainty (Rauhut et al. 2019: p. 5), the type of *Alcmonavis* is considered the 13th specimen. Thus, the Karlsruhe and Chicago specimens become the 14th and 15th specimens, respectively, rather than the 13th and 14th specimens, as stated by O'Connor and Marugán-Lobón (2026). Finally, whereas the latter authors identified the type of *Alcmonavis* only by its specimen number (SNSB-BSPG 2017 I 133), the name Mühlheim specimen is also used for this fossil, following Rauhut et al. (2019).

All specimens of *Archaeopteryx* were examined first-hand, except for the Maxberg and Chicago specimens. However, casts of the Maxberg specimen are available at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, and a cast of the main slab is also deposited in the Museum für Naturkunde Berlin.

Anatomy

Because crown birds represent the only living lineage of dinosaurs (e.g., Gauthier 1986; Rauhut and Foth 2020), the anatomical and directional terminology traditionally used in vertebrate anatomy, as established by Owen (1854), is adopted; this terminology is also standard in descriptions of non-avian dinosaurs (Wilson 2006). Accordingly, the terms "anterior" and "posterior" are used instead of "cranial"/"rostral" and "caudal," because the latter terms may be confused with specific skeletal regions. Common English names for bones (e.g., "frontal" instead of "*os frontale*") are likewise preferred. The surfaces of long bones are described according to their orientation in the resting posture of a theropod dinosaur. For anatomical structures unique to birds and absent in non-avialan dinosaurs, the terminology of the "Nomina Anatomica Avium" (Baumel and Witmer 1993) is applied.

Morphometry, allometric scaling, and statistical comparison

For each Urvogel specimen, bone measurements were collected from Wellnhofer (2008), Foth et al. (2014), Rauhut et al. (2018, 2019), and O'Connor et al. (2025) (Suppl. material 2).

To test whether the two fragmentary Haarlem and Mühlheim specimens are morphometrically comparable to the sample of *Archaeopteryx*, a bone-by-bone length comparison was performed for both specimens. The estimated measurements of the tibia and metatarsus in the Haarlem specimen (provided by Wellnhofer 2008, 2009) were not included in the main analysis because both bones are highly incomplete (but see Discussion). The *Archaeopteryx* sample included the fairly complete Altmühl, Berlin, Chicago, Eichstätt, London, Munich, Schamhaupten, Solnhofen, and Thermopolis specimens. The Daiting and Karlsruhe specimens were not included in the comparison because of the lack of available measurements for manual elements.

Size differences among the Urvogel specimens indicate allometric relationships between bones (Houck et al. 1990; Senter and Robins 2003; Bennett 2008; O'Connor and Marugán-Lobón 2026). Thus, prior to the statistical analysis, the lengths of all bones (log-transformed) were compared with each other using ordinary least-squares (OLS) regression analyses, in which the longer bone was set as the independent variable (x). To control for allometry, the residuals of the dependent variable (y) from the regression were estimated and subsequently used for the statistical comparison. For the latter, a modified t test for the comparison of a single specimen with the mean of a given sample (Sokal and Rohlf 1995; Crawford and Howell 1998) was performed to examine whether the non-allometric residuals of the Haarlem and Mühlheim specimens fell within the population of *Archaeopteryx*. For small sample sizes ($n < 50$), this test is preferred over the z test (Crawford and Howell 1998) and is generally more conservative than the parametric one-sample t test or the non-parametric one-sample Wilcoxon signed-rank test, which examine whether a single sample comes from a population with a given mean or median, respectively (Hammer and Harper 2024). Significant differences between a sample and the population were considered to be indicated by a p value of less than 0.05.

The protocol was repeated for the two incomplete Ottmann and Steil and Maxberg specimens, whose assignment to *Archaeopteryx* is probable but cannot be demonstrated based on clearly diagnostic characters (Rauhut et al. 2018). Given that the Ottmann and Steil specimen has the right forelimb preserved, a direct comparison with the Mühlheim specimen is possible, except for the first manual ungual, which is not visible on the slab. For the Maxberg specimen, measurements that overlap with those of the two fragmentary specimens were selected, creating two datasets that included the elements preserved in the Haarlem specimen, except for metatarsus I and pedal phalanx IV-5 (dataset I), and the Mühlheim specimen (dataset II), respectively.

Finally, an additional bone-by-bone comparison was performed to test whether the Haarlem and Mühlheim specimens are comparable to the samples of the volant dromaeosaurid *Microraptor* and the basal non-volant avialan *Anchiornis*. Because the number of hindlimb measurements for *Microraptor* is limited, the main statistical comparison was restricted to the Mühlheim specimen using forelimb measurements only. However, a bone-by-bone comparison between *Microraptor* and the Haarlem specimen was performed for all overlapping elements preserved, and the results are presented in the supplementary information. Additional comparisons among the Ottmann and Steil specimen, *Microraptor*, and *Anchiornis* are also provided in the supplementary information (see Suppl. material 1: tables S2–S13).

To illustrate the statistical differences, the p values from the bone-by-bone length comparisons were summarized in a similarity matrix and visualized as a heatmap. In addition, the collected p values from each comparison

were log-transformed and visualized as boxplots to illustrate the differences among the comparisons. The equality of the medians and distributions among the log-transformed *p*-value samples was tested using two non-parametric tests: the Kruskal–Wallis test for equal medians (Hammer and Harper 2024) and the Anderson–Darling test for equal distributions (Scholz and Stephens 1987), respectively. All statistical tests were performed in PAST v. 5.3 (Hammer et al. 2001).

Specimen-based phylogenetic analyses

In paleontology, the distinction of taxa is primarily based on comparative anatomy. However, this process is not always trivial because fossils are often incomplete and taphonomically deformed. Furthermore, knowledge of different types of intraspecific variation in extinct taxa is very limited because many fossil species are known only from a single, often fragmentary individual. Even in extant taxa, studies of intraspecific variation within the skeleton are rare. Thus, determining whether a certain morphology found in one specimen is representative of the entire species or is influenced by individual, ontogenetic, or sexually dimorphic variation is difficult and requires multiple individuals. Here, specimen-based phylogenies provide a means of assigning very fragmentary specimens to better-known taxa. In addition, this approach provides an opportunity to learn more about intraspecific and intrageneric variation in taxa known from multiple specimens and can also help resolve taxonomic issues involving these taxa. In the past, this method has been applied, for instance, to resolve the taxonomy of basal sauropodomorphs (Yates 2003), Diplodocidae (Tschopp et al. 2015), *Archaeopteryx* (Pei et al. 2020), and *Allosaurus* (Malafaia et al. 2025).

The phylogenetic dataset is based on Foth et al. (2025) and was adapted for the purpose of a specimen-based analysis to test whether all Urvogel specimens from the Late Jurassic limestones of southern Germany form a monophylum. The outcome allows the diagnosis of *Archaeopteryx* to be updated and potentially helps clarify the ingroup relationships within the genus. Thus, all 15 known Urvogel specimens were added separately to the dataset as substitutes for a compound taxon, *Archaeopteryx*. The lost Maxberg specimen was scored based on Steiner (1962), Wellnhofer (2008, 2009), and a cast of the main slab housed in the Museum für Naturkunde in Berlin. Within the framework of regular updates to the data matrix, the following taxa were also added to the dataset: *Asteriornis*, *Baminornis*, *Chongmingia*, *Cratonavis*, *Fujianvenator*, *Fukuipteryx*, *Janavis*, *Kompsornis*, *Navaornis*, *Parahesperornis*, *Vegavis*, and *Yuornis*. Thus, the current version of the dataset contains 202 operational taxonomic units (OTUs) and 628 characters. In addition to the diagnostic characters for the genus *Archaeopteryx* based on Rauhut et al. (2018), further characters were added from Foth et al. (2021), which is based on O'Connor and Zhou (2013), to obtain better resolution of the tree within Avialae. Both the character list and the phylogenetic dataset are provided in the supplementary information (Suppl. materials 1, 3, 4).

The dataset was analyzed in TNT v. 1.6 (Goloboff and Morales 2023), using the New Technology Search with all four search methods—sect. search, ratchet, drift, and tree fusing—to find the minimum tree length 30 times, followed by tree bisection–reconnection (TBR) branch swapping, with 200,000 trees kept in memory. One analysis was run with all characters assigned equal weights and one with implied weights (Goloboff et al. 2018). The latter was performed to reduce the impact of homoplasy, which, in a specimen-based phylogeny, can encode different types of polymorphism (e.g., variation related to ontogeny or sex) within a taxon, making the character less phylogenetically informative (Tschopp et al. 2015). For a matrix with approximately 200 taxa, the optimal *k* value ranges between 12 and 21 (Ezcurra 2024). The results presented here are based on an intermediate *k* value of 16. The most parsimonious trees were summarized in the form of strict consensus and reduced strict consensus trees (Wilkinson 1995; Pol and Escapa 2009). The consistency index (CI), retention index (RI), and character evolution along the topology of the most parsimonious trees were explored in Mesquite v. 3.81 (Maddison and Maddison 2023).

Principal coordinate analyses

To explore the morphological distances among the different Urvogel specimens from the Late Jurassic of Germany, a morphospace was calculated in R, version 4.4.2 (R Core Team 2025), using a principal coordinates analysis (PCoA) implemented in the R package *Claddis* (Lloyd et al. 2024). Using phylogenetic data as input for the analysis, Maximum Observed Rescaled Distances (MORD) was chosen as the preferred distance matrix (Lloyd 2016).

Because only 10–18% of all characters could be scored for the five most fragmentary Urvogel specimens (i.e., the Ottmann and Steil, Haarlem, Karlsruhe, Maxberg, and Mühlheim specimens), the first PCoA was not performed using the complete matrix. Because all fragmentary specimens preserve the forelimb, a reduced matrix that included only forelimb characters was analyzed instead. Although the Haarlem specimen is still scored for only 31% of the characters, the Mühlheim specimen reaches 76%. To verify these results, five additional matrices were created that included the sample of all characters scored for the Ottmann and Steil, Maxberg, Karlsruhe, Haarlem, and Mühlheim specimens, respectively. Given that all fragmentary specimens are scored slightly differently because of their poor preservation, this subsampling helps explore the robustness of the first analysis, which included only forelimb characters.

Subsequently, a regression of humeral length (log-transformed) against the first principal coordinate (PCo 1) was performed for each PCoA. Given that no humerus is preserved in the Haarlem specimen, the log-transformed length of manual phalanx I-1 was used. The respective PCo 1 values and their non-allometric residuals were applied to the single-case test mentioned above to evaluate whether the Mühlheim and Haarlem specimens are part of the *Archaeopteryx* sample.

An additional PCoA was performed that included not only the German Urvogel specimens but also other non-ornithothoracine Avialae for a broader comparison, allowing visualization of whether the Haarlem and Mühlheim specimens are positioned within the *Archaeopteryx* sample. These taxa included *Anchiornis*, *Baminornis*, *Caihong*, *Chongmingia*, *Confuciusornis*, *Cratonavis*, *Fujianvenator*, *Fukuipteryx*, *Jeholornis*, *Jinguofortis*, *Jixiangornis*, *Kompsornis*, *Sapeornis*, *Serikornis*, and *Xiaotingia*.

Results

Statistical comparison of non-allometric measurements

The overall differences between the Mühlheim, Ottmann and Steil, and Maxberg specimens (dataset I) and *Archaeopteryx*—indicated by the log-transformed *p* values from the non-allometric bone-by-bone comparisons using the single-case test—cannot be statistically differentiated from one another (Table 1; Fig. 1). Except for a total of three outliers, all comparisons performed for the three specimens are not significant and fall within the variation shown by other specimens of *Archaeopteryx*. In contrast, both the Mühlheim and Ottmann and Steil specimens are more different from *Anchiornis* than from *Archaeopteryx*, with approximately one-fourth of the comparisons showing a significant difference in their proportions. The Mühlheim and Ottmann and Steil specimens are also more different from *Microraptor* than from *Archaeopteryx*, although not as strongly, given that less than 20% of all comparisons were found to be significant.

For the Mühlheim specimen, the only significant difference from *Archaeopteryx* was found for the comparison between metacarpal I (*x*) and manual phalanx III-2 (*y*). No difference was found for the Ottmann and Steil specimen. The Maxberg specimen differs from *Archaeopteryx* in the comparisons between manual phalanges I-1 (*x*) and III-2 (*y*) and PII-2 (*x*) and III-3 (*y*).

The heatmaps comparing the Mühlheim, Ottmann and Steil, and Maxberg specimens with *Archaeopteryx* show very similar color patterns, suggesting an overall similar variation in the proportions of all three specimens. In contrast, the color patterns of the comparisons of the Mühlheim specimen with *Anchiornis* and *Microraptor* differ from those of the previous comparisons but are not identical between *Anchiornis* and *Microraptor*.

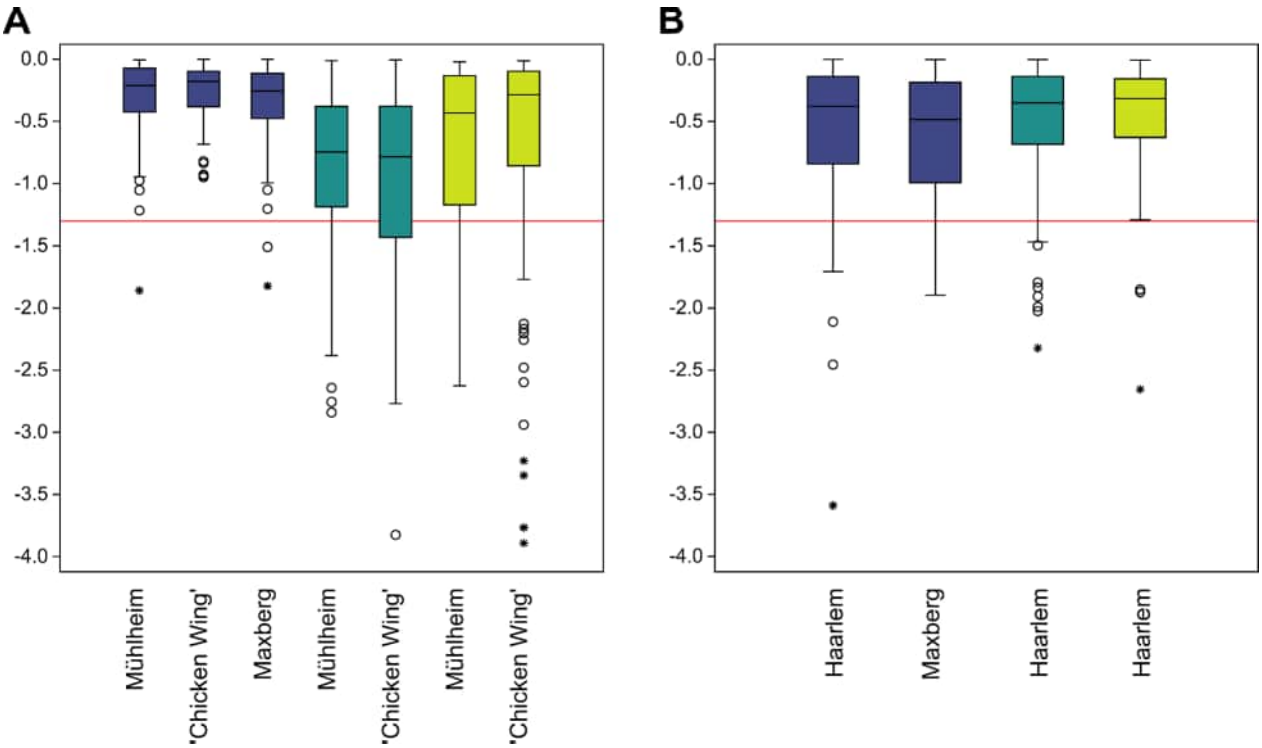

Figure 1. Boxplot comparisons showing the distribution of log-transformed *p* values from the various bone-by-bone comparisons. **A.** Comparison of the Mühlheim, Ottmann and Steil ("chicken wing"), and Maxberg specimens with *Archaeopteryx* (purple boxes), *Anchiornis* (dark green boxes), and *Microraptor* (light green boxes); **B.** Comparison of the Maxberg and Haarlem specimens with *Archaeopteryx* (purple boxes), *Anchiornis* (dark green boxes), and *Microraptor* (light green boxes). Statistical outliers are shown as empty circles or stars. The red line marks the 0.05 threshold for *p* values.

Overall, the proportions of the Haarlem specimen cannot be differentiated from those of *Archaeopteryx*, *Anchiornis*, or *Microraptor*. Likewise, the Maxberg–*Archaeopteryx* comparison (dataset II) shows no statistically significant differences from the Haarlem–*Archaeopteryx* comparison (Table 2; Fig. 1).

The great majority of all bone-by-bone length comparisons (more than 75%) are not significant in all four analyses. Although the Maxberg specimen is slightly more different from *Archaeopteryx* than the Haarlem specimen, the latter is slightly more similar to *Microraptor* and *Anchiornis* than to *Archaeopteryx*. However, as stated above, none of these differences are significant.

The Haarlem specimen was found to differ from *Archaeopteryx* in the following comparisons: manual phalanx I-1 (*x*) vs. pedal phalanx III-3 (*y*); manual phalanx III-4 (*x*) vs. I-2 (*y*); pedal phalanx II-3 (*x*) vs. manual phalanx I-2 (*y*); pedal phalanx II-3 (*x*) vs. metatarsus I (*y*); pedal phalanx III-1 (*x*) vs. pedal phalanx II-2 (*y*); pedal phalanx III-2 (*x*) vs. pedal phalanx II-2 (*y*); pedal phalanx II-2 (*x*) vs. pedal phalanx IV-1 (*y*); pedal phalanx II-2 (*x*) vs. pedal phalanx IV-3 (*y*); and pedal phalanx III-1 (*x*) vs. pedal phalanx IV-1 (*y*).

The heatmaps visualizing the differences between the Haarlem and Maxberg specimens and *Archaeopteryx*, respectively, show very different patterns in the individual bone-by-bone length comparisons. In contrast, the distribution patterns from comparisons of the Haarlem specimen with *Archaeopteryx* and *Anchiornis* are more similar to each other. Although the Maxberg and Haarlem specimens resemble each other in the variation in the lengths of pedal phalanges II-2, II-3, and IV-1, the Maxberg specimen is more different from the *Archaeopteryx* sample in the proportional lengths of pedal phalanges II-1 and IV-2 (Fig. 2; Suppl. material 1: tables S2–S13).

Table 2. Statistical comparison of log-transformed *p* values based on the modified *t* tests for the bone-by-bone comparisons of the Mühlheim and Haarlem specimens with *Archaeopteryx* and other comparisons. Significant differences in medians (Kruskal–Wallis) and distributions (Anderson–Darling) are marked in colored cells.

	Kruskal–Wallace		Anderson–Darling	
Mühlheim vs. *Archaeopteryx*	***H***	***p***	***Z***	***p***
Ottmann and Steil vs. *Archaeopteryx*	0.688	0.407	0.473	0.220
Maxberg vs. *Archaeopteryx*	0.300	0.584	−0.221	0.458
Mühlheim vs. *Anchiornis*	45.900	0.000	29.581	0.001
Ottmann and Steil vs. *Anchiornis*	33.890	0.000	23.833	0.001
Mühlheim vs. *Microraptor*	15.380	0.000	10.932	0.001
Ottmann and Steil vs. *Microraptor*	4.943	0.026	4.371	0.012
Haarlem vs. *Archaeopteryx*	***H***	***p***	***Z***	***p***
Maxberg vs. *Archaeopteryx*	3.945	0.047	2,3004	0.033
Haarlem vs. *Anchiornis*	1.009	0.315	−0.161	0.424
Haarlem vs. *Microraptor*	9.002	0.003	6,7789	0.002

Specimen-based phylogeny

Equal-weight analysis

Under equal weights, the New Technology Search found more than 200,000 most parsimonious trees with a total length of 4167 steps (CI: 0.194; RI: 0.731). The strict consensus tree recovered a large polytomy at the base of Coelurosauria, which included Compsognathidae, Alvarezsauroidea, and Therizinosauria (with *Fukuivenator* excluded), as well as subclades of Tyrannosauroidea, Oviraptorosauria, Dromaeosauridae, and Troodontidae. Avialae is excluded from this polytomy but shows another polytomy at its base, including the Late Jurassic taxa *Anchiornis*, *Pedopenna*, *Fujianvenator*, and *Xiaotingia*, *Serikornis*+*Caihong*, and all Urvogel specimens except for the Mühlheim specimen. Within this polytomy, the Berlin, Chicago, Ottmann and Steil, Eichstätt, Karlsruhe, and Maxberg specimens form their own clade.

The Mühlheim specimen, *Alcmonavis poeschli*, which is excluded from this polytomy, represents the sister taxon to the clade containing *Sapeornis* and Euavialae. This position of the Mühlheim specimen is supported by an angle between the proximal part of the humerus and the humeral shaft that is larger than 35° (char. 387/1); the presence of a facet for the attachment of *m. deltopectoralis* on the deltopectoral crest of the humerus (char. 413/1); a proximal articular surface of the ulna that forms an oval concavity with slightly raised rims (char. 422/1); a radial diameter that is between 0.5 and 0.7 times the ulnar diameter (char. 425/1); and a dorsal surface of manual ungual I that arches higher than the level of the dorsal extremity of the proximal articular surface when oriented vertically (char. 477/1). The recently discovered Late Jurassic taxon *Baminornis* (Chen et al. 2025) is found within Euavialae, representing a member of Jeholornithiformes (Suppl. materials 3, 5).

The pruning of the basal coelurosaurs *Aniksosaurus*, *Aristosuchus*, *Bagaraatan*, *Coelurus*, *Mirischia*, *Tugulusaurus*, *Xinjiangovenator*, *Xunmenglong*, the alvarezsaurid *Albinykus*, the troodontid *Xixiasaurus*, and the dromaeosaurids *Balaur*, *Dineobellator*, *Dromaeosaurus*, *Graciliraptor*, *Hesperonychus*, *Linheraptor*, *Mahakala*, *Pyroraptor*, *Saurornitholestes*, *Tsaagan*, and *Zhenyuanlong* using reduced-consensus methods results in improved resolution of the topology, especially at the base of Coelurosauria. Paraves still forms a polytomy, including *Jinfengopteryx*, *Jianianhualong*, *Liaoningvenator*+*Daliansaurus*, and a clade containing the remaining Troodontidae and Dromaeosauridae (Fig. 3A; Suppl. materials 3, 6).

After the Haarlem specimen is excluded from the tree sample, the polytomy at the base of Avialae resolves such that the remaining *Archaeopteryx* specimens form a monophylum that is the sister taxon to the *Alcmonavis*–Euavialae clade. The *Archaeopteryx* clade is defined by the following character states: a triangular, anteriorly tapering snout (char. 24/1); a rod-like jugal quadratojugal

process (char. 76/1); an anteroventral margin of the infratemporal fenestra with a sharply angled incision separating the quadratojugal and postorbital processes of the jugal (char. 79/1); fewer than 10 cervical vertebrae (char. 241/0); 14 dorsal vertebrae (char. 266/1); a gently rounded ventral surface of the posterior sacral centra (char. 294/0); a notch at the base of the ischial peduncle of the pubis in the position of the pubic obturator foramen in basal theropods (char. 521/1); pubic aprons that do not contact each other along the entire shaft (char. 526/2); and a non-ginglymoid distal end of metatarsal III (char. 603/0) (Fig. 3C).

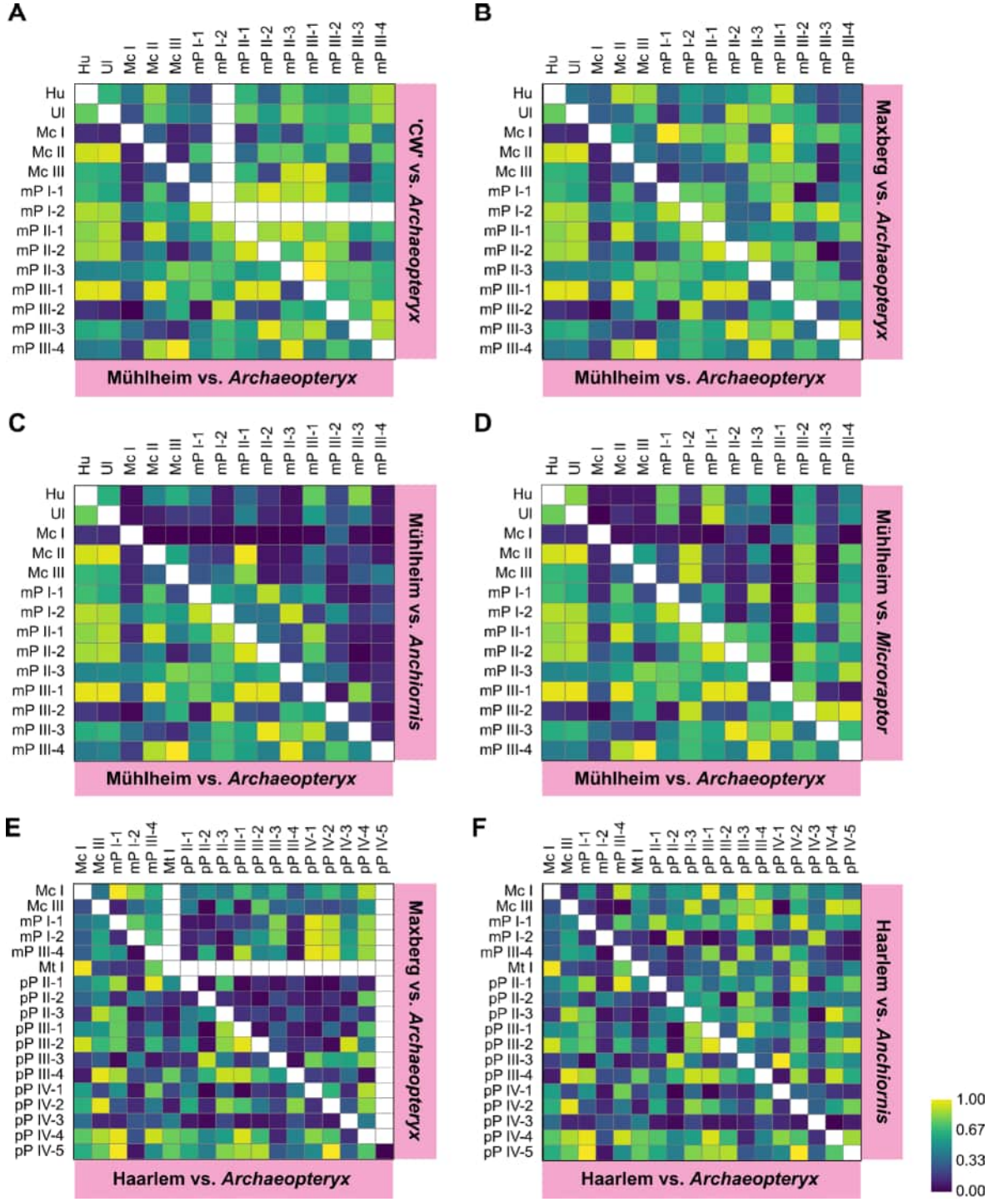

Figure 2. Heatmaps of the bone-by-bone comparisons showing the *p* values. The cells below the diagonal show the comparisons of the Mühlheim and Haarlem specimens with *Archaeopteryx*, respectively. The cells above the diagonal show alternative comparisons (see Table 1). **A.** Mühlheim specimen vs. *Archaeopteryx* and Ottmann and Steil specimen ("chicken wing") vs. *Archaeopteryx*; **B.** Mühlheim specimen vs. *Archaeopteryx* and Maxberg specimen vs. *Archaeopteryx*; **C.** Mühlheim specimen vs. *Archaeopteryx* and Mühlheim specimen vs. *Anchiornis*; **D.** Mühlheim specimen vs. *Archaeopteryx* and Mühlheim specimen vs. *Microraptor*; **E.** Haarlem specimen vs. *Archaeopteryx* and Maxberg specimen vs. *Archaeopteryx*; **F.** Haarlem specimen vs. *Archaeopteryx* and Haarlem specimen vs. *Anchiornis*. White cells indicate comparisons that were not possible.

Because the resolution of the internal relationships within the genus *Archaeopteryx* is beyond the scope of the current paper and requires additional detailed comparisons of character distributions among the different specimens, only brief comments on the internal relationships recovered here are provided, and the characters supporting the different groupings are not discussed further. A detailed analysis of the internal topology within the genus *Archaeopteryx* is currently in preparation and will be presented elsewhere. The Altmühl and London specimens represent two independent lineages at the base of the *Archaeopteryx* clade. The remaining specimens form a polytomy that contains the Munich, Solnhofen, and Thermopolis specimens, a Daiting+Schamhaupten clade, and a second clade. The latter includes the Berlin specimen and two subclades, one including the Chicago+Eichstätt specimens and the other including the Ottmann and Steil+Karlsruhe+Maxberg specimens. If the Munich specimen is additionally pruned from the tree sample, the basal polytomy resolves into a large clade including the Thermopolis, Solnhofen, and Daiting+Schamhaupten specimens (Fig. 3D).

Implied weight analysis

With implied weights (k = 16), the New Technology Search found 110,250 most parsimonious trees with a score of 145.23472 and 4,178 steps (CI: 0.193; RI: 0.730). The strict consensus tree shows a large polytomy at the base of Coelurosauria, also including the groups Compsognathidae, Alvarezsauroidea, and Therizinosauria (with *Fukuivenator* included), as well as subclades of Tyrannosauroidea and Oviraptorosauria.

Avialae, Dromaeosauridae, and Troodontidae, which are commonly grouped as Eumaniraptora, are excluded from this large polytomy. In accordance with the results

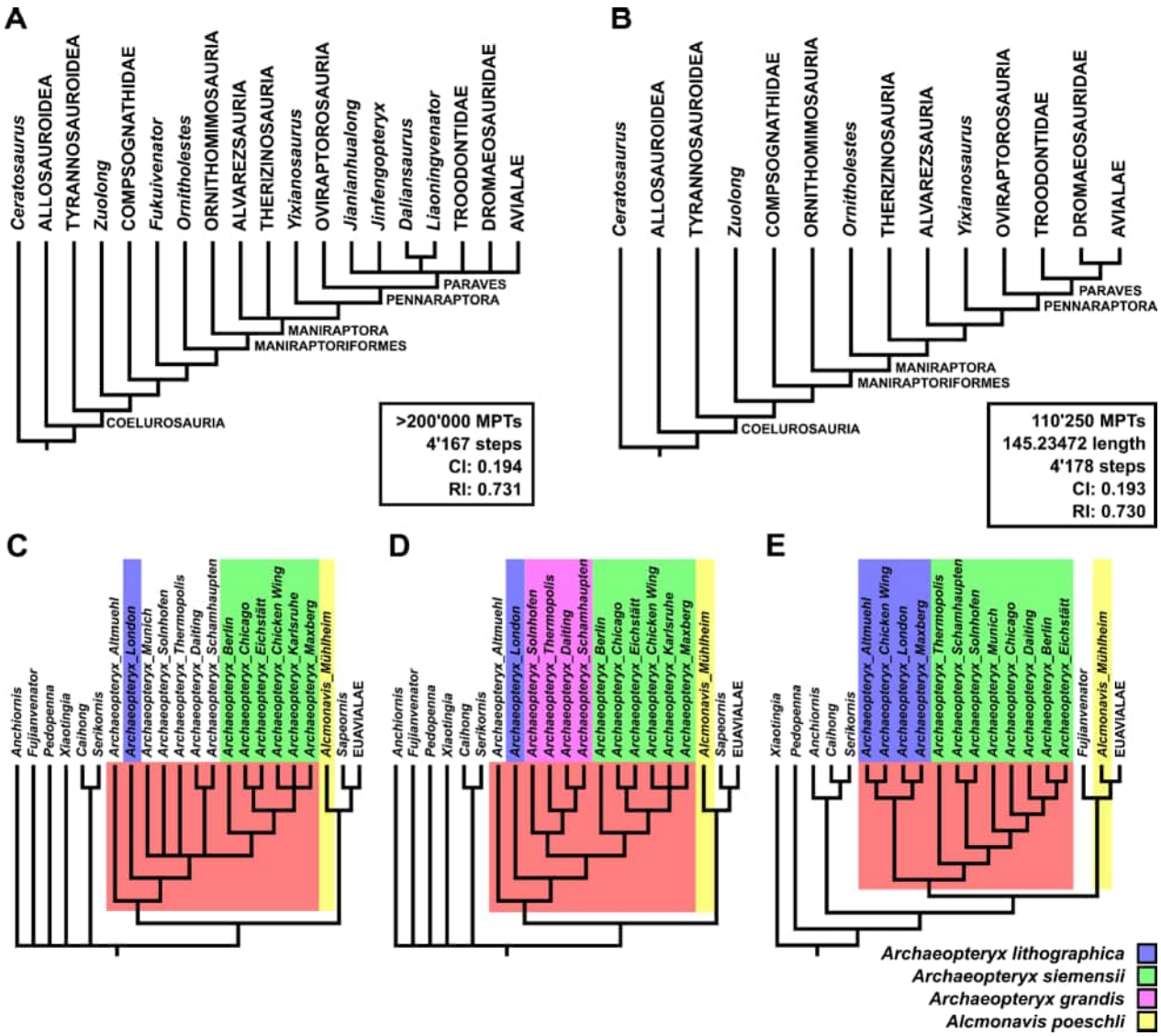

Figure 3. Specimen-based phylogeny of *Archaeopteryx*. **A.** Main topology of the reduced consensus tree under equal weights; **B.** Main topology of the reduced consensus tree under implied weights; **C.** Topology of basal Avialae under equal weights after the Haarlem specimen was pruned; **D.** Topology of basal Avialae under equal weights after the Haarlem and Munich specimens were pruned; **E.** Topology of basal Avialae under implied weights after the Haarlem specimen was pruned. Based on the topology, different species of *Archaeopteryx* can be assigned (see Suppl. materials 3–8 for details).

of Foth et al. (2025), Dromaeosauridae represents the sister clade to Avialae, whereas troodontids are recovered here as the earliest-branching clade within Paraves. The Chinese taxa *Xiaotingia* and *Pedopenna* form two independent lineages at the base of Avialae. More crownward, there is a large polytomy containing *Fujianvenator*, the Altmühl, Ottmann and Steil, Haarlem, Karlsruhe, London, Maxberg, Munich, Schamhaupten, Solnhofen, and Thermopolis specimens, a clade including *Anchiornis*+*Caihong*+*Serikornis*, and a second clade including the Chicago+Daiting+Berlin+Eichstätt specimens. The Mühlheim specimen is excluded from this polytomy and forms the sister taxon to the clade including *Kompsornis*, *Jeholornis*+*Jixiangornis*, *Baminornis*, and Pygostylia. The position of the Mühlheim specimen is supported by an angle between the proximal part of the humerus and the humeral shaft that is larger than 35° (char. 387/1); a radial diameter that is between 0.5 and 0.7 times the ulnar diameter (char. 425/1); a robust metacarpal II that is wider than metacarpal I (char. 436/1); and a strongly broadened manual phalanx II-1 that is more than 1.5 times the width of phalanx II-2 (char. 465/1) (Suppl. materials 3, 7).

Pruning the basal coelurosaurs *Aristosuchus* and *Xinjiangovenator* resolves the polytomy at the base of Coelurosauria. The general topology of the non-paravian taxa is consistent with the results of the implied-weight analysis of Foth et al. (2025). The exclusion of the dromaeosaurids *Dakotaraptor*, *Hesperonychus*, and *Pyroraptor* from the tree sample helps resolve relationships within Microraptorinae and Velociraptorinae, respectively (Fig. 3B; Suppl. materials 3, 8).

After the Haarlem specimen is pruned, the polytomy at the base of Avialae resolves into three independent lineages. The first lineage includes *Anchiornis*+*Caihong*+*Serikornis* and thus corresponds to Anchiornithinae. The second lineage, which is closer to the crown, represents a monophyletic *Archaeopteryx* clade. Except for the presence of nine cervical vertebrae, all autapomorphic characters of this clade (chars 24/1, 76/1, 79/1, 266/1, 294/0, 521/1, 526/2, and 603/0) that were identified in the equal-weight analysis were also found in the implied-weight analysis. In addition, this analysis found further characters supporting this clade, including the development of a small preotic pendent by the otosphenoidal crest (char. 158/1); procumbent maxillary teeth in the mesial portion of the tooth row (char. 225/1); fewer than 25 caudal vertebrae (char. 298/0); no tuber along the dorsal edge of the ilium (char. 499/0); a pubic apron that measures approximately half the length of the pubic shaft (char. 525/0); a large, hooked proximodorsal process of the ischium that is separated from the iliac peduncle of the ischium by a notch (char. 548/2); and an enlarged hallucal ungual on the first toe (char. 617/1). *Fujianvenator* is placed more crownward than *Archaeopteryx*, forming the sister taxon to the clade containing the Mühlheim specimen and the remaining Euavialae.

After pruning, the *Archaeopteryx* clade consists of two main subclades. The first includes the Altmühl, Ottmann and Steil, Karlsruhe, London, and Maxberg specimens, which form a polytomy. After the Karlsruhe specimen is excluded, the topology becomes balanced, resolving into two subclades including the Altmühl+Ottmann and Steil specimens and the London+Maxberg specimens.

The other main subclade has a pectinate topology, including, from base to tip, the Thermopolis, Schamhaupten+Solnhofen, Munich, Chicago, Daiting, Berlin, and Eichstätt specimens (Fig. 3E).

Principal coordinate analyses

Based on the forelimb characters, basal Avialae, *Archaeopteryx*, and Euavialae form three distinct clusters in the PCoA that are well separated from one another. The fragmentary Ottmann and Steil, Haarlem, Karlsruhe, and Maxberg specimens are placed within the *Archaeopteryx* cluster. In contrast, the Mühlheim specimen is neither part of the *Archaeopteryx* cluster nor of the other two clusters but is located in isolation in the middle of the three main clusters (Fig. 4A). When the 15 Urvogel specimens from the Solnhofen Archipelago are analyzed alone, the Haarlem specimen is located at the margin of the *Archaeopteryx* cluster, surrounded by the Altmühl, Daiting, London, and Maxberg specimens. Located at the opposite corner of the plot, the Mühlheim specimen remains isolated from the *Archaeopteryx* cluster (Fig. 4B).

The first PCo of the analysis using only the Solnhofen avialans accounts for more than 19.4% of the total variation in the forelimb characters. It has a weak but nonsignificant positive correlation with the length of the humerus (slope: 1.652; R^2: 0.032; p: 0.542) and manual phalanx I-1 (slope: 2.591; R^2: 0.072; p: 0.355), which is mainly due to the outlier position of the Mühlheim specimen (Fig. 4C, D). The first PCo value of the Mühlheim specimen (t: 3.773; p: 0.003) and its residual (t: 3.066; p: 0.010) are significantly different from those of the remaining *Archaeopteryx* specimens, indicating a certain phylogenetic distance. This significance also persists for the other character subsamples analyzed (Fig. 4E; Table 3). The first PCo value of the Haarlem specimen is part of the *Archaeopteryx* sample (t: −1.475; p: 0.166) when the forelimb characters are applied. This is also true for all subsamples. Using the residuals of PCo 1 from the forelimb character sample (t: −2.258; p: 0.048) and the Maxberg subsample (t: −2.693; p: 0.023), the Haarlem specimen is significantly different from *Archaeopteryx*. However, the residuals from the other subsamples do not indicate any difference from *Archaeopteryx* (Table 3). Comparing the PCo 1 scores of the different character samples, the Haarlem specimen overlaps primarily with the Daiting, Solnhofen, and Thermopolis specimens and marginally with the Berlin, Chicago, Ottmann and Steil, Maxberg, and Munich specimens (Fig. 4F).

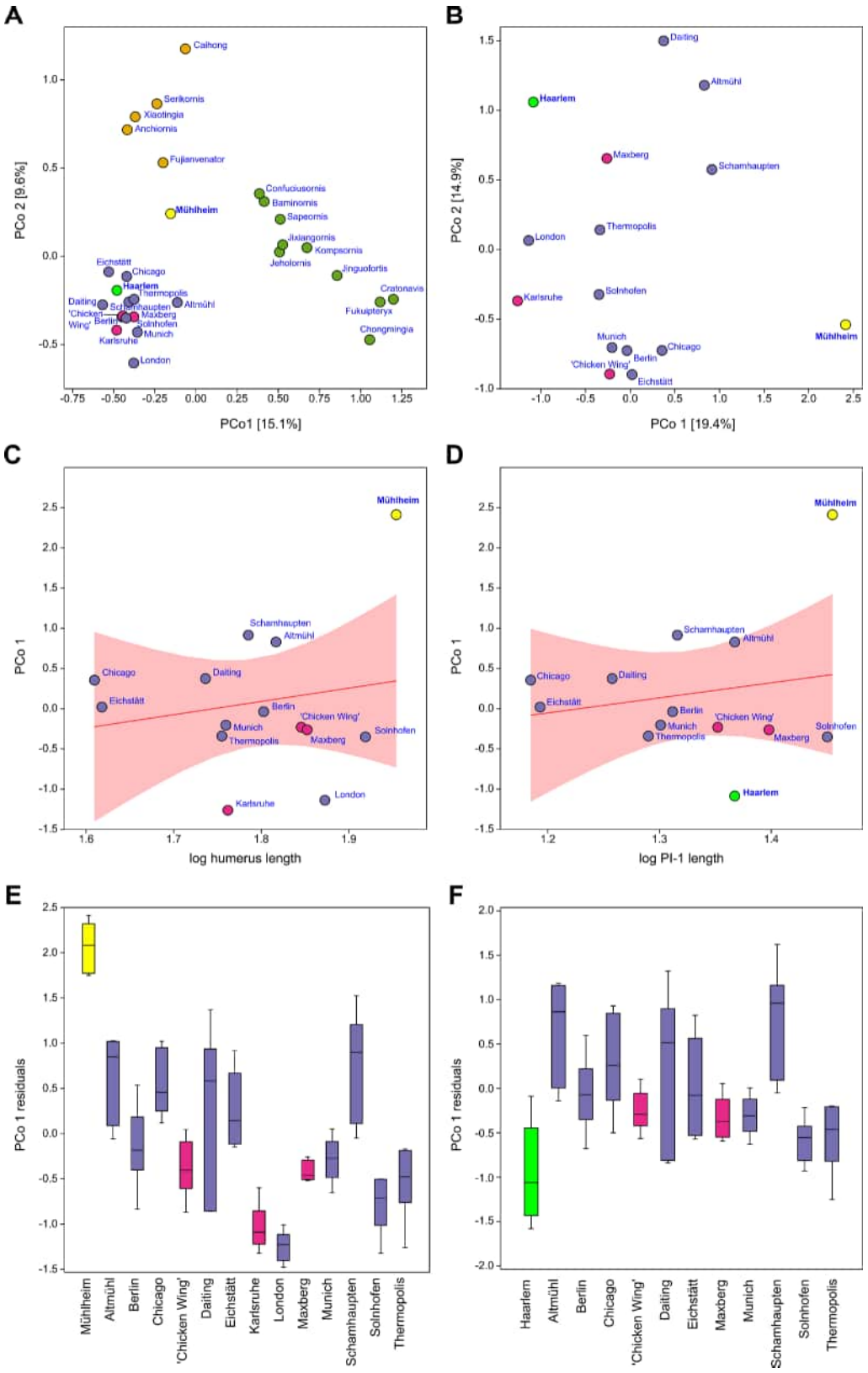

Figure 4. Principal coordinate analyses (PCoAs) of the phylogenetic dataset showing the positions of the Mühlheim (yellow) and Haarlem specimens (green). **A.** PCoA morphospace based on the forelimb characters of basal Avialae; **B.** PCoA morphospace based on the forelimb characters of basal Avialae from the Solnhofen Archipelago; **C.** Regression of PCo 1 for Solnhofen Avialae against log-transformed humeral length; **D.** Regression of PCo 1 for Solnhofen Avialae against the log-transformed length of manual phalanx I-1; **E.** Boxplots showing the variation in the residuals of PCo 1 against log-transformed humeral length for different character subsamples; **F.** Boxplots showing the variation in the residuals of PCo 1 against the log-transformed length of manual phalanx I-1 for different character subsamples. *Archaeopteryx* specimens are shown in purple, with those used for the statistical comparisons highlighted in pink.

Table 3. Results of the modified *t* test comparing the Mühlheim and Haarlem specimens with *Archaeopteryx* for different character samples based on the PCo 1 values and their residuals. Significant differences are marked in colored cells.

	Mühlheim				Haarlem			
	PCo1		Residuals		PCo1		Residuals	
Characters	***t***	***p***	***t***	***p***	***t***	***p***	***t***	***p***
Forelimb	3.773	0.003	3.066	0.010	−1.475	0.166	−2.258	0.048
Mühlheim	−3.093	0.009	2.340	0.037	0.860	0.407	1.291	0.226
Haarlem	4.743	0.000	3.392	0.005	−1.782	0.100	−1.928	0.083
Maxberg	5.664	0.000	3.995	0.002	−1.989	0.070	−2.693	0.023
Ottmann and Steil	3.234	0.007	2.465	0.030	−0.658	0.523	−0.940	0.369
Karlsruhe	−3.317	0.001	−2.341	0.037	−0.064	0.950	0.108	0.916

Discussion

The monophyly of *Archaeopteryx*

According to Rauhut et al. (2018), the genus *Archaeopteryx* can be diagnosed based on the following characters: a maxilla with only eight to nine tooth positions (see also Elzanowski 2002; Kundrát et al. 2019); a jugal with a longitudinal groove on the medial side of the suborbital process; an anteroventral margin of the infratemporal fenestra that forms a sharply angled incision separating the quadratojugal and postorbital processes in the jugal (see also Kundrát et al. 2019; specimen-based phylogenetic analysis); a very slender quadratojugal process of the jugal, less than half the minimum height of the suborbital process (specimen-based phylogenetic analysis); a depressed rim around the posterior margin of the trigeminal foramen in the prootic; the absence of a mandibular fenestra (see also Elzanowski 2002; Kundrát et al. 2019); premaxillary and anteriormost dentary teeth with a straight basal part and a bulbous, strongly recurved apical part; nine cervical and 14 dorsal vertebrae (see specimen-based phylogenetic analysis); and an ischium with a well-developed, triangular "intermediate process" posteriorly at approximately mid-shaft (see also Elzanowski 2002; Kundrát et al. 2019).

Kundrát et al. (2019) proposed three additional diagnostic characters: at least some teeth exhibit crown tips that are slightly curved distally (*sensu* Elzanowski 2002); 10–12 dentary teeth, including non-erupted teeth; and a promaxillary fenestra whose most anterior extension is situated between the fifth and sixth maxillary teeth. Although *Archaeopteryx* indeed has a distinct tooth shape, the preserved maxillary teeth of the Daiting and Schamhaupten specimens and the lateral dentary teeth of the Schamhaupten and Altmühl specimens are not strongly recurved and do not match the morphology described by Elzanowski for *Archaeopteryx* (Rauhut et al. 2018). Furthermore, the position of the anterior margin of the promaxillary fenestra varies in *Archaeopteryx*: its anterior margin is situated between the sixth and seventh maxillary teeth in the Schamhaupten specimen (Rauhut et al. 2018). Thus, the latter two characters may not be diagnostic of the genus *Archaeopteryx* but seem to show variation within the genus.

In their specimen-based analyses, Pei et al. (2020) identified four characters as apomorphic for the *Archaeopteryx* clade: metatarsal III with a smooth, non-ginglymoidal distal end; a notch between the iliac peduncle and the distal dorsal process of the ischium; a tapering posterior (jugal) ramus of the maxilla; and a lesser trochanter that is placed more distally than the greater trochanter. The smooth distal end of metatarsal III was also found to be apomorphic for *Archaeopteryx* in the present study and can be added to the list of diagnostic characters. A posterior process that is separated from the iliac peduncle of the ischium by a distinct notch is more common and is also present in the dromaeosaurids *Rahonavis*, *Unenlagia*, and *Balaur* (Brusatte et al. 2013; Forster et al. 2020; Novas et al. 2021) and the basal euavialans *Jeholornis*, *Sapeornis*, *Confuciusornis*, and *Jinguofortis* (Chiappe et al. 1999; Zhou and Zhang 2002, 2003; Wang et al. 2018). Furthermore, the notch cannot be confirmed with certainty in every *Archaeopteryx* specimen because the region is often covered by the femur or ilium. Given that this morphology is frequently developed in taxa closely related to *Archaeopteryx*, the use of this feature as a diagnostic character depends on the topology of the phylogeny. Although this character state was found to be apomorphic for the *Archaeopteryx* clade in the current implied-weight analysis, for instance, it was apomorphic for a clade including *Archaeopteryx* and Euavialae in the equal-weight analysis. The presence of a maxillary jugal ramus that tapers posteriorly is a common feature among coelurosaurs (Pei 2015) and is absent only in Troodontidae and Alvarezsauroidea. Given that the relationships among Avialae, Troodontidae, and Dromaeosauridae are still debated (see, e.g., Turner et al. 2012; Agnolín and Novas 2013; Godefroit et al. 2013; Foth et al. 2014, 2025; Rauhut et al. 2019; Pei et al. 2020), it should first be tested whether this character state remains apomorphic for *Archaeopteryx* across the different topologies. The same is true for the distal position of the lesser trochanter relative to the greater trochanter, which is also present in many basal paravians, including *Anchiornis*, *Mahakala*, *Microraptor*, and *Sinovenator* (Xu et al. 2002; Turner et al. 2011; Pei et al. 2014, 2017).

The two specimen-based phylogenetic analyses in this study suggest further characters that could be autapomorphic for the genus *Archaeopteryx*. These include fewer

than 25 caudal vertebrae (char. 298/0); a ventral notch at the base of the ischial peduncle of the pubis (char. 521/1); a divided pubic apron that does not contact its counterpart along a portion of the pubic shaft (char. 526/2); and a metatarsal III without a ginglymoid distal end (char. 603/0; see Pei et al. 2020). The number of caudal vertebrae in *Archaeopteryx* ranges from 21 to 24 (Wellnhofer 2008, 2009; O'Connor et al. 2025) and is lower than that in most long-tailed paravians, including *Anchiornis* and *Jeholornis* (O'Connor et al. 2012; Pei et al. 2017). The distal half of the pubic shaft of *Archaeopteryx* bears a prominent apron that extends medially. As visible in the London and Solnhofen specimens, the proximal portion of the apron has no medial contact but is divided by a narrow slit (Wellnhofer 2008, 2009). Given that the apron of the right pubis in the Eichstätt specimen is taphonomically rotated anteriorly, this condition might also apply to this specimen.

A revised diagnosis of the genus *Archaeopteryx*

Based on the current revision of the characters, the genus *Archaeopteryx* can be diagnosed by the following combination of characters: a jugal with a longitudinal groove on the medial side of the suborbital process (Rauhut et al. 2018); an infratemporal fenestra with a sharply angled incision at the anteroventral margin separating the quadratojugal and postorbital processes in the jugal (Rauhut et al. 2018; Kundrát et al. 2019); a very slender quadratojugal process of the jugal, less than half the minimum height of the suborbital process (Rauhut et al. 2018); a depressed rim around the posterior margin of the trigeminal foramen in the prootic (Rauhut et al. 2018); the lack of a mandibular fenestra (Elzanowski 2002; Rauhut et al. 2018; Kundrát et al. 2019); a maxilla with only eight to nine tooth positions (Elzanowski 2002; Rauhut et al. 2018; Kundrát et al. 2019); 10–12 dentary teeth (Kundrát et al. 2019); premaxillary and anteriormost dentary teeth with a straight basal part and a bulbous, strongly recurved apical part (Rauhut et al. 2018); nine cervical and 14 dorsal vertebrae (Rauhut et al. 2018); fewer than 25 caudal vertebrae (new); a pubic obturator foramen that opens ventrally (new); a pubic apron that is divided along parts of the shaft (new); an ischium with a well-developed "intermediate process" posteriorly at approximately mid-shaft (modified from Elzanowski 2002; Rauhut et al. 2018; Kundrát et al. 2019); and metatarsal III with a smooth distal end (Pei et al. 2020).

Archaeopteryx can be further distinguished from *Anchiornis* and other more basal Avialae by the presence of a large, hooked proximodorsal process of the ischium (modified from Pei et al. 2020) and an enlarged hallucal ungual on the first toe. In contrast, the genus differs from more crownward taxa by the absence of a facet for the attachment of *m. deltopectoralis* on the deltopectoral crest of the humerus (see Discussion below) and a more robust radius with a shaft diameter greater than 0.7 times the ulnar diameter.

The Maxberg specimen can be assigned to *Archaeopteryx* based on the lack of a ginglymoid distal end in metatarsal III. None of the diagnostic characters can be established for the Ottmann and Steil specimen or the Karlsruhe specimen. Their assignment to *Archaeopteryx* is based on character states that they share with a subset of other specimens referred to the genus.

The intrageneric taxonomy of *Archaeopteryx*

In the past, limited specimen-based phylogenies for *Archaeopteryx* were performed by Kundrát et al. (2019) and Foth et al. (2025) to evaluate the taxonomy of the incomplete Daiting and Karlsruhe specimens, respectively. However, in these analyses, the genus *Archaeopteryx* was still represented by a single OTU. Pei et al. (2020) performed the first true specimen-based analysis of *Archaeopteryx*, including eight Urvogel specimens (London, Berlin, Haarlem, Eichstätt, Solnhofen, Munich, Thermopolis, and Altmühl). Although the specimens were not resolved in the strict consensus tree, the pruning of the Haarlem specimen resulted in a monophyletic *Archaeopteryx* clade, with the Solnhofen specimen excluded and placed closer to Euavialae. Within the *Archaeopteryx* clade, Pei et al. (2020) found a polytomy of the Eichstätt specimen with two subclades, including the Thermopolis+Berlin specimens and the London+Altmühl+Munich specimens, respectively.

In contrast to Kundrát et al. (2019) and Pei et al. (2020), a monophyletic *Archaeopteryx* clade including the Solnhofen specimen was recognized in the current analyses after the Haarlem specimen was pruned from the tree sample. Thus, the current results do not support the classification of the Solnhofen specimen as a separate genus ("*Wellnhoferia*") outside the *Archaeopteryx* clade (Elzanowski 2001). In the majority of trees, the Haarlem specimen was part of the *Archaeopteryx* clade, but alternative, equally parsimonious positions at the base of Avialae were also found (see below).

The results for the internal *Archaeopteryx* topology differ between the equal-weight and implied-weight analyses. However, both topologies show that the London and Altmühl specimens are separated from the Thermopolis and Berlin specimens, which was also found by Pei et al. (2020). Although the Munich specimen is part of the London+Altmühl cluster in Pei et al. (2020), the current analyses place this specimen closer to the Thermopolis and Berlin specimens. Furthermore, the Chicago, Daiting, Eichstätt, Solnhofen, and Schamhaupten specimens were found to be closer to the Berlin and Thermopolis specimens, whereas the fragmentary Maxberg, Karlsruhe, and Ottmann and Steil specimens vary in position: the equal-weight analysis placed them within the Berlin cluster, whereas the implied-weight analysis found them within the London cluster.

In general, the equal-weight analysis is less well resolved than the implied-weight analysis. The sister-

group relationship between the Eichstätt and Chicago specimens is based on a radius that is shorter than the femur. However, this proportion might be ontogenetically variable in *Archaeopteryx* (Wellnhofer 1974), showing positive allometry of the forelimbs relative to the hindlimbs (Senter and Robins 2003; Foth et al. 2021; O'Connor and Marugán-Lobón 2026). Consequently, the pairing of these specimens might be an artifact related to their younger ontogenetic stages. The sister-group relationship between the Daiting and Schamhaupten specimens is better justified by their shared characters (e.g., the presence of a tubercle-like hypocleidium), but, ironically, this clade is formed by the stratigraphically youngest and oldest specimens in the sample. The exclusion of the Munich specimen from the equal-weight analysis separates the Thermopolis specimen from the Berlin specimen (contra Mayr et al. 2007) and places it with the Solnhofen, Daiting, and Schamhaupten specimens.

The implied-weight analysis recovers two distinct main clusters, one including the London specimen and the other the Berlin specimen. Thus, based on this topology, the genus *Archaeopteryx* could be split into *A. lithographica* von Meyer, 1861 and *A. siemensii* Dames, 1897, which were previously recognized by Elzanowski (2002) and Mayr et al. (2007). As mentioned above, the Munich and Solnhofen specimens, which have each been described as separate species (Wellnhofer 1993; Elzanowski 2001), are found to be part of the Berlin cluster in the current analysis. The Solnhofen specimen forms a subclade with the Schamhaupten specimen that is supported by various dentition characters (see above), which, however, show considerable variability in *Archaeopteryx* (Rauhut et al. 2018).

In summary, the current results of the specimen-based analyses do not help resolve the internal taxonomy of *Archaeopteryx* conclusively. Based on the results, either one, two, three, or more species can be justified, depending on the analytical protocol (unweighted vs. weighted analysis) or how the topology or noted differences are interpreted. If all specimens are interpreted as representing the same species, the name of this species would be *Archaeopteryx lithographica*, following the decision of the International Commission on Zoological Nomenclature to accept the London specimen as the neotype of the species instead of the single feather (ICZN 2011).

However, there are good reasons to assume that more than one species is represented by the 13 specimens that can now be referred more confidently to *Archaeopteryx*. First, and most importantly, the different specimens show considerable variation. This variation is evident in the morphometric characters, for which several specimens show at least a few values that fall outside the 95% confidence interval calculated for the values of all specimens (see, e.g., Rauhut et al. 2018; this paper). However, there are also significant differences in concrete morphological characters (Howgate 1984; Elzanowski 2001, 2002; Mayr et al. 2007; Kundrát et al. 2019). Indeed, no two known specimens are identical in all aspects of their dentition, and the marked difference in the shape of the lateral teeth, in particular, is unlikely to be purely ontogenetic or due to individual variation (Rauhut et al. 2018). This high variation is also reflected in the fact that distinct clusters are found in the different phylogenetic analyses instead of a simple polytomy within the genus (as was found, e.g., for *Efraasia* in the specimen-level analysis of Yates 2003). Despite the differences between the topologies of the equal-weight and implied-weight analyses, this additional structure indicates that differences among specimens are not random but probably represent some internal evolutionary history within the genus. Furthermore, the different specimens come from different depocenters within a tropical or subtropical archipelago and from different stratigraphic ages, spanning approximately 700,000 to one million years (Rauhut et al. 2018). Although this does not exclude the possibility that all specimens represent a single species, modern archipelagos are often characterized by rapid speciation after colonization from a source area and a high degree of endemism on different islands (Sulloway 1982; Grant and Grant 1996). However, distinguishing the possible different species and referring the different specimens to any one of them remain problematic.

As noted above, if the two clusters of the implied-weight analysis are considered to represent different species, these would correspond to *Archaeopteryx lithographica* (for the cluster including the London, Altmühl, Ottmann and Steil, and Maxberg specimens) and *Archaeopteryx siemensii* (for the cluster including the Berlin, Eichstätt, Daiting, Chicago, Munich, Solnhofen, Schamhaupten, and Thermopolis specimens). Based on the results of the equal-weight analysis, the species *Archaeopteryx lithographica* would be restricted to the London specimen, whereas *Archaeopteryx siemensii* could be represented by the Berlin, Eichstätt, Chicago, Ottmann and Steil, Maxberg, and Karlsruhe specimens. Because the Solnhofen, Thermopolis, Daiting, and Schamhaupten specimens form a separate cluster after the exclusion of the Munich specimen in this analysis, this cluster could correspond to a further species, for which the name *Archaeopteryx grandis* would be available, as this name was suggested for the Solnhofen specimen (Elzanowski 2001). However, because these specimens are nested within other species of *Archaeopteryx*, a separate genus for this species (Elzanowski 2001) does not seem justified. The Altmühl specimen falls outside the remaining *Archaeopteryx* specimens in this analysis and would thus require its own species if the division of the other specimens into different species, as outlined above, is accepted. However, given the widely differing results of the unweighted and weighted analyses, as well as the differences between the present analysis and the specimen-based analysis of Pei et al. (2020), no new species name is proposed for this specimen here. Furthermore, the subdivisions of the genus *Archaeopteryx* outlined above, guided by the assumption that the specimens represent more than a single species and by the different clusters of specimens found in the analyses, would represent

only a minimum estimate of the species present. Single specimens or smaller subclusters, such as the sister-taxon relationship between the Solnhofen and Schamhaupten specimens found within the "*Archaeopteryx siemensii*" cluster of the implied-weight analysis, could still represent additional species, depending on how the observed differences are evaluated. Thus, the present study should be regarded as a further step toward understanding the taxonomy of the genus *Archaeopteryx*, but a more detailed evaluation of the differences observed among specimens that are now clearly referable to this genus is needed to further elucidate its species taxonomy.

The use of morphometrics for taxonomy in early avialans

As alleged differences in skeletal proportions were used to distinguish species within the genus *Archaeopteryx* (Howgate 1984; Wellnhofer 1993; Elzanowski 2001, 2002), several studies have presented morphometric analyses of the different specimens to test for such differences. Thus, Houck et al. (1990) and Senter and Robins (2003) presented major-axis regressions of various proportions and concluded that all specimens can be shown to follow the same allometric scaling of the variables compared. They thus concluded that such proportions cannot be used to separate species within the genus *Archaeopteryx*, although Senter and Robins (2003: 964) cautioned that "allometric coefficients may be similar in closely related species. Our results therefore do not demonstrate that the six *Archaeopteryx* specimens are conspecific." They thus noted that species differences might be found in other characters but discarded all such characters mentioned by other authors as insufficient for taxonomic separation without further discussion.

Although Houck et al. (1990) noted that many of the allometries seen in *Archaeopteryx* were similar to patterns seen in other coelurosaurian theropods, both their analysis and that of Senter and Robins (2003) suffer from the fact that no other small maniraptoran theropods or early birds were included to test whether morphometric differences might separate *Archaeopteryx* from other paravian taxa. As hinted at by Mayr et al. (2007: 113), if different taxa show similar proportions, then the similarity of proportions among specimens referred to a single taxon might have little taxonomic meaning. Indeed, if only the major forelimb or hindlimb elements are scaled against each other (e.g., humerus vs. ulna and femur vs. tibia), the regressions for different taxa (including, e.g., *Archaeopteryx*, *Anchiornis*, *Microraptor*, and *Confuciusornis*) show no statistically significant differences (based on a one-way ANCOVA test run in the program PAST). At least for the tibia–femur proportions, this very similar scaling seems to apply to a broad range of theropods (see Xing et al. 2020). Thus, the fact that the humerus and ulna of the Mühlheim specimen—the only measurements for this specimen used by O'Connor and Marugán-Lobón (2026)—scale with the values found in other *Archaeopteryx* specimens has little taxonomic value.

The main difference between *Archaeopteryx* and *Anchiornis* found by O'Connor and Marugán-Lobón (2026) was in the proportions of the forelimbs when compared with the hindlimbs, which they convincingly argued represent volant versus non-volant behavior in the two taxa. However, given that the humerus–ulna scaling in the two taxa shows no statistically significant differences, any imputation of the hindlimb proportions for a specimen for which only the forelimb is known, such as the Mühlheim specimen, will inevitably follow the model used for the imputation (see example in Suppl. material 1: fig. S1, table S1). Thus, if data for *Archaeopteryx* are used to impute the missing hindlimb elements, the resulting known and imputed values will plot with *Archaeopteryx*, whereas when values of *Anchiornis* are used for the imputation, the resulting values will plot with *Anchiornis*. If a pooled dataset of *Anchiornis* and *Archaeopteryx* values is used, the imputed values will be placed between the plots for the two taxa. The same applies to the imputed values for the Haarlem specimen; because only the tibia was used to impute the other values for this specimen, its placement depends on the model used for the imputation of the data.

A multivariate analysis of limb elements using data from all major axes of the limbs (humerus, ulna, radius, metacarpals I–III, femur, tibia, and metatarsals II–IV) might provide better insights not only into taxonomic differences among paravians and basal Avialae but also potentially into macroevolutionary patterns across the origin of birds and their flight. In this case, stochastic imputation might be useful for estimating missing values within distinct taxonomic groups, but for the use of this method, the coherence of such taxonomic groups should be established *a priori* based on diagnostic morphological characters. However, such a multivariate study across a broad range of paravians and basal Avialae is beyond the scope of the current paper.

The taxonomic identity of the Haarlem specimen

The highly incomplete Haarlem specimen has a complicated taxonomic history (see Wellnhofer 2008, 2009). After being erroneously identified as a new species of pterosaur under the name *Pterodactylus crassipes* (von Meyer 1857, 1860), it was later assigned to *Archaeopteryx lithographica* by Ostrom (1970, 1972). However, Foth and Rauhut (2017) excluded the Haarlem specimen from *Archaeopteryx* and referred it to its own genus under the name *Ostromia crassipes* (von Meyer, 1857). Differences from other *Archaeopteryx* specimens noted by these authors included the presence of longitudinal furrows on both sides of all preserved manual phalanges and at least metacarpal III, an unusually small first manual ungual, a flexed pubic shaft and a triangular rather than cup-shaped pubic boot, and various differences in proportions. Based on the phylogenetic analysis

by Foth and Rauhut (2017), the Haarlem specimen was placed within Anchiornithinae based on a curved pubic shaft and the presence of longitudinal furrows. Recently, the specimen was reassigned to *Archaeopteryx* by O'Connor and Marugán-Lobón (2026), based on their morphometric analysis and a critical re-evaluation of the characters noted by Foth and Rauhut (2017). Given the poor preservation of the specimen, a further critical re-evaluation of these characters is presented here.

In addition to strong bone compaction, which is especially visible in the hindlimb region, the fossil suffered heavily from corrosion. This corrosion is characterized by more or less irregular dissolution pits, often with ragged and irregular margins. This type of corrosion is very typical of the plattenkalks of Jachenhausen, from which this specimen originates, but is rare or absent in other plattenkalk localities in Bavaria (Mäuser 1985). This phenomenon can be best observed in the area of the second digit of the right manus. With the majority of the bones missing, this digit is largely preserved as a mold with corroded margins. Although the mold on the main slab still allows the identification of individual phalangeal elements, the digit is barely recognizable on the counterslab (Fig. 5A).

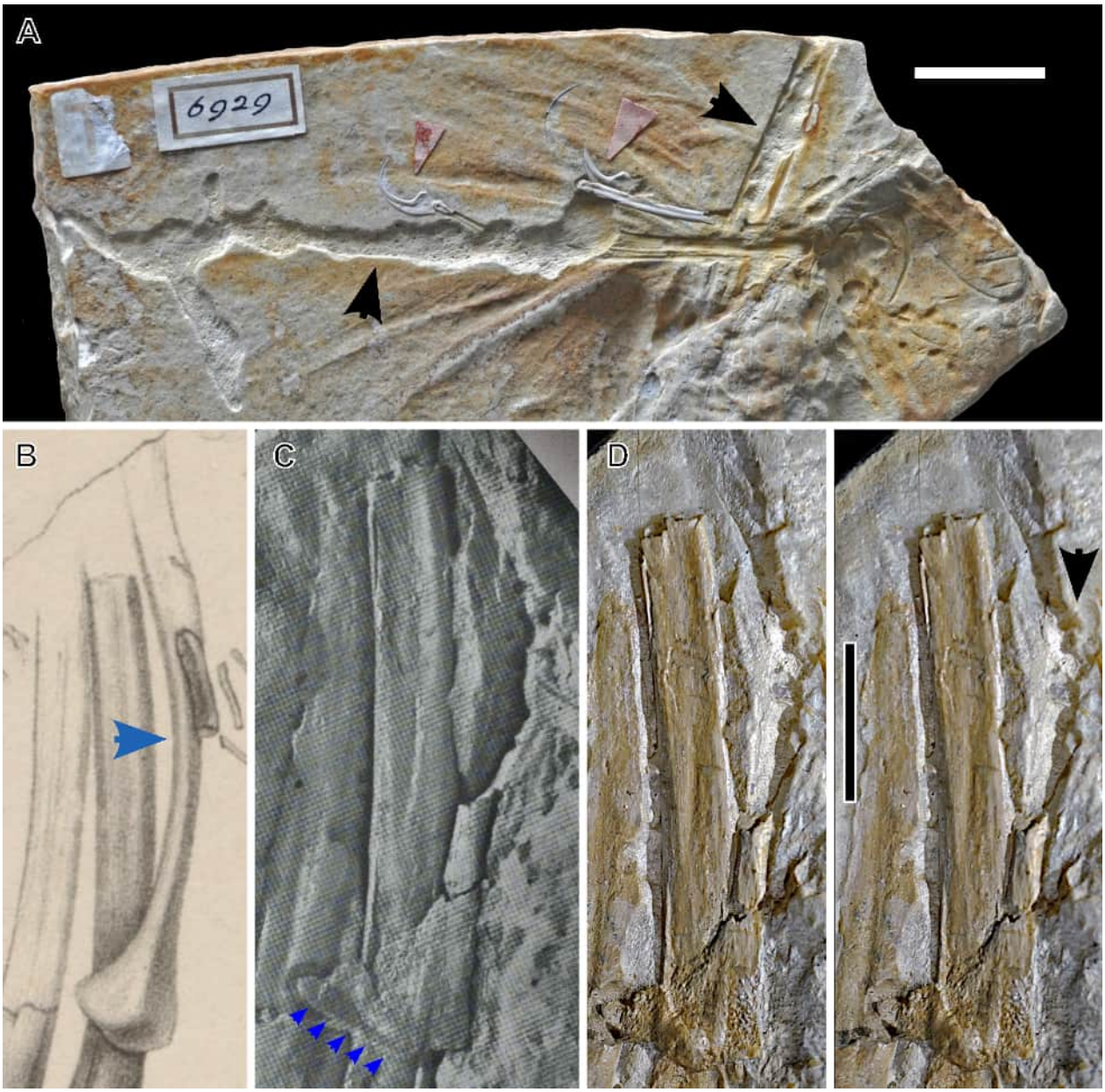

Figure 5. Haarlem specimen. **A.** Counterslab showing corrosion (black arrow) in the forelimb (scale bar: 20 mm); **B.** Illustration of the pelvic region of the Haarlem specimen by von Meyer (1860), showing the presence of a curved pubic shaft (dark blue arrow); **C.** Photograph of the same region by Ostrom (1972), showing the intact ventral margin of the pubic boot (small blue arrows); the remains of the shaft illustrated by von Meyer are no longer present; **D.** Stereophotograph of the preserved pubic remains, taken from a high-quality cast at the BSPG produced in 1971. The cast shows the same morphology of the pubic boot as illustrated by Ostrom (1972), as well as the heavy corrosion associated with the mold of the pubic shaft (scale bar: 10 mm).

In comparison, the few preserved remains of manual bones from the first and third digits appear quite intact at first glance, showing only minor signs of crushing. The preserved manual phalanges show remarkably regular-looking longitudinal furrows, and molds of such furrows are also present in the elements that are preserved only as impressions in the rock. These furrows were already noted by von Meyer (1860: 64), who stated, "Dieses Glied besitzt eine Furche, die auch an den anderen Knochen der Hand wahrgenommen wird, und um so weniger vom Druck auf einen Röhren-förmigen Knochen hergeleitet werden kann, als sie an beiden Seiten des Knochens auftritt und der Knochen keine Sprünge zeigt." ("This digit possesses a furrow, which is also seen in the other bones of the hand and which cannot be explained as a result of pressure on a tubular bone, as it is present on both sides of the bone and shows no cracks.").

Lacking obvious signs of crushing, the longitudinal grooves that are visible on the bone and in the molds were identified by Foth and Rauhut (2017) as probably "true" features that distinguish the Haarlem specimen from *Archaeopteryx*. Furthermore, these furrows were considered to represent a feature shared with the Late Jurassic Chinese avialan *Anchiornis*. Mulder et al. (2024) indicated that these furrows are probably taphonomic, despite their regular appearance, and Foth et al. (2025) also expressed caution based on CT data from the Karlsruhe specimen, which shows similar furrows. Finally, O'Connor and Marugán-Lobón (2026) argued strongly that the apparent furrows in *Anchiornis* are preservational artifacts caused by compression of the specimens and suggested that this is also the case in the Haarlem specimen, noting that similar furrows are found in other specimens of *Archaeopteryx*. However, all the examples of furrows in other *Archaeopteryx* specimens provided by O'Connor and Marugán-Lobón (2026: supplementary information) are clearly recognizable as breaks because they show irregular edges, broken margins, and breaks in the depths of the furrows or extend only over parts of the bone, as is the case with some already noted by Foth and Rauhut (2017). In contrast, as far as they are preserved, the furrows extend over the entire length of the phalanges in the Haarlem specimen, lack clearly recognizable breaks either at their margins or in their deepest parts, and are present on both sides of the bones, as shown by the partially preserved phalanx III-3 and the impression of its other side. Furthermore, in phalanx III-3 of the Haarlem specimen, which has the distal articular end preserved, the furrow is confluent distally with the collateral ligament groove, again without visible breaks separating it from this undoubtedly true structure (see Ostrom 1972: plate 4). This preservation is certainly different from the collapse structures common in tetrapods from other localities within the Solnhofen Archipelago (pers. obs. in hundreds of specimens of lepidosaurs, pterosaurs, and theropod dinosaurs), most of which are from localities other than Jachenhausen. Although the possibility that these structures are indeed taphonomic cannot be ruled out, a careful analysis of synchrotron data from the Haarlem specimen, as referred to by Mulder et al. (2024), is needed to finally settle this question. Such an analysis would need to show that the furrows can be completely explained by breaks that are not visible on the outside of the bone and that the grooves are not true features that might simply be exaggerated by compaction. However, given the uncertainty surrounding these features, this character was already removed from the phylogenetic dataset (see also Foth et al. 2025) and is no longer considered taxonomically important for the Haarlem specimen. It should be noted, however, that such grooves are present in manual phalanx I-1 of the three-dimensionally preserved basal tyrannosauroid *Guanlong*. Thus, the character could still be phylogenetically informative but should be carefully re-evaluated among theropod dinosaurs and not applied to specimens that suffered from compaction and for which no scan data are available to check for taphonomic artefacts.

Although not included in the diagnosis, the posteriorly curved pubic shaft was identified as a character that the Haarlem specimen shares with Anchiornithinae (Foth and Rauhut 2017). As preserved, the pubic shaft of the Haarlem specimen is highly incomplete and preserved mainly as a mold. This mold is clearly curved, with the anterior and posterior margins running parallel to each other. However, on the main slab, the anterior margin of the mold suffered from corrosion similar to that affecting other parts of the slab, such that this margin no longer represents the original condition of the mold (Fig. 5C, D). These corrosion marks were identified as a possible break in the shaft by O'Connor and Marugán-Lobón (2026), who argued that the curved appearance of the shaft is due to this break. However, the general shape of the mold seems to be otherwise unaffected by these corrosion marks, as can be seen in its uninterrupted posterior margin, although the area where a possible break might occur is poorly preserved. A break in the shaft is evident in the Munich specimen, resulting in the appearance of a slightly flexed shaft, although not to the degree seen in the Haarlem specimen (Wellnhofer 1993, 2008, 2009). It should be noted, however, that in this specimen, the break has clearly displaced the ends, whereas there is no evidence of such displacement in the mold of the Haarlem specimen.

Interestingly, in the original description, von Meyer (1860: p. 65) states that "Unmittelbar vor dem linken Oberschenkel erkennt man einen langen, dünnen, schwach gekrümmten Knochen, der mit seinem ausgebreiteten Ende auf der Innenseite des linken Oberschenkels liegt. Es wird dies das eine der beiden Schambeine seyn, …" ("Immediately in front of the left femur, a long, thin, slightly curved bone can be observed, which overlays the inner surface of the left femur with its expanded end. This should be one of the two pubes"), and his illustration of the specimen (von Meyer 1860: pl. 3, fig. 3) shows the pubic shaft to be present as bone, whereas the shaft of the right femur, the proximal end of the left femur, and several other bones are indicated as impressions. The

small fragment of the right pubic shaft that is still present in the counterslab of the specimen is also indicated in the drawing, in which von Meyer obviously used the then-common method of graphically transferring elements from both slabs into a single drawing (Fig. 5B). Because historic Solnhofen fossils, such as the Haarlem specimen, were often damaged through handling, a lack of treatment with consolidants, and especially casting, it thus seems that the left pubic shaft was still present at the time of the original description. Von Meyer's drawing shows the pubic shaft without a break or displacement and with a natural curve, as reconstructed by Foth and Rauhut (2017: fig. 6C). However, because this matter cannot currently be verified, the character of a flexed pubic shaft was scored as "?" for the Haarlem specimen in the current analysis to apply the most cautious interpretation possible (see below).

Another character related to the pubis and noted by Foth and Rauhut (2017) to differ from other specimens of *Archaeopteryx* was the shape of the pubic boot. Whereas *Archaeopteryx* usually has a ladle-shaped distal end of the pubis, with a well-rounded ventral margin and an acuminate posterodorsal tip, Foth and Rauhut (2017: fig. 6B) reconstructed the boot of the Haarlem specimen as rather triangular, with a tapering posteroventral tip. O'Connor and Marugán-Lobón doubted this reconstruction and instead indicated a reconstruction of the pubic boot similar to that found in other *Archaeopteryx* specimens (O'Connor and Marugán-Lobón 2026: fig. 3C). This interpretation was based on the mold of the boot in a probably relatively recent post-1990 photograph of the specimen provided by Luis Chiappe, as indicated in the figure legend. The reconstruction presented by Foth and Rauhut (2017) was based on a research-quality cast of the Haarlem specimen held in the collections of the Bavarian State Collection of Paleontology in Munich. This cast has the specimen number SNSB-BSPG 1971 I 211 and was donated to the BSPG by John Ostrom in November 1971 (SNSB-BSPG archive) during the time he was preparing the detailed description of the recently recognized Urvogel specimen (Ostrom 1972). In this cast, only the anteroventral edge and minor parts of the dorsal border of the boot are missing. Foth and Rauhut (2017) also indicated that the posterior tip was missing, but this was an error resulting from tracing the structure in photographs of the cast rather than directly from the cast. Indeed, the photograph of the hindlimb and pubis in Ostrom (1972: plate 5) shows the same morphology seen in the cast at the BSPG, with a triangular outline and a straight ventral margin (Fig. 5C, D). Photographs of the Haarlem specimen taken in July 2016 indicate that the posterior end of the boot must have gone missing at some stage after Ostrom's description of the specimen, leading to the erroneous impression of a rather rounded pubic boot, as reconstructed by O'Connor and Marugán-Lobón. Thus, the shape reconstructed by Foth and Rauhut (2017: fig. 6B) seems to be correct and represents a difference from other specimens of *Archaeopteryx*.

The remaining characters used to distinguish the Haarlem specimen from *Archaeopteryx* and also used by Foth and Rauhut (2017) to diagnose *Ostromia crassipes* are based on the proportions of certain elements. In revising these differences, it was noted that the value given by Foth and Rauhut (2017) for the probable length of metacarpal III is erroneous, probably because of transposed digits: the estimated length of metacarpal III—the distal end of which is not preserved and whose impression is obliterated by corrosion—is approximately 32 mm, not 23 mm, as given by Foth and Rauhut. After this error is corrected, all significant proportional differences between the Haarlem specimen and *Archaeopteryx* involving the length of metacarpal III become statistically nonsignificant (Suppl. material 1: table S10).

The heatmap visualizing the differences in the bone-by-bone comparison between the Haarlem specimen and the *Archaeopteryx* sample, based on the measurements of Wellnhofer (2008, 2009), shows nine significant differences in the proportions of the elements. Based on the color distribution of the heatmap, the Haarlem specimen is more similar to *Anchiornis* and *Archaeopteryx* than the Maxberg specimen is to *Archaeopteryx* (Fig. 2E, F). Most of the differences observed occur in the pedal elements of the Haarlem and Maxberg specimens (Suppl. material 1: tables S9, S11, S12) and may indicate that the feet of volant Avialae were less constrained than the forelimbs, showing greater disparity in proportional ranges. The ratio between pedal phalanges II-1 and II-2, for instance, is significantly different from that of the *Archaeopteryx* sample in the Maxberg specimen because of the very elongated PII-2 (Wellnhofer 2008, 2009). The Solnhofen specimen even lacks a phalangeal element in the fourth toe, which was one reason why the specimen was separated from *Archaeopteryx* (Elzanowski 2001). This pattern is, however, consistent with the findings of Wang and Zhou (2023), who showed that the functional constraints of flight resulted in lower variation in forelimb proportions compared with hindlimb proportions.

The majority of the diagnostic proportions identified by Foth and Rauhut (2017) cannot be reproduced by the current bone-by-bone length comparison using the measurements of Wellnhofer (2008, 2009). When the bone-by-bone length comparison is performed based on the measurements provided by Foth and Rauhut (2017), after correcting the length of metacarpal III, the Haarlem specimen differs from the *Archaeopteryx* sample in the proportions of the tibia and metatarsus III and those of metatarsus III and pedal phalanx III-4 (Suppl. material 1: table S10). These measurements indicate that the Haarlem specimen has a relatively longer metatarsus than *Archaeopteryx*. This difference can also be confirmed by testing the measurements of tibial and metatarsal length provided by Wellnhofer (2008, 2009) ($t = 4.119, p = 0.003$).

As previously recognized, the ungual shape of the Haarlem specimen overlaps with the variation seen in both *Archaeopteryx* and *Anchiornis* (Foth et al. 2025). Although the principal component analysis (PCA) placed

the Haarlem specimen directly in the middle of the *Anchiornis* sample, it does not correspond to the latter in the canonical discriminant analysis (CDA). In contrast, the specimen clusters with the *Archaeopteryx* sample but still represents an outlier that is somewhat distinct from *Archaeopteryx* (Foth et al. 2025). As in *Archaeopteryx*, the flexor tubercles are slightly distally displaced. However, the apex of the flexor tubercle of the third ungual of the Haarlem specimen is not rounded but straight. Whether this represents a difference from *Archaeopteryx* or merely individual variation remains unclear.

The specimen-based phylogenetic analyses identified the Haarlem specimen as a wildcard taxon at the base of Avialae that must be pruned from the tree sample to recover a monophyletic *Archaeopteryx* clade. In many of the most parsimonious trees, the Haarlem specimen was found at the base of *Archaeopteryx* but also within the *Archaeopteryx* clade, pairing with different *Archaeopteryx* specimens. In the equal-weight analysis, the Haarlem specimen paired only with specimens outside the clade containing the Berlin+Eichstätt+Maxberg specimens. Nevertheless, the Haarlem specimen was also frequently found outside the *Archaeopteryx* clade and instead placed at different positions at the base of Avialae.

In summary, the Haarlem specimen cannot currently be placed with certainty. None of the diagnostic characters of *Archaeopteryx* are preserved in this specimen, and the phylogenetic analysis does not place it consistently within this taxon, in contrast to the Karlsruhe and Ottmann and Steil specimens, which also preserve none of the diagnostic characters but are consistently found within *Archaeopteryx*. Despite the poor preservation, there are a few notable differences from other *Archaeopteryx* specimens, especially in the shape of the pubic boot and the tibia-to-metatarsus ratio, but also potentially in the flexed pubic shaft (see above). It remains unclear, however, whether these differences are sufficient to exclude the specimen from *Archaeopteryx* or whether they might represent intrageneric variation and possibly indicate that this specimen represents a species different from the other specimens. Indeed, the shape of the pubic boot is somewhat variable among the known specimens of *Archaeopteryx*. For example, compare the elongate—and still partially cartilaginous—boot of the Eichstätt specimen (Wellnhofer 1974) with the typical, ladle-shaped boot of the Berlin specimen (see Tischlinger and Unwin 2004). Likewise, the Thermopolis specimen seems to have a slightly curved pubic shaft, although not to the degree seen in the mold of the shaft or von Meyer's drawing of it in the Haarlem specimen. On the other hand, a character potentially linking the Haarlem specimen to anchiornithines might be the curved pubic shaft, which, however, cannot currently be shown without doubt to represent the natural condition. This uncertainty is reflected in the phylogenetic analysis, which cannot place the specimen beyond a probable basal position within Avialae. It should be noted that if the morphology of the pubis is coded according to the illustration of von Meyer (1860) and the mold of the shaft in the slab, and the pubic boot is coded as preserved in the Munich cast and shown by Ostrom (1972), the Haarlem specimen is again found to be a basal anchiornithine in both the reduced consensus tree resulting from the equal-weight analysis and the strict consensus tree of the implied-weight analysis (see also Foth et al. 2025). Thus, given the lack of clearly diagnostic characters, the few differences observed, and the phylogenetic uncertainty, there seems to be little reason to refer this specimen to *Archaeopteryx* and even less reason to refer it to any of the named species within this genus. At present, *Ostromia crassipes* (von Meyer, 1857) should be regarded as an indeterminate early avialan and, given its poor preservation and resulting lack of clearly diagnostic characters, probably also as a *nomen dubium*.

The taxonomic status of the Mühlheim specimen

The Mühlheim specimen, which is known only from its right forelimb, was diagnosed as a new genus and species, *Alcmonavis poeschli*, that differs from *Archaeopteryx* and other theropods based on the combination of the following characters (Rauhut et al. 2019): a humerus with a large deltopectoral crest, the maximum expansion of which exceeds the width of the humeral shaft; the proximal part of the humerus strongly angled at approximately 38° relative to the distal shaft; an ulna with a well-defined, single, oval, concave proximal cotyle and a small lateral tubercle; the distal end of the ulna slightly asymmetrically expanded; a large, crest-like biceps tubercle on the proximal radius; a longitudinal groove along the medial side of the radial shaft; metacarpal II considerably more robust than metacarpals I and III; phalanx I-1 with a longitudinal groove; phalanx II-1 very robust but with a rounded rather than flattened cross-section; phalanx II-1 slightly twisted; and manual unguals with strongly developed and palmarly transversely expanded flexor tubercles.

O'Connor and Marugán-Lobón (2026) argued that all the diagnostic characters listed above are either artifacts of taphonomic compaction and breakage or result from allometric growth, as the specimen is the largest of the known Urvogel specimens from the Late Jurassic limestones of southern Germany. Given that the specimen is very incomplete and crushed, the following characters proved problematic and should be deleted from the original diagnosis. The deltopectoral crest is not notably enlarged but is comparable in relative size to that of various *Archaeopteryx* specimens (see also O'Connor and Marugán-Lobón 2026). Although the distal end of the ulna appears more or less symmetrical in the Daiting, Berlin, London, Maxberg, and Schamhaupten specimens, strong asymmetry can be observed in the left ulna of the Chicago specimen (O'Connor et al. 2025; O'Connor and Marugán-Lobón 2026). In contrast, the asymmetry in the Mühlheim specimen is less pronounced than that in the Chicago specimen and more similar to the condition observed in the Thermopolis specimen. The observed

variation is not necessarily caused by individual variation but may partly be an artifact produced by how the bone was rotated along its long axis when originally embedded on the seafloor. As discussed for the Haarlem specimen, the longitudinal grooves along the radial shaft and manual phalanx I-1 are questionable and could be artifacts of compaction. However, given that some three-dimensionally preserved species of Enantiornithes possess such a groove on the radius (e.g., Chiappe and Calvo 1994; Chiappe and Walker 2002), this character remains phylogenetically informative, but its absence or presence should be scored only for taxa that have not been affected by taphonomic compaction (see Foth et al. 2025) or for which it can clearly be shown to be a true feature based on scan data.

The second metacarpal of the Mühlheim specimen is considerably more robust than metacarpal III. The ratio of the mid-shaft diameters of the two elements is approximately 0.7; because of damage, the proportional difference between the widths of metacarpals I and II cannot be established. Depending on the specimen, the ratio between metacarpals II and III varies between 0.8 and approximately 1.0 in *Archaeopteryx*. The only exceptions are the Solnhofen specimen, in which the ratio varies between 0.6 and 0.7 in the left and right wings, respectively, and the Eichstätt specimen, with a ratio of approximately 0.7. The length-to-width proportion of metacarpal II in both specimens is similar to that of the Mühlheim specimen. Therefore, in agreement with O'Connor and Marugán-Lobón (2026), the robustness of metacarpal II relative to metacarpal III or its length-to-width ratio does not allow discrimination between the Mühlheim specimen and *Archaeopteryx*. However, based on its variation in the *Archaeopteryx* sample, this character is not related to size and is thus ontogenetically uninformative. This variation is either a product of polymorphism, possibly also reflecting taxonomic differences at the species level, or a result of different degrees of taphonomic compaction. To what extent the slight twist observed in manual phalanx II-1 also results from compaction is unclear because the bone is obviously taphonomically flattened. This compaction also potentially affects the original interpretation that the bone is more robust than the other manual elements. However, as noted by Rauhut et al. (2019), the size of the proximal articulation of manual PII-1 fits the proportions of the distal condyle of metacarpal II, indicating that the preserved robustness most likely represents the actual morphology, similar to that in *Jeholornis* (Lefèvre et al. 2014), *Kompsornis* (Wang et al. 2020), *Sapeornis* (Provini et al. 2009; Gao et al. 2012), and *Confuciusornis* (Chiappe et al. 1999; Duan et al. 2025), and is not an artifact of compaction. However, some specimens of *Archaeopteryx* also have a more robust manual PII-1, namely the Altmühl, Berlin, Chicago, and Ottmann and Steil specimens. Thus, the robustness of manual PII-1 alone cannot be used to distinguish the Mühlheim specimen from *Archaeopteryx* with certainty and might be an adaptation to volant behavior, as the second manual digit carried the primary wing feathers.

Several of the characters proposed by Rauhut et al. (2019) require more detailed discussion. According to O'Connor and Marugán-Lobón (2026), the increased angle between the proximal part of the humerus and the humeral shaft of the Mühlheim specimen is questionable. The bone obviously suffered from compaction, as indicated by multiple cracks, and is missing its proximal end. Although the anterolateral side of the bone is missing half of the deltopectoral crest, the posteromedial margin extends almost to the level of the humeral head and is thus fairly complete. The curved trajectory of this margin is smooth throughout its course, showing no signs of breakage that could have caused an offset or disarticulation. The curvature of the posteromedial margin in the Mühlheim specimen is greater than that in any *Archaeopteryx* specimen, independent of size and preservation quality. The Daiting, Karlsruhe, and Solnhofen specimens also suffered from heavy compaction but still retain curvature similar to that in the better-preserved *Archaeopteryx* specimens (Fig. 6A). Given that the London and Solnhofen specimens, which represent the largest specimens in the *Archaeopteryx* sample, possess the same morphology, the greater curvature of the Mühlheim specimen can be explained neither as an artifact of taphonomy nor by ontogenetic variation and thus represents an actual morphology that distinguishes this specimen from *Archaeopteryx*.

The elongate oval facet for the insertion of *m. pectoralis*, which is located distally at the anteromedial margin of the deltopectoral crest in the Mühlheim specimen, cannot be found in *Archaeopteryx*. However, the anterior view of the humerus can be observed only in the Thermopolis and London specimens and in the 3D reconstruction of the Karlsruhe specimen. Because the outer margins of the deltopectoral crests in the London and Thermopolis specimens are slightly eroded, O'Connor and Marugán-Lobón (2026) argued that the absence of this facet in *Archaeopteryx* is uncertain or that it formed at a very late ontogenetic stage. Given that the distal portion of the deltopectoral crest in the London specimen is fairly intact, the distal extent of the facet should be visible in the specimen if it were originally present. Consequently, its absence is considered to represent the actual morphology of *Archaeopteryx*. The fact that the facet also appears in immature individuals of *Sapeornis* (Provini et al. 2009) indicates that, at least in this species, the feature does not develop only during late ontogeny.

O'Connor and Marugán-Lobón (2026) further argued that a well-defined, single, oval, concave proximal cotyle in the ulna of the Mühlheim specimen (Fig. 6B) is also present in the Chicago *Archaeopteryx*. However, the morphology of the cotyle is difficult to assess in the latter because the region seems to be slightly damaged, based on the photograph provided by O'Connor and Marugán-Lobón (2026: fig. 3E). Although the articular surface seems to be bordered, the outer margin does not appear raised, as in the Mühlheim specimen. Furthermore, the articular surface

in the Chicago *Archaeopteryx* seems to bear a large hole that most likely resulted from damage, limiting comparability between the two specimens. However, the proximal articular surface is also visible in the left ulna of the London *Archaeopteryx*, the right ulna of the Munich specimen, and the right ulna of the Ottmann and Steil specimen. Here, the articulation does not show a raised, well-defined margin, and the preserved portion of the surface appears flat rather than concave (Fig. 6C). Although slightly damaged, the proximal end of the left ulna in the Solnhofen specimen resembles the condition in the London, Munich, and Ottmann and Steil specimens. Furthermore, the CT data for the Karlsruhe specimen also indicate a rather flat articular surface. Therefore, this character can be retained to distinguish the Mühlheim specimen from *Archaeopteryx*.

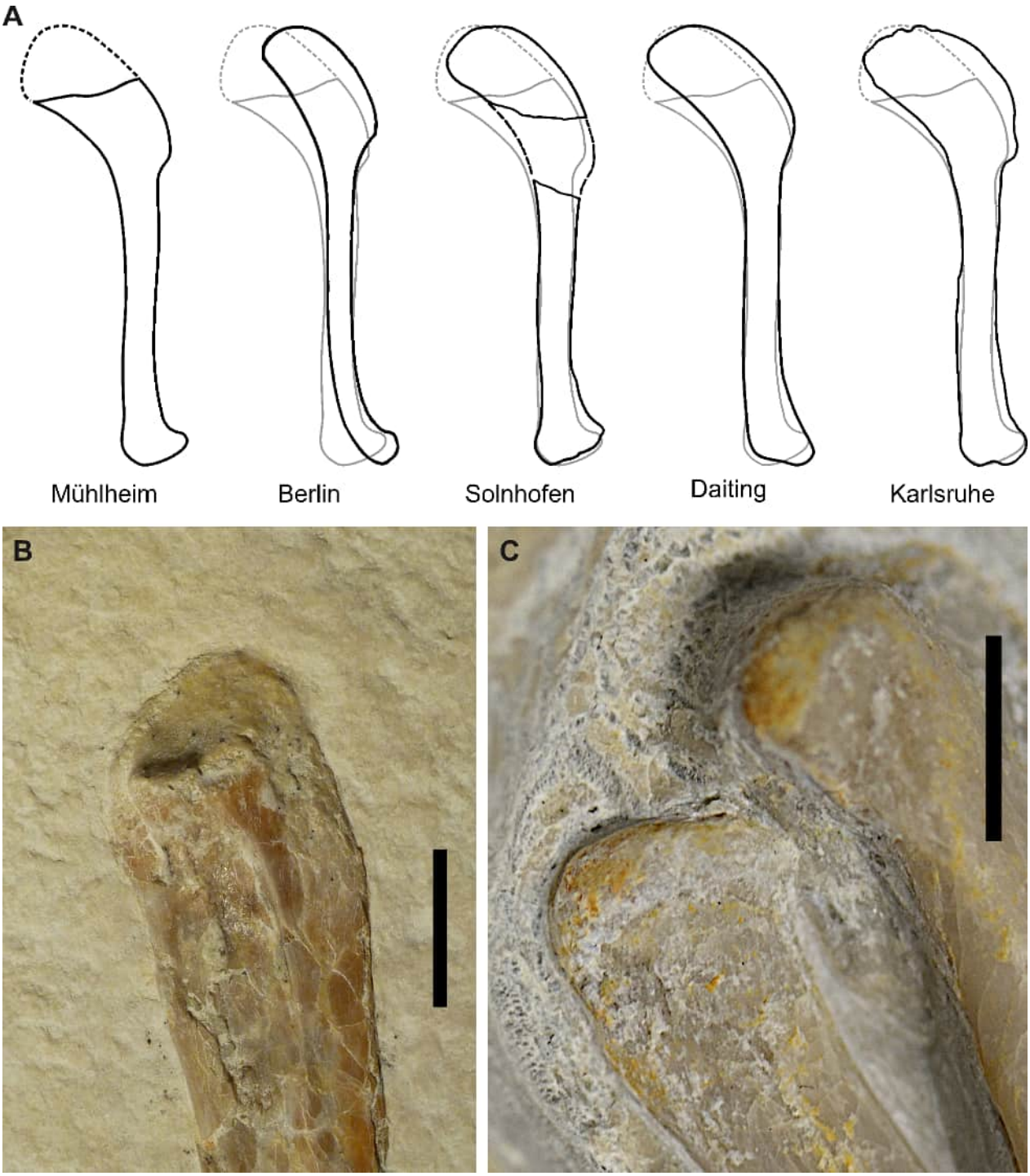

Figure 6. Mühlheim specimen. **A.** Comparison of the humeral outline of the Mühlheim specimen (gray) with those of various *Archaeopteryx* specimens, showing the different angulation of the posteromedial margin of the humerus; **B.** Proximal end of the right ulna in the Mühlheim specimen, showing a well-defined, single, oval, concave proximal cotyle (scale bar: 5 mm); **C.** The same region in the Ottmann and Steil specimen, showing a flat articular surface (scale bar: 5 mm).

Like *Archaeopteryx*, the Mühlheim specimen bears a biceps tubercle on the proximal radius (Rauhut et al. 2019), which represents a muscle attachment site that supports elbow flexion in modern birds (Vazquez 1994). Although the process is small and triangular in *Archaeopteryx* (see Rauhut et al. 2019: fig. 17A, B), it is large and crest-like in the Mühlheim specimen. O'Connor and Marugán-Lobón (2026) argued that, because of damage and compaction in the proximal region of the radius, the size and morphology of the biceps tubercle cannot be deduced. Although the process itself is missing its midsection, the proximal and distal ends are well preserved, allowing its length to be estimated. Despite the strong compaction of the radius, the two fragments of the biceps tubercle can be clearly evaluated on the flattened bone. The reconstructed midsection of the process is simply straight, connecting the two ends without adding further size to the process. Thus, if the apex of the process were located within the reconstructed midsection, the biceps tubercle would be even larger. Based on the preserved original bone, the present reconstruction therefore represents the most conservative morphology of the process. Consequently, the size and shape of the biceps tubercle can be used to distinguish the Mühlheim specimen from *Archaeopteryx*. As the shape and size of the tubercle are very comparable in the differently sized Munich and Ottmann and Steil specimens, the latter being 22% larger than the former, there is also little reason to believe that the increased size in the Mühlheim specimen simply represents ontogenetic variation.

Finally, O'Connor and Marugán-Lobón (2026) argued that the manual unguals of the Mühlheim specimen do not differ from those of *Archaeopteryx* and that the Solnhofen specimen possessed palmarly and transversely expanded flexor tubercles. In *Archaeopteryx*, as well as in the Haarlem specimen, the flexor tubercles are distally displaced from the articular surface. Such distal displacement can be observed only in the second ungual of the Mühlheim specimen, whereas in unguals I and III, the strongly developed flexor tubercles are positioned closer to the proximal articular surface. The transverse expansion of the flexor tubercles described for the Solnhofen specimen (O'Connor and Marugán-Lobón 2026) is usually associated with collapse of the tubercle base and multiple cracks in the bone surface caused by compaction, indicating that the morphology in the Solnhofen specimen is a taphonomic artifact. Such collapse of the flexor tubercles is not evident in the Mühlheim specimen. The holotype of *Jeholornis* also bears unguals with transversely expanded flexor tubercles (Chiappe and Meng 2016). Finally, the Mühlheim specimen differs from *Archaeopteryx* in the curvature of unguals I and II. In the Mühlheim specimen, the dorsal surface of ungual I arches higher than the dorsal extremity of the proximal articular surface when the latter is oriented vertically, whereas both structures are level in ungual II, as in *Jeholornis* (Chiappe and Meng 2016). In contrast, *Archaeopteryx* shows the opposite pattern, with a high arch in ungual II but not in ungual I.

Although the shape analysis provided by Foth et al. (2025) did not find significant differences in the overall ungual shape between *Archaeopteryx* and the Mühlheim specimen, the landmark configuration for this analysis was adapted to the preserved ungual of the Karlsruhe specimen, which lacks the proximal articular surface, including the dorsal lip, and most of the flexor tubercle. Thus, to quantify and verify or falsify these differences in detail, a shape analysis capturing the entire ungual morphology, including the proximal articular facet, proximal lip, and flexor tubercle, should be performed; however, this is beyond the current scope of the paper.

The phylogenetic analyses support the distinction between the Mühlheim specimen and *Archaeopteryx*, placing it consistently in a more crownward position, as originally proposed by Rauhut et al. (2019) and Foth et al. (2025). The Mühlheim specimen differs from *Archaeopteryx* and other basal Avialae in the following characters: an angle between the proximal part of the humerus and the humeral shaft that is larger than 35° (char. 387/1); a facet for the attachment of *m. deltopectoralis* on the deltopectoral crest of the humerus (char. 413/1); a proximal articular surface of the ulna that forms an oval concavity with slightly raised rims (char. 422/1); a radial diameter that is between 0.5 and 0.7 times the ulnar diameter (char. 425/1); and a dorsal surface of manual ungual I that arches higher than the level of the dorsal extremity of the proximal articular surface when oriented vertically (char. 477/1). These characters are not unique to the Mühlheim specimen and are also present in various species of Euavialae from the Early Cretaceous of China, as discussed by Rauhut et al. (2019). The exclusion of the Mühlheim specimen from the *Archaeopteryx* sample is further supported by the PCoA, which places the specimen outside the *Archaeopteryx* population with statistical significance, independent of the character sample (Fig. 4). Correcting the phylogenetic differences for size did not change the statistical outcome, indicating that these differences cannot be explained by allometry but instead reflect intergeneric taxonomic differences. Thus, based on the evidence presented in this study, the Mühlheim specimen retains its original status as a separate genus and species, namely *Alcmonavis poeschli*, as proposed by Rauhut et al. (2019).

Revised diagnosis

Based on the present evaluation, *Alcmonavis poeschli* can be distinguished from *Archaeopteryx* and more basal Avialae by the following characters: an angle of approximately 38° between the proximal part of the humerus and the humeral shaft; a facet for the attachment of *m. deltopectoralis* on the deltopectoral crest of the humerus; an ulna with a well-defined, single, oval, concave proximal cotyle and a small lateral tubercle; a slender radius with a diameter less than 0.5 times that of the ulna; a large, crest-like biceps tubercle on the proximal radius;

manual unguals with strongly developed, palmarly and transversely expanded flexor tubercles that are positioned close to the articular surface; a dorsal margin of manual ungual I that arches higher than the proximal articular surface; and a dorsal margin of manual ungual II that is level with the proximal articular surface. The Mühlheim specimen can be distinguished from Avialae closer to the crown group by having an ulna that is shorter than the humerus. It differs from Jeholornithidae by possessing a straight, closely appressed metacarpal III and lacking an intermetacarpal space. It differs from Sapeornithidae by having a fully developed third manual digit consisting of four phalanges, including the ungual.

Conclusion

Apart from the Haarlem and Mühlheim specimens, the specimen-based phylogeny found that all Urvogel specimens from the Late Jurassic of southern Germany, including the Solnhofen specimen, form a monophyletic group that represents the genus *Archaeopteryx*. Based on these findings, the diagnosis of *Archaeopteryx* was updated. The internal topologies of the analyses did not yet allow the distinction of different *Archaeopteryx* species. Thus, further anatomical comparisons are necessary to identify additional intrageneric variation that can be conceptualized as morphological characters.

Because of inconsistencies in its phylogenetic position, it is unclear whether the Haarlem specimen represents another *Archaeopteryx* specimen or a more basal representative of Avialae. Although several morphological features previously described by Foth and Rauhut (2017) as distinguishing the specimen from *Archaeopteryx* and linking it to anchiornithines might be taphonomic artifacts of compaction, potential differences from *Archaeopteryx* remain. Furthermore, the specimen still differs in various skeletal proportions from *Archaeopteryx*, but because of its fragmentary nature and the lack of any indisputable diagnostic features, it should be classified as Avialae *indet*.

In contrast, the incomplete Mühlheim specimen is very similar to *Archaeopteryx* in its general forelimb proportions but differs from the paravians *Anchiornis* and *Microraptor* in its manual proportions. However, morphological comparisons, phylogenetic analyses, principal coordinate analyses, and subsequent statistical tests indicate that the specimen is anatomically distinct from *Archaeopteryx*, supporting the validity of the taxon *Alcmonavis poeschli*. Although some of the original diagnostic characters are now also interpreted as preservational artifacts, the remaining differences from *Archaeopteryx* are distinct and cannot be explained by ontogeny or other types of intrageneric variation. The strong similarities observed in forelimb proportions are most likely due to functional constraints in the forelimbs of early Avialae related to volant behavior (Wang and Zhou 2023) and thus do not reflect taxonomic similarities. In contrast, the hindlimb proportions are less constrained in volant (*Archaeopteryx*) and non-volant (*Anchiornis*) taxa, showing a similar degree of statistical difference.

Based on the different statistical outcomes for the measurements of the Haarlem specimen provided by Wellnhofer (2008, 2009) and Foth and Rauhut (2017) (supplementary material), the use of distal limb elements can be problematic because their smaller size can introduce measurement errors. Nevertheless, the use of actual data is preferred over imputation methods. Although the imputation of missing values based on maximum likelihood is a valid strategy for estimating a certain number of missing values in well-constrained samples (see Marugán-Lobón and Chiappe 2022), it reaches its limitations when the input data are too fragmentary and biased in their distribution.

In addition, the phylogenetic analyses support the previous findings of Foth et al. (2025), indicating that Dromaeosauridae is the sister group of Avialae (see also Agnolín and Novas 2013), contradicting previous results that recovered either a monophyletic Deinonychosauria (Troodontidae+Dromaeosauridae) or Troodontidae as the sister group of Avialae (e.g., Turner et al. 2012; Godefroit et al. 2013; Foth et al. 2014). Thus, the internal relationships of Paraves remain controversial (Pol and Goloboff 2020), with significant implications for evolutionary scenarios concerning the origin of Avialae, active flight behavior, and feeding ecology.

Finally, the forelimb morphospace of basal Avialae shows three distinct clusters for non-volant Avialae, *Archaeopteryx*, and Euavialae. However, the arrangement of the clusters does not indicate a linear evolutionary trend from non-volant to volant taxa in the forelimbs because of the outlier position of the *Archaeopteryx* cluster along PCo 2. This finding may indicate that flight adaptations occurring in the forelimbs followed mosaic-like evolution, which requires a more sophisticated macroevolutionary analysis.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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Author contributions

CF and OWMR designed the project; CF performed all analyses; CF and OWMR wrote the manuscript; CF prepared all tables, figures and supplementary files.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Supplementary tables, figures and character list for phylogenetic analysis

Authors: Christian Foth, Oliver W. M. Rauhut
Data type: pdf

Link: https://doi.org/10.3897/fr.29.200245.suppl1

Supplementary material 2

Measurements used for statistical analyses

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Supplementary material 3

Mesquite data file

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Supplementary material 4

TNT data file

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Supplementary material 5

Strict consensus tree of phylogenetic analysis with all characters equally weighted

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Supplementary material 6

Reduced consensus tree of phylogenetic analysis with all characters equally weighted

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Supplementary material 7

Strict consensus tree of phylogenetic analysis with implied weighted

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Supplementary material 8

Reduced consensus tree of phylogenetic analysis with implied weighted

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