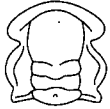


The skeletal taphonomy of *Archaeopteryx*: a quantitative approach

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A new technique is described for taphonomic investigation of fossil vertebrates with a high degree of skeletal articulation and completeness, and applied to analysis of the taphonomy of *Archaeopteryx*. The known skeletal remains of *Archaeopteryx* can be assigned to two preservational types: (A) well-articulated and almost complete skeletons, and (B) less complete and more disarticulated skeletons, but with some well-articulated sub-units. Differences between these categories are most likely a function of time elapsed between death and burial, and these groups are interpreted as samples of a larger possible range of taphonomic variation. The specimens represent parts of a decay spectrum rather than a decay sequence, and there is no evidence for a regional drift pattern. Digital crossover in the hands of *Archaeopteryx*, previously considered an anatomical condition, is interpreted as a post-mortem artefact. □ *ARCHAEOPTERYX*, taphonomy, Solnhofen Plattenkalk, palaeoecology, Jurassic, birds.

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Archaeopteryx from the Upper Jurassic (Tithonian) Solnhofen Plattenkalk of Bavaria has attracted considerable attention, not least because of its intermediate evolutionary position between reptiles and birds (see Hecht *et al.* 1985 and Barthel *et al.* 1990 for discussions). Two species are currently recognized: *A. lithographica*, represented by six skeletons and possibly an isolated feather specimen (Griffiths 1996), and *A. bavarica*, known from a single skeleton (Wellnhofer 1993; Figs. 1 and 2 herein). There has been considerable debate regarding the anatomy, functional morphology, and ecology of this early bird (Hecht *et al.* 1985), and a clear understanding of the taphonomy of *Archaeopteryx* may help to resolve some of these issues.

So far, taphonomic investigations have been confined to observational studies (Barthel 1970, 1978; Barthel *et al.* 1990; Rietschel 1976; de Buissonjé 1985; Viohl 1985; Davis 1996). Since Rietschel's (1976) comprehensive account, the discovery of two relatively complete specimens of *Archaeopteryx* (Wellnhofer 1988, 1993) enables further development of ideas regarding the taphonomy of *Archaeopteryx*.

In contrast to previous workers, we took a quantitative approach to this problem. A database was compiled from standardized observations of completeness and articulation, and used to search for taphonomic patterns and to test the observations and interpretations of earlier workers. Quantitative analyses have often been employed in

vertebrate taphonomy and zooarchaeology (see Grayson 1984; Lyman 1994a, b and references therein). However, these have generally been applied to investigations of the relationship between numbers of skeletal parts and numbers of individuals in faunal assemblages where the material is substantially disarticulated. Here, we describe a new technique that can be applied to instances where the specimens are relatively well articulated. *Archaeopteryx* provides an ideal test case for this approach, as it is represented by a small number of well-documented specimens with a high degree of articulation.

Methods

The database was constructed from observations of original specimens and casts of *Archaeopteryx* held in the Bayerische Staatssammlungen für Paläontologie und historische Geologie, München, the Jura-Museum, Eichstätt, and the Natural History Museum, London. This was supplemented by details from the literature (de Beer 1954; Hecht *et al.* 1985; Heller 1959; Ostrom 1970, 1972, 1978; Wellnhofer 1974, 1988, 1992, 1993).

Specimens were assessed according to two main sets of criteria: completeness and degree of articulation. For completeness, major skeletal elements ($n_{\max} = 130$) were scored according to their presence or absence. Elements

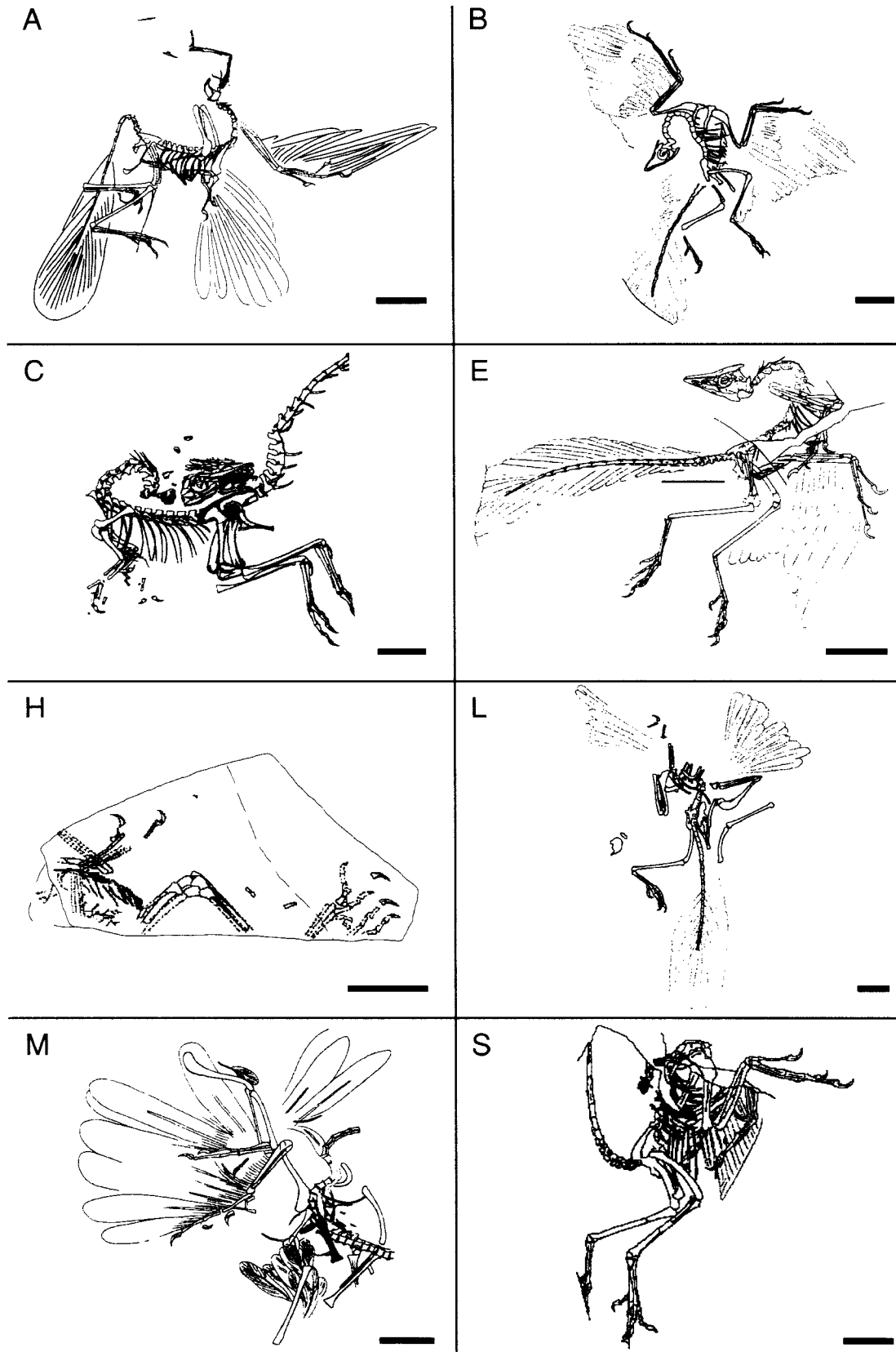


Fig. 1. The specimens of *Archaeopteryx* and *Compsognathus*. A=Aktien-Verein specimen, B=Berlin specimen, C=*Compsognathus*, E=Eichstätt specimen, H=Haarlem specimen, L=London specimen, M=Maxberg specimen, S=Solnhofen specimen. Scale bars 50 mm. (Redrawn from de Beer 1954; Heller 1959; Ostrom 1972, 1978; Wellnhofer 1974, 1992, 1993.)

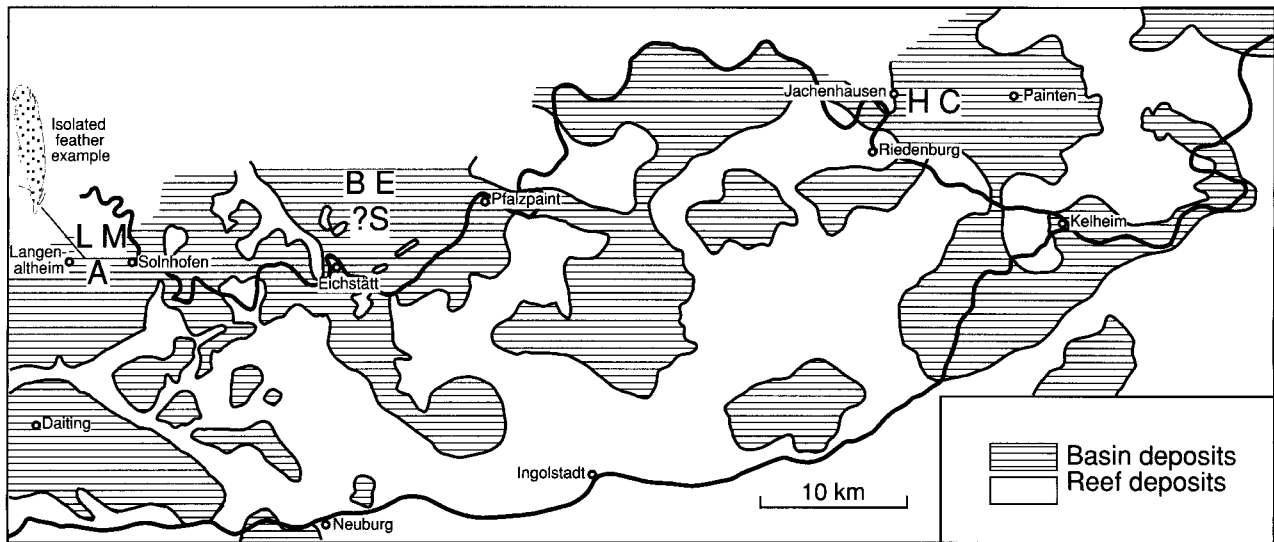


Fig. 2. Locality map for the specimens of *Archaeopteryx* and *Compsognathus*. Specimen labels as for Fig. 1. The Solnhofen–Langenaltheim basin lies to the west, the Eichstätt basin is central, and the Painten basin lies to the east. (Adapted from Barthel *et al.* 1990.)

that were not visible, but could be reasonably inferred to be present (for example, the dorsal and cervical vertebrae of the Solnhofen specimen), were also scored (unshaded section of bar charts), but differentiated from observed elements. Where it seemed doubtful to infer elements as originally present, although they may well have been (for example, the digits of the left manus of the Haarlem specimen and the caudal vertebrae of the Maxberg specimen), they were counted as absent: the graphs (Figs. 3A–C, G, 4A–C, 5) thus indicate minimum completeness for each specimen. The furcula was interpreted as originally present in all the specimens, but the presence of an ossified sternum in *A. bavarica* (Wellnhofer 1993) was omitted from the analysis. The presence of only four phalanges in digit IV of the Solnhofen specimen was treated as an anomaly (Wellnhofer 1992). For those elements that could not be scored reliably, such as ribs and gastralia, qualitative observations were made.

Joint articulations were classified in four main categories: (1) articular surfaces in contact and natural orientation; (2) surfaces in contact, but in an unnatural orientation (using the Berlin specimen as a reference standard, because its position displays the least post-mortem alteration); (3) articular surfaces slightly separated; and (4) fully disarticulated. In the case of the vertebral column, class 2 was discounted, as it was impossible to gauge accurately the orientation of individual vertebrae. Where neither side of a joint could be viewed (20.4% of all potential articulations; $n=1095$), or its orientation could not reasonably be inferred (1.55%), maximum 2.99% in any one specimen) it was omitted from the analysis. Joints not visible (obscured by overlying bone material, or matrix), but whose position could be reasonably inferred from the rel-

ative positions of the bone shafts, were scored, but with an indication of uncertainty. It was later found that inclusion of these 'inferred observations' (8.22% of all observations; $n=864$; maximum 14.3% in any one specimen) in the analyses did not significantly affect the results, and so they are included in the graphs presented below (Figs. 3D–G, 4D–F, 5).

Bivariate plots of different classes of joints were used to search for patterns within the database and to assess the degree of bias in the classification system. Relationships between specimen completeness and articulation were investigated with respect to the decay sequence of Rietchel (1976; Fig. 3A–G) and supplemented with observations from the *Compsognathus longipes* burial site within the Solnhofen area (Fig. 4). This small theropod dinosaur, represented at Solnhofen by a single specimen, is of similar size and morphology to *Archaeopteryx*, and provides an additional point of comparison.

In addition to overall completeness and articulation, individual regions of the body were assessed as separate units. 'Arms' are defined here as the entire forelimb, but not including the shoulder joint, and 'legs' as the entire hind limb, but not including the hip joint.

Results

Relative completeness and articulation of the specimens

The data for minimum completeness and different articulation classes were plotted against the decay sequence of Rietchel (1976; Fig. 3A–G herein, see discussion), with

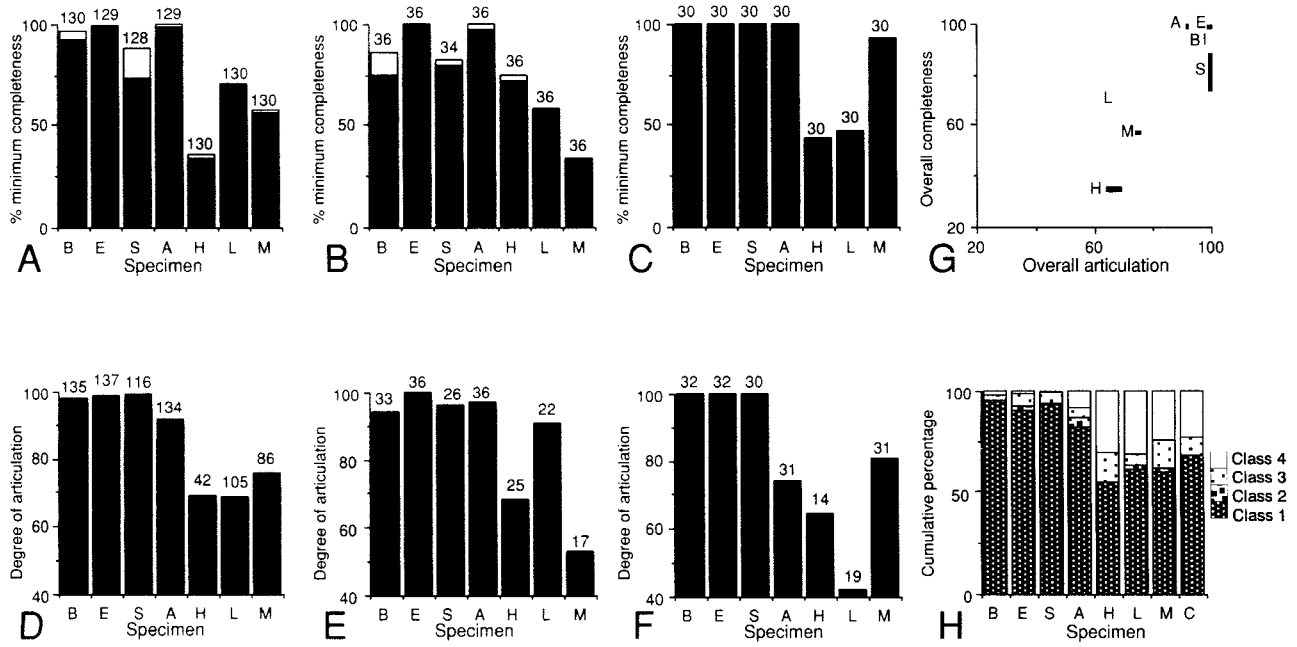


Fig. 3. The relationship between articulation and completeness to the decay sequence of Rietschel (1976). □A, D. Completeness and articulation of 'overall' values. □B, E. 'Leg' subunits. □C, F. 'Arm' subunits. Specimen labels as for Fig. 1; black infill indicates observed entries; white infill inferred entries. □G. Comparison of overall articulation and completeness for the *Archaeopteryx* specimens. Width of rectangles indicates discrepancy between observed and inferred values. □H. Disarticulation class distributions (see text). The labels at the tops of columns represent the number of data points from which the percentage was calculated (see methods).

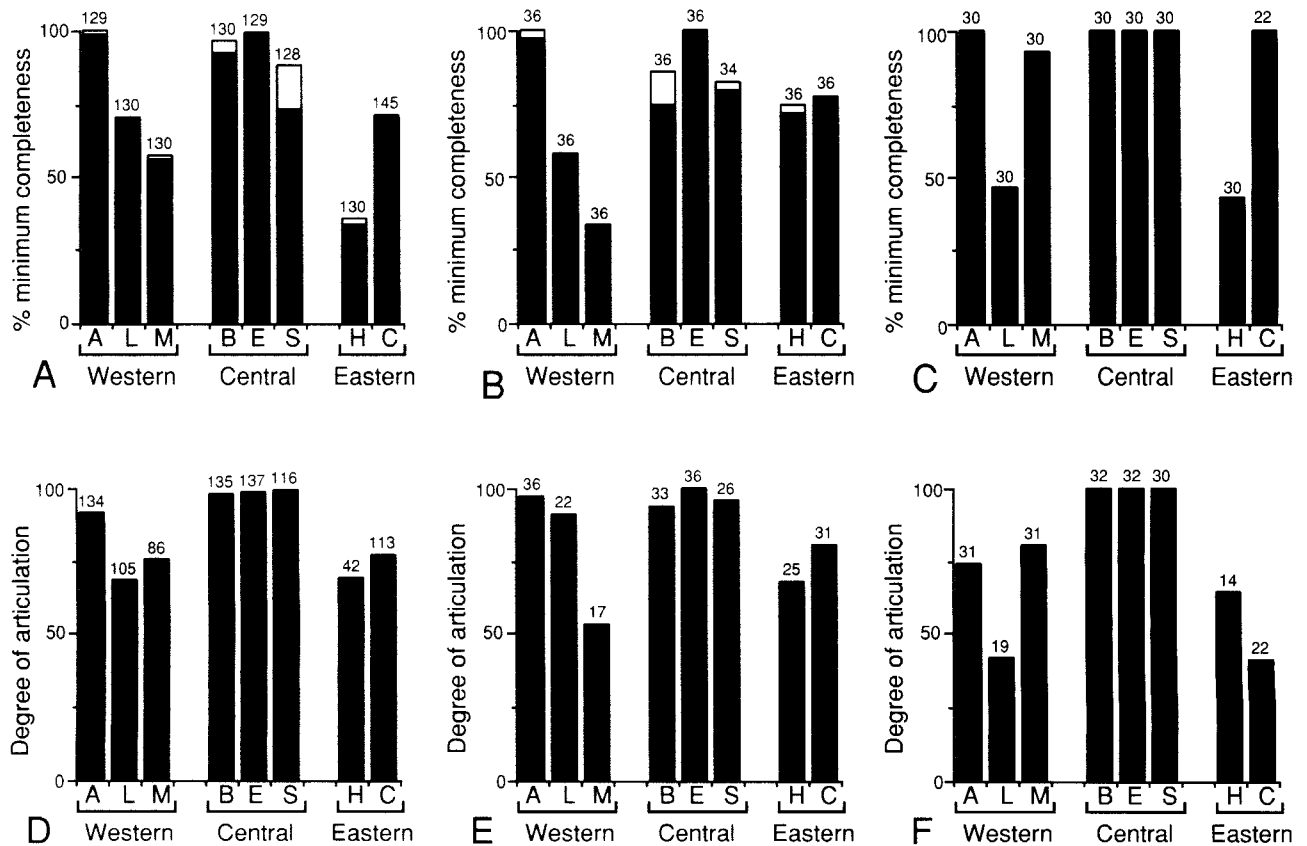


Fig. 4. The relationship of articulation and completeness to geographic distribution. Specimen labels and units as for Fig. 1. Bracketed groups correspond to Western, Central and Eastern basins of deposition (see Fig. 2). □A, D. Completeness and articulation of 'overall' values. □B, E. 'Leg' subunits. □C, F. 'Arm' subunits.

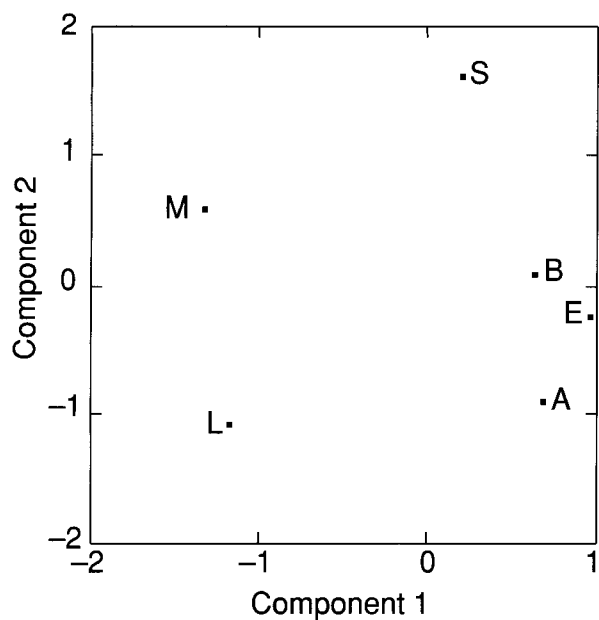


Fig. 5. Principal Component Analysis of the two preservational types. Abbreviations as for Fig. 1.

the inclusion of the Aktien-Verein and Solnhofen specimens. The degree of completeness and articulation is shown for 'Overall' values (all data points, Fig. 3A, D) and for 'leg' (Fig. 3B, E) and 'arm' (Fig. 3C, F) subunits. The labels at the top of columns represent the number of data points from which the percentage was calculated.

The number of joints falling within classes 2 and 3 was relatively small (8.45%; $n=864$; maximum 16.3% in any one specimen; Fig. 3H), and did not influence any of the observed trends. Accordingly, the graphs presented here (Figs. 3D–G, 4D–F, 5) show the degree of 'articulation' as the sum of classes 1, 2 and 3 expressed in terms of the number of joints visible in the specimen. It was also found that inclusion or exclusion of the furcula, sternum, and the anomalous phalanges of the Solnhofen specimen had negligible impact on the final results.

The specimens consistently grouped into two types:

- A Well-articulated and almost complete skeletons (Berlin, Eichstätt, Solnhofen and Aktien-Verein).
- B Less complete and more disarticulated skeletons (London, Maxberg), but with some well-articulated subunits. For example, the forelimbs of the Maxberg specimen have a high degree of articulation (Fig. 3C, F), unlike those of the London specimen, but in the latter the left hind limb is fully articulated (Fig. 3B, 3E).

Relationship to burial site

The same data, supplemented by *Compsognathus*, was then used to discover whether there were any relationships between articulation, completeness and burial site within the Solnhofen area (Fig. 4). Here, the three bracketed groups correspond to Western, Central and Eastern basins of deposition (see Fig. 2), and graphs are shown for 'Overall' values (4A, D) and for 'leg' (4B, E) and 'arm' (4C, F) subunits. The following is demonstrated in the geographic distribution of the specimens (Fig. 4A–F):

- 1 All three specimens from the central Altmühl–Alb region (Eichstätt basin) have a high degree of completeness and articulation. These specimens all belong to preservational type A, described above.
- 2 Different preservational types can be present within a single basin as, for example, in the Solnhofen–Langenaltheim basin, in the west part of the Altmühl–Alb region.
- 3 There are no general patterns across the region.

Relationship to stratigraphy and size/ontogeny

Unfortunately, other than probable confinement to the Upper Solnhofen Plattenkalk (ti_{2b}), the exact stratigraphic horizon for all the *Archaeopteryx* specimens is not known. The three specimens found in the Langenaltheimer Haardt (Wellnhofer 1993) may suggest a crude link of taphonomy with stratigraphy. The youngest specimen (*Archaeopteryx* des Solenhofer Aktien-Verein) is the most complete and articulated of the three. It would be unwise, however, to base a trend upon only three specimens, and in any case the well-articulated Eichstätt specimen comes from the lower half of the Upper Solnhofen Plattenkalk (Wellnhofer 1974), implying that across the whole depositional area, well-articulated specimens are not recovered from the youngest strata alone.

The degree of completeness and articulation was also investigated with respect to specimen size/ontogenetic status (Houck *et al.* 1990). As with stratigraphy, there may be a crude relationship with size in the western basin in that the only well-articulated (and also youngest) specimen is the smallest of the three. However, this relationship does not hold across the whole region, as the largest known example, the Solnhofen specimen, has a high degree of articulation.

Discussion

Decay sequence or decay spectrum?

Based on observational evidence, Rietschel (1976) proposed the following decay stages for the five specimens

known at that time, identifying the Berlin specimen as the least decayed prior to burial:

Berlin→Eichstätt→Haarlem(?)→London→Maxberg

Davis (1996) has interpreted the seven currently known specimens of *Archaeopteryx* according to a disarticulation sequence. By contrast to both these authors, we found that the specimens fall into two preservational types and cannot be ordered into a strict hierarchy. The preservational types identified in this study, when ordered A>B, correspond roughly to the decay stages proposed by Rietschel (1976). However, the results of our work emphasize the general similarity of preservational type-A specimens and do not encourage the idea that they can be arranged in a particular order. The Aktien-Verein specimen is notable in that the forelimbs show a greater degree of disarticulation (Fig. 3F), there is a pronounced upturn of the tail (which occurs in the four basal caudal vertebrae), and disarticulation of the bones of the skull (Wellnhofer 1992; Elzanowski & Wellnhofer 1996). It might be supposed that the Aktien-Verein *Archaeopteryx* had reached a slightly more advanced stage of decay than other type-A individuals. This is complicated, however, by the presence of an upturned tail and the partially disarticulated occipital region of the skull in the Solnhofen specimen (Wellnhofer 1992; Elzanowski & Wellnhofer 1996), which is otherwise, where comparable, more complete and better articulated than the Berlin specimen, supposedly the best preserved individual. Identification of the Berlin *Archaeopteryx* as the 'best' specimen (e.g., Rietschel 1976) is questionable, in that it is by no means the most complete example, having already lost some parts of the foot skeleton. The furcula, previously assumed as absent, is in fact present, but only preserved in a fragmentary condition (P. Wellnhofer, personal communication, October, 1996).

Thus, comparisons of type-A individuals suggests a spectrum of decay, via a range of taphonomic pathways, rather than a particular decay sequence where disarticulation proceeds in a constant manner. The incomplete nature of the Solnhofen and Haarlem specimens almost certainly reflects loss of parts of the skeleton during collection. Given the completeness and articulation of the remaining skeleton, it seems reasonable to assume that the Solnhofen specimen had lost few, if any, elements at burial. The Haarlem specimen shares some features with individuals of type A, for example, intact gastralia, suggesting that it too may well have been largely complete at burial. However, this is less certain than in the Solnhofen specimen, because the hands and feet are somewhat disarticulated. The overall low collection and poor preservation of the Haarlem specimen prohibits a reliable assessment of the skeletal remains (Rietschel 1976).

Specimens of preservational type B (London and Maxberg) undoubtedly experienced a greater degree of

preburial decay than those of type A, as shown by their more incomplete and disarticulated nature. For example, unlike type-A specimens, the gastralia and ribs have been scattered. The distinction between types A and B is a little blurred, however. For example, the left foot of the London specimen (type B) is fully articulated, yet some parts are missing in the feet of the Berlin specimen (type B). Again, although previous studies ranked the London specimen as better preserved than the Maxberg, quantitative analysis (Fig. 3A–G) does not reveal a significant distinction between these two.

The difficulty of distinguishing, in terms of degree of decay, between individuals within particular preservational types, and the blurring of the boundaries between types, further emphasize our interpretation of the *Archaeopteryx* specimens as representative of a decay spectrum, rather than a decay sequence. This is hardly surprising, given that differing environmental conditions frequently produce variations in disarticulation sequences (Hill 1979).

Two discrete groups or continuous spectrum? – The two preservational types suggested by the bivariate plots would appear to have two possible origins. Either the two types represent two distinct modes of preservation, or their appearance as groups is a statistical artefact related to the very small sample size, and they merely represent different regions of a larger spectrum. The first explanation would indicate two markedly different taphonomic pathways, possibly representing those fossils that were delivered directly to the hypersaline pools and those that drifted around in the surface waters before becoming entombed in the sediment (Barthel *et al.* 1990). The second explanation is supported by the observation that, where large numbers of individuals have been recovered (e.g., Solnhofen fish), all stages of decay are present (Viohl 1994).

To test these explanations, Principal Component Analysis (using the correlation matrix) of the specimens was conducted using SYSTAT (Wilkinson 1989). Analyses of the data for overall completeness and articulation are shown in Fig 5. Component 1 accounts for 84.056% of the total variance, and shows the two nominal preservational types as represented by the left-hand (type B) and right-hand sectors (type A). However, the overall spread of values shows that these two types cannot be statistically separated on the basis of major elements alone. This suggests that the two types are more likely to form part of a continuous spectrum rather than distinct groups, an assertion supported by our preliminary investigations into the taphonomy of another Solnhofen tetrapod, *Rhamphorhynchus*, which is represented by more than 100 specimens.

Functional and anatomical implications

Sub-units of the skeleton. – The vertebral column remains remarkably intact, with substantial disarticulation evident in only the London specimen. Similarly, the tail of *Archaeopteryx* appears to have been a remarkably coherent unit, fully articulated in five out of the seven specimens. The tail is missing in the Maxberg and Haarlem specimens, but this is probably because it would have lain in a region of the slab that was not collected. Given that the skeletons of the Solnhofen and Eichstätt specimens are otherwise fully articulated, the lack of an ossified sternum suggests that it was only weakly attached or was absent in the living animal (Rietschel 1976). A calcitic mass in the Berlin specimen may indicate the existence of a cartilaginous sternum (P. Wellnhofer, personal communication, October, 1996).

The ‘arms’ of *Archaeopteryx* are better represented in the sample (i.e. exhibit higher completeness) than the ‘legs’, but are not necessarily better articulated, as the London and Aktien-Verein specimens show. Interestingly, the shoulder joint seems to have been a robust structure, as the scapula, coracoid, and humerus are found in close articulation even in those specimens most decayed prior to burial. Comparisons with experimental work on bird taphonomy (Davis & Briggs 1998) show that the integrity of this association and its early separation from the thorax are features shared by *Archaeopteryx* and modern birds. The digits of the Berlin, Eichstätt and Aktien-Verein specimens all show some signs of disarticulation, suggesting that these elements may separate early relative to a more coherent vertebral column. If a true feature of the animal, this early disarticulation of foot and hand digits in *Archaeopteryx* differs from the decay stages observed in recent forms (Davis & Briggs 1998) and is possibly related to its basal position within Aves. Further investigations of the articulation and completeness of other sub-units of the skeleton and individual joints did not reveal any particular patterns, but perhaps this is not surprising given the small number of specimens.

Taphonomic modification. – Failure to identify the effects of taphonomic modification has led to differing interpretations regarding the anatomy of *Archaeopteryx*. For example, the early post-mortem displacement of the shoulder girdle of *Archaeopteryx* (best exhibited in the Berlin specimen) led to misinterpretations of the point of wing insertion on some reconstructions of the animal (Rietschel 1976). Similarly, post-mortem rotation of the pubis resulted in much debate concerning its original orientation (Wellnhofer 1985). Diagenetic modification of the bone material itself has been limited (Davis 1996). With the exception of the Haarlem specimen, which has

been subject to extensive dissolution (Ostrom 1972), the elements are usually preserved intact but may have suffered some crushing and fracturing.

The ventral cross-over between digits II and III in the manus of *Archaeopteryx* is a feature that has been noted by several authors (Wellnhofer 1988, 1992; Ostrom 1992; Griffiths 1993). This has been interpreted (Griffiths 1993) as the natural configuration of the digits and not a post-mortem artefact, based in part on the high incidence of crossover among the skeletal specimens. However, the strength of evidence for this is questionable. Crossover is only definitely present in six out of the nine hands that are articulated and well preserved, and some of these cases are equivocal. The Eichstätt specimen has a clear crossover in its right hand, but in the left one this crossover is only achieved by a backwards flexion of digit II between the first and second phalange. When this digit is restored to a straight orientation (as is common to the situations above), no crossover is present. In a similar manner, when the left hand of the Solnhofen specimen (which has folded at the wrist) is restored to form a continuous line through the metacarpals, the natural configuration of these digits as crossed is questionable.

While *Archaeopteryx* might have crossed its fingers during flight (Ostrom 1992; Griffiths 1993), we propose that crossover is more easily explained as a post-mortem artefact and related to the inertia of digit II, the feather-bearing digit (Yalden 1985), when compared to the relatively unrestricted mobility of the ‘free’ digits, I and III. Alternatively, Yalden (1985) has proposed that crossover arose when the claws became twisted from their natural orientation, as can be observed in the Berlin, Eichstätt and Solnhofen specimens (Yalden 1985; Stephan 1994). Crossover also occurs between digits II and III in both feet of the Eichstätt specimen and, to a lesser extent, in the right foot of the Solnhofen and London specimens. This is almost certainly a post-mortem artefact.

Curvature of the neck. – Previous discussion of *Archaeopteryx* taphonomy has often centred around its characteristic death posture, a distinctive feature of which is the sharply recurved neck, a condition also exhibited by some Solnhofen pterodactyls (Wellnhofer 1970). Curvature can be explained in a number of ways: (1) the consequences of a pendulant head and neck while drifting (Rietschel 1976; de Buissonjé 1985); (2) arrival of the carcass at the sea floor (Frey & Martill 1994); (3) differential contraction of muscles in the neck region; and (4) contraction of the ligaments (Heinroth 1923; Ostrom 1978), due either to mummification (Schäfer 1962; Barthel 1970; Wellnhofer 1970; Davis 1996) or osmotic dehydration in a hypersaline layer (Seilacher *et al.* 1985; Davis 1996), as has also been suggested for Solnhofen fish (Viohl 1994). The results of this study do not help us to resolve this

problem, but experimentation, and comparison with other Solnhofen tetrapods should yield further insights.

Martin's (1995) unorthodox three-dimensional reconstruction of *Archaeopteryx*, using casts of actual bone material, is consistent with its taphonomy and falls within the range of poses exhibited by the well-articulated fossil specimens. However, at least some features of the model may incorporate artefacts of taphonomic modification rather than reflecting a natural posture. For example, the extreme curvature of the basal caudal vertebrae in the model is apparent in the Solnhofen and Aktien-Verein specimens, but in the fossils this deflection is almost certainly due to post-mortem modification.

Regional drift pattern

A regional drift pattern for *Archaeopteryx*, inferred from a supposed increase in specimen disarticulation from east to west, has been based on the first five specimens to be found (Barthel 1970, 1978; de Buissonjé 1985), and more recently upon all seven (Davis 1996). This pattern has also been suggested for the Solnhofen pterodactyls (Wellnhofer 1970) and for Solnhofen fossils in general (de Buissonjé 1985). By contrast, von Ammon (1907, cited in Weigelt 1989, p. 83) maintained that at Kelheim, a locality in the east of the region (Fig. 2), vertebrate carcasses were more disarticulated than those in other areas. Quantitative analysis of completeness and articulation of the specimens shows that, for *Archaeopteryx*, the data do not support the idea of a regional drift pattern. Data for completeness, articulation, and size do not exhibit any clear patterns across the entire region. Indeed, different preservational types can be present within a single basin. Certainly, drift from east to west seems unlikely given that the Aktien-Verein specimen is complete, suggesting that an animal could be delivered directly to the westerly plattenkalk basin (compare with Davis 1996, Fig. 2). This can also be seen in vertebrates from the Green River Formation (Grande 1984) and in the Crato Member of the Santana Formation (Maisey 1991).

Taphonomic history

Given the small number of specimens it is difficult to define a distinct taphonomic history for *Archaeopteryx*. A number of factors (time spent in the water column, time spent on the lagoon floor before final burial, regional variation in the stratification of the water column, and chemistry of the lagoonal water and sediment) must underlie the observed variations in patterns of decay of the specimens.

A principal goal of taphonomy is to establish the length of time elapsed between death and final burial. There are various lines of evidence that help to constrain this time

interval: in the case of *Archaeopteryx*, they can be divided into two phases: (1) predepositional and (2) postdepositional, preburial.

The predepositional phase extends from the point of death to arrival at the lagoon floor. The high degree of articulation and completeness for type-A specimens would seem to preclude a prolonged period of transport and suggests only a short interval of time before they became deposited. Even the most disarticulated example, the Aktien-Verein specimen, has all its skeletal elements present, suggesting that even in this case there was rapid delivery of the entire carcass to the bottom. The high degree of articulation as well as evidence for soft-tissue preservation are also consistent with a short predepositional phase. For type-B individuals, their lower completeness suggests that the length of time involved was significantly longer.

The postdepositional, preburial phase covers the time interval between arrival of the carcass at the bottom and final burial. The presence of articulated gastralia in type-A specimens indicates that some soft tissues still existed at burial (Wellnhofer 1992), and hence for these individuals the postdepositional, preburial phase was probably short. Gastralia are also present in type-B specimens and, as these elements were originally embedded in the dermis, the integument must have been intact upon arrival at the bottom. However, the gastralia are scattered in type-B specimens, indicating a period of decay and dispersal and thus a longer postdepositional, preburial phase than in type-A specimens. This is also supported by the disarticulation and scattering of the skull bones seen in the London specimen (Rietschel 1976).

Though variable, there are impressions of feathers in all seven specimens (Swinburne 1988; Fig. 1), indicating that some soft-tissues were present when individuals reached the bottom. Such exceptional preservation requires inhibition of decay and little or no disturbance of the individual once on the lagoon floor. At present, the rate at which preservation took place is unclear, and thus this does not provide insights into the length of the postdepositional, preburial phase.

Death, transport and burial. – The evidence presented above suggests that in most cases the length of time from death to deposition was probably no more than a few days, and possibly only a few hours. In any case, experimental evidence from modern birds (Davis & Briggs 1998) suggests that the maximum time interval is unlikely to have been more than four days (for type-A specimens) to 27 days (for type-B specimens). The exceptional preservation of the Berlin and Eichstätt specimens has been attributed to drowning of these animals during a storm, with rapid sinking facilitated by water-filled lungs and a soaked plumage (Rietschel 1976; Viohl 1985; Barthel *et al.* 1990).

The high degree of articulation (especially in type-A specimens) shows that there was little postdepositional movement of the skeletal elements (Ostrom 1978; Elzanowski & Wellnhofer 1996); this is also consistent with the preservation of recalcitrant soft-tissues (e.g., feathers) which occurs in all specimens (Swinburne 1988). The low numbers of class-3 articulations in type-A individuals (Fig. 3H), some of which can be attributed to compactional modification, also argues against substantial dispersal of skeletal elements. This is not surprising, given that the floor of the Solnhofen lagoon was generally an area of minimal current activity (Viohl 1985; Barthel *et al.* 1990).

In comparison to other type-A specimens, the high degree of completeness of the Aktien-Verein specimen contrasts with its relatively greater degree of disarticulation (cf. Fig. 3A and D). Unlike the Berlin and Eichstätt specimens, however, where elements are lacking, the disarticulated parts have remained in close association with the skeleton, suggesting that, in this case, there was at least some movement of the skeletal elements on the lagoon floor before final burial. A similar situation also applies to *Compsognathus* (Ostrom 1978). This observation may explain the different preservation seen across the region, with better preservation in the central basin than in those to the east and west, although undoubtedly other factors may be important.

It is generally assumed that the total length of time from deposition to burial was short. The exceptional preservation of the specimens has been attributed to delivery straight to the deeper hypersaline pools and rapid cover by sediment (Barthel *et al.* 1990; Davis 1996). It has also been proposed that the climatological event that delivered the animal to the lagoon resulted in its immediate burial (Davis 1996). It is nevertheless conceivable that specimens may have spent long periods (possibly weeks or months) on the lagoon floor before burial, particularly if subject to bacterial sealing or hypersaline conditions inhibiting decay, as has been proposed for Solnhofen fossils (Keupp 1977; Seilacher *et al.* 1985; Barthel *et al.* 1990).

Palaeoecological significance

The lack of a regional drift pattern means that post-mortem transport from a supposed habitat in a tree-less land mass immediately to the north of the lagoon cannot be confidently invoked, and palaeoecological arguments over the interpretation of anatomical details (Hecht *et al.* 1985) must remain speculative (Viohl 1985; Barthel *et al.* 1990). The presence of a decay spectrum suggests that the sequence of disarticulation differed between individuals, and biostratigraphic conditions varied between individual basins. Further *Archaeopteryx* discoveries may display intermediate, or possibly even more decayed, states.

The exceptional preservation of all seven specimens and the lack of any clear taphic bias (size, drift time) may indicate that, once dead, any individual *Archaeopteryx* had an equal chance of being preserved. Given this, the prevalence of immature specimens (Houck *et al.* 1990) in the current sample cannot be adequately explained by post-mortem factors. The low numbers of *Archaeopteryx* specimens in relation to the more abundant pterosaurs (more than 200) may be a true reflection of their relative abundance in a terrestrial ecosystem (Davis 1996), but given their differing ecologies it would seem more likely that other biotic factors are involved (Wellnhofer 1995).

Conclusions

The quantitative approach taken here provides a means of testing the various taphonomic hypotheses proposed for *Archaeopteryx* and has enabled us to clarify some important issues, such as the question of drift. A major problem with *Archaeopteryx* is the low number of specimens, which, unfortunately, precludes effective use of statistical techniques. Studies, now underway, on taxa represented by larger numbers of specimens (e.g., pterosaurs) will be able to take greater advantage of the quantitative approach and will help to resolve some remaining questions regarding the palaeoecology and taphonomy of the Solnhofen tetrapods.

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