

Biostratinomic Patterns in Archosaur Fossils: Influence of Morphological Organization on Dispersal

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The dispersal of 122 specimens of fossil archosaurs and lepidosaurians from different localities throughout the world, catalogued as fossil-lagerstätten, has been characterized. The analysis is based on the quantification of dispersal by the evaluation of burial position, anatomical disarticulation, overlap and significant absences of bony elements. Our goal is to identify commonalities of morphological organization, and to reveal dispersal patterns. First, we explore a theoretical space of burial positions, and seek logical alignments of variables in order to understand the sequence of the earliest biostratinomic phenomena. Dinosauria and the basal avian specimens (*Archaeopteryx*-like organisms) are biased towards lateral burials with crossed forelimbs or hindlimbs. Pterosauria and Ornithuromorpha have ambivalent burial positions, while Enantiornithes and Confuciusornithidae adopt preferentially dorso-ventral burial positions. There is a significantly negative regression coefficient relating overlap and disarticulation-absence. A high percentage overlap corresponds to a high percentage articulation and completeness of body elements, particularly in laterally lying fossils. Conversely, overlap and disarticulation are not significantly related in specimens with a dorso-ventral burial position. Ambivalence in burial positions is associated with singularities in disarticulation patterns. Aves and Pterosauria both diverge from the general disarticulation sequence of diapsids. The results indicate that dispersal has a strong biological component at least in the initial steps of the biostratinomic process.

Keywords: TAPHONOMY, BIOSTRATINOMY, DISPERSAL STAGES, DISPERSAL SEQUENCES, ARCHOSAURS

Introduction

Taxonomic differences between biostratinomic patterns must be determined to know the extent to which morphological

organization influences taphonomic processes, that is, to understand how information is transferred from the biosphere to the lithosphere. The biostratinomic phase begins with death and/

or biogenic production, and although it could also be the starting point for fossilization and fossilization (Fernandez-López, 2000; Fernandez-López & Fernández-Jalvo, 2002; Müller, 1963), biostratinomy (prior to burial) is the main source of paleoecological and paleobiological information. Most approaches have addressed the importance of environmental conditions in biostratinomic patterns. Weigelt (1989) noted that carcasses adopt different spatial configurations (e.g., sigmoidal-shaped, circular-shaped or bowled) in dry and wet milieus. Subsequently, Schäfer (1972), Hill (1979), Bickart (1984) and Oliver & Graham (1994) studied vertebrate carcass disarticulation during decay under several environmental models. Their conclusions endorse a set of disarticulation sequences, and discuss the parameters involved in the biostratinomic process in different environments. Davis & Briggs (1998) quantified the disarticulation in their study with an actual bird carcass (*aktuopaläontologie*). Davis was the first to attempt a comparative study of fossil and extant aves, pioneering the taphonomic interpretation of *Archaeopteryx* (Davis, 1994, 1996). Each specimen of *Archaeopteryx* shows a particular stage of taphonomic disarticulation that is related to the hydrodynamics of Solnhofen during the Upper Jurassic. There are other landmark papers in avian taphonomy; Brain (1980) and Andrews (1990) address the pattern of bone accumulation in caves while Dodson & Wexlar (1979), Emslie & Messenger (1991), Denys *et al.* (1995), Fisher (1981), Mellet (1974), and Bochenski *et al.* (1993) studied association and transformation in avian bones (e.g., pellets, scatological and

digestive remains).

Ecological observations and aktuopaläontologie have aided in moving the field of paleoecology beyond the study of a set of isolated variables to a more specific complex set of mechanisms and processes that address a particular order in fossil associations (Behrensmeier, 1978, 1982; Behrensmeier & Hill, 1980). Herein we stress the notion that biological organization is crucial to understanding the biostratinomic patterns found in the fossil record. We taphonomically characterize 122 specimens of fossil archosaurs (aves, dinosaurs, pterosaurs, crocodiles) and lizards from different localities throughout the world that have mostly been catalogued as *fossil-lagerstätten*. The analysis is based on the quantification of dispersal by means of the evaluation of burial position, disarticulation, overlapping and significant absences of anatomical elements. Our goal is to highlight commonalities of morphological organization and to reveal trends in dispersal patterns. We are concerned with the integrated interpretation of the preservation processes and their effects on the data collected (Behrensmeier & Kidwell, 1985). In that sense, we are looking for a model that enables a parsimonious explanation for dispersal in a broad spectrum of localities and paleoenvironmental conditions. We contrast our hypothesis evaluating the behavior of dispersal variables among well known *fossil-lagerstätten*. If dispersal as understood here were fully dominated by particular external factors (related with the sedimentological, paleoecological and taphonomical regime) similar dispersal values would be expected no matter which biological group was considered, clustering

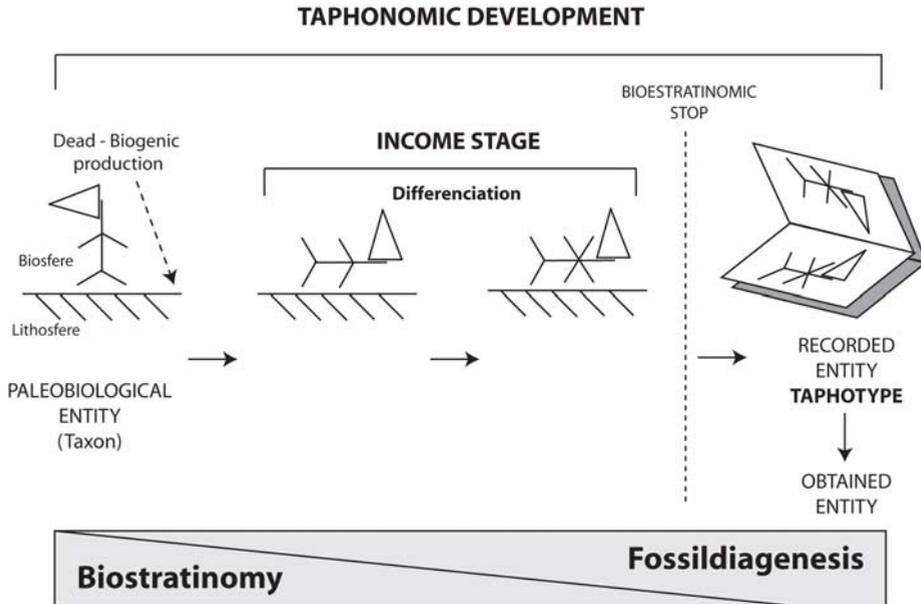


Figure 1. Transference of information from biosphere to lithosphere: we propose that biological influence could be greater at least during the first steps of the biostratinomic process where *postmortem* processes and carcass decomposition begins. The “income stage” shows that the taphonomic bias is biologically constrained.

fossils according the common properties of these localities. We discuss the strength of the model and consider how internal and external factors may affect dispersal.

Theoretical background

We are able to overcome the obstacles posed by incomplete fossil record that shows the destructive dynamics of fossildiagenesis (Efremov, 1940), not only by the increasing number of fossils described, but also by the introduction of a new conceptual system in taphonomy (Fernandez-López, 2000). Taphonomic entities defined as taphon can be

characterized according to their chemical, mineralogical and structural composition. Here, we recognize biostratinomy with a developmental process in which paleobiological entities taphonomically differentiate into organized taphons depending upon not only the environmental conditions under which they were produced and preserved, but also on their former morphological organization (Figure 1). Quantifying the extent to which biological organization affects taphon organization is the objective of this research. We will use the term taphotype to refer to a set of fossils that share a common process of taphonomic differentiation.

The biological component of dispersal

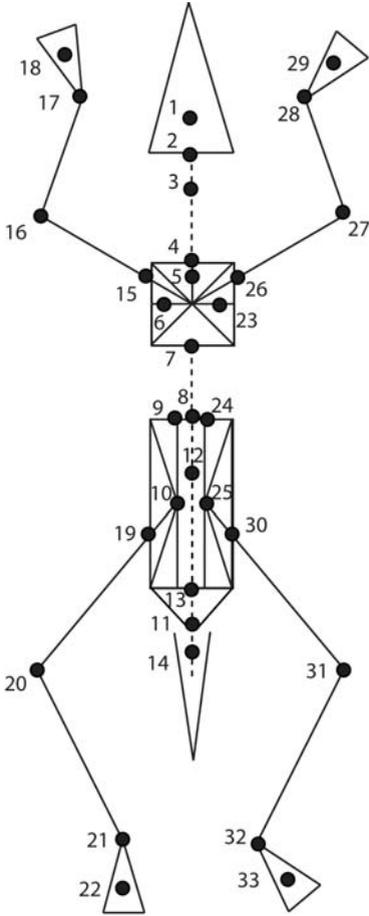
Dispersal has been interpreted and quantified in term of lateral displacement. Lyman (1994) compiles data about the study of dispersal according to the disposition of elements on horizontal and inclined surfaces. Dispersal measurement is based on the quantification of the energetic and transport capabilities of the environment characterized. Dispersal and necrolysis have been related to external factors (Behrensmeyer, 1982). However, we consider that dispersal also involves internal biological factors, which we define as the resistance of the phenotypic organization of organisms to disarticulation. The pattern of dispersal is thus characterized by combination of variables that aim to describe those biological aspects that will influence taphonomic processes: 1) the degree of disarticulation; 2) the disposition of the body after burial; 3) the mapping of overlapping elements; and 4) significant absences of morphological elements. Thus, we use more dispersal variables than did Davis (1996), Davis & Briggs (1998) and Hill (1979). Our initial hypothesis is that taphotypes (quantified using these variables) are significantly linked to their taxonomic group, so that each paleobiological group will have different taphonomic behavior.

Methodological approach

Variables and characters: Based on the biological organization of a tetrapod we use a modular prototype (Figure 2) to summarize complexity (i.e., number of elements and shape). The variables explored are referred to as tetrapod

prototype. The disposition of the body after burial is defined by a combination of stages defined by percentages of articulation, overlap and loss of modules representing biological and taphonomical information. The disarticulation variable is characterized according to 33 joints with significant location. Overlap is defined by the lateral and antero-posterior crossing of a module with the remainder. All possible crossing combinations make up the 153 overlapping characters. The number of characters for the variable absence corresponds to the eleven modules used for the prototype: head, cervical vertebrae, pectoral girdle, dorsal vertebrae, pelvic girdle, sacral vertebrae, forelimb, hand, hindlimb and pes. Significant absences are explored by examining how ontogeny may affect biostratigraphic processes (Marugán *et al.*, 2002), since the connectivity pattern of each module is either ontogenetically or phylogenetically significant. We have used juvenile to immature individuals to track dispersion and absences in these specimens.

Articulation, overlap and significant absences were coded as discrete binary variables in three independent matrices (Appendix 2A, B and C). In the binary code for articulation (1) represents the occurrence of natural articulation or the maintenance of elements' biological orientation, while (0) indicates that elements are neither oriented nor articulated. Overlap of elements within and between modules is given a value of (1). Significant absences are coded as (1) when more than 50% of elements of one module are lost. Each matrix includes particular cases that represent ideal cases of complete articulation (T_{dmin}, minimum theoretical disarticulation) or complete disarticulation



MODULE (abbreviation)	VARIABLE	
HEAD (Head)	1	Head - Head
	2	Head - Neck
CERVICAL VERTEBRAE (Neck)	3	Neck - Neck
	4	Neck - Dorsal
PECTORAL GIRDLE (Pect)	5	Pect (r) - Pect (l)
	6	Pect (r) - Pect (l)
DORSAL VERTEBRAE (Dorsal)	7	Dorsal - Dorsal
	8	Dorsal - Sacral
PELVIC GIRDLE (Pelv)	9	Sacral - Pelv (l)
	10	Pelv (l) - Pelv (l)
	11	Pelv (i) - Pelv (r)
SACRAL VERTEBRAE (Sacral)	12	Sacral - Sacral
	13	Sacral - Caudal
CAUDAL VERTEBRAE (Caudal)	14	Caudal - Caudal
FORELIMB (Fore)	15	Pect (l) - Fore (l)
	16	Fore (l) - Fore (l)
ANTERIOR AUTOPOD (Hand)	17	Fore (l) - Hand (l)
	18	Hand (l) - Hand (l)
	19	Hand (l) - Hand (l)
HINDLIMB (Hind)	20	Pelv (l) - Hind (l)
	21	Hind (l) - Hind (l)
POSTERIOR AUTOPOD (Pes)	22	Hind (l) - Pes (l)
	23	Pect (r) - Pect (r)
	24	Pelv (r) - Pes (r)
	25	Pelv (r) - Pelv (r)
	26	Pect (r) - Fore (r)
	27	Fore (r) - Fore (r)
	28	Fore (r) - Hand (r)
	29	Hand (r) - Hand (r)
	30	Pelv (r) - Hind (r)
	31	Hind (r) - Hind (r)
	32	Hind (r) - Pes (r)
	33	Pelv (r) - Pes (r)

Figure 2. Tetrapod prototype. Note that variables representing connections, within and between modules, are indicated by circles. Variables describe individual disarticulation.

(T_{dmax}), overlap (T_{omax}), or non-overlap (T_{omin}), and likewise for absence (T_{abmax} and T_{abmin}). Articulation data were transformed to disarticulation data (100 % of articulation) to obtain more information about the biostratinomic process. We have used also the sum of two matrixes (disarticulation + absences) as a sole matrix for the sake of simplicity (see below).

The null hypothesis: It is reasonable to assume that, in the absence of any biological bias, the biostratinomic process could be driven purely by external environmental factors. However, an organism's properties stem from its morphological organization: a) modular arrangement of structures; b) relative proportions of bony elements; c) degree of internal connectivity that each module presents (i.e., compactness); d) number of articulations; and e) relationship between body surface area and volume. We hypothesize that earliest biostratinomic stages could be influencing more dispersal due to the imprint of these biological properties.

To deduce how this bias arises we first explore a theoretical space of burial positions in order to determine trends within the sample and then seek logical alignments between the overlap, disarticulation and absence variables. We introduce the idea of logical *alignment of variables* as a sequential set of phenomena. We explore how these three variables could be related, whether overlap takes place during the production of carcasses, and whether disarticulation process precedes the absence of elements (in adults). We tackle the issue of which types of organic properties limit the taphonomical preferences of each group.

The sample

The sample comprises 122 specimens taken from published photographs and drawings (see Appendix 1 for data sources). All of them are of diapsid reptiles, mostly archosaurians (Crocodylomorpha, Pterosauria, Dinosauria and Aves) and a few squamata lepidosaurians (representing Lacertidae and Varanidae groups). Aves (Sanz, 1999; Chiappe & Witmer, 2002) is represented by 39 cases: 13 Ornithuromorpha representing the modern avian forms (basal forms like *Apsaravis* genus and Neornithes orders as Charadriiformes, Piciformes, Coraciiformes, Psittaciformes, Ciconiiformes); 7 Archaeopteryx-like forms gathering almost all the *Archaeopteryx* examples plus *Jeholornis prima*, *Rahona ostromi*, and *Sapeornis chaoyangensis*; 11 Enantiornithes (*Iberomesornis*, *Noguerornis* and Euenantiornithes genera such as *Concornis*, *Eoalulavis*, *Eocathayornis*, *Sinornis*, *Protopteryx* and *Neuquenornis*); 7 members of the family Confuciusornithidae (*Confuciusornis*, *Changchengornis* and one juvenile exemplar *Lianxornis*). Dinosauria is represented by 30 cases: *Lagosuchus*, 11 Ornithischia (Thyreophora, Ceratopsia and Ornithopoda) and 18 Saurischia (Theropoda and Sauropoda). Crocodylomorpha is represented by only 5 cases, gathering members of the clade Neosuchia (MCCM LH-6009, *Atoposaurus oberndorferi*, and *Montsecosuchus*, all of them from the family Atoposauridae. A form related probably to an advanced Neosuchia MCCM LH 7287), and 2 basal crocodiles one is *Crocodylaemus robustus* and the other a Gobiosuchidae from the outcrop of Las

Table 1. Pair-wise comparison of fossil-lagerstätten. Values represent the analysis of means for independent samples (“T Test”) for the percentages of disarticulation-absence and overlapping. Note that means are significantly different for $p < 0.05$.

		Solnhofen (lagoon)	Las Hoyas (lake)	Yixian Formation (lake)
Messel (lake)	Disarticulation- Absence	$t_{44} = 0.53; p = 0.60$	$t_{21} = -2.15; p = 0.05$	$t_{27} = -1.51; p = 0.14$
	Overlapping	$t_{44} = 0.50; p = 0.04$	$t_{21} = 1.56; p = 0.13$	$t_{27} = -1.82; p = 0.08$
Solnhofen (lagoon)	Disarticulation- Absence		$t_{47} = -3.53; p < 0.01$	$t_{53} = -2.95; p = 0.01$
	Overlapping		$t_{47} = 1.56; p < 0.01$	$t_{53} = 4.90; p < 0.01$
Las Hoyas (lake)			Disarticulation- Absence	$t_{30} = 0.46; p = 0.65$
			Overlapping	$t_{30} = -0.26; p = 0.80$

Hoyas MCCM LH-7991). Pterosauria is represented by 38 cases: 20 members of suborder Rhamphorhynchoidea (including families Dimorphodontidae, Eudimorphodontidae, Rhamphorhynchidae and Anurognathidae) and 16 Pterodactyloidea (Pterodactylidae, Germanodactylidae and Ctenochasmatidae) and two unclear classified exemplars.

Specimens come from differently aged (Eocene, upper Cretaceous, lower Cretaceous and upper Jurassic) continental or transitional *Konservat lagerstätten* from all over the world (Europe, Asia, North and South America). To diversify and expand the preservational and environmental background of the sample, other Jurassic to Cretaceous fossil sites famous and dinosaurian assemblages were added (see Appendix 1). The sample size ranged from 113.54 mm² for juvenile and immature individuals, through 35,860.49 mm² for the fossil lagerstätten specimens, to 4.8-x-10⁷ mm² for the large dinosaurs.

Results

Testing the null hypothesis

To test the influence of external factors in the present study we have selected those localities better sampled with a significant sample size: Solnhofen, Messel, Las Hoyas and Yixian Formation. These localities are well known fossil *Konservat-lagerstätten*. Solnhofen sedimentary environment is interpreted as lagoon waters with high salinity density stratification, resulting in stagnation and hostile bottom environment with no indications of strong bottom currents (Viohl, 1990). Las Hoyas consists of lacustrine deposits of shallow freshwater formed in a subtropical and semiarid climate with alternating annual wet and dry seasons (Fregenal-Martínez & Meléndez, 1995). The formation of sediments was driven by the autochthonous carbonate production (i.e., chemical precipitation and bioinduction with algal and bacterial mats).

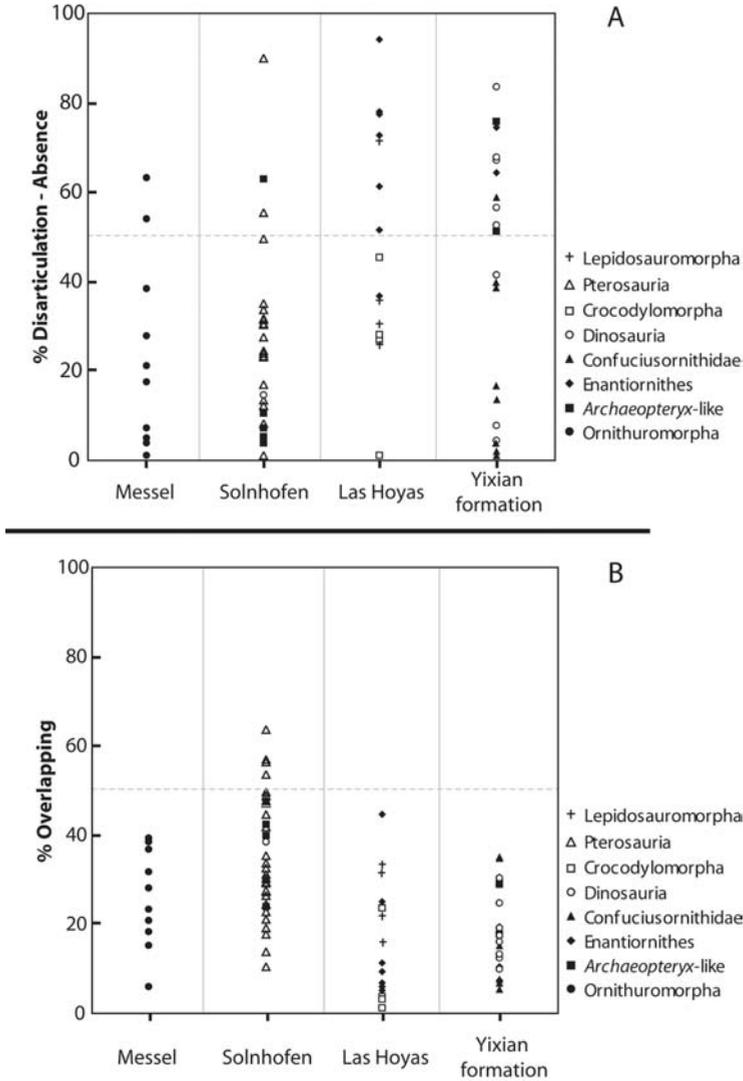


Figure 3. Representation of the values of A) disarticulation and absence, and B) overlapping of fossils from Messel (Eocene), Solnhofen (Upper Jurassic), Las Hoyas and Yixian (Lower Cretaceous).

The delicate laminated preservation of facies indicates an anoxic bottom due to the high production of organic matter. The Yixian Formation is composed of alternate

series of lacustrine and volcanic sediments that were deposited in the bottom of freshwater shallow rivers and lakes (less than 10 m). The climate was semi-arid and

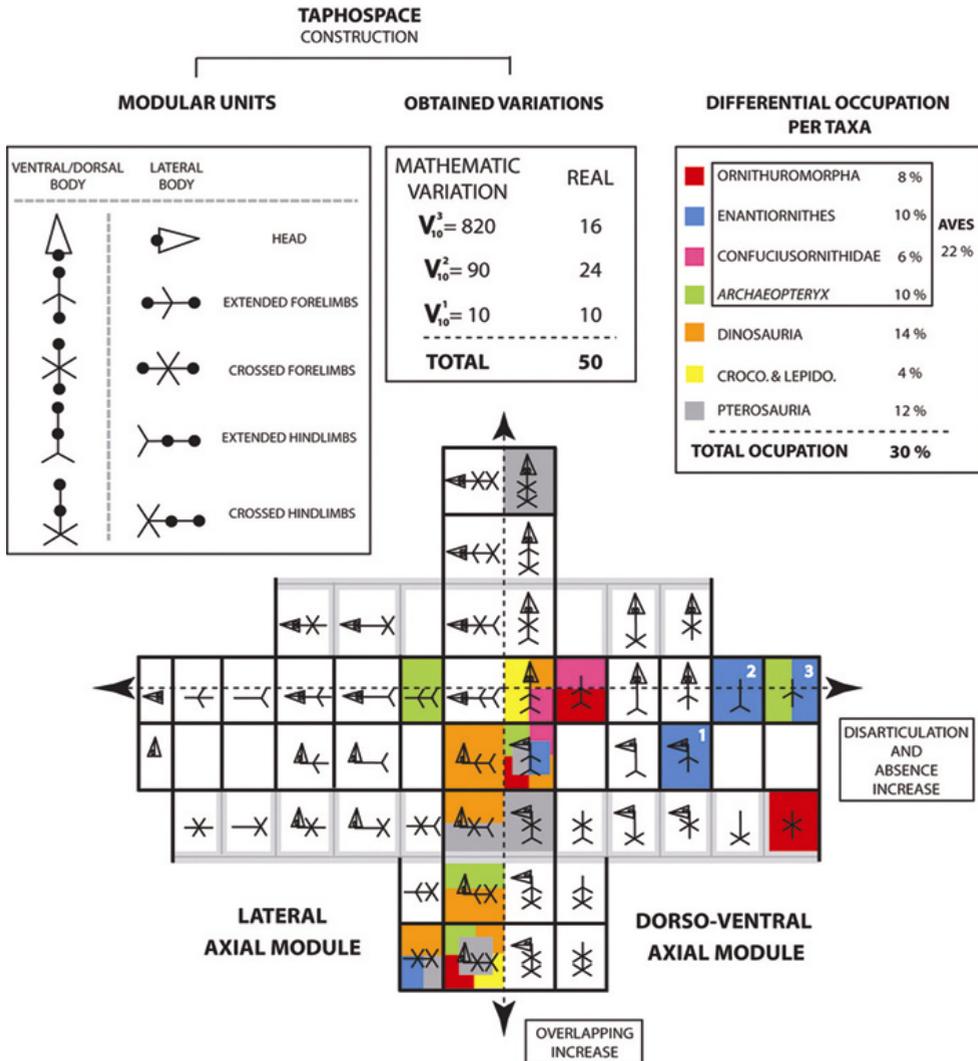


Figure 4. Theoretical taphospace. Left and middle top show modular units and mathematics variations calculated to construct the theoretical taphospace. The representation of the taphospace combines data on disarticulation, overlap and absence. Grey lines mean not overlapping increase zones, and white boxes represent configurations not found in the sample. Top right shows the different colours selected to represent each taxa. Over taphospace different colours represent the spatial configurations occupied by each group. Boxes 1, 2 and 3 represent specimens that are incomplete due to particular circumstances of fieldwork bias or posterior fossil-diagenetic alteration. They are *ex situ* specimens and/or broken slabs (*Eoalulavis hoyasi*, Sanz et al. 1996; *Noguerornis gonzalezi*, Lacasa 1986; *Eo-cathayonis walkeri*, Zhou 2002). The incompleteness of these specimens biases the sample of enantiornithines towards an extreme percentage in the bivariate plot of overlap and disarticulation-absence (see also figure 5).

the volcanic horizons likely correlate with mass mortality events that probably would have entombed most of the organisms present in the water column (Zhou *et al.*, 2003). Grube Messel fossil content was deposited on the bottom of a small lake that has been interpreted as warm-monomictic subtropical type. It has been considered *Konservat-lagerstätten* with limnic stagnation, with anoxic conditions, and without bioturbation. Messel claystones are rich in algal layers that would contribute as conservational traps (Franzen, 1990).

External factors (e.g. sedimentary rate, nature of sediment, presence or absence of algal mats, pH, oxygenate or anoxia of the environment, the hydrodynamic regime, etc.) should exert their imprint differentiating and clustering localities, hence sorting out taphons with equivalent taphonomical characteristics.

Table 1 shows that the sole locality in which disarticulation and overlapping differ from the remainder is Solnhofen. We presume that this locality contributes its own sedimentary, paleoecological and taphonomical regimes influencing dispersal (i.e., percentage of disarticulation-absence and percentage overlapping). Figure 3 A and B shows the distribution of fossils per locality. The range of the variable Disarticulation-Absence (Figure 3A) is similar in all the analysed localities. The percentage of disarticulation comprises all values, being more packed in Solnhofen (between 0 and 40 with the exception of few pterosaurs and one *Archaeopteryx* specimen). The variable overlapping (Figure 3B) is less than 50% in all the localities except Solnhofen that cross this threshold.

Taphospace: body burial disposition

The disposition of the body after burial is analysed using a combinatorial taphospace to reveal all the theoretically possible situations (Figure 4). For the sake of simplicity, we have used only the three principal modules: the head, forelimb and hindlimb. We consider that each could be orientated in profile (laterally left, or right) or lying (downward or upward). Furthermore, forelimbs or hindlimbs may overlap. The resulting ten possible conditions (modular units in Figure 4) can be combined according to their articulation (elements remain fully or partially articulated or isolated). The combinatorial calculation yields a total of 50 biological meaningful burial dispositions (Figure 4). The taphospace has two principal axes: the horizontal one deals with disarticulation (preservation of one, two or three modules), and the vertical deals with overlap. Theoretical taphospace has 30% occupancy when natural occurrences are indicated (see different colours plot in the taphospace; Figure 4).

Gaps in the taphospace show the stages in the biostratinomic process that are least likely to occur. For example, taphospace is biased, especially with respect to the presence-absence of the skull. The skull is recurrently absent especially in flying reptiles. There seems to be a greater skull loss in lateral than in dorso-ventral burial positions. Skull should be the earliest module to disappear as deduced from the interplay of the presence or absence of the remaining modules. Lateral and dorso-ventral burial patterns without the skull retain the articulation between forelimbs and hindlimbs, and there is no match combining the presence of skull with the

Table 2. Representation of data obtained in the correspondence analysis of different taxa versus the burial position of each specimen. A contingency test shows that the difference between the lateral and dorso-ventral groups is significant ($\chi^2 = 18.086$; $p = 0.021$).

Taxa	Dorso-ventral position	Lateral position	Number of individuals
Ornithuromorpha	7	6	13
<i>Archaeopteryx</i> -like	2	6	8
Enantiornithes	7	4	11
Confuciusornithidae	7	0	7
Dinosauria	9	21	30
Crocodylomorpha	5	2	7
Pterosauria	18	20	38
Lepidosauromorpha	6	2	8
Number of individuals	61	61	122

absence of appendages. Three particular cases (1-3) are also highlighted at theoretical taphospace. These concern unnatural burial positions due to particular bias arising during the recovery of fossils or due to special biostratigraphic processes (see Figure 4 and 5 captions).

Differential occupation by taxa may be appreciated in the 50 real burial positions described in the taphospace. Aves (22%): Ornithuromorpha (8%), Enantiornithes (10%), Confuciusornithidae (6%) and *Archaeopteryx*-like forms (10%); Dinosauria (14%); Pterosauria (12%); and Crocodylomorpha plus Lepidosauromorpha (4%). It may be of particular significance that the value for the latter group is so low, although as it is the most poorly represented, the small sample size prevents any firm conclusion being drawn. Flying organisms (pterosaurs + active flying Aves)

adopt a wider variety of burial positions than do non-flying animals (Dinosauria + basal Aves).

The crucial point in the evaluation of taphospace occupation is whether any group follows a pattern of burial position. Significance has been tested using correspondence analysis of the two categories (lateral and dorso-ventral) for all the biological groups. Dinosauria and the basal avian specimens (*Archaeopteryx*-like organisms) are biased towards lateral burials with crossed forelimbs or hindlimbs (see Table 2). Otherwise, Pterosauria and Ornithuromorpha do not show any preference, while Enantiornithes adopt dorso-ventral burial positions preferentially to lateral ones.

Alignment of dispersal variables

To describe each group with respect to the variables of overlap, disarticulation and significant absences, we performed a cluster analysis of each matrix to obtain the symmetric distance matrix using the ideal extreme cases (Tdmax, Tomax and Tabmax) as a reference. Estimates of percentage disarticulation, overlap and absences were obtained for each specimen using PAST software (Harper, 2003).

Examining the covariation of significant absences and disarticulation revealed a positive linear relationship (ANOVA, $F_{1,121} = 291.481$; $p = 0.0004$; $R^2 = 0.708$). This suggests that the absence of a module is somehow related to its former disarticulation. This is especially meaningful for terminal units such as the skull and autopod. Otherwise, there would also be disarticulated elements that are not absent from the specimen.

Figure 5 shows a bivariate graph in which overlap is plotted against the sum of two matrices (Disarticulation + Absences). Overall, although the regression model has a small correlation coefficient ($R^2 = 0.140$), the ANOVA confirms the dependence between the two variables (see Table 3). The entire sample follows a general trend of negative association between overlap and disarticulation. In Table 3 we have included regression model data for the various taxa included in the sample. Significant values are observed for Ornithuromorpha and Confuciusornithidae groups. In particular, Confuciusornithidae has a positive relation between disarticulation and overlap. We have grouped the sample into two categories, lateral and dorso-ventral. Only the group of lateral individuals is

significantly dependent on the relation with both variables, while the dorso-ventral position showed no dependency between overlap and disarticulation-absence. Overlap and disarticulation are not significantly related in specimens with a dorso-ventral configuration. Specimens with a low or high degree of overlap may be highly disarticulated.

In lateral burial configurations the slope of the regression is significantly negative (Figure 5) and a high percentage overlap is associated with a high percentage of articulation and completeness of body elements (low disarticulation). Furthermore, the percentage of overlap in the lateral burial configuration is significantly higher than in the dorso-ventral configuration (see Table 3 and top right square of Figure 5). This latter result introduces a discordance when sequences of disarticulation are explored (see sequences of disarticulation). Finally, we checked whether individual size has an effect on burial position. Table 4 shows that the mean area of specimens (Appendix 1) does not significantly differ for lateral and dorso-ventral burial positions ($t_{90} = -1.471$; $p = 0.145$).

Sequences of disarticulation

Common patterns have been sought to describe the sequence of disarticulation. A general sequence for diapsid reptiles overall, and particular sequences for Aves, Pterosauria, and non-avian dinosaurs have been obtained. We compare our results with those disarticulation sequences described empirically in mammals and birds using actuo-taphonomy (Hill, 1979; Schäfer, 1972; Davis & Briggs, 1998).

The general sequence in Diapsida

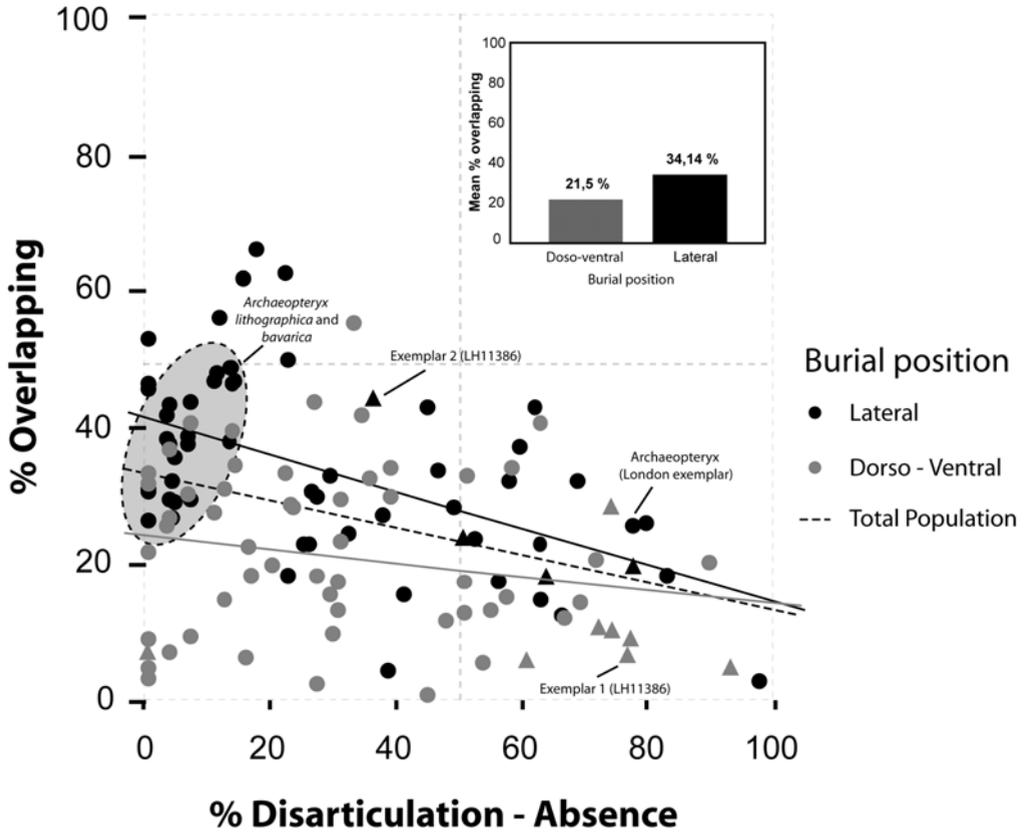


Figure 5. Empirical taphospace: relationship between overlap and disarticulation plus absence. The sample follows a general trend with a negative slope. In the upper-right square are plotted the significantly different means of overlap for lateral and dorso-ventral positions. All *Archaeopteryx* exemplars fall within the grey circle except for the London specimen, which has a different pattern. Exemplars 1 and 2 (LH11386) are special cases within the Enantiornithes (represented by triangles). Two individuals are found in association with other specimens (isolated elements of other unknown archosaurs, Sanz et al. 2001). These two present different dispersal stages. Exemplar 2 LH 11386 shows an extreme overlap value with low disarticulation, while Exemplar 1 (LH11386, same slab) is placed close to the greatest disarticulation values and low overlapping. The association itself is evidence that it was probably produced by separate biostratinomic processes, and not by the same biostratinomic event (the association was formerly interpreted as the result of the accumulation by a biological agent, dinosaur pellet, Sanz et al. 2001).

highlights how disarticulation follows modular body organization (see Figure 6A), rather than random isolated elements. Four units of disconnection are recognised:

pelvic girdle and thoracic cage with dorsal vertebrae, head plus cervical vertebrae, posterior limbs, and pectoral girdle including forelimbs. Figure 6A shows the

direction of disarticulation of this sequence: pectoral girdle, forelimbs, hindlimbs and the column including neck and skull. Despite the large number of boxes without a skull that we found in the taphospace, the disarticulation sequence shows that the skull is not among the first disarticulation stages.

The axial line starts its disarticulation from skull to caudal vertebrae after the left and right halves of the pelvic girdle becomes separated. This sequence may be compared with that obtained by Hill (1979) for the African bovid *Damaliscus korrigum*. Hill localized an equivalent number of units that followed a similar disconnection pattern (see Figure 6B). Figure 6 also includes the disarticulation sequence of specimens that have a significant (see Tables 2 and 3) lateral burial position (i.e. *Archaeopteryx* and non-avian dinosaurs, Figure 6C). Disarticulation follows a similar modular pattern of disconnection to that of the general sequence. The result resembles that of mammals quite closely.

The sequence obtained for flying archosaurs, Aves (Ornithuromorpha, *Archaeopteryx*, Enantiornithes and Confuciusornithidae) and Pterosauria, is represented in Figure 7A and B. Pterosaurs does not present a modular pattern in the disarticulation process (Figure 7B). This could be the result of their singular (autopomorphic) anatomical configuration. The sequence obtained for Aves features a set of variations on the general patten described above (Figure 7A). The most relevant aspect is the disarticulation of the forelimb in association with the anterior-mid axial column and skull. On the other hand, the hindlimb is more closely related

to the posterior axial column and hips. This has morphological foundations in the development of the anterior locomotor apparatus as it becomes a flying apparatus (Sanz, 1999).

Discussion

The sample includes individuals produced in different *Konservat lagerstätten* (see Appendix 1): Las Hoyas, Spain (Sanz *et al.*, 1988, Martínez-Delclós, 1991, Fregenal-Martínez & Meléndez, 1995); Yixian Formation, China (Zhou *et al.*, 2003); Solnhofen, Germany (Davis, 1996); Messel, Germany (Briggs & Crowther, 2001). The sampled individuals were produced under different environmental and taphonomical conditions; nonetheless, all of them share a high degree of skeletal completeness that permit us suppose that fossildiagenesis phase was reduced (some of the specimens have mineralized soft tissues as feathers, scales). We provide paleobiological criteria for the understanding of skeletal dispersal in fossils that were rapidly buried by biostratinomic processes.

Variables coded using discrete binary states are a simple way to survey overlap, articulation and absence of skeletal units (see data Appendix 2A, B and C). Ambiguous choices occurred mainly due to variable disarticulation, and were resolved by attributing the state of maximum taphonomical alteration, i.e., if one natural articulation was not evident the character was assigned a code of 0.

Theoretical and empirical taphospace illustrate that variability of dispersal taphonomic factors is also constrained by morphological features and

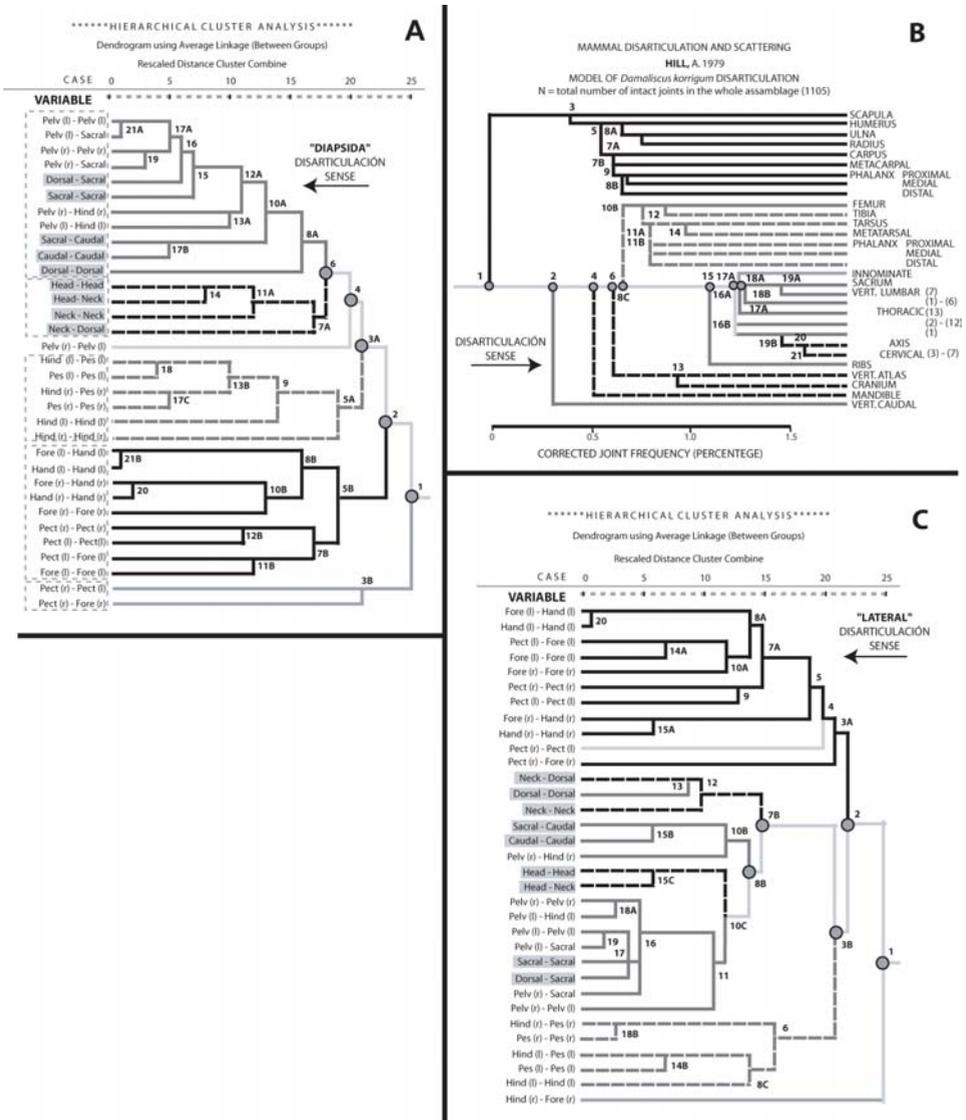


Figure 6. Disarticulation sequence. A) Consensus disarticulation sequence for the entire selected sample (n = 122). B) Disarticulation sequence proposed by Hill (1979) for mammal's carcass (*Damaliscus korrigum*) in Lake Turkana (Kenya). In this case, n = 1115 (articulations by area unit). C) Sequence of disarticulation in exemplars with lateral burial position. Note the modular pattern in the different sequences. Four units of disconnection are recognised: pelvic girdle and thoracic cage with dorsal vertebrae, head plus cervical vertebrae, posterior limbs, and pectoral girdle including forelimbs.

burial position (Figures 4 and 5). Morphological features concern body organisation, either as a compendium of morphological analogies or as singular body plans (apomorphies). Morphology conditions trends in burial position and sequence of disarticulation patterns.

The entire sample follows a general pattern of negative correspondence between overlap and disarticulation-absence. It should be stressed that the *Chi*-square contingency test confirms that this trend is highly significantly different in taphotypes with lateral burial positions (Table 3). In other words, overlapping is positively correlated with articulation. In addition, overlap and disarticulation depend

on individual size (represented in the area enclosed by each specimen, $F_{2,91} = 3.564$, $p = 0.032$), showing that the greatest area correlates with the most highly overlapping and articulated specimens. Thus, it is not surprising that the lateral burial position predominates in dinosaurs and in basal avian birds, such as *Archaeopteryx*-like. In both groups the two pairs of extremities overlap, and the head is exposed laterally (Figure 4).

The disarticulation sequence for dinosaurs and basal birds is similar to that proposed for bovids by Hill (1979, Figure 6B). These similarities have three major implications. First, there is an analogous sequence in which head and neck are placed

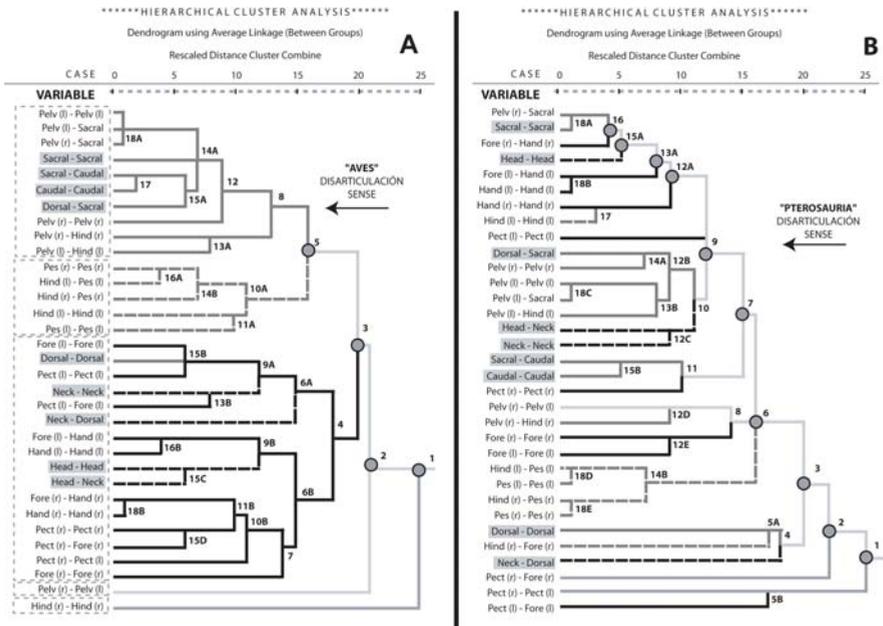


Figure 7. Disarticulation sequences of flying archosaurs. A) Aves disarticulation sequence (n = 39: *Archaeopteryx*, Confuciusornithidae, Enantiornithes and Ornithuromorpha). B) Pterosauria (n = 38) have a unique disarticulation sequence in which the earliest forelimb disconnection from pectoral girdle is the most striking feature. In Aves sequences the pattern of disarticulation is characterized by a link between the disarticulation of head and neck with pectoral girdle disarticulation.

Table 3. Linear regression statistics for relationship between overlap and disarticulation-absence for each taxonomic group in our sample. Modern birds (*Ornithuromorpha*), *Confuciusornithidae* and *Dinosauria* have particularly significant results (in bold).

TAXA	Linear Regression Model Overlap / Disarticulation-Absence			Regression Slope
	Correlation coefficient (R ²)	ANOVA		
		F	p	
Ornithuromorpha	0.703	F _{1,12} = 26.018	<0.05	–
<i>Archaeopteryx</i> -like	0.493	F _{1,7} = 5.852	0.052	–
Enantiornithes	0.093	F _{1,10} = 0.926	0.361	–
Confuciusornithidae	0.876	F _{1,6} = 35.181	0.001	+
Dinosauria	0.150	F _{1,29} = 4.924	0.034	–
Crocodylomorpha	0.026	F _{1,6} = 0.136	0.727	–
Pterosauria	0.140	F _{1,37} = 5.841	0.020	–
Lepidosauromorpha	0.325	F _{1,7} = 2.892	0.139	–
Lateral position	0.288	F _{1,60} = 23.942	<0.05	–
Dorso-ventral position	0.043	F _{1,60} = 2.660	0.108	–
Total population	0.140	F_{1,121} = 19.528	<0.05	–

in different branches (Figure 6C), implying a two-stage disarticulation. Cervical vertebrae become disarticulated before (branch 15, Figure 6C) the connection between atlas-axis complex and head (branch 12, Figure 6C). Second, it may be stressed that the lateral burial position prevails over the dorso-ventral position in all these cases. It is suspected that morphological analogies (such as forelimb and hindlimb proportions, relative size and number of connections between biological modules) are important in determining

burial position. This hypothesis should be investigated in future work. Third, it is striking that actuo-taphonomy provides similar results to those analyses that use fossils exclusively; in other words, actualism is perfectly applicable.

In contrast, pterosaurs and birds (archosaurs with active flight) have no preferential burial position. There are similar percentages for lateral and dorso-ventral positions (Table 4). Aves contains groups that follow the general lateral trend (e.g., the *Ornithuromorpha* group has an

Table 4. Comparison of means of the two categories established in the empirical taphospace (lateral and dorso-ventral burial position). The mean overlap of the two groups differs significantly ($t_{120} = -5.312$; $p < 0.05$). The mean of specimens per burial categories does not.

Group	Mean overlap (%)	Mean area (mm ²)	Number of individuals
Dorso-ventral	21.556	48657.722	50
Lateral	34.141	1396578.116	42
Total population	27.848	664012.684	92

extremely significant linear regression; Table 2: $F_{1,12} = 26.018$; $p < 0.05$; $R^2 = 0.703$), and others like Confuciosornithidae that possess a singular regime of overlap and disarticulation ($F_{1,6} = 35.181$; $p = 0.001$; $R^2 = 0.876$; positive slope, see Table 2). Ambivalence in burial positions is associated with the singularity of the disarticulation patterns in Aves and Pterosauria, which both diverge from the general sequence of diapsid disarticulation.

Aves and Pterosauria disarticulation sequences (Figure 7) reflect unique and very distinct patterns. Some particular aspects may be relevant in Aves, such as the relationship between the disarticulation of the pectoral girdle-forelimbs closely associated with the neck, head and dorsal vertebrae disarticulation. This suggests that the anterior half of the axial module is strongly connected to the pectoral girdle standing out morphological factors associated with the flight apparatus (Sanz, 1999). On the other hand, Pterosauria have a unique disarticulation sequence whose most striking feature is the early forelimb disconnection from pectoral girdle (see Figure 7 A and B for comparison. In Aves the disarticulation takes place in branches 11 and 13, while in Pterosauria it occurs in branches 1 and 2).

This particular pattern could be due to the special pterosaurian body plan, which features: 1) the presence of an extra, autapomorphic bone (the pteroid) in the pterosaur wrist that supports a small anterior flight membrane; and 2) the connection between forelimbs and hindlimbs through the patagio. This second trait reflects a strong phylogenetic influence that highlights the primitive condition exhibited by the Rhamphorhynchoidea group. The Pterosaur disarticulation sequence also features the loss of the modular regime that occurs in the sequences of Dinosauria, Mammals and Aves.

The last group comprises crocodiles and lizards that represent the smallest sample in taphospace. They are largely included within the dorso-ventral configurations with the head in dorsal or ventral view (Figure 4). They usually present the extremities extended. Crocodylomorpha have a more compact axial module associated with their bony dermal armour representing a key limitation on the burial position. However, basal taxa (LH 13777 a Gobiosuchidae from the Las Hoyas outcrop) that has reduced armour occupies a different place within taphospace. To be precise, this specimen is

situated next to the dinosaur and basal bird groups (*Archaeopteryx*).

Fossil lagerstätten maintain exceptional preservation (fossils usually are preserved in two dimensions). They are herein regarded as the product of a set of ordered processes that took place during the dispersal and disarticulation sequence. Depending on their morphology, carcasses adopt a preferential position. A lateral burial position favours the overlap of anatomical units that, in turn, prevents disarticulation and absence (loss) of elements (circular highlighted zone, Figure 5). A dorso-ventral position does not involve overlap. In general, this taphotype has a low percentage of overlap and a wide range of disarticulation-absence values. When overlap increase in dorso-lateral taphotypes they may exhibit a high percentage of disarticulation-absence (e.g., *Confuciusornithidae*).

We have considered dispersal to be synonymous with scattering (page 122, Lyman 1994). However, we have explored dispersal as the resistance of the phenotypic organization of organisms to disarticulation, introducing variables that might quantify the differential compactness of connectivity among skeletal modules, or skeletal features that could be involved in overlapping (e.g. the proportion of fore and hindlimbs with body length). We have left for future studies other potential variables that should affect dispersal such as the nature of epidermal tegument (presence/absence of feathers, osteoderms, and scales). The results show that dispersal has a biological component (see Figure 4, and sequences of disarticulation in figures 6 and 7). Biological influence can be estimated comparing disarticulation-absence and

overlapping percentages inside each taxonomic group. The different groups show significantly different means of these variables (for disarticulation-absence $F_{7,114} = 3,016$, $p = 0,006$ and for overlapping $F_{7,114} = 5,637$, $p = <0,05$). Therefore, the taxonomical attribution of each specimen can be predicted from dispersal variables using discriminant analysis (via cross-validation). Results show that values of disarticulation-absence and overlapping match significantly in 24.6% of the cases. This percentage identifies paleobiological impact on the dispersal of the fossil considered, although the influence of external factors and their influence in disarticulation and overlapping (see below) cannot be denied.

We have interpreted the influence of internal-biological factors in two ways. First, the biological factor conditions burial position, and three categories of burial may be drawn in our study: a) a group with clear lateral position; b) a group with ambiguous lateral or dorso-ventral positions; and c) a group with clear dorso-ventral position. These categories reflect analogical features in a phenotypic organisation especially concerning size and proportions. Overlap, disarticulation and absence are clearly sequentially aligned variables for those fossils with lateral position (e.g. dinosaurs, and basal birds *Archaeopteryx*-like forms): the more articulation the more overlapping, when modular disconnection happen overlapping decrease, and distal elements may disappear.

Second, the disarticulation sequence shows a modular disconnection pattern that we interpret as characteristic depending upon specific features of phenotypic organisation. At the same time

disconnection pattern is in relation to the loss of volume. The disconnections, highlighted in gray for each sequence (Figures 6 and 7), depict relations between morphological units (i.e., head, thorax and pelvis) along the axial module. These units are the zones of greatest volume in the carcass. The disconnections of these units permit the loss of volume during the decay process. A progressive loss of volume is necessary in order to avoid the severe destruction of the carcasses before the inclusion of individuals in the sediment. The way that carcass volume fades is related to their internal organisation. The fossil record retains the logic and biological order in the pattern of disarticulation sequence.

Our results suggest that there are no significant differences when disarticulation and overlapping per localities are compared. The degree of dispersal of skeletal parts in our sample is reduced by rapid burial. Selected *Fossil lagerstätten* have rather homogeneous preservational conditions (concerning articulation), although differences can be detected for the Solnhofen lagoon deposit. Overlapping is particularly notorious in Solnhofen probably due to the high salinity of the paleoenvironment. Further, the sample is under-represented in localities and in data from other depositional environments (fluvial, transitional, deltaic, etc.). A broader sample will lead us to specify dispersal categories with each sedimentary and taphonomical environment.

Nevertheless, external-environmental factors incorporate new solutions and combinations to dispersal variables. We do not find that external and

internal factors were antagonists. The action of external factors could promote the increase (or decrease) of element dispersal and of its rate following the proposed general trend. For example, the London exemplar of *Archaeopteryx* has a different dispersal condition from all other specimens of *Archaeopteryx*. Davis (1996), taking into account the average hydrodynamic flotation in the Solnhofen paleoenvironment, suggesting that the former specimen had been transported longer. In Figure 5 *Archaeopteryx* specimens are highlighted, and one can trace the particular position of the London exemplar. All the *Archaeopteryx* specimens possess a definite value of overlap and disarticulation and present no significant differences with individuals related taxonomically and from different fossil sites. The London specimen is by far the most disarticulated. However, the taphonomic transformations of those specimens from the same fossil site, since they are taxonomically and biologically related, maintain the general trend described for the entire set of specimens with lateral burial positions, implying a negative relationship between overlap and disarticulation.

With the present work we want to face a general model in which paleobiology and phenotypic organisation are underlying dispersal explanations. Our objective is to build up a model that would enable us to query more on biostratigraphic conditions, and therefore we have to work more in the direction of how internal and external factors are involved in the taphonomic processes.

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References

- Andrews, P. (1990). *Owls, Caves and Fossils*. Natural History Museum publications. Cromwell Road, London SW7 5BD.
- Behrensmeyer, A. K. (1978). Taphonomy and ecologic information from bone weathering. *Paleobiology*, 4(2): 150-162.
- Behrensmeyer, A. K. & Hill, A. P. (1980). *Fossils in the making: Vertebrate taphonomy and paleoecology*. The University of Chicago Press. Chicago.
- Behrensmeyer, A. K. (1982). Time resolution in fluvial vertebrate assemblages. *Paleobiology*, 8(3): 211-227.
- Behrensmeyer, A. K. & Kidwell, S. M. (1985). Taphonomy's contribution to paleobiology. *Paleobiology*, 11: 105-119.
- Bickart, K. J. (1984). A field experiment in avian taphonomy. *Journal of Vertebrate Paleontology*, 4 (4): 525-535.
- Bochenski, Z. M.; Tomek, T.; Boev, Z. & Mitev, I. (1993). Patterns of bird bone fragmentation in pellets of the tawny owl (*Strix aluco*) and the eagle owl (*Bubo bubo*) and their taphonomic implications. *Acta Zool. Cracov.*, 36 (2): 313-328.
- Brain, C. K. (1980). Some criteria for the recognition of bone-collecting agencies in African caves. In (Behrensmeyer, A. K. & Hill, A. P., eds.) *Fossils in the making: Vertebrate taphonomy and paleoecology*. The University of Chicago Press, pp.107-130.
- Briggs, D. E. G. & Crowther, P. R. (2001). *Palaeobiology II*. Blackwell Science Publications, Osney Mead, Oxford, London.
- Chiappe, L. M. & Witmer, L. M. (2002). *Mesozoic Birds. Above the heads of dinosaurs*. University of California Press, Ltd. Berkeley and Los Angeles, California.
- Davis, P. G. (1994). *The taphonomy of birds*. Unpublished Ph.D. thesis. University of Bristol, Bristol, England.
- Davis, P. G. (1996). *The taphonomy of Archaeopteryx*. Bulletin of the National Science Museum. Series C, 22(3, 4): 91-106.
- Davis, P. G. & Briggs, D. E. G. (1998). The impact of decay and disarticulation on the preservation of fossil birds. *Palaios*, 13: 3-13.
- Denys, C. Dauphin, Y. & Fernandez-Jalvo, Y. (1995). Experimental taphonomy: preliminary results of the digestion of micromammal bones in the laboratory. *C. R. Acad. Sci.*, 321(IIa): 803-809.
- Dodson, P. & Wexlar, D. (1979). Taphonomic investigations of owl pellets. *Paleobiology*, 5(3): 275-284.
- Emslie, S. D. & Messenger, S. L. (1991). Pellet and bone accumulation at a colony of western gulls (*Larus occidentalis*). *Journal of Vertebrate Paleontology*, 11(1): 133-136.
- Efremov, J. A. (1940). Taphonomy: a new branch of Paleontology. *Pan-American Geologist* 74(2): 81-93.
- Fernández-López, S. R. (2000). *Temas de Tafonomía*. Departamento de Paleontología, Universidad Complutense, Madrid.
- Fernández-López, S. R. & Fernández-Jalvo, Y. (2002). The limit between biostratigraphy and fossilization. In (De Renzi, M; Pardo Alonso, M. V.; Belinchón, M.; Peñalver, E.; Montoya, P. & Márquez-Aliaga, A., eds.) *Current Topics on Taphonomy and Fossilization*, Ajuntament de Valencia, pp. 27-37.
- Fisher, D. C. (1981). Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth. *Paleobiology*, 7(2): 262-275.
- Franzen J. L. Grube (1999). Messel. In (Briggs, D. E. G. & Crowther, P., eds.) *Paleobiology A synthesis*. p: 289-294. Blackwell Scientific Pub.
- Fregenal-Martinez, M. A. & Meléndez, N. (1995). *Las Hoyas. A lacustrine Konservat lagerstätte*. II International Symposium on the Lithographic

- Limestones, Field Trip Guidebook, Cuenca, Spain.
- Harper, D. A. T. (2003). Past, version 1.04. Obtained from <http://fok.uio.no/ohammer/past>. Freely distributed program.
- Hill, A. (1979). Disarticulation and scattering of mammal skeletons. *Paleobiology*, 5(3): 261-274.
- Lacasa, A. (1986). Nota preliminar sobre el hallazgo de restos fósiles de un ave fósil en el yacimiento neocomiense del Montsec, provincia de Lérida, España. *Institut D' Estudis Ilerdencs*, 203-206.
- Lyman, R. L. (1994). *Vertebrate taphonomy*. Cambridge Manuals on Archaeology. Cambridge University Press, Cambridge.
- Martínez-Delclós, X. (1991). *Les calcàries litogràfiques del Cretaci inferior del Montsec. Deu anys de campanyes paleontològiques*. Institut D' Estudis Ilerdencs. Lleida.
- Marugán-Lobón, J.; Cambra-Moo, O.; Martínez-Delclós, X.; Sanz, J. L., & Buscalioni, A. D. (2002). Juvenile Enantiornithine skeleton from Montsec (Catalonia, Spain) lower cretaceous revisited: taphonomy and morphometrics to assess ontogenetic stage. 62nd Annual Meeting of the Society Vertebrate Paleontology. *Journal of Vertebrate Paleontology* 22(3)- Abstracts (84A).
- Mellet, J. S. (1974). Scatological origin of microvertebrate fossil accumulations. *Science*, 185: 349-350.
- Müller, A. H. (1963). *Lehrbuch der Paläozoologie*. I. Allgemeine Grundlagen. C. Die Fossilisationslehre. Fischer, Jena: 17-134.
- Olivier, J. S. & Graham, R. W. (1994). A catastrophic kill of ice-trapped coots: time-averaged versus scavenger-specific disarticulation patterns. *Paleobiology*, 20: 229-244.
- Sanz, J. L.; Wenz, S.; Yebenes, A.; Estes, R.; Martínez-Delclós, X.; Jiménez-Fuentes, E.; Diéguez, C.; Buscalioni, A. D.; Barbadillo, L. J. & Via, L. (1988). An early cretaceous faunal and floral assemblage: Las Hoyas fossil site (Cuenca, Spain). *Geobios*, 21 (fasc. 5): 611-635.
- Sanz, J. L.; Chiappe, L. M.; Pérez-Moreno, B. P.; Buscalioni, A. D.; Moratalla, J. J.; Ortega, F. & Poyato-Ariza, F. J. (1996). An early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature*, 382: 442-445.
- Sanz, J. L. (1999). *Los dinosaurios voladores. Historia evolutiva de las aves primitivas*. Colección Mundo Vivo. Ediciones Libertarias/Prodhufl, S. A., Madrid.
- Sanz, J. L.; Chiappe, L. M.; Fernández-Jalvo, Y.; Ortega, F.; Sánchez-Chillón, B.; Poyato-Ariza, F. J. & Pérez-Moreno, B. (2001). An early Cretaceous pellet. *Nature*, 409: 998-999.
- Sanz, J. L.; Fregebal-Martínez, M. A.; Melendez, N. and Ortega, F. (2001b). Las Hoyas. In (Briggs, D. E. G. & Crowther, P. R., eds). *Palaeobiology II*. Blackwell Science Publications, Osney Mead, Oxford, pp 356-359.
- Schäfer, W. (1972). *Ecology and Palaeoecology of marine environments*. Chicago University Press, Chicago.
- Viohl, G. 1990. Solnhofen lithographic Limestones. In (Briggs, D. E. g and Crowther, P., eds.) *Paleobiology A synthesis*, pp. 285-289. Blackwell Scientific Pub.
- Weigelt, J. (1989). Recent vertebrate carcasses and their paleobiological implications. The University of Chicago Press, Chicago.
- Zhou, Z. (2002). A new and primitive Enantiornithine birds from the early cretaceous of China. *Journal of Vertebrate Paleontology*, 22(1): 49-57.
- Zhou, Z.; Barrett, P. M. & Hilton, J. (2003). An exceptionally preserved Lower Cretaceous ecosystem. *Nature*, 421: 807-814.

Appendix legends

Appendix 1. Data matrix describing taxonomic group, source of data, fossil localization, burial position, total area (mm²), % Disarticulation-Absence and % Overlapping, of each specimen.

Appendix 2. Binary data extracted from the description of articulation (A), overlapping (B) and Absence (C) of bony elements.