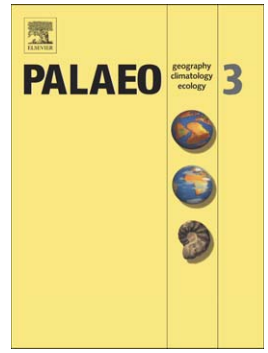

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Death, decay and disarticulation: modelling the skeletal taphonomy of marine reptiles demonstrated using *Serpianosaurus* (Reptilia; Sauropterygia)

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Abstract

Taphonomic models for fossil vertebrates are designed to reconstruct processes that affected carcasses during the transition from biosphere to geosphere, in particular in the interval between death and burial. To circumvent various limitations in existing methodologies, a new taphonomic method, assessing vertebrate skeletons as nine anatomical units (the head, neck, dorsal, tail, ribs and four limbs) scored independently for two characters (articulation and completeness), was developed.

The potential of the method is demonstrated using the Triassic marine reptile *Serpianosaurus* from Monte San Giorgio, Switzerland. Specimens are preserved in alternations of black shale and dolomite, representing normal background sediment and event beds respectively, deposited into a shallow, intraplatform basin. All specimens exhibit disarticulation of skeletal elements though loss of completeness varies considerably. Minor loss of fidelity occurred during the 'floating phase', but individuals reached the sediment-water interface relatively soon after death, and largely intact, where they decayed during the 'residence phase'. Carcasses allowed to reach extensive states of decay became prone to the effects of weak bottom currents, resulting in removal of elements. The episodic deposition of event beds rapidly buried individuals at various stages of decay, inhibiting further disarticulation and loss of completeness.

Keywords: skeleton, articulation, completeness, taphonomy, Pachypleurosauridae.

1. Introduction

Elucidating the taphonomic history of any fossil assemblage is a crucial part of interpreting its palaeobiology (Behrensmeyer and Kidwell, 1985; Brett and Baird, 1986; Brandt, 1989; Briggs, 1995). Vertebrates, and various invertebrate groups (notably echinoderms), possess multi-element skeletons, a suite of biomineralised tissues that are held together in life by 'soft tissues'. The term 'soft tissues' is a colloquial descriptor for various types of non-biomineralised tissue, including ligaments, tendons, and musculature. These vary in their resistance to decay (recalcitrance), but collectively can be considered as 'decay prone' relative to biomineralised tissues (Briggs, 1995). Decay of these non-biomineralised 'soft tissues' is effected by two biological agents, autolysis and degradation by endogenous and exogenous microbes, resulting in the carcass separating into a series of co-joined, and, ultimately, individual skeletal elements. Any additional biostratinomic processes tend to exacerbate the loss of skeletal fidelity. A skeleton can collapse passively under sediment loading or gravity as it decays, and skeletal elements that are free to rotate become oriented into more stable orientations than those in which they came to rest (McNamara et al. 2011). Disarticulation and removal of skeletal elements from a carcass can occur more actively via various biostratinomic processes, most notably transport, and scavenging by metazoans, before burial. Disarticulation of the skeleton after burial is possible, as a result of bioturbation of the host lithologies, and remobilisation of sediments, e.g. slumping. Loss of skeletal fidelity (i.e. from a complete, fully articulated, skeleton) can therefore be assessed using two variables: whether skeletal elements are present or absent (completeness) and whether those present are in life position, or not (articulation). The two variables are partially coupled:

disarticulation of the skeleton precedes, but does not automatically result in, skeletal elements being removed from the carcass.

Multi-element skeletons are most likely to retain a high degree of skeletal fidelity if the organisms were buried alive or shortly after death. Examples include the burial of echinoderms below obrution deposits (Brett and Baird, 1986; Dornbos and Bottjer, 2001; McIntosh, 2001), and, for vertebrates, entombment within rapidly accumulated sediments, such as volcanic ash or mud flows (Smith, 1993; Mastrolorenzo et al., 2001; Zhou et al., 2003). In such examples, the preservation of ‘soft-tissues’ may accompany, but is not necessary for, preservation of the skeleton in a fully articulated state. Conversely, soft-tissues may be preserved even in specimens that are incomplete and extensively disarticulated (Briggs, 1995).

Almost all existing models that describe the loss of skeletal fidelity of vertebrates after death use a qualitative ‘flashcard’ approach (e.g. Martill, 1985; Smith, 1997; Soares, 2003). The skeletal fidelity of a specimen as a whole is determined by comparison to images representing a series of preservational states. The approach is advantageous in that specimens can be classified visually and a dataset assembled rapidly. There are, however, limitations. Preservational states are typically defined using verbal descriptors (e.g. “moderately complete”; “extensively disarticulated and lacking many elements”), with the chosen characters, e.g. articulation and completeness, combined rather than analysed separately. The descriptors are rarely quantified, and, even if circumscribed using values (e.g. less than 40% complete), cannot accommodate the possibility that two or more specimens may reach the same state of fidelity via different taphonomic processes. Such models potentially underestimate how complicated loss of skeletal fidelity can be, instead giving the impression the same series of incremental, sequential, steps are consistently involved. Experimental data and retrospective reconstruction of the decay patterns from fossils both indicate, however, that at a given time the state of fidelity often varies systematically between different parts of a carcass (Schäfer, 1972; Briggs, 1995; Kemp and Unwin, 1997).

The alternative approach is to extract the maximum amount of information possible from each fossil by considering the presence/absence of individual skeletal elements, and the state of articulation of each joint. While comprehensive, the approach is time-consuming for all but the smallest datasets. McNamara et al. (2011) coded the presence/absence of elements in salamanders as a percentage of the 172 total in a pristine carcass, and the number of articulated joints between. In their study of the skeletal taphonomy of the reptile *Tanytrachelos*, Casey et al. (2007) coded disarticulation using three semi-quantitative states (based on those of Behrensmeyer, 1991) but assessed completeness based on the presence of 128 separate skeletal elements. For *Archaeopteryx*, Kemp and Unwin (1997) noted what proportion of the 130 skeletal elements, and 1095 articulations, were present to differentiate between “well articulated and complete” and “less complete and more disarticulated” skeletons.

Herein we describe a novel method that not only quantifies how much skeletal fidelity has been lost in fossil vertebrates, but identifies how this has occurred, thus allowing the taphonomic pathway to be reconstructed. In the new method, vertebrate skeletons are sub-divided into a series of smaller units (Figure 1), with the taphonomy of each unit defined using semi-quantitative measures for articulation and completeness (see Appendix 1). The fidelity of the entire skeleton, i.e. a single value for each of completeness and articulation, is calculated based on aggregating values for the preservational states of the different units. As well as providing greater detail regarding the specific loci at which skeletal fidelity is reduced, the method can potentially differentiate whether loss of completeness occurred before or after deposition, allowing the taphonomic history to be resolved in detail. We describe first the method (sections 2-3) then illustrate its potential by reconstructing the taphonomic history (sections 4-7) of the pachypleurosaurid (Reptilia; Sauropterygia) *Serpianosaurus mirigiolensis* from the Middle Triassic Besano Formation, Monte San Giorgio, Switzerland. The method can, however, be applied to a wide range of fossil vertebrates throughout the geological record.

2. Methodology

2.1. Definition of skeletal units

The vertebrate skeleton is divided into nine ‘skeletal units’ that can be readily identified in a wide range of tetrapod groups: the head, ribs, left and right front limbs, left and right back limbs, neck, dorsal, and tail vertebrae. The skeletal fidelity of each is considered separately. For convenience, the visual illustration of these units (Figure 1) uses a pachypleurosaurid skeleton, as the case study herein focuses on these reptiles.

2.2. Collection of data

Loss of skeletal fidelity (from a pristine, fully complete and articulated carcass) is assessed using two variables: articulation (A) and completeness (C), each scored semi-quantitatively using five categories, from 4 to 0. In descriptive terms, articulation ranges from fully, near-fully, moderately, limited to entirely disarticulated, and completeness, from fully, nearly, moderately, limited to absent. Visual representations of each category of completeness and articulation for the nine units are presented in Appendix 1. There is no reason to assume that the categories are equally spaced between the two end-members, i.e. that the carcass has experienced the same amount of decay between each successive stage.

2.3. Defining articulation and completeness

In the most obvious example of a disarticulated joint the two relevant bones are separated spatially. In other cases a joint can be considered disarticulated even if the bones are in contact, if they occur in an attitude that is not possible in life.

Skeletal completeness is more difficult to quantify for two reasons. Firstly, it is necessary to define a threshold distance beyond which a disarticulated element, or a series of elements that are themselves articulated, is no longer in association with the carcass as a whole. In practice, this is controlled strongly by the collection strategy, and in particular, the size of the specimen and that of the slab removed from the field. Systematic excavation of a relatively small specimen is most likely to recover those elements distributed close to but beyond the periphery of the main part of the carcass. Many specimens may be trimmed to remove peripheral parts of the slab, although presumably after any preparation, in which case skeletal elements in peripheral positions are likely to be retained. In the case study herein, such problems are minimal as the specimens are (relative to many tetrapods) small (less than 400mm long) and most were collected during systematic scientific sampling of outcrops.

How completeness is defined is sensitive to whether any weighting is given to bones or joints. In this study, no weighting is given to the presence or absence of specific bones, or whether specific joints are articulated. In certain cases, a skeletal ‘element’ will comprise a single bone; for example, the humerus is relatively large, easily recognisable, and will be either present or absent, and the shoulder joint disarticulated or articulated. In contrast, other skeletal ‘elements’ consist of numerous small bones. For example, in pachypleurosaurids there are 16 phalangeal bones in the front limbs, and 12-15 in the back limbs (Rieppel, 1989). Unless the strict proviso that the absence of any is sufficient to render that part of the unit incomplete, it is clearly subjective as to what proportion of the total should be present to define a particular category of completeness (see Appendix 1). Herein the phalanges are considered present if more than 50% are present.

2.4. Missing data

Invariably, it is not possible to return a score for every unit in each specimen. This occurs for one of two reasons. A specimen may be truncated by the edge of a slab so that one or more units are missing (coded 'Xp' in the data matrix). Alternatively parts of the skeleton may be juxtaposed and one unit concealed by another (Xh). The sub-division of the skeleton into a series of units means an incomplete, or partly obscured, specimen can still be included in certain analyses. Specimens in which either category of X was present for more than three units are omitted from all analyses.

2.5. Analysis of data

2.5.1. Overall completeness and articulation of specimens

Single values for each of completeness and articulation are derived by summing the scores for each character across the nine units, and expressing this as a percentage of the total possible score (36 = 9 (units) x 4 (score for a fully complete/articulated unit)). In specimens with 1 to 3 units missing (X), the total possible score is adjusted accordingly, i.e. percentages are based on a total of 32 where 1 X is present, and 28 where there are two. The percentage data is displayed using bivariate, scatter plots constructed in Microsoft Excel. Articulation (A) is always shown on the X-axis, and completeness (C) on the Y-axis (Figure 2 and 3).

The distribution of the data is considered relative to 4 trends defining broad regions (Figure 2). In Trend 1 data exhibit variable values for articulation but consistently high values for completeness, i.e. skeletal elements can be separated from, but remain associated with, the carcass. In Trend 2 completeness and articulation both decrease, i.e. isolated skeletal elements were removed from the vicinity of the carcass. Trend 3 encompasses a series of variants between Trends 1 and 2. Skeletal elements or units must disarticulate from the remainder of the carcass before they can be removed, i.e. before loss of completeness (see further discussion in section 2.5.3), thus, and therefore data cannot plot in the area labelled Trend 4 (Figure 2). Finally, the data need not form a continuous sequence or trend. If all specimens exhibit broadly similar values for completeness and articulation the data will clump or pool.

The trends are defined quantitatively for each dataset examined using a trend parameter "T". T is defined on a plot of articulation (A) versus completeness (C) (Figure 3) by the intersect with the completeness axis of a best-fit linear trend line forced through the taphonomic origin of the data (the condition of the specimen immediately after death; 100% completeness, 100% articulation). Values of T between 0-25% represent Trend 2, between 75-100%, Trend 1, and 25-75%, variants of Trend 3 (Figure 2).

The T value is calculated by plotting 100-A as the x-value against 100-C as the y-value in Microscoft Excel, and fitting a linear trend-line forced through the origin (0,0) of this plot. The value of T is then determined by subtracting the *y*-value of the reported trend line at a value of *x*=100, from 100. Although somewhat convoluted, this procedure allows the properties of the desired trend-line to be calculated using the in-built Excel functions. The trend line calculated by Excel assumes that the parameter plotted on the X-axis is the independent variable, and that plotted on the Y-axis is the dependent one, and a different value of T would be appropriate if these dependencies were reversed or if the two variables were mutually independent. However, loss of articulation must precede loss of completeness so C depends on A and the statistical assumptions in the Excel trend-fitting procedure are appropriate.

The strength of the trend can be expressed parametrically by the goodness of fit of the regression line (Pearson's r^2 value) reported by Excel. Additionally, a nonparametric measure of the strength of correlation between articulation and completeness can be given by the Spearman rank-order correlation coefficient (rs, calculated in PAST (PAlaeontological STatistics program); Hammer et al. 2001), which does not assume any particular form for the trend, but merely reports the similarity of a ranking between the two properties. Both r^2 and rs have values of zero in the absence of any correlation and values of 1.0 for a perfect positive correlation. Use of both is appropriate in the present analysis as they can highlight different aspects of the data. For example, high values of both imply that the data are well fitted by a linear model of Trend 2 or 3. Alternatively, a high rs value but a low r^2 implies that the data contain a significant trend, but not one which is adequately described by our simple linear trend lines: the trend may, for example, have significant curvature in A/C space. Some variants of Trend 1 are not captured by either the rs or the r^2 value. If most specimens exhibit the same completeness (most likely 100%) these values will be low. If completeness is invariant, neither an r^2 or rs value can be generated. Therefore visual examination of the plots, as well as an examination of the statistics, is required to evaluate the appropriateness of the modelled trends. T, r^2 and rs values are shown at the bottom of the plot (Figure 3).

2.5.2. Completeness and articulation of individual units

The relationship between completeness and articulation for each unit can be determined by plotting the corresponding score values directly on a bivariate plot. However, the number of specimens for each unit varies due to missing data (indicated by 'X') within the dataset. The number of individuals at each score combination is therefore calculated as a percentage of those available in the dataset, with the percentages then visualised on 5 x 5 bivariate bubble plots in Microsoft Excel (Figure 4). As each bubble is to the same scale the distribution of data can be compared directly across the nine units. Trends in the unit plots are identified by the method used for the percentage analysis (see section 2.5.1), with the straight line used to obtain T constrained to pass through the maximum articulation and completeness score values of 4. T values between 0 and 1 represent Trend 2, between 3-4, Trend 1, and 1-3 variants of Trend 3. As before, Pearson's r-squared (r^2) and Spearman rank-order (rs) values are used to determine the strength of the relationship between articulation and completeness; these are shown below the bubble plot for each unit (Figure 4).

2.5.3 Relationship between completeness and articulation

The two variables, articulation and completeness, are partially coupled: disarticulation of individual or co-joined skeletal elements is a pre-requisite for, but does not automatically result in, removal of elements (i.e. loss of completeness). For example, a unit cannot be fully articulated (4) but missing any elements (3 or less for completeness). Only some of the 25 score combinations are therefore possible. For the head, rib and limb units there are 15 possible combinations; a value of articulation greater than that for completeness is not possible. For the neck, dorsal and tail units there are, however, 18 score combinations, reflecting how the categories of articulation are defined on the basis of 'breaks' (gaps, rotations, imbrications) between vertebrae (see Appendix 1). The additional three combinations are possible as in certain circumstances articulation can be greater than completeness for these units (Figure 5). For example, the absence of the distal part of the tail can reduce completeness markedly; if the remainder of the tail is articulated only a single point at which disarticulation occurred can be proven, thus the value for articulation can be higher.

Similarly, it is not possible to score the articulation of a unit absent in its entirety (completeness = 0). In such cases the articulation of the unit is also returned as zero. This scenario remains distinct from units that are entirely disarticulated, as in the latter completeness will be ≥ 1.

2.5.4. Patterns of limb articulation and completeness

The semi-quantitative method described above codes for the extent of any disarticulation and loss of completeness in the limbs, but cannot identify which joints or bones are affected. Use of what are herein termed ‘limb tables’ resolves this (Table 1). For each limb, which joints are articulated or elements present are recorded. The total number of articulated joints and elements is four. The four relevant joints for the front and rear limb are: phalangeal-metacarpal/metatarsal, wrist/ankle, elbow/knee, and shoulder/hip. The relevant elements are the phalanges, metacarpals/metatarsals, radius/ulna, and tibia/fibula, and humerus/femur. For the phalanges to be considered complete a minimum of 50% of the individual bones must be present. Three metacarpals/metatarsals must be present. If either the radius or ulna in the front limbs, or the tibia or fibula in the back limbs, is missing, this part of the limb unit is scored as absent.

Articulation and completeness are treated separately for each limb (Table 1, upper and lower respectively). The number of either articulated joints or elements present is shown in columns against the score for articulation and completeness for that limb as a whole (rows). The data is ordered such that the more proximal joint or bone is in the column to the right. The final row sums the number of times a particular joint is articulated or skeletal element present. The final column is the number of specimens that correspond to each score of articulation or completeness. Marked differences in the number of articulated joints or elements present thus indicates whether some joints are more likely to be disarticulated, or elements absent, than others. Differences in how the data are distributed between two or more rows indicate variation as to which joints are articulated, or elements present, as the skeletal fidelity of the limb as a whole changes.

2.5.5. Recurrent patterns of rib articulation

Values for the articulation of the rib unit as a whole cannot indicate where disarticulation occurred. A semi-quantitative approach has been devised that codes for the loci of disarticulation. The thoracic cavity is sub-divided into six regions, three running anterior to posterior either side of the vertebral column (Figure 6). *Serpianosaurus* possess 20 pairs of ribs, thus 6-7 ribs occur in each region of the grid. Regions coded as articulated have 4 or more ribs in life position; these are identified by shading the appropriate region. These values can be recalibrated for taxa with a different number of ribs. The notations 6A to 0A indicate the number of articulated regions (6A = 6 articulated regions); the number of specimens in the dataset exhibiting a particular configuration is shown. Visual comparison of these grids indicate which patterns recur, and whether articulation is similar between the left and right sides of the body, or the anterior and posterior of the torso.

2.5.6 Paired appendage analysis

It is possible to detect whether completeness and/or articulation is similar on opposite sides of the body by comparing data for the two corresponding limbs, herein termed ‘paired appendage analysis’ (Figure 7). Values of completeness *or* articulation for the left versus right of a limb pair are visualised as bubble plots on a 5 x 5 grid in Microsoft Excel. The left limb is plotted on the X-axis, and the right, on the Y-axis. As the preservational state of one limb is independent of the other, all 25 combinations are possible. The plots identify concentrations of data, if any, on the diagonal line bisecting the score combinations 0,0 and 4,4, a line indicating levels of fidelity are similar on either side of the body.

3. Using assessments of skeletal fidelity to reconstruct the taphonomic history of vertebrates

The taphonomic history of most fossil vertebrates preserved in a marine or lacustrine system comprises the following stages: (a) transport and *entry* into the depositional system (not applicable to autochthonous taxa); (b) post-mortem *floating* at the water-air interface; (c) vertical *sinking* through the water column; (d) *residence* at the sediment-water interface during which progressive *burial* under depositing sediment occurs. One of the strengths of the method herein is that it can be used to distinguish the relative importance of the floating and residence phases in the taphonomic history of a vertebrate skeleton. This is based on two observations.

Firstly, disarticulation while floating in the water column will be followed automatically by loss of completeness, as skeletal elements that become detached cannot remain associated with the carcass (Schäfer, 1972; Davis and Briggs, 1998). The same could, but need not, happen if disarticulation occurred after deposition on the sediment-water interface; separated elements may remain in association with the carcass. A strong positive correlation between articulation and completeness (Trend 2) does not necessarily indicate during which phase skeletal fidelity was lost. However, a weak correlation, and especially high levels of completeness coupled with relatively low levels of articulation (Trend 1) implies disarticulation occurred after deposition.

Secondly, the vertebrate body is bilaterally symmetrical. In the floating phase the left and right hand sides of the body should disarticulate and lose completeness symmetrically. This may, but need not, occur if specimens disarticulate while on the sediment-water interface. Any variation in skeletal fidelity between the left and right sides of the body would favour disarticulation having occurred after deposition (i.e. during the residence phase). This can be tested for using the paired appendage analysis.

4. Material

Excavations at Monte San Giorgio on the Switzerland-Italy border have recovered numerous Middle Triassic marine reptile fossils (Figure 8) (Furrer, 2004). Skeletons of the small pachypleurosaurid *Serpianosaurus* (Reptilia; Sauropterygia) from the Besano Formation, or Grenzbitumenzone, are one of the most abundant (Rieppel, 1989; Sander, 1989; Furrer, 1995; Röhl et al., 2001). Descriptions of this pachypleurosaurids, and others from the younger Meride Limestone Formation, are provided by Carroll and Gaskill (1985), Rieppel (1989) and Sander (1989).

Forty-four of 52 prepared specimens of *Serpianosaurus* used herein are from the collections of the Paläontologisches Institut und Museum der Universität, Zürich (PIMUZ). The remainder are from the Museo Civico di Storia Naturale di Milano (MCSN), Italy. Most specimens are of single skeletons, though two slabs have more than one. Almost all specimens are in a dorso-ventral orientation and parallel to bedding, the remainder are laterally orientated (Sander, 1989). For most, no orientation or way-up data is available; 'left' and 'right' herein are therefore used in an anatomical sense, as viewed from the dorsal surface (Sander, 1989). Preservation of specimens ranges from well articulated and complete to disarticulated and incomplete.

5. Geological setting

During deposition of the Besano Formation, the Monte San Giorgio region was a subsiding intra-platform basin on an extensive carbonate platform on the western margin of the Neo-Tethys (Furrer, 1995; Röhl et al., 2001; Etter, 2002). Its depth is estimated to have been around 30-100 metres, well below storm wave-base (Bernasconi, 1991; Furrer, 1995; Röhl et al., 2001; Etter, 2002). The upper part of the water column was stenohaline as indicated by the presence of ammonoids, conodonts and marine reptiles, and a weak connection to adjacent basins and open water was maintained (Furrer, 1995). Circulation lower in the water column was inhibited by the carbonate platform, however, a dysaerobic transitional layer occasionally mixed with bottom waters, resulting in at least temporary or partial oxygenation of the latter (Bernasconi, 1991; Furrer, 1995; Röhl et al., 2001). Bivalves at certain horizons are interpreted as either adapted to low oxygen conditions or as opportunistic colonisers (Röhl et al. 2001; Schatz, 2005). Other benthos is limited to dasycladacean algae, gastropods, one echinoid spine and rare crustaceans, which were probably swept into the basin during storms (Furrer, 1995).

The 16 metres thick Besano Formation consists of alternations of black shale and dolomitic layers. The black shales are organic rich (up to 40wt %) marls and claystones derived from nearby land and primary productivity in the overlying water column (Bernasconi, 1991; Tintori, 1992). Deposition of the black shale layers was continuous, but slow, at an average rate of 1-5 mm per thousand years (Röhl et al., 2001). Layers are typically less than 0.1 m thick, and are thicker and more common in the middle part of the formation (Bernasconi, 1991; Röhl et al., 2001; Etter, 2002). Bioturbation and evidence of current activity are absent in the shales. The dolomite layers are 0.1-0.3 m thick and either massive or thinly laminated mud-, wacke- and packstones. Some of the thicker layers are normally graded (Bernasconi, 1991). Organic carbon content is less than 10wt % (Röhl et al., 2001). The dolomites formed from calcitic muds introduced to the basin as low-density and detached turbidites (Bernasconi, 1991; Röhl et al., 2001; Etter, 2002). Oxygenation rarely penetrated the sediment surface; only Bed 17 in the lower Besano Formation shows evidence of bioturbation

(Bernasconi, 1991; Röhl et al., 2001). Contacts between the dolomite and shale layers are generally sharp, consistent with abrupt switching between these two modes of sediment deposition (Bernasconi, 1991).

6. Results for *Serpianosaurus*

Values for overall completeness and articulation are extremely variable (between 17% and 97% for articulation, and 25% and 100% for completeness) although the majority of specimens are more than 60% articulated and 75% complete (Figure 3). The T value of 44% indicates a variant of Trend 3. The r^2 is moderate (0.62) and the rs relatively high (0.82), suggesting the relationship between articulation and completeness is strong and, although slightly non-linear, is nonetheless adequately defined by the linear trend.

Of the nine skeletal units, only the head exhibits Trend 2 (Figure 4a): T is low (0.74), and r^2 (0.82) and rs (0.89) are both high, indicating articulation and completeness are strongly, and positively, correlated. The remaining units show three more complex patterns. Disarticulation and loss of completeness of the neck vertebrae (Figure 4b), the ribs (Figure 4e) and, especially, the dorsal vertebrae (Figure 4c) are limited; in most specimens these units are fully complete and articulated. The moderate T values indicate variants of Trend 3. In particular, the high T value for the dorsal unit (2.97) is very close to the boundary between Trend 1 and 2; disarticulated vertebrae tended to remain associated with the carcass. In contrast, the T value for the ribs (2.23) and neck (1.8) units imply removal of bones after disarticulation was more extensive. The high rs values (neck: 0.74; dorsal: 0.62; and ribs 0.78) suggest strong positive relationships between articulation and completeness, but the low corresponding r^2 values (neck: 0.34; dorsal: 0.39; ribs: 0.5) suggest these are not defined by the linear model. The tail vertebrae (Figure 4d) data show the greatest scatter with most of the possible combinations represented and no evidence of the data being concentrated at any single combination; reflecting this the r^2 (0.2) and rs (0.43) values are particularly low. Articulation and completeness patterns for the four limb units (Figure 4f-i) are broadly similar (Trend 3 in all). Subtle differences, however, between the limb pairs are indicated by higher T values for the back limb pair (compare Figure 4f-g to 4h-i). The rear limbs are fully complete and articulated in proportionally more specimens, and few specimens show moderate to low completeness and articulation.

The results of the paired appendage analyses are shown in Figure 7. In each case, any tendency for the data to lie on the diagonal line bisecting the plot is weak. Symmetrical loss of articulation and completeness either side of the body occurred in relatively few specimens.

Limb tables (Table 1) reveal a tendency for the shoulder/hip, and less frequently the elbow/knee, joint to be articulated when overall values for disarticulation are low (scores of 1 or 2). At moderate values for articulation (scores of 3) the phalanges are less frequently articulated than other elements. For low values of completeness (scores of 1 or 2), only the humerus and radius/ulna, and the femur and tibia/fibula, are present. A wider variety of bones are present when specimens are moderately complete (scores of 3), although the phalanges tend to be absent more frequently than other elements. Disarticulation and loss of completeness therefore followed a distal to proximal trend in each limb. For both articulation and completeness, a score of 4 occurred more frequently for the back limbs than the front.

Twenty-six (50%) of the *Serpianosaurus* specimens possess intact ribcages (6A). Of the remainder, two individuals were coded X, and not included, leaving 24 specimens in various states of disarticulation (Figure 6). Disarticulation was initiated in the posterior regions of the ribcage (5A). As specimens disarticulated further the middle parts of the ribcage were affected least. At moderate to low values (3A-0A), articulation patterns are almost always strongly asymmetrical between opposite sides of the body. In extreme cases all the ribs on one side can be disarticulated with no, or at most, only one region on the other side affected. Many of these show a recurrent feature: the disarticulated ribs lie in a narrow band extending 7-10 centimetres away from, and perpendicular to, the vertebral column (Figure 9a). A second recurrent feature is the occurrence of disarticulated ribs parallel to each other and equidistantly spaced, as they would have been in life (Figure 9b). These have clearly separated at the same time as a co-joined series.

7. Conclusions: a taphonomic model for *Serpianosaurus*.

The nine skeletal units show four different patterns of completeness and articulation, illustrating how complex variation in the fidelity of skeletal preservation is amongst specimens. The pattern exhibited by the tail (Trend 3) has the most variation, and is most complicated to interpret. The head unit is distinct from other units in exhibiting a strong positive relationship between articulation and completeness (Trend 2). This unit, relative to others, is heavy, especially if all the elements are present, and most likely was prone to hanging below a floating body. This scenario places the cervical vertebrae under tension to a point where the vertebral column eventually separates. Separation of the head from the remainder of the carcass is therefore potentially indicative of the floating phase (Boaz and Behrensmeyer, 1976; Schäfer, 1972; Schäfer, 1972; Allison et al., 1991; Davis and Briggs, 1998; Esperante et al., 2002). It should, however, be borne in mind that the orientation of the carcass can be affected by retention of gas and fluids, less dense than the surrounding water, in the lungs, guts and eyes; the latter may be sufficient to buoyantly lift the head until decay is advanced (Renesto, 2006; Davis and Briggs, 1998). Overall, as only four specimens of *Serpianosaurus* lack the entire head unit, the duration of the floating phase was short.

The neck, dorsal and rib units disarticulated during the residence phase with a tendency for elements to remain in the vicinity of the carcass. In their study of *Archaeopteryx* Kemp and Unwin (1997, p235) also found the dorsal vertebral column to be what they termed 'coherent'. In some *Serpianosaurus*, centra from the dorsal vertebrae have separated from the neural arches and processes, and occur scattered beyond the rib cage; the skin had reached an advanced state of decay before burial but not before arrival at the sediment-water interface (Brand et al., 2003; Renesto, 2006). Only three specimens of *Serpianosaurus* show symmetrical loss of ribs either side of the vertebral column; the left and right sides of the ribcage routinely experienced different patterns in the loss of skeletal fidelity. There is a tendency in some for the posterior region of the ribcage to be preferentially disarticulated. In others, one side of the ribcage can be fully, or near fully, articulated, but the other entirely disarticulated (Figure 6 and Figure 9a). These loci of disarticulation are evidence for gut rupture, where, gas built up in the abdomen region due to postmortem bacterial decay, is released abruptly. This occurrence is controlled by the balance between hydrostatic pressure and that inside the abdomen (Allison et al. 1991). The basinal setting into which the *Serpianosaurus* carcasses were deposited was not deep enough to prevent gut rupture and this phenomenon has been identified previously in other marine reptiles from the Besano Formation (Sander, 1989). Gut rupture during the residence phase, as opposed to during floating, is more likely. It is difficult to envisage how ribs separated as co-joined series from the vertebral column, or their tendency to occur as a narrow band of disarticulated ribs, perpendicular to the body, could otherwise be generated. Secondly, in no specimens do the ribs occur juxtaposed on or by any skeletal elements, something that might be expected to occur if gut rupture had occurred during the floating phase.

All limbs exhibit a Trend 3 pattern. The combination of variable articulation and higher completeness is more prevalent in the back limbs; decay of the back limbs either began later, or progressed more slowly (Figure 4; Davis and Briggs, 1998; Casey et al, 2007). The lack of any consistent relationship between articulation and completeness, and especially the different sides of the body (Figure 7) indicates loss of fidelity occurred predominantly in the residence phase. As skeletal fidelity deteriorated loss of completeness was exacerbated, affecting the front and back limb pairs. The limb tables indicate loss of articulation and completeness progressed from the distal to proximal parts of each limb, i.e. from where the volume of soft tissue is limited to where it was greater during life. A similar trend has been observed previously, e.g. by Oliver and Graham (1994), Casey et al (2007) and McNamara et al. (2012).

The patterns of articulation and completeness for each skeletal unit suggest processes that reduced the fidelity of specimens of *Serpianosaurus* occurred predominantly, or exclusively, during the residence phase. The individuals died in the water column, underwent a short floating phase and were transferred relatively rapidly to the sediment-water interface, before extensive decay of soft tissue. Disarticulation affected all skeletal units subsequently. Loss of completeness occurred preferentially at the periphery of the carcass, in particular in the distal parts of the limbs; the medial part of the carcass (especially the dorsal vertebrae) was affected least. There is little sedimentological evidence to identify the process by which elements were removed. The depositional setting for the Besano Formation was a subsiding basin below storm wave-base, and scavenging was inhibited by the dysaerobic, and occasionally anoxic, bottom waters (Bernasconi, 1991; Röhl et al., 2001). Weak, and possibly intermittent, bottom currents are considered the most likely agent. Their presence is implied by the similar alignment of skeletal units such as the head and neck in two individuals (Figure 9b), and the neck and tail in individual skeletons (Figure 9c; Table 1). Taphonomic differences amongst specimens can therefore be explained best by residence phases having varied in duration and exposure to current activity. This is consistent with the vast majority of specimens having arrived at the sediment-water interface during the extended intervals between deposition of event beds when black shales were accumulating; different specimens on the same bedding plane, or separated by very short vertical distances, can thus exhibit marked variation in skeletal fidelity (Figure 9b).

8. Wider implications

Testing of the method herein confirms its potential as a technique by which the taphonomic history of a fossil vertebrate can be reconstructed in detail. In particular, how specific skeletal units lose articulation and completeness allows the relative duration of the floating phase (when in the water column) and the residence phase (while on the sediment surface) to be distinguished. The methodology, including the various units into which the skeleton is divided, can be applied to any vertebrate with the basic tetrapod body plan (Beardmore et al. 2012). Direct comparison of the skeletal taphonomy of two or more taxa from the same assemblage, or different assemblages, is therefore possible.

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Figure 1: The vertebrate skeleton is sub-divided into nine skeletal units, shown using the pachypleurosaurid *Neusticosaurus* (Sander, 1989). The completeness and articulation of each is assessed separately using the categories described in Appendix 1.

Figure 2: Theoretical trends for the percentage and unit analyses. Plots of overall articulation versus completeness (as percentages), and scores for each unit (0 to 4), allow three trends to be defined: Trend 1, decreasing articulation but consistently high completeness; Trend 2, decreasing articulation accompanied by

loss of completeness; and Trend 3, variants between Trends 1 and 2. Trend 4 is not possible as loss of articulation is a pre-requisite to loss of completeness.

Figure 3: Bivariate plot showing percentage articulation (A%) versus percentage completeness (C%) for *Serpianosaurus* from the Besano Formation.

Figure 4: Bubble plots of articulation (A) versus completeness (C) in *Serpianosaurus* for each of the nine skeletal units (5a, head; 5b, neck vertebrae; 5c, dorsal vertebrae; 5d, tail vertebrae; 5e, ribs; 5f, front left limb; 5g, front right limb; 5h, back left limb; and 5i, back right limb). Articulation and completeness are scored from 0-4 (as Figure 4a); each of these categories is defined in Appendix 1. Values for Pearson's r-squared (r^2), Spearman rank-order (rs), and intercept (T) are shown for each skeletal unit.

Figure 5: Possible score combinations in the unit analysis. Possible combinations for, the head, rib and four limb units (5a), and the neck, dorsal and tail units (5b) are indicated by 'Y'; bold type and grey boxes indicate those combinations that are different between the two groups.

Figure 6: Results of the rib unit analysis. Articulation ranges from 6A (all six regions are fully articulated) to 0A (none articulated). Numbers in the grids are the number of specimens exhibiting that configuration.

Figure 7: Paired appendage plots for *Serpianosaurus*. 6a, articulation of the front limbs; 6b, completeness of the front limbs; 6c, articulation of the back limbs; and 6d, completeness of the back limbs.

Figure 8: Map and stratigraphic section of Middle Triassic outcrop in the Monte San Giorgio region (after Furrer (1995) and Stockar (2010)). The pachypleurosaurid *Serpianosaurus* (inset) is from the Besano Formation, which spans the Anisian-Ladinian boundary.

Figure 9: Key features of the taphonomy of *Serpianosaurus*. 9a, preferential disarticulation of the ribs on one side of the body. Disarticulated ribs are grouped into a narrow band extending perpendicular to the body

(PIMUZ T3683); 9b, variation in the skeletal fidelity of two individuals that are closely spaced vertically and preserved in the same lithology (PIMUZ T1071a-b). Variation is attributed to differences in the duration of the residence phase. Similar alignment of the anterior vertebrae in each was caused by current activity. The ribs in one specimen (circled) are disarticulated but parallel to each other and equally spaced as in life; 9c, similar alignment of the neck and tail is attributed to current activity (PIMUZ T3677).

Table 1: Limb tables for articulation (upper), and completeness (lower) in *Serpianosaurus*. Abbreviations: ph – phalanges; met – metacarpels/metatarsals; wr – wrist; ank – ankle; sh – shoulder; hip – hip; r/u – radius/ulna; t/f – tibia/fibula; hu –humerus; fem – femur.

Appendix 1.1: stage definitions for the head for articulation (top) and completeness (below).

Appendix 1.2: stage definitions for the neck vertebrae for articulation (top) and completeness (below).

Appendix 1.3: stage definitions for the dorsal vertebrae for articulation (top) and completeness (below).

Appendix 1.4: stage definitions for the tail vertebrae for articulation (top) and completeness (below).

Appendix 1.5: stage definitions for the ribs for articulation (top) and completeness (below).

Appendix 1.6: stage definitions for the front limbs for articulation (top) and completeness (below).

Appendix 1.7: stage definitions for the back limbs for articulation (top) and completeness (below).

Table 1

Artic	Front left					Front right					Back left					Back right				
	ph	wr	elb	sh	**TOT**	ph	wr	elb	sh	**TOT**	ph	ank	kne	hip	**TOT**	ph	ank	kne	hip	**TOT**
4	7	7	7	7	*7*	5	5	5	5	*5*	14	14	14	14	*14*	10	10	10	10	*10*
3	1	5	5	4	*5*	1	8	8	7	*8*	2	6	6	4	*6*	3	6	7	5	*7*
2	0	1	8	9	*9*	1	1	7	7	*8*	1	1	4	6	*7*	3	3	4	5	*8*
1	1	1	1	14	*17*	2	3	1	12	*18*	2	3	1	2	*7*	1	1	1	5	*8*
0	0	0	0	0	*12*	0	0	0	0	*10*	0	0	0	0	*17*	0	0	0	0	*15*
X					*2*					*3*					*1*					*4*
present	**9**	**14**	**21**	**34**		**9**	**17**	**21**	**31**		**19**	**24**	**25**	**26**		**17**	**20**	**22**	**25**	

Compl	Front left					Front right					Back left					Back right				
	ph	met	r/u	hu	**TOT**	ph	met	r/u	hu	**TOT**	ph	met	t/f	fem	**TOT**	ph	met	t/f	fem	**TOT**
4	20	20	20	20	*20*	18	18	18	18	*18*	25	25	25	25	*25*	27	27	27	27	*27*
3	1	4	5	5	*5*	0	9	9	9	*9*	2	9	10	9	*10*	3	8	9	7	*9*
2	0	0	15	15	*15*	0	0	12	12	*12*	0	2	4	6	*6*	0	0	4	4	*4*
1	0	0	0	8	*8*	0	0	1	8	*9*	0	0	0	3	*3*	0	0	0	4	*4*
0	0	0	0	0	*2*	0	0	0	0	*1*	0	0	0	0	*5*	0	0	0	0	*4*
X					*2*					*3*					*3*					*4*
present	**21**	**24**	**40**	**48**		**18**	**27**	**40**	**47**		**27**	**35**	**39**	**43**		**30**	**35**	**40**	**42**	

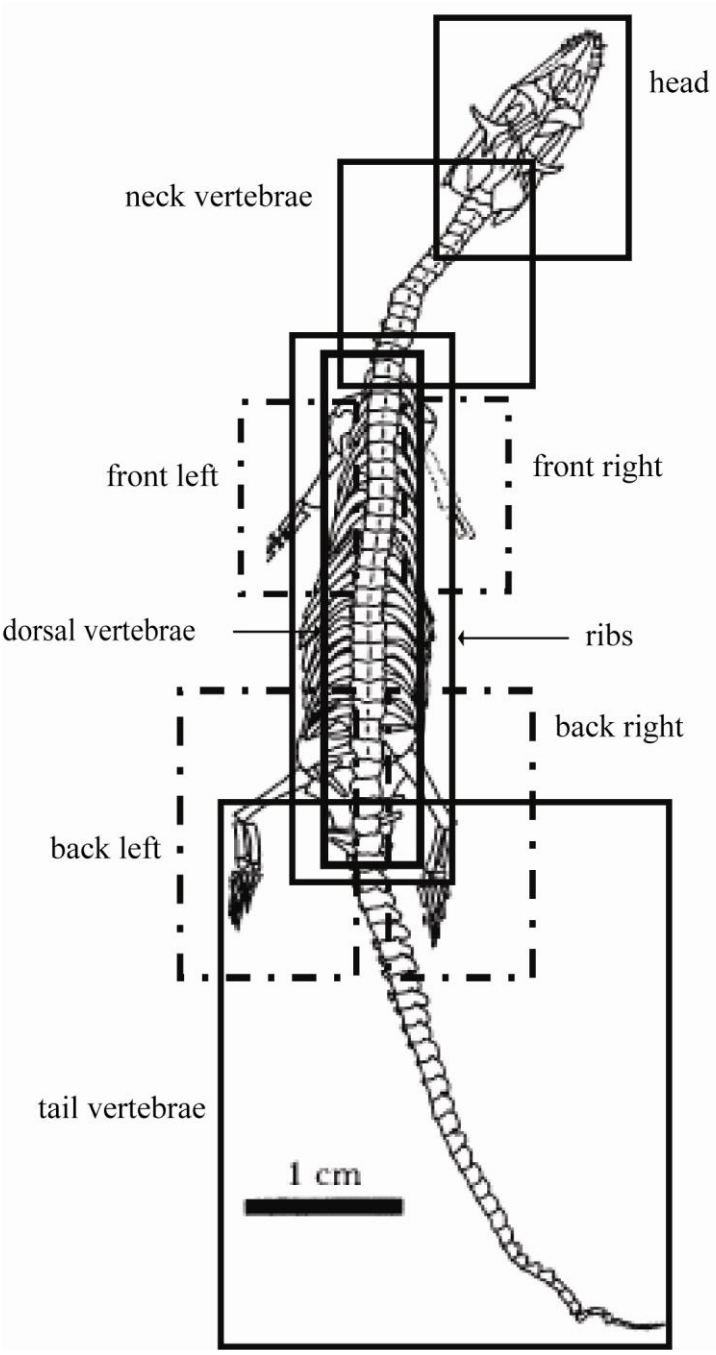

head
neck vertebrae
front left
front right
dorsal vertebrae
ribs
back right
back left
tail vertebrae
1 cm

Figure 1

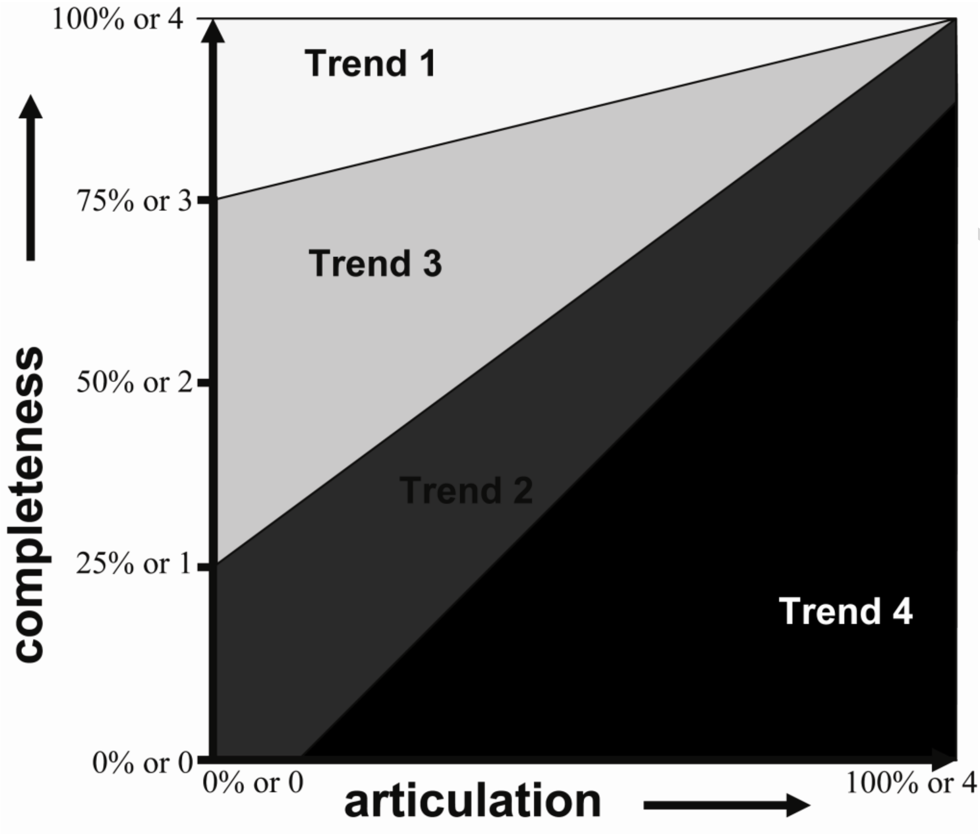
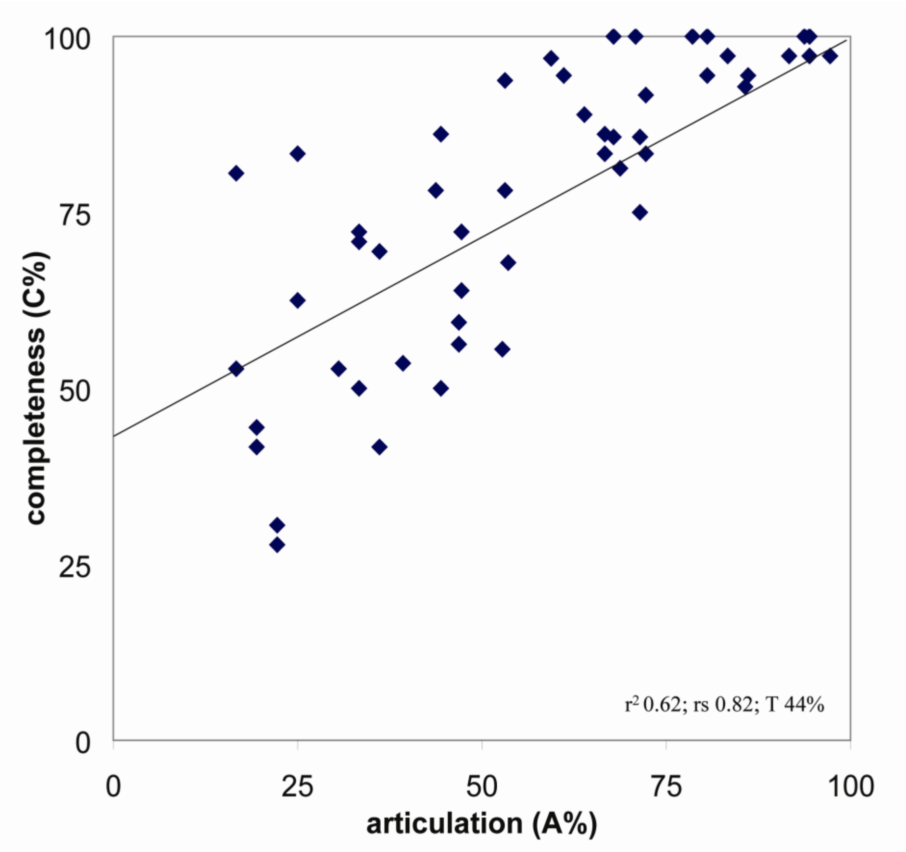

100% or 4
Trend 1
75% or 3
Trend 3
50% or 2
completeness
Trend 2
25% or 1
Trend 4
0% or 0
0% or 0
articulation
100% or 4

Figure 2



100
75
50
25
0
completeness (C%)
0
25
50
75
100
articulation (A%)
r² 0.62; rs 0.82; T 44%

Figure 3

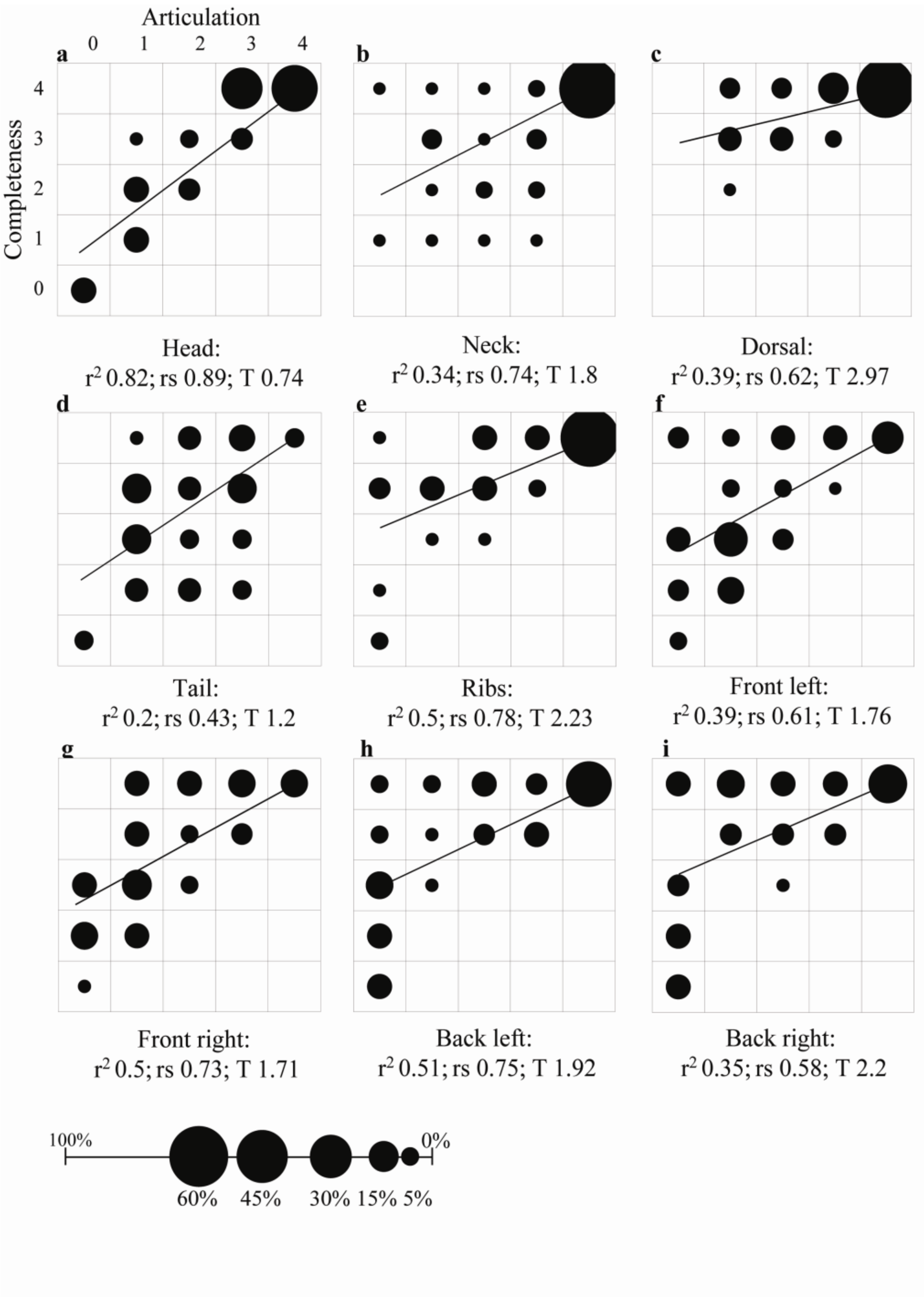

Articulation
0 1 2 3 4
Completeness
0 1 2 3 4
a
b
c
Head:
r^2 0.82; rs 0.89; T 0.74
Neck:
r^2 0.34; rs 0.74; T 1.8
Dorsal:
r^2 0.39; rs 0.62; T 2.97
d
e
f
Tail:
r^2 0.2; rs 0.43; T 1.2
Ribs:
r^2 0.5; rs 0.78; T 2.23
Front left:
r^2 0.39; rs 0.61; T 1.76
g
h
i
Front right:
r^2 0.5; rs 0.73; T 1.71
Back left:
r^2 0.51; rs 0.75; T 1.92
Back right:
r^2 0.35; rs 0.58; T 2.2
100%
0%
60% 45% 30% 15% 5%

Figure 4

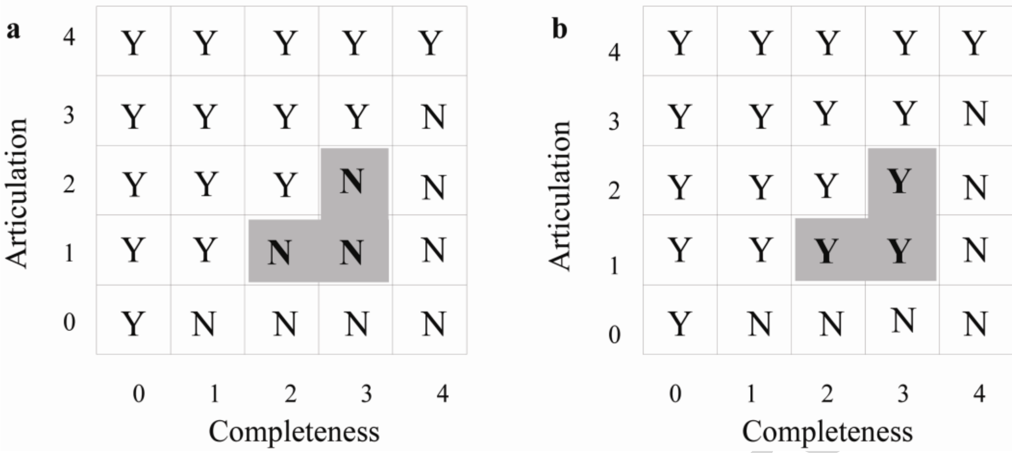


Figure 5

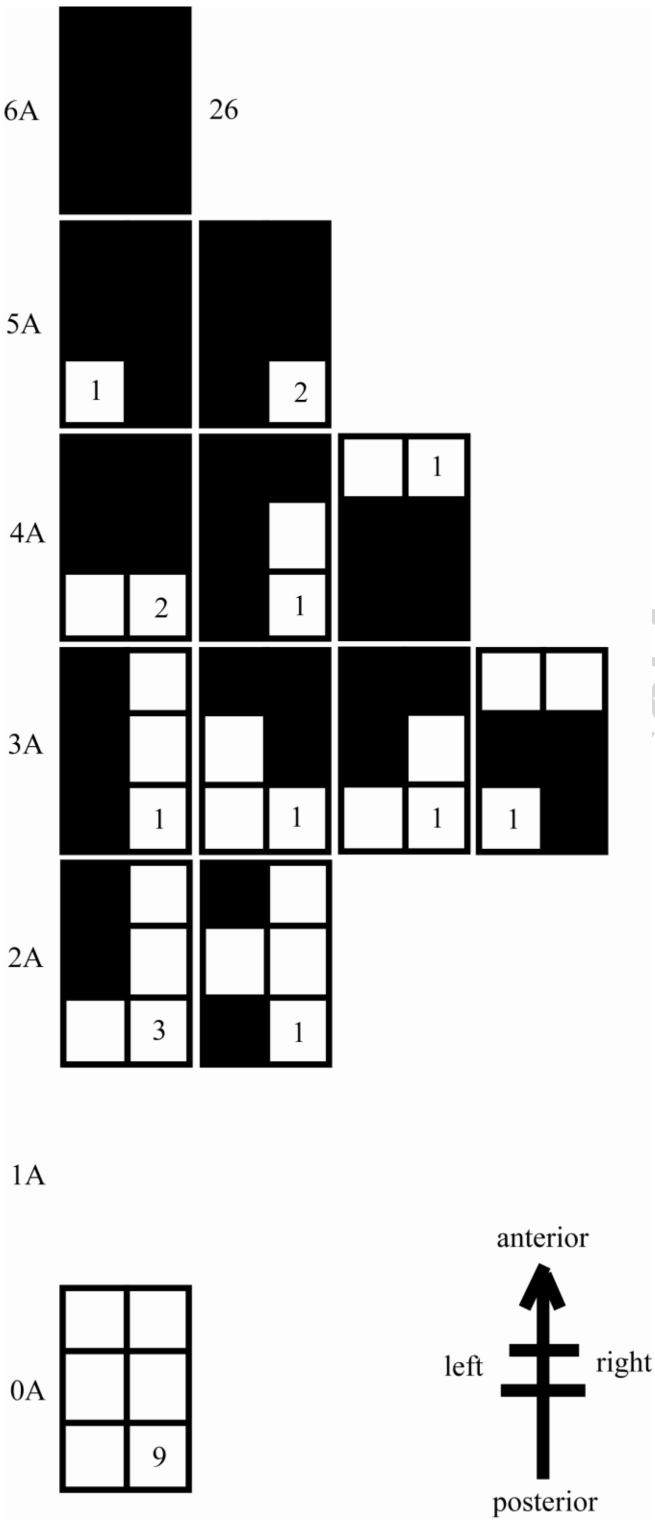

6A
26
5A
1
2
4A
1
2
1
3A
1
1
1
1
2A
3
1
1A
0A
9
anterior
left
right
posterior

Figure 6

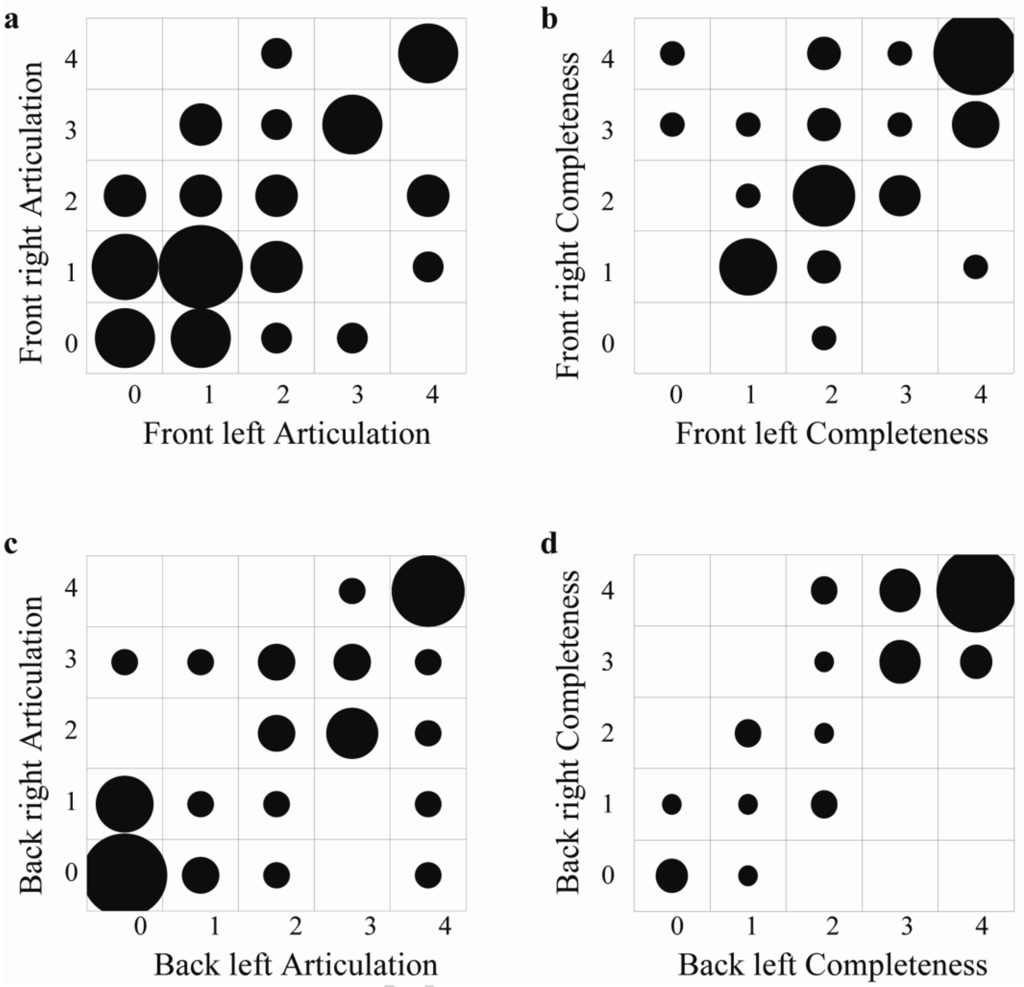

a
Front right Articulation
4
3
2
1
0
0
1
2
3
4
Front left Articulation
b
Front right Completeness
4
3
2
1
0
0
1
2
3
4
Front left Completeness
c
Back right Articulation
4
3
2
1
0
0
1
2
3
4
Back left Articulation
d
Back right Completeness
4
3
2
1
0
0
1
2
3
4
Back left Completeness

Figure 7

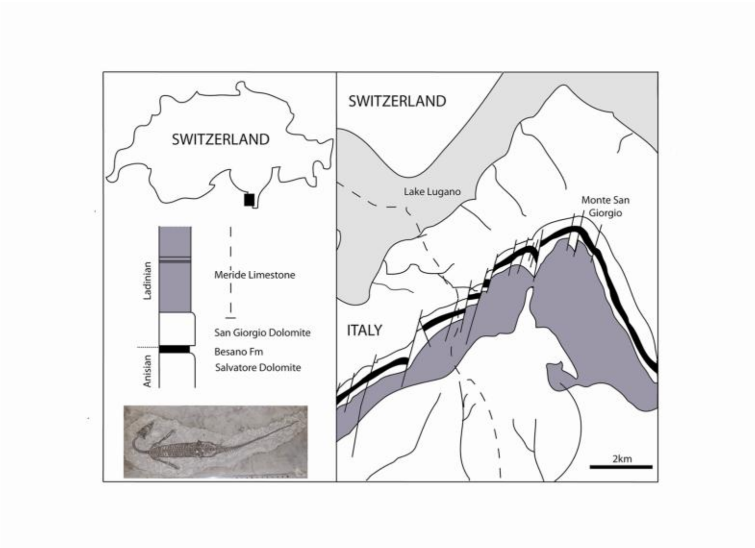

SWITZERLAND
SWITZERLAND
Lake Lugano
Monte San Giorgio
Ladinian
Meride Limestone
San Giorgio Dolomite
Besano Fm
Salvatore Dolomite
Anisian
ITALY
2km

Figure 8

Figure 9

Appendix 1.1: head

1.1: Head	Score	Articulation
	4	Description: head fully articulated, including skull (quadratojugal) with both lower jaws (angular). *Serpianosaurus* T0951: fully articulated skull including lower jaws.
	3	Description: near fully articulated, typically only one or both lower jaws lost. *Serpianosaurus* T0090: one lower jaw separated, the other near place of articulation at posterior of skull.
	2	Description: moderate articulation, approximately half of skull pieces articulated. *Serpianosaurus* T1074: parts of the skull articulated but anterior separated from posterior; jaws missing
	1	Description: limited articulation; majority of bones out of life position. *Serpianosaurus* T3709: elements scattered in vicinity of head; parietal, postfrontal and frontal bones still articulated.
	0	Description: no articulated elements. *Serpianosaurus* T0950: neck is articulated but nothing further anterior.

1.1: Head	Score	Completeness
	4	Description: head unit is fully complete; all skull elements present. *Serpianosaurus* T0951: complete skull.
	3	Description: near fully complete; 1-2 elements missing, typically 1 or both lower jaws. *Serpianosaurus* T3685: Skull and lower jaws present but frontal bone missing.
	2	Description: moderately complete; three or more elements remaining, typically the frontal bone and lower jaws. *Serpianosaurus* T1080: upper and lower jaws with frontal bone between; all are near life position.
	1	Description: limited completeness; 1-2 bones remaining, typically frontal bone. *Serpianosaurus* T1081: frontal bone is recognisable, amongst other fragmented elements.
	0	Description: head unit absent. *Serpianosaurus* T3807: part of neck articulated but nothing further anterior.

Appendix 1.2: neck

1.2: Neck vertebrae	Score	Articulation
	4	Description: vertebrae fully articulated. No breaks (imbrications, rotations or spaces between vertebrae). *Serpianosaurus* T1071a: all vertebrae articulated.
	3	Description: near fully articulated; 1-2 breaks between vertebrae. *Serpianosaurus* T0132: break at anterior end and midway along neck vertebrae.
	2	Description: moderate articulation; 3-7 breaks. Vertebrae can occur as short chains or piled in heaps. *Serpianosaurus* T3683: half articulated neck with other half piled to one side.
	1	Description: limited articulation; more than 8 breaks. Vertebrae generally scattered. *Serpianosaurus* T0961: Scattered vertebrae
	0	Description: no articulation. No photo

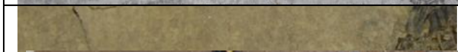
1.2: Neck vertebrae	Score	Completeness
	4	Description: 75-100% of vertebrae present (14 or more in *Serpianosaurus*). *Serpianosaurus* T1071a: all vertebrae present.
	3	Description: 50-75% complete (10-13 vertebrae in *Serpianosaurus*). *Serpianosaurus* T3807: 12 vertebrae.
	2	Description: 25-50% complete (6-9 vertebrae in *Serpianosaurus*). *Serpianosaurus* T0950: 7 vertebrae.
	1	Description: 10-25% complete (3-5 vertebrae in *Serpianosaurus*). *Serpianosaurus* T0964: 4 adjacent vertebrae, 1 separated (bottom left of photo).
	0	Description: 0-10% complete. Few, if any, vertebrae present (>2 in *Serpianosaurus*). *Serpianosaurus* T4821: no neck vertebrae.

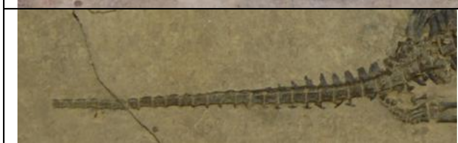
Appendix 1.3. dorsal

1.3: Dorsal vertebrae	Score	Articulation
	4	Description: fully articulated vertebrae. No breaks (imbrications, rotations or spaces). *Serpianosaurus* T0090: all vertebrae articulated without breaks
	3	Description: near fully articulated; 1-2 breaks. *Serpianosaurus* T3675: vertebrae posteriorly (left) rotated and therefore disarticulated.
	2	Description: moderate articulation; 3-10 breaks. *Serpianosaurus* T0950: anterior vertebrae articulated but posterior scattered.
	1	Description: limited articulation; more than 11 breaks; vertebrae generally scattered. *Serpianosaurus* T1046: vertebrae scattered.
	0	No articulations. No photo.

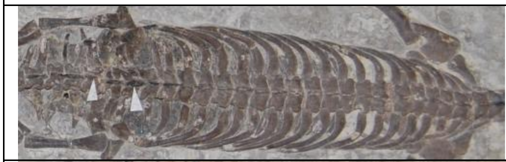
1.3: Dorsal vertebrae	Score	Completeness
	4	Description: 75-100% of vertebrae present (20 or more in *Serpianosaurus*). *Serpianosaurus* T3685: all present.
	3	Description: 50-75% complete (15-19 vertebrae in *Serpianosaurus*). *Serpianosaurus* T0950: 16 vertebrae.
	2	Description: 25-50% complete (8-14 vertebrae in *Serpianosaurus*). No photo
	1	Description: 10-25% complete (3-7 vertebrae in *Serpianosaurus*). No photo.
	0	Description: 0-10% complete. Few or no dorsal vertebrae present (<2 in *Serpianosaurus*). No photo

Appendix 1.4: tail

1.4: Tail vertebrae	Score	Articulation
	4	Description: fully articulated without breaks (imbrications, rotations or spaces). *Serpianosaurus* T3406: no breaks.
	3	Description: near fully articulated; 1-2 breaks. *Serpianosaurus* T3677: distal part of tail missing, only one break proven.
	2	Description: moderately articulated; 3-10 breaks. *Serpianosaurus* T3675: 7 breaks at various points.
	1	Description: limited articulation; >11 breaks. *Serpianosaurus* T3678: vertebrae disarticulated and piled.
	0	Description: no articulations. *Serpianosaurus* T3473: tail absent.

1.4: Tail vertebrae	Score	Completeness
	4	Description: 75-100% present (more than 45 in *Serpianosaurus*). *Serpianosaurus* T3931: 50 vertebrae.
	3	Description: 50-75% complete (31-45 vertebrae in *Serpianosaurus*). *Serpianosaurus* T1045: 28 vertebrae.
	2	Description: 25-50% complete (16-30 vertebrae in *Serpianosaurus*). *Serpianosaurus* T3677: 29 vertebrae
	1	Description: 10-25% complete (5-15 vertebrae in *Serpianosaurus*). *Serpianosaurus* T0950: 1 isolated and 7 ‘chained’ vertebrae.
	0	Description: 0-10% complete (<5 vertebrae in *Serpianosaurus*). *Serpianosaurus* T3473: tail absent.

Appendix 1.5: ribs

1.5: Ribs	Score	Articulation
	4	Description: 75-100% of ribs articulated (over 16 pairs or 30 single ribs in *Serpianosaurus*). *Serpianosaurus* T3685: all articulated.
	3	Description: 50-75% articulated (11-15 pairs or 20-30 single ribs in *Serpianosaurus*). *Serpianosaurus* T1045: only mid-region of ribcage articulated.
	2	Description: 25-50% articulated (6-10 pairs or 10-20 single ribs in *Serpianosaurus*). *Serpianosaurus* T3583: ribs disarticulated along one side.
	1	Description: 10-25% articulated (3-5 pairs or 5-10 single ribs in *Serpianosaurus*). *Serpianosaurus* T3810: articulation limited to several ribs on one side.
	0	Description: 0-10% articulated (<2 pairs or <4 single ribs in *Serpianosaurus*). *Serpianosaurus* T1278: few remaining ribs scattered.

1.5: Ribs	Score	Completeness
	4	Description: 75-100% complete (over 16 pairs or 30 single ribs in *Serpianosaurus*). *Serpianosaurus* T0090: all present.
	3	Description: 50-75% complete (11-15 pairs or 20-30 single ribs in *Serpianosaurus*). *Serpianosaurus* T0964: rib articulation lost on one side.
	2	Description: 25-50% complete (6-10 pairs or 10-20 single ribs in *Serpianosaurus*). *Serpianosaurus* T3810: 18 single ribs scattered.
	1	Description: 10-25% complete (3-5 pairs or 5-10 single ribs in *Serpianosaurus*). *Serpianosaurus* T1074: approximately 10 scattered ribs.
	0	Description: 0-10% complete (<2 pairs or <4 single ribs, in *Serpianosaurus*). *Serpianosaurus* T0950: 2-3 scattered ribs.

Appendix 1.5: stage definitions for the ribs for articulation (top) and completeness (below).

Appendix 1.6: front limbs

1.6: Front limbs	Score	Articulation
	4	Description: four joints (shoulder, elbow, wrist and hand) articulated. *Serpianosaurus* T3685: fully articulated.
	3	Description: three of 4 joints articulated, typically the shoulder, elbow and wrist. *Serpianosaurus* T3810: phalangeal-metacarpal joint absent.
	2	Description: two of 4 joints articulated; typically the shoulder and elbow. *Serpianosaurus* T3678: phalanageal-metacarpal and wrist joints only.
	1	Description: 1 of 4 joints articulated; typically the shoulder. *Serpianosaurus* T3683: humerus articulated at shoulder.
	0	Description: no articulated joints. *Serpianosaurus* T3810: scapula, humerus, radius and ulna not closely spaced or in life position.

1.6: Front limbs	Score	Completeness
	4	Description: humerus, radius and ulna, 50% of metacarpals (>3 in *Serpianosaurus*) and 50% of phalanges (>8 in *Serpianosaurus*) present. *Serpianosaurus* T0961: above bones present.
	3	Description: 3 of 4 subunits present, typically the phalanges are absent. *Serpianosaurus* T3675: humerus, radius/ulna and metacarpals retained.
	2	Description: 2 subunits present, typically metacarpals and phalanges are absent. *Serpianosaurus* T3683: humerus and radius/ulna retained.
	1	Description: only 1 subunit present, typically the humerus. *Serpianosaurus* T3683: humerus retained.
	0	Description: all limb bones absent. *Serpianosaurus* T0964: no bones present.

Appendix 1.7: back limbs

1.7: Back limbs	Score	Articulation
	4	Description: four joints (hip, knee, ankle and foot) articulated. *Serpianosaurus* T3933: fully articulated.
	3	Description: 3 of 4 joints articulated, typically the hip, knee and ankle. *Serpianosaurus* T3677: Foot, ankle and knee articulated but not hip.
	2	Description: 2 of 4 joints articulated, typically the hip and knee. *Serpianosaurus* T1045: femur articulated with hip and tibia/fibula; digits disarticulated.
	1	Description: 1 of 4 joints articulated, typically the hip. *Serpianosaurus* T3678: metatarsals and phalanges articulated.
	0	Description: no joints articulated. *Serpianosaurus* T0964: all elements present but not articulated.

1.7: Back limbs	Score	Completeness
	4	Description: femur, tibia and fibula, 50% of metatarsals (>3 in *Serpianosaurus*) and 50% of phalanges (>8 in *Serpianosaurus*) present. *Serpianosaurus* T3675: All bones present adjacent to body and tail.
	3	Description: 3 of 4 subunits present, typically the phalanges are absent. *Serpianosaurus* T3678: femur, tibia/fibula, and the metatarsals present; phalanges missing.
	2	Description: 2 of 4 subunits present, typically the femur and tibia/fibula. *Serpianosaurus* T3679: femur with tibia and fibula.
	1	Description: 1 of 4 subunits present, typically the femur. *Serpianosaurus* T3683: femur only.
	0	Description: all limb bones absent. *Serpianosaurus* T0964: no limb bones.

Highlights

We model vertebrate taphonomy using an innovative new method.

The method identifies the ‘phases’ responsible for loss of fidelity after death.

The intrinsic and extrinsic processes causing variation can thus be investigated.

Minor loss in *Serpianosaurus* was whilst floating, but most was *in situ* on the seabed.