

The Taphonomy of *Archaeopteryx*

By

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Abstract *Archaeopteryx* is the oldest known undisputed bird. It is also the most famous and well studied fossil bird taxa. Although the taxonomy of the two known species of *Archaeopteryx* has been discussed, little information on the taphonomy of the skeletal specimens has been included in these papers. The aim of this paper is to review the mainly anecdotal information published upon the taphonomy of *Archaeopteryx* and in the light of new techniques in avian taphonomy, reassess and produce a taphonomic history for the specimens.

Introduction

The fauna of the Solnhofen Lithographic Limestone (Tithonian, Upper Jurassic) of Bavaria, Germany is one of the most famous among Konservat Lagerstätten due to the occurrence of *Archaeopteryx*, the so called Darwinian “missing link” between dinosaurs and birds. Apart from *Archaeopteryx* this Lagerstätte contains other taphonomically similar vertebrates such as rhamphorhynchoid and pterodactyloid pterosaurs, and the small coelurosaurian dinosaur *Compsognathus longipes*, which may for all taphonomic intents and purposes be treated as a small featherless bird [although some authors—e.g. PAUL (1988) and BAKKER (1986)—contend that some dinosaurs, especially their ‘avetheropods’ (like *Compsognathus*) were feathered].

Most of the literature on the two species of *Archaeopteryx* (*lithographica* and *bavarica*) is concerned with the taxonomy, evolution and palaeobiology of the seven known skeletal specimens (e.g. OSTROM, 1972, 1973, 1974, 1975a, b, 1976; WALKER, 1972, 1980, 1985; WELLNHOFER, 1974, 1985, 1988a, 1993). Aspects of the taphonomy of *Archaeopteryx* have also been investigated (e.g. HELLER, 1959; RAU, 1969; BARTHEL, 1970, 1978; RIETSCHER, 1976; HELMS, 1982; WELLNHOFER, 1983; DE BUISONJÉ, 1985; VIOHL, 1985; SWINBURNE, 1988; BARTHEL *et al.*, 1990), and the recent controversy upon the authenticity of the specimens inadvertently added further taphonomic data to the literature (e.g. HOYLE *et al.*, 1985; WATKINS *et al.*, 1985a, b, c; HOWGATE, 1985; CHARIG *et al.*, 1986; HOYLE & WICKRAMASINGE, 1986; SWINBURNE, 1988).

Study Methods

All the skeletal specimens of *Archaeopteryx* and *Compsognathus* were reviewed for this study. This review took the form of making taphonomic observations upon every specimen from the literature and replicas except in the case of the London specimen of *Archaeopteryx* where direct observations were conducted. Records were made of the amount and type of disarticulation, presence/type of soft tissues, compaction, diagenesis etc. The data for each specimen was recorded on a *pro forma* and then summarized (this data does not appear here as it is easily extractable from the literature). Previous work upon the taphonomic aspects of *Archaeopteryx*, *Compsognathus* and the pterosaurs is reviewed in the following sections.

Review of Previous Research

Sedimentology and palaeoenvironment: SEILACHER *et al.* (1985) remarked that diagenesis is traditionally viewed as the result of physiochemical processes, but in Solnhofen the preservation of soft tissues and the solution of aragonite seem to have been controlled by microbiological activity. SEILACHER *et al.* (1985) illustrated preserved trackways and roll marks which demonstrate that a macroscopic scum occurred on the sediment surface. They argued that the effects of such a scum are:—

1. To protect soft sediments against erosion.
2. To favour the preservation of tracks and other markings.
3. To serve as a food source during benthic events.
4. To protect carcasses against decay.
5. To act as a carbonate pump into the sediment.
6. To seal the particular microenvironments responsible for the absence of bioturbation and for the unusual preservational histories of ordinary fossils such as ammonite shells.

The most important factors in the preservation of *Archaeopteryx* are 1, 2, and 4.

BARTHEL *et al.* (1990) stated that *Archaeopteryx* lived in a terrestrial environment to the north of the lagoon. Because there is no trace of this terrestrial environment this palaeoecological reconstruction must be somewhat speculative, but up to the present time the theory presented by BARTHEL *et al.* (1990) is the most complete that is available. The following is their description of this landmass.

.... In all probability the land was low-lying and of no great areal extent because it did not supply any appreciable amount of terrigenous sediment to the lagoon. River channels were not a permanent feature of the landscape, but freshwater ponds probably existed seasonally. There

may have been a belt of wide sandy beaches fringing the land.

In the hinterland, the stunted, shrubby growth consisted mostly of gymnosperms, able to survive in this dry, salty soil. Seed ferns, particularly the widely dispersed and presumably hardy *Cycadopteris*, formed a scanty undergrowth whilst squat, cone-bearing cycadophytes, deciduous-leaved ginkgos and stunted, scaly conifer bushes were present as isolated shrubs. No logs have ever been recovered from the Solnhofen Plattenkalk and one conclusion may be that trees were either very rare or absent from the land immediately adjacent to the lagoon. However, further to the north lay the landmasses of the 'Mitteldeutsche Schwelle' and the London-Brabant Massif and they most probably held richer plant as well as animal communities. The plants produced various megaspores, cones and pollen, which would have supported a diverse insect population. Of the insects recovered from the Solnhofen Plattenkalk, most are dependent on a freshwater habitat for the larval stages of their life cycle.

Into this setting we can place the land reptiles and the renowned *Archaeopteryx*. The rhynchocephalians and small lizards most likely spent much of their lives basking in the sun and running under stones. They probably ate insects and were themselves eaten by the fast-running little dinosaur *Compsognathus* (a lizard has been found in the gut contents of the one known specimen of *Compsognathus*). The relatively common pterosaurs lived in close proximity to the lagoon and with their large wings and light bodies they must have been adept fliers. Some were probably water animals as they have webbing between their hind toes and many ate fish, judging from the stomach contents. However, one [pterosaur] genus, *Ctenochasma*, has teeth, which suggest that it was more likely to have been an insectivore.

BARTHEL *et al.*, 1990, p. 86.

BARTHEL *et al.* (1990) speculated that *Archaeopteryx* would have lived an arboreal existence (to avoid predators and because *Archaeopteryx* could not have run fast enough for take off). No trees are found fossilized in the lagoon, implying that *Archaeopteryx* could have been buried at quite some distance from its normal habitat.

BARTHEL *et al.* (1990) also considered the biostratinomy of *Archaeopteryx* and concluded that airborne individuals were caught in high winds and waves and were drowned. With the lungs full of water and the plumage soaked, the bodies sank to the bottom. They noted that modern bird carcasses show the same initial stages of decay as in *Archaeopteryx* i.e. in *Archaeopteryx* feathers are only preserved on the wings and the tail (and possibly the back of the head). DAVIS and BRIGGS (1995, in press) also noted that these feathers are the most recalcitrant.

The transport of Archaeopteryx and causes of disarticulation: DE BEER (1954) stated that some earlier authors, particularly R. OWEN and H. STEINER, believed, erroneously, that the London specimen was prey to other animals before entombment and that this explained the disarticulation pattern. He suggested that the specimen was more likely to have fallen onto a mud-flat near the shore of the Solnhofen sea where it underwent gentle disarticulation before becoming covered with sediment. DE BEER (1954, p. 7) went on to remark that the way up of the slabs was not recorded when collected but, because the feather impressions on the main slab were more distinct, then this must be the underslab, for the following

reason:

.... It must be supposed that when the body of the bird fell on to the surface of the mud, the impressions made by the impact of the feathers on that surface were protected from disturbance and water movement by the overlying feathers themselves. The subsequent deposition of the fine grained matter on the upturned surface of the feathers would, however, not be so protected from the limited movement of the water which, it is clear, must have taken place and been responsible for the displacement of the head a few inches from its original resting place.

BARTHEL (1970) stated *Archaeopteryx* specimens had been found in “awkward mummy-like conditions” which are consistent with birds that dry and mummify on a shoreline. These shoreline mummies can be buried at sea if a very high tide coupled with a seaward wind drifts the mummies offshore where they eventually sink.

BARTHEL (1970) noted that the distance from the palaeo-shoreline could be directly correlated with the degree of preservation in *Archaeopteryx*, i.e. those in a near-shore environment (the Berlin *Archaeopteryx*) are well preserved and the further away from the shoreline the more decay the specimens have undergone.

BARTHEL (1970) also noted that *Archaeopteryx* would be less subject to prolonged drift because the bones are less pneumatic than modern birds. It also has a large heavy tail, therefore only the feathers and the mummified soft tissues remaining would have retarded sinking.

VIOHL (1985) stated that *Archaeopteryx* was undoubtedly capable of powered flight (a view supported by NORBERG, 1985) and this flight ability is indicated by the complete preservation of the Berlin and Eichstätt specimens. His theory precludes long transport and rapid burial. He assumed that the birds flew across the sea, perhaps from one island to another, when they were caught in a storm or monsoonal shower and drowned. The lungs then filled with water, and the plumage was soaked. Only in this condition would the carcasses sink down quickly, as was stated by RIETSCHER (1976). Otherwise they would have floated for a prolonged time, becoming more disarticulated (as noted by SCHÄFER 1955, 1962, 1972, 1976).

Pose of the Archaeopteryx skeletons: HEINROTH (1923) used magpies (*Pica pica*) and pheasant coucals (*Centropus phasianinus*) in experiments to investigate the ‘bicycling pose’ of the Berlin *Archaeopteryx* (‘bicycling pose’ is my term for the pose that is seen in all *Archaeopteryx* specimens—(except the London and Maxburg)—see Fig. 1). HEINROTH arranged fresh unplucked, plucked and defleshed cadavers in the position of *Archaeopteryx*. He ascertained that after artificial detachment of the muscles and also some slight decay the carcass adopted a position similar to *Archaeopteryx*. He noted that, after muscle tension has disappeared, the pull of the ligaments creates the neck curvature as seen in *Archaeopteryx*. Also in *rigor mortis*, the antagonistic muscles all contract at the

same time giving the same appearance as in *Archaeopteryx specimens*.

MOODIE (1923) noted that *Archaeopteryx*, *Compsognathus* and some pterosaurs exhibit a pronounced opisthotonos, “a tetanic spasm in which the spine and extremities are bent with convexity forward, the body resting on the head and heels” (MOODIE, 1923, p. 323). He attributed such a spastic spasm to the poisoning of the central nervous system by bacterial poisons, mineral poisons or other toxins, which when liberated in the blood, attack the brain and spinal cord. This, however, is not believed to be correct. It is more likely to be due to desiccation as HEINROTH (1923) assumed.

WEIGELT (1989/1927, p. 105–106) argued that the curvature of the neck (the backward bend placing the head above the centre of the back) in the land/flying vertebrates from Solnhofen is a result of desiccation and shortening of muscles and tendons after *rigor mortis* has finished.

RIETSCHEL (1976) indicated that wind-driven near-surface currents operated from east to west which led to the transport of *Archaeopteryx* on the water surface in an east to west direction. He also suggested that *Archaeopteryx* died by eating poisoned fish or invertebrates that were washed up on the lagoon shoreline. The dead *Archaeopteryx* then would have floated for several days before sinking with the head and neck dorsally bent. He postulated that the head and neck would have come to rest in this position on the sediment surface thus explaining this configuration in the fossil specimens.

To further ascertain the cause of the bicycling pose I repeated HEINROTH's basic experiment using a pigeon (*Columba livra*). The pigeon was defleshed by removing all muscle tissues by dissection. The pigeon was then placed in a fume cupboard with the extraction unit switched on. This allowed a constant stream of air of room temperature (20°C) to pass over the specimen. The specimen was left for three days. As in HEINROTH's (1923) experiment the neck curved backwards and the legs assumed the ‘bicycling pose’ evident in *Archaeopteryx*. The carcass adopts this pose because, without the muscles to act as an antagonistic force to the desiccating and shortening tendons, the skeleton contorts into the ‘bicycling pose’. It is reasonable to assume that this same pose would occur if the muscle tissue of *Archaeopteryx* had first decayed away naturally before desiccation. This experiment is not sufficient, however, to indicate whether this desiccation was on land or due to being immersed in the hypersaline lagoonal waters (i.e. osmotic desiccation) although in light of other evidence the latter is most likely.

Preservation of the feathers of Archaeopteryx: RIETSCHEL (1985) summarized previous interpretations of the preservation of the feathers of *Archaeopteryx* as “impressions” of the feathers on the soft sediment surface. He argued that this was impossible (based on current understanding of how the Solnhofen limestone was deposited) and that preservation could only have resulted from:—1) the

plumage being covered with a very fine grained sediment or, 2) conserved by an overgrowth of bacteria and algae. He termed these mechanisms "precipitation". A thorough review of the preservation of the feathers of *Archaeopteryx* was presented by DAVIS and BRIGGS (1995). This work need not be further repeated here except to say that the preservation of the feathers is due to the growth of bacteria on the feathers (by glycocalyx attachment) which in turn creates a localized area of early lithified sediment which retains the 'imprint' of the feather surface.

Taphonomy of the pterosaurs and Compsognathus: The pterosaurs provide comparative data as the only other group of flying vertebrates represented in the Solnhofen Limestone. *Compsognathus* is very similar both morphologically (osteologically and presumably physiologically) and taphonomically to *Archaeopteryx*, even though *Compsognathus* did not fly.

DE BUISONJÉ (1985) suggested that the backward twist of the neck in pterosaurs (similar to the 'bicycling pose' in *Archaeopteryx*) was due to death by ingestion of toxin-filled coccolithophorans or fish poisoned by such a bloom (modern coccolithophoran blooms may poison fish: see BRONGERSMA-SAUNDERS, 1957) and then drifting for some days before sinking to the bottom. Some buoyancy in the chest region kept the carcasses afloat with the head and neck hanging dorsally bent, essentially in the same position in which they finally came to rest on the bottom.

WELLNHOFER (1970) looked at the preservation of the pterodactyloid pterosaurs, and made similar observations to those of BARTHEL (1970) on *Archaeopteryx*. He noted that mummification of Solnhofen pterosaurs on the lagoon shoreline must have occurred before entombment, and he also observed that the further from the palaeo-shoreline the animal was buried (i.e. the longer the carcass had drifted) the more disarticulated it became.

OSTROM (1978) studied the osteology of *Compsognathus longipes* and noted that the bones are preserved as actual bony elements or as impressions; the bony elements are completely replaced by calcite with no re-crystallization and consequent distortion or loss of detail. The specimen was close to the ground surface in the quarries and consequently subject to solution by sub-surface run-off. This weathering caused unusual textures which have been interpreted as skin and muscle preservation by other authors (e.g. VON HUENE, 1901; NOPSCA, 1903) or eggs (GRIFFITHS, 1992).

OSTROM further noted that the specimen is preserved on its right hand side and the hands, skull, cervical ribs and posterior gastralia show some disarticulation. According to OSTROM this disarticulation pattern is due to scavengers or more likely the action of gentle bottom currents which dispersed the bones after their connecting tissue decayed. The fact that stomach contents are present

indicates that the peritoneal cavity was not breached before burial. The disarticulation of the posterior gastralia may be due to eruption of decomposition gases from this region when the carcass was on the lagoon floor.

WELLNHOFER (1988b) noted that if Solnhofen pterosaurs were bipedal, their mode of preservation would be as in *Archaeopteryx* and *Compsognathus* (i.e. spread wings embedded dorso-ventrally and hind legs still in acetabular articulation, although directed to one side). He used this to support the case for pterosaur quadrupedal locomotion.

Results and Discussion

Cause of death: The cause of death of *Archaeopteryx* can never be ascertained although it was not due to predation (as revealed by the fully articulated nature of the specimens and the fact that no bones of *Archaeopteryx* show signs of biting/gnawing, fracturing etc.). MOODIE (1923) argued that the 'bicycling pose' was due to poisoning of the nervous system. It is more likely that this is incorrect and the posture of *Archaeopteryx* and *Compsognathus* is due to osmotic desiccation of the tendons caused by immersion in the hypersaline lagoon. This assumption is further supported by the curved posture evident in some fish and crustaceans specimens.

Biostratinomy: If *Archaeopteryx* and *Compsognathus* were terrestrial animals and they lived on the supposed land mass to the north of the lagoon (BARTHEL *et al.*, 1990) then we must explain their presence within the Solnhofen sediments. We must also explain their rarity in relation to the pterosaurs (pterosaurs are more numerous in the ratio 186+ pterosaurs: 7 *Archaeopteryx*: 1 *Compsognathus*). The pterosaurs of Solnhofen have two principal feeding habi-

Table 1. Pterosaur species of the Solnhofen Limestone with diet and a minimum estimated number of known specimens (primary data from WELLNHOFER, 1990).

Pterosaur species	Diet	Number of species
<i>Rhamphorhynchus gemmingi</i>	Piscivore	108+
<i>Odontorhynchus aculeatus</i>	?	?
<i>Scaphognathus crassirostris</i>	Piscivore	2
<i>Anurognathus ammoni</i>	Insectivore	1
<i>Pterodactylus antiquus</i>	Insectivore?	60+
<i>Gallodactylus suevicus</i>	Piscivore	2
<i>Germanodactylus cristatus</i>	Piscivore	1
<i>Germanodactylus rhamphastinus</i>	Piscivore	3
<i>Ctenochasma procristata</i>	Filter	1
<i>Ctenochasma gracile</i>	Filter	6
<i>Gnathosaurus subulatus</i>	Filter	2

tats (see Table 1) and these indicate two differing ecologies. The piscivorous forms must have fed over the sea (there is no evidence that any fish lived in the lagoon (BARTHEL *et al.*, 1990)) and the insectivorous forms would have fed near to the land mass (very few modern insects live over salt-water, and the insects preserved at Solnhofen all belong to modern families that are closely associated with freshwater in their adult and larval stages). As can be deduced from Table 1 the piscivorous forms probably flew regularly over the lagoon to their marine feeding habitats, thus giving them a higher preservation potential in the lagoon sediments i.e. if they were regularly flying over the lagoon they had a higher chance of 'dropping' into it and hence being preserved. But if the insectivorous forms were mainly 'terrestrial', like *Archaeopteryx*, why are they more numerous than *Archaeopteryx*? I suggest six possible explanations:

- 1) Terrestrial pterosaurs were more common than *Archaeopteryx*, i.e. the apparent relative abundances seen in Table 1 are an actual representation of the real abundances in this terrestrial ecosystem.
- 2) The flying ability of *Archaeopteryx* was poor and it behaved ecologically like a small coelurosaurian dinosaur. This can probably be discounted as there is convincing evidence that *Archaeopteryx* was a capable flier (RIETSCHEL, 1985; NORBERG, 1985).
- 3) Insectivorous pterosaurs were more likely to frequent the lagoonal area than *Archaeopteryx* and hence have a higher preservation potential.
- 4) Insectivorous pterosaurs spent more time on the wing than *Archaeopteryx* and therefore had a higher chance of being blown over the lagoon and drowned by storms and strong winds (the palaeo-latitude of the lagoon was within the monsoonal region, so severe seasonal storms would have been frequent. The affect of such storms on pterosaurs can be inferred as it is known that modern birds can be drowned by such storms—see NAKAMURA, 1973).
- 5) Pterosaurs had a waterproof pelage which allowed them to settle on water hence increasing their preservation potential.
- 6) *Archaeopteryx* was a migrating bird, and its migration path was across the lagoon. During the migration disorientated sick, elderly, or young birds may have died and fell into the lagoon.

Of all of these hypothetical solutions I regard the first as the most probable in light of the available evidence. It is most likely that *Archaeopteryx* and *Compsognathus* were the top predators on the land mass (as there is no evidence of the presence of larger predators, apart from crocodilians). As ecological studies have shown that the numbers of individuals at the top of an ecosystem or food web is small, the apparent rarity of *Archaeopteryx* and *Compsognathus* in relation to the pterosaurs can easily be explained.

The biostratinomy of *Archaeopteryx* has been explained (by others authors

e.g. VIOHL, 1985) by high winds and storms blowing individuals over the lagoon where they were drowned. This cannot be true for *Compsognathus*. The specimen of *Compsognathus* is well articulated and there is no evidence that the soft tissues decayed before the specimen reached the lagoon floor. As palaeo-temperatures for the surface waters of the lagoon were in the region of 26°C (ENGST, 1961), temperatures on land must have been higher. These temperatures are similar to those used in the actualistic experiments of DAVIS and BRIGGS (in press). In these experiments the rate of decay was shown to be very rapid (skeletonisation within 1 to 3 days). Therefore the period of time from the point of death to entombment in the sediments, for *Archaeopteryx* and *Compsognathus*, is unlikely to have been very long (1 to 2 days). This now begs the question of how *Archaeopteryx* and *Compsognathus* became entrained in the lagoon so quickly.

I believe that if the climate were semi-arid with a low annual rainfall (as envisaged by BARTHEL *et al.*, 1990) then a storm or heavy rain would have created flooding. This water would be subject to rapid surface runoff. It is possible that a recently deceased *Compsognathus* was caught by this fast moving water and swept into the lagoon and buried quickly by the turbid water and sediment. The more exquisitely preserved *Archaeopteryx* specimens (the Berlin, Eichstätt and Solnhofen) may well have been preserved in this way although the hypothesis that they were caught in high winds and drowned could still be valid.

All the terrestrial animals have been found in the Kelheim and Eichstätt regions (BARTHEL *et al.*, 1990) (Fig. 1), which is also the source of the best preserved *Archaeopteryx* specimens. Therefore I have assumed that these well preserved *Archaeopteryx* specimens had a similar taphonomic history to *Compsognathus*, because to be well preserved *Archaeopteryx* could not have been transported far from its place of death. The other three *Archaeopteryx* specimens show a greater degree of disarticulation (corresponding to stage 3e on the disarticulation sequence proposed by DAVIS & BRIGGS, in press) and this is to be expected if the specimens were transported for a greater distance (Fig. 2). This point raises the further question of why some specimens were transported further than others. I believe that the following factors explain this anomaly:

- 1) *Archaeopteryx* was carried out over the lagoon, whilst still alive, and then drowned.
- 2) The currents in the lagoon, created by the surface runoff, were stronger due to very high levels of rainfall.
- 3) Not all birds float (*contra* SCHÄFER, 1972; see DAVIS & BRIGGS, in press) and this may have been true for *Archaeopteryx*, whose bones were much more dense and less pneumatized than 'modern birds'. In order to allow *Archaeopteryx* to float for long periods of time, the carcass must have been filled with decay gases, rendering it neutrally buoyant. The decay processes creating the decay gas could only have persisted for

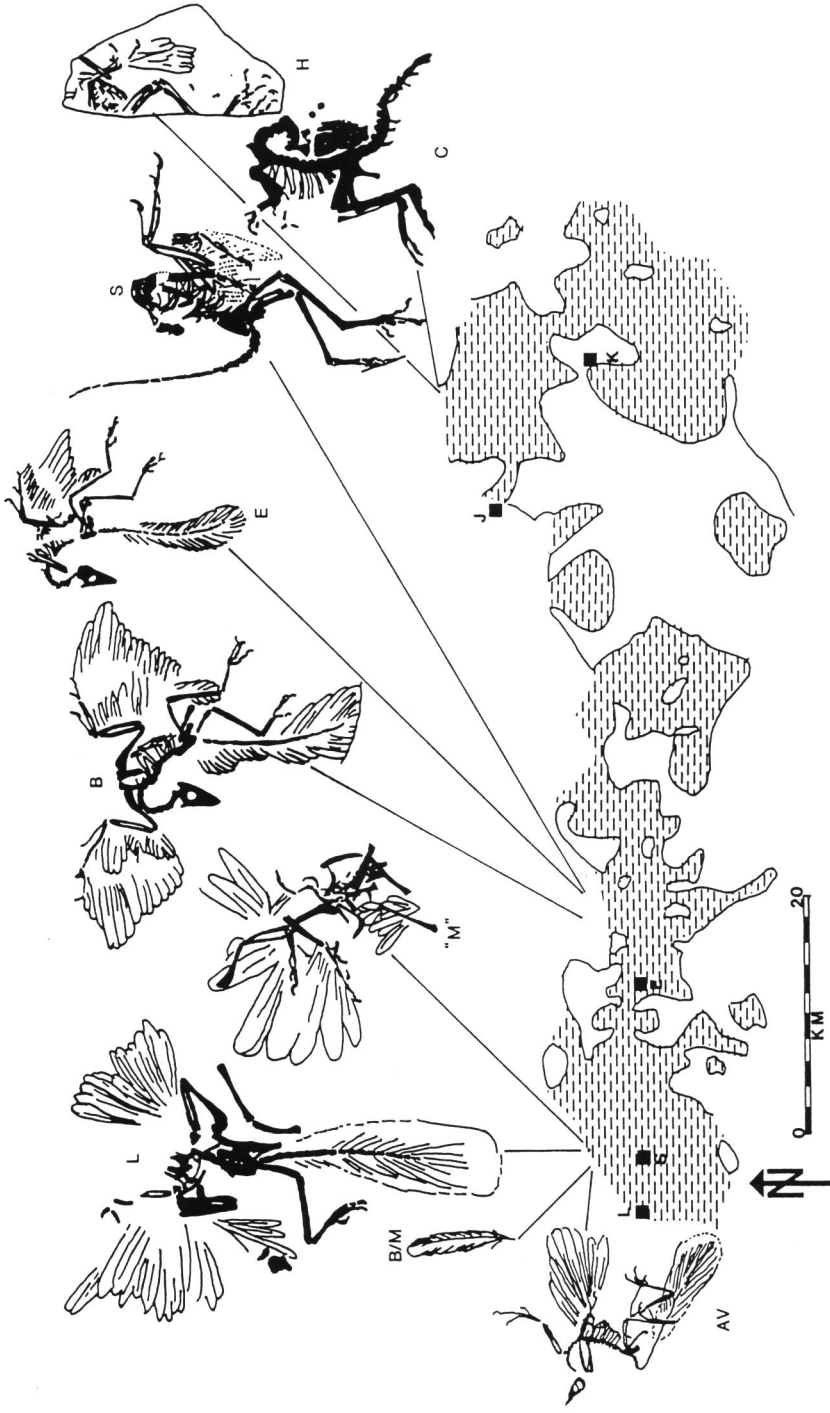


Fig. 1. Geological map of the Solnhofen area with the discovery localities of *Archaeopteryx* and *Compsognathus* marked on. Disarticulation of the specimens increases from East to West. The outcrop of Solnhofen Lithographic Limestone is indicated by dashed fill. Abbreviation: L, Langenaltheim; S, Solnhofen; E, Eichstätt; J, Jachenhausen; K, Kelheim; AV, Aktein-Vereins specimen; B/M, Berlin/Munich feather; L, London specimen; B, Berlin specimen; E, Eichstätt; S, Solnhofen specimen; C, *Compsognathus*; H, Haarlem specimen (adapted from WELLNHOFER, 1988a).

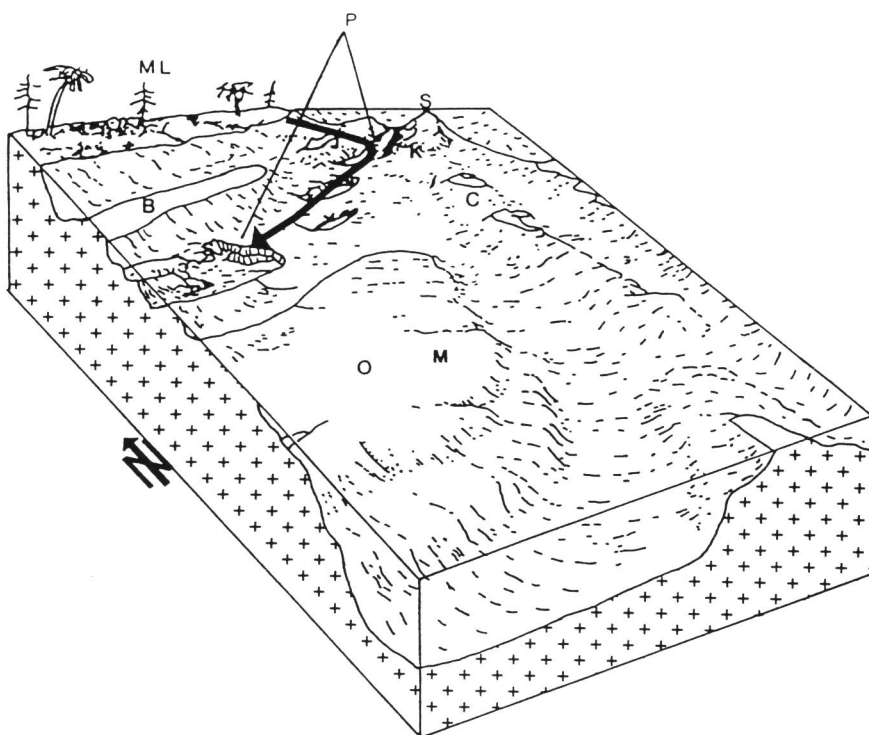


Fig. 2. Palaeogeography of the Solnhofen area. Arrow shows possible direction of transport for *Archaeopteryx* and *Compsognathus* specimens. Direct transport from the westerly Plattenkalk basin was prevented by a barrier, possibly a coral reef/sponge mound/ooid shoal. Abbreviation: ML, Middledeutsch landmass; B, barrier; P, Plattenkalk basin; O, ooid shoal; S, sponge mound; C, coral reef; K, Kelheim; M, Munich; S, Solnhofen (adapted from BARTEL *et al.*, 1990).

several days or the specimen would have disarticulated to a greater extent.

- 4) It is accepted that Solnhofen was hypersaline, which of course would have increased its buoyancy properties (e.g. the Dead Sea) but BARTHEL *et al.* (1990) noted that the climatological factors that created the preservation opportunity would also destroy this hypersalinity by mixing of the water. Therefore hypersalinity cannot explain the floating of the carcasses for prolonged periods.

Further evidence for the above factors can be deduced from Fig. 3. This graph of percentage of specimens in category versus morphological decay stage shows two peaks corresponding to stage 2 (complete skeleton) and stage 3e (skeleton disarticulated: ribs disarticulated from the thoracic vertebrae and the thoracic vertebrae disarticulated into individual vertebrae). If there were only

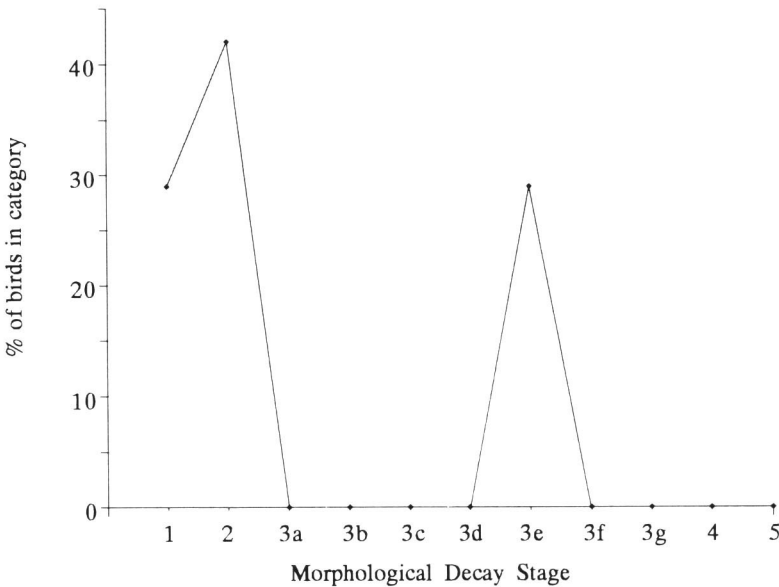


Fig. 3. Graph of the percentages of *Archaeopteryx* specimens from the Solnhofen Lithographic Limestone in each morphological decay stage. The nomenclature and theory behind morphological decay stages follows that of DAVIS and BRIGGS (in press) and is summarised here. 1. The skeleton remains intact and the feathers are still attached to the dermal layers. The internal soft tissues remain, but are undergoing autolysis and bacterial decay. 2. The skeleton is still complete, but the soft tissues have decayed and loosely attached feathers (down, contour etc.) are starting to become detached. 3. The skeleton is now starting to disarticulate. Disarticulation occurs in a set order though some overlap occurs. 3a. The skull and cervical vertebrae detach from the thorax. The skull may remain attached to some cervical vertebrae but it is more usual for these two elements to be totally separated from each other. 3b. The femur disarticulates from the synsacrum. 3c. The pectoral girdle becomes detached from the thorax. The pectoral girdle and forelimbs (wings, sternum, clavicle, coracoids and scapulae) remain articulated as a unit. 3d. The vertebrae in the abdominal region disarticulate. This causes the thorax to separate from the synsacrum. 3e. The ribs disarticulate from the thoracic vertebrae and the thoracic vertebrae disarticulate into individual vertebrae. 3f. The legs separate into individual elements (femur, tibiotarsus, tarsometatarsus and digits). 3g. Final disarticulation occurs between elements of the pectoral girdle (the wings, sternum, clavicle, coracoids and scapulae). 4. The skeleton disarticulates completely and external forces may remove skeletal elements. 5. Only isolated, completely disarticulated, skeletal elements remain. These elements may exhibit damage caused by external forces.

two basins in which the preservation could have occurred, and transport occurred from one basin to the other, then the *Archaeopteryx* skeletons deposited in the nearest basin to the shore (the Eichstätt basin) would be better preserved than those in the further basin (the Solnhofen basin). Because the specimens are

disarticulating whilst being transported only certain morphological decay stages would be preserved. The two peaks in Fig. 3 correspond to deposition in each of the two basins (see Fig. 2). This further emphasizes that transport was from east to west and that the exceptional preservation was limited to these basins of deposition.

Preservation : Once the well preserved *Archaeopteryx* and *Compsognathus* had reached the lagoon floor they would have been covered quickly with sediment that had been resuspended by the turbulent action of the currents transporting the carcass. The carcass would have decayed undisturbed under the sediment so preventing further disarticulation. The preservation of the feathers requires special conditions (DAVIS & BRIGGS, 1995). The other specimens of *Archaeopteryx* (the London, MAXBERG and TAYLOR) specimens eventually came to rest on the lagoon floor, but not in turbid conditions thus allowing them to disarticulate further before being covered with sediment. There is evidence of periodic current activity on the lagoon floor (BARTHEL *et al.* 1990) and this would further disarticulate and scatter the skeletal elements (DAVIS, 1994).

SEILACHER *et al.* (1985) and GALL (1990) demonstrated that microbial films (bacterial jelly) are very important in the preservation of soft bodied fossils in lithographic limestones, and it is likely that they affect the preservation of all fossils in lithographic limestones. There is a smooth area of sediment around the skeleton of the London *Archaeopteryx* which differs markedly in texture to the surrounding matrix. This was used to argue that *Archaeopteryx* is a forgery (by HOYLE & WICKRAMASINGE, 1986). CHARIG *et al.* (1986), however explained the smooth area as "the impression of the animal's cadaver upon parts of the surface". They further elucidated this sentence by saying that "A similar difference in texture may be seen between a human footprint on a mud-flat and the general surface of the surrounding mud".

In the light of SEILACHER *et al.* (1985) and GALL (1990) this duality of texture is more likely to be the effect of a microbial veil/sediment interaction. The sedimentary layers around *Archaeopteryx* have not been compacted to the same degree as the surrounding limestone. This too can be explained by the microbial veil theory. If the cadaver had a veil covering it and extending into the surrounding sediment, it would promote early diagenesis (e.g. PYE *et al.* 1990 described early diagenesis of siderite due to microbial activity). If diagenesis in these regions is early then the differential compaction observed will occur. The diagenesis of the *Archaeopteryx* fossils is quite straightforward in comparison to their biostratinomy. Once the carcass had been covered with sediment this effectively sealed it from the porewaters. It would rapidly form a micro-environment in which reducing conditions predominated (due to decomposition of the organic matter). These conditions would retard decay and increase soft

tissue preservation (DAVIS & BRIGGS, 1995 & in press).

The actual skeletal elements have undergone little diagenetic change. The bone is still preserved as calcium phosphate (hydroxyapatite), the organic constituents (e.g. collagen) having decayed away. The cavities within the bone have formed sites of diagenetic calcite growth and this is evident where the fragile fossil bone is flaked away on the London specimen.

Summary

The Solnhofen Lithographic Limestone has yielded 7 specimens of *Archaeopteryx* (taxonomically divided into two species). As far as can be assessed this represents the complete diversity of birds present in the Upper Jurassic. *Archaeopteryx* was a volant bird which lived on the landmass to the north of the lagoons and transport (with desiccation and decay) to its place of deposition accounts for the nature of the preservation. The specimens are diagenetically well preserved which has allowed much data of taxonomic significance to be obtained from the skeletons.

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