



Biological controls upon the physical taphonomy of exceptionally preserved salamanders from the Miocene of Rubielos de Mora, northeast Spain

MARIA E. MCNAMARA, PATRICK J. ORR, TOM MANZOCCHI, LUIS ALCALÁ, PERE ANADÓN AND ENRIQUE PEÑALVER

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The middle Miocene Rubielos de Mora Konservat-Lagerstätte of northeast Spain is hosted within profundal, finely laminated, lacustrine mudstones. The diverse biota includes abundant salamanders. Most individuals died during separate episodes and sank rapidly postmortem. Specimens are typically preserved in dorso-ventral aspect, the most hydrodynamically stable orientation. The near-cylindrical morphology of the body, however, allowed some carcasses to settle in or subsequently re-orientate into, lateral orientations. Loss of skeletal elements (i.e. reduced completeness) reflects their location within the body and followed a distal to proximal trend. Two stages are identified: initial loss of a small number of phalanges, followed by loss of more proximal limb bones plus additional phalanges. Disarticulation is more complex: it occurred *via* several mechanisms (notably, abdominal rupture and re-orientation of part of the body and limbs during decay) and shows no consistent pattern among specimens. The physical taphonomy of the salamanders is controlled predominantly by intrinsic biological factors, i.e. the geometry of the body and of individual skeletal elements, the orientation, inherent strength and location of specific joints and the extent to which soft tissues, particularly the skin, persist during decay. These biological factors probably control patterns of physical taphonomy of other fossil tetrapods with a similar skeletal configuration. □ *Articulation, completeness, Konservat-Lagerstätten, orientation, quantitative taphonomy, salamanders.*

Maria E. McNamara* [maria.mcnamara@yale.edu], Patrick J. Orr [patrick.orr@ucd.ie], and Tom Manzocchi [tom@fag.ucd.ie], UCD School of Geological Sciences, University College Dublin, Belfield, Dublin 4, Ireland; *Current address: Department of Geology and Geophysics, Yale University, New Haven, CT 06520-8109, USA; Luis Alcalá [alcala@dinopolis.com], Fundación Conjunto Paleontológico de Teruel-Dinópolis, Avda. Sagunto s/n, 44002 Teruel, Aragón, Spain; Pere Anadón [panadon@ija.csic.es], Consejo Superior de Investigaciones Científicas, Institut de Ciències de la Terra 'Jaume Almera', Lluís Solé i Sabarís s/n 08028, Barcelona, Spain; Enrique Peñalver [e.penalver@igme.es], Instituto Geológico y Minero de España, C/Ríos Rosas 23, E-28003, Madrid, Spain; manuscript received on 24/9/2010; manuscript accepted on 01/4/2011.

Konservat-Lagerstätten are celebrated for the exceptional preservation of articulated multi-element skeletons and details of the soft tissue anatomy of ancient organisms and provide insight into palaeodiversity, organism morphology, evolution and taphonomic processes (Bottjer *et al.* 2002). The physical taphonomy (i.e. the completeness and articulation of the skeleton and the attitude of part or all of the skeleton with respect to bedding) of exceptionally preserved organisms can also yield useful palaeobiological information. Variation in the physical taphonomy of exceptionally preserved vertebrates can originate *via* extrinsic or intrinsic factors that relate to the physical and chemical aspects of the depositional system, and to the biology of the organism respectively. Various

studies of exceptionally preserved vertebrates have identified extrinsic factors that impact upon physical taphonomy, e.g. water depth (Elder & Smith 1988; Barton & Wilson 2005), water temperature (Barton & Wilson 2005), sediment consistency (Martill 1993) and concentrations of dissolved ions (Etter 2002). Previous taphonomic studies of exceptional vertebrate faunas have considered birds (Davis & Briggs 1998; Dyke & Lindow 2009), fish (McGrew 1975; Smith & Elder 1985; Elder & Smith 1988; Ferber & Wells 1995; Barton & Wilson 2005), frogs (Wuttke 1988) and reptiles (Casey *et al.* 2007). In each study, the authors related taphonomic patterns primarily or exclusively to extrinsic, environmental factors; the extent to which intrinsic factors impact upon physical

taphonomy is not well understood. Recent investigations of fossil anurans demonstrate that patterns of physical taphonomy can primarily reflect attributes of the biology of the animal itself, in particular, gross body geometry (McNamara *et al.* 2010), the orientation of specific skeletal elements relative to bedding and the presence of preserved skin (McNamara *et al.*, unpublished data). Other biological factors that may influence physical taphonomy include organism size and the strength of specific joints (Cambra-Moo & Buscalioni 2003).

In this article, we hypothesise that such intrinsic factors play an important role in the physical taphonomy of other vertebrate taxa, potentially explaining much of the taphonomic variation among taxa within and between different lagerstätten in broadly similar depositional settings. Herein, we test this using the example of fossil salamanders from the Miocene Rubielos de Mora Konservat-Lagerstätte of northeast Spain. These specimens comprise an ideal dataset as they are abundant and vary markedly in their taphonomy. Notably, the taphonomy of fossil salamanders has not been investigated previously, despite the preservation of abundant, well-articulated specimens in several Konservat-Lagerstätten (e.g. Gao & Shubin 2001, 2003; Wang & Rose 2005; Wang & Evans 2006). The taphonomic model presented herein can thus be tested by applying it to exceptionally preserved salamanders in other Konservat-Lagerstätten. We do so using data from the coeval lacustrine-hosted Lagerstätte of Libros (northeast Spain); the taphonomy of these salamanders has not been studied in detail; their taphonomic history is known to include organic preservation of bone marrow (McNamara *et al.* 2006).

Quantitative techniques are used infrequently in investigations of the physical taphonomy of exceptionally preserved vertebrates. Kemp & Unwin (1997) quantified percentage completeness and articulation for specimens of *Archaeopteryx*; Casey *et al.* (2007) in their study of exceptionally preserved tetrapods from the Virginia Solite Quarry (Triassic, USA) quantified percentage completeness, but used only qualitative data for articulation. Cambra-Moo & Buscalioni (2003) used semi-quantitative data for skeletal element overlap, completeness and articulation for various fossil vertebrates, and applied cluster analysis to investigation of disarticulation patterns. In a forthcoming study, we will integrate fully quantitative (i.e. percentage) and qualitative data for completeness and articulation to reveal subtle patterns in the physical taphonomy of exceptionally preserved frogs from the Miocene Libros biota. Herein, we build upon this approach, most notably *via* the novel application of trend analysis and further development of cluster

analysis applications, to identify the controls upon the physical taphonomy of fossil salamanders.

Geological setting

The Rubielos de Mora lacustrine system developed within a strongly asymmetric half-graben during the early–middle Miocene (Anadón *et al.* 1990). The basin-fill comprises ca. 800 m of lacustrine carbonates and alluvial and fluvial siliciclastics, and crops out near the village of Rubielos de Mora in the province of Teruel (Anadón *et al.* 1990, 1991) (Fig. 1). The deepest water facies of the Rubielos de Mora sequence is the 250-m-thick, middle Miocene, Facies Assemblage C1 (Anadón *et al.* 1989, 1991). It comprises laminated organic-rich mudstones (oil shales) interbedded with carbonate-clay rhythmites (herein referred to collectively as ‘laminated mudstones’) (Anadón *et al.* 1988, 1989), massive bioturbated mudstones and rare thin (10–30 mm thick) sandstone beds; these lithologies grade laterally into conglomerates and breccias deposited close to the fault-bounded western margin of the basin (Anadón *et al.* 1990, 1991). During deposition of the laminated facies, the lake was hydrologically open, perennial and meromictic, with extensive swamp-like littoral zones in its eastern parts, and a permanently anoxic monimolimnion. The lake was up to ca. 30–40 km² and a few tens of metres deep (de las Heras *et al.* 2003).

The laminated mudstones host an exceptional biota of abundant leaves (Fernández-Navarro 1914; Barrón & Diéguez 2001), insects (Peñalver 1998; Peñalver *et al.* 1999) and salamanders (Sanchiz 1977; Barrón & Diéguez 2001); two frog specimens are known (Martínez-Delclòs *et al.* 1991; and M.E.McN. personal

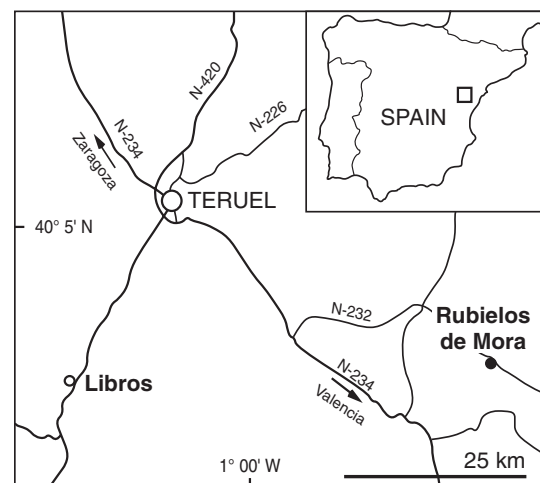


Fig. 1. Map of the Teruel region of northeast Spain showing the location of Rubielos de Mora and Libros with, inset, position within Spain.

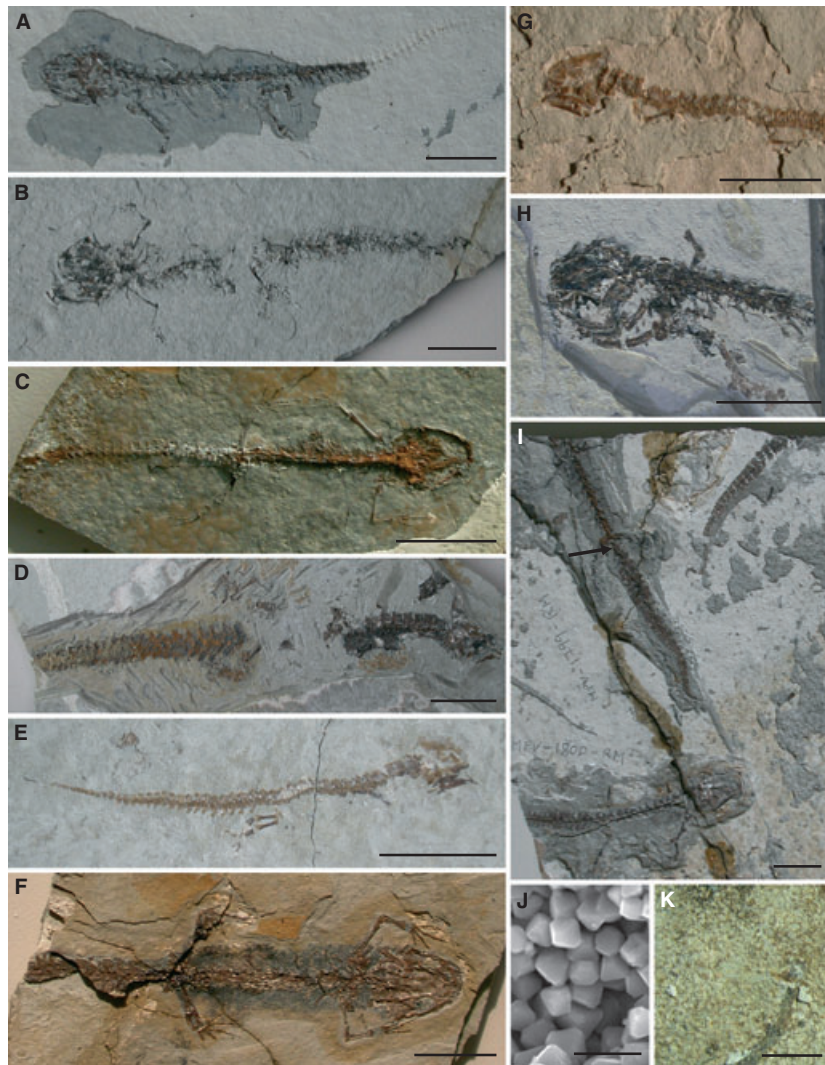


Fig. 2. Representative examples of exceptionally preserved salamanders from minor unit C1 of the Rubielos de Mora sequence, showing variation in orientation with respect to bedding, completeness, articulation and the extent of preserved soft tissues. A, MPV-1815-RM. Dorso-ventral orientation, moderate degree of completeness, well-articulated, rare soft tissues. B, MPV-1087-RM. Dorso-ventral orientation, high degree of completeness, well-articulated, no soft tissues. Note disarticulation in posterior thorax. C, MPV-864-RM. Dorso-ventral orientation, complete, fully articulated, no soft tissues. Note iron oxide void fill of bones. D, MPV-1819-RM. Lateral orientation, high degree of completeness, well-articulated, rare soft tissues. Note disarticulation in posterior thorax and iron oxide void fill of bones. E, MPV-423-RM. Lateral orientation, high degree of completeness, well-articulated, no soft tissues. F, MPV-1923-RM. Dorso-ventral orientation, complete, well-articulated, extensive soft tissues. G, MPV-1948-RM. Variable orientation (cranium dorso-ventral, rest of body lateral), moderate degrees of completeness and articulation, no soft tissues. H, MPV-1835-RM. Dorso-ventral, moderate degrees of completeness and articulation, rare soft tissues. I, MPV-1798-RM (top right). Lateral, no soft tissues. MPV-1799-RM (top left). Variable orientation (tail lateral, rest of body dorso-ventral), high degree of completeness, well-articulated, rare soft tissues. MPV-1800-RM (bottom). Dorso-ventral orientation, moderate degrees of completeness and articulation, no soft tissues. Scale for A–I = 10 mm. J, SEM micrograph of loosely packed octahedra of iron oxide (after pyrite) infilling void space within the cranium bones of MPV-1866-RM. Scale = 10 μ m. K, light micrograph of (brown) soft tissues showing subtle polygonal texture overlying the (pale-coloured) sediment (MPV-1911-RM). Scale = 2 mm.

observation). Taxa adapted to hot, humid, tropical conditions dominate (Peñalver *et al.* 1999; Barrón & Diéguez 2001). Salamanders (Fig. 2) typically occur as well-articulated skeletons; in some specimens, a dark brown carbonaceous layer defines part, or all, of the outline of their soft tissues (e.g. Fig. 2F), including details such as gill filaments. An orange-coloured decay halo can occur around part, or all, of a

specimen (Fig. 2D, F); iron oxide (after pyrite) can occur as a void fill of the bones (Fig. 2C, D, J).

Other facies of the Rubielos de Mora lacustrine sequence contain disarticulated skeletal remains of mammals, amphibians, reptiles and birds. Eggs of the cladoceran crustacean *Daphnia*, ostracods and gastropods are common throughout the sequence (Montoya *et al.* 1996).

Materials and methods

Skeletal anatomy

The skeleton of salamanders comprises three units: the cranium, axial skeleton and appendicular skeleton. The axial skeleton comprises the following types of vertebrae: cervical (the atlas); trunk (the vertebrae between the atlas and the sacrum to which ribs are attached); sacral (the vertebra to which the hindlimbs are attached); caudosacral (the two to four vertebrae immediately posterior to the sacrum); and caudal (tail vertebrae). The appendicular skeleton comprises the forelimbs (scapula, humerus, radius, ulna, carpals and phalanges) and hindlimbs (pelvis, femur, tibia, fibula, tarsals and phalanges). The term 'thorax' herein refers collectively to the atlas, trunk vertebrae and ribs.

Fossil material

A total of 160 specimens were examined from the collections of the following institutions in Spain: Museu de Geologia de Barcelona, Barcelona (MGB); Museu de Geologia del Institut Paleontològic Dr M. Crusafont, Sabadell, Barcelona (IPC); Museu de Geologia de la Universitat de València, Valencia (MGUV); Museo Paleontológico Municipal de Valencia, Valencia (MPV); and the Museu del Seminari, Barcelona (MSB). The fossil salamanders were originally identified as *Chelotriton paradoxus* (Fernández-Navarro 1914), but the taxonomy of the specimens is under revision; preliminary investigations by M. Böhme indicate that *Triturus*, *Pleurodeles* and *Chelotriton* (all members of Salamandridae) are represented (E.P. 2006 personal communication). This is not considered to impact significantly upon reconstructions of the taphonomic history of the salamanders as the anatomy of all specimens is fundamentally similar. Most specimens (85%) were recovered during field excavations by one of us (E.P.) in 1994, whereby a block of laminated mudstone of dimensions 650 × 500 × 280 mm was extracted and split as finely as possible in the laboratory. All salamander specimens recovered were archived by one of us (E.P.) at the MPV regardless of the quality of preservation and most received minimal or no further preparation; these specimens are therefore considered to represent an unbiased dataset. Variation in the fidelity of preservation of specimens archived in other institutions is similar to that of specimens from the MPV. The dataset as a whole is therefore considered to have sampled, at the very least, the most important of any differences in preservational conditions during deposition of the

laminated mudstones. Bioclastic material is associated with only 10% of salamander specimens and, where present, typically comprises rare, short (<5 mm) fragments of plant material, bivalves or ostracods.

Identification of adults, juveniles and larvae is not possible. Larvae of modern salamanders are typically smaller than adults and possess characteristic soft tissue features such as external gills and caudal fins. None of these anatomical features is a reliable indicator of life cycle stage in fossil salamanders. In particular, these soft tissue features, which have limited preservation potential, can be retained in neotenic taxa and individuals (the latter can coexist with metamorphic forms in a single population of a species; Duellman & Trueb 1986).

All specimens used in this study are preserved in laminated mudstones. The lithology of each fossil-bearing slab was classified according to the relative proportions of the different types of laminae present. The lamina succession of each slab was compared with that of all other slabs (using the method of McNamara *et al.* (2010)) to determine whether two or more slabs include the same fossiliferous horizon.

Eighty-five specimens were omitted from the study, as a large part of the body (greater than one foot, half of the tail or the cranium) is concealed by sediment or truncated by the edge of the slab. For 25 of the remainder ($n = 75$), only their orientation with respect to bedding could be determined, as part of the skeleton was not visible. Completeness, articulation and the extent of soft tissues were assessed for 50 specimens.

Sixteen salamander specimens from the Libros Lagerstätte were studied from the collections of the following institutions: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany (FNS); Museu del Colegio de la Salle, Teruel, Spain (MCS); Museu de Geologia de Barcelona, Barcelona (MGB); Museu de Geologia del Institut Paleontològic Dr M. Crusafont, Sabadell, Barcelona (IPC); Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN); and the Natural History Museum, London (NHM).

Orientation

Herein, we define the orientation of a specimen as *dorso-ventral*, *lateral* or *variable*. In the first two categories, the whole body is in the same orientation with the sagittal plane perpendicular (dorso-ventral) or parallel (lateral) to bedding respectively. Specimen orientation is classified as variable if different parts of the body are orientated differently. Way-up data are not available for any specimen and thus whether a specimen was deposited ventral side up or down, is unknown. These data are summarized in Figure 3.

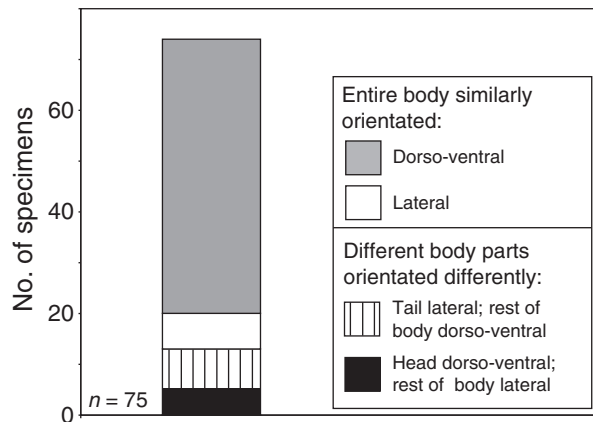


Fig. 3. Number of specimens in each orientation.

Completeness

All bones are present as entire non-fragmented elements. Bones were coded as present if they are preserved in or less than 20 mm from, life position; complete specimens may therefore be disarticulated. Due to their small size, the number of caudal vertebrae, cranial bones, carpals, tarsals and phalanges could not be determined precisely in the fossil material. Estimates for the total number of these elements were therefore determined using the skeleton of the extant salamander *Ambystoma*, as its skeletal configuration is essentially similar to that of the Rubielos de Mora salamanders and is representative of crown group salamanders (including salamandrids) (Duellman & Trueb 1986). Combination of these data, with that from the fossils, allows the total number of bones present in a fully articulated fossil specimen to be estimated as 172.

For each specimen ($n = 50$), completeness was assessed in two ways: (1) the percentage of the total number of bones present ('percentage completeness') (Fig. 4A); and (2) which skeletal elements are present (e.g. femur, humerus, etc.) (Fig. 5). Completeness was not assessed for: (1) the scapula and pelvis, as these bones were often obscured by the vertebrae; (2) the tarsals and carpals, as they are not ossified in larval salamanders; and (3) individual elements of the cranium, which are characteristically superimposed upon each other.

The absence of each trunk vertebra (V1–V13) (Fig. 4B), rib (Fig. 4C) and caudal vertebra (V18–V53) (Fig. 4D) was recorded. The significance of variation among the specimens could not be tested using χ^2 analysis (as $n < 5$ for some expected values); instead, differences were tested statistically using trend analysis (see Data S1 Supporting information and Fig. 1F, therein) (Fig. 6A, B).

Data on which particular skeletal elements are missing from each specimen ($n = 50$) formed the basis of

cluster analyses conducted using the Euclidean un-weighted pair-group method with arithmetic mean (UPGMA) algorithm using PAST (PALaeontological STatistics) v. 2.07 (Hammer *et al.* 2001; Fig. 7). This method was chosen as it performs equally well with data that form natural distinct groupings, as well as with data that comprise elongated chain-like groupings (Hill & Lewicki 2007). Cluster groups were identified visually and are the basis of 'completeness categories' defined by the types of element(s) lost (if any); each category does not have an identical level of support.

Articulation

Articulation can be assessed only for those skeletal elements that are present in the fossils. For example, given the absence of all skeletal elements distal of an articulated femur, only the bones at the knee joint can be coded as disarticulated. The bones at a particular joint were coded as articulated if they are juxtaposed in life position. For each specimen, articulation was assessed in two ways: (1) the percentage of the total number of joints that are articulated ('percentage articulation') (Fig. 4A); and (2) which of the individual joints (e.g. shoulder, knee, etc.) are articulated (Fig. 5). For specimens in which the exact positions of the scapula and pelvis could not be determined, the bones at the shoulder and hip joints were considered articulated if the humeri, and femora, respectively, were in life position. Where possible, the articulation of successive trunk vertebrae (Fig. 4B), ribs and the associated vertebra (Fig. 4C) and caudal vertebrae (Fig. 4D) was recorded. Differences in the number of specimens in which each of the trunk vertebrae (V1–V13) and caudal vertebrae (V18–V53) are disarticulated were tested statistically using χ^2 analysis; differences in the number of specimens in which each of the ribs are disarticulated were tested using trend analysis (Fig. 6C).

Data on which joints are disarticulated (if any) in a specimen are the basis of cluster analyses conducted using the methodology described above (Fig. 8). The bones at the following joints were chosen for further consideration: (1) the shoulder; (2) the hip; and (3) V7–V13. Specimens were assigned to 'articulation categories': (1) fully articulated; (2) shoulder disarticulated; (3) hip disarticulated; and (4) any of the posterior thoracic vertebrae disarticulated) based on the states of articulation of the bones at each of these joints.

Extent of soft tissues

Soft tissues are preserved as a thin (up to 250 μm thick) carbonaceous layer that often exhibits a

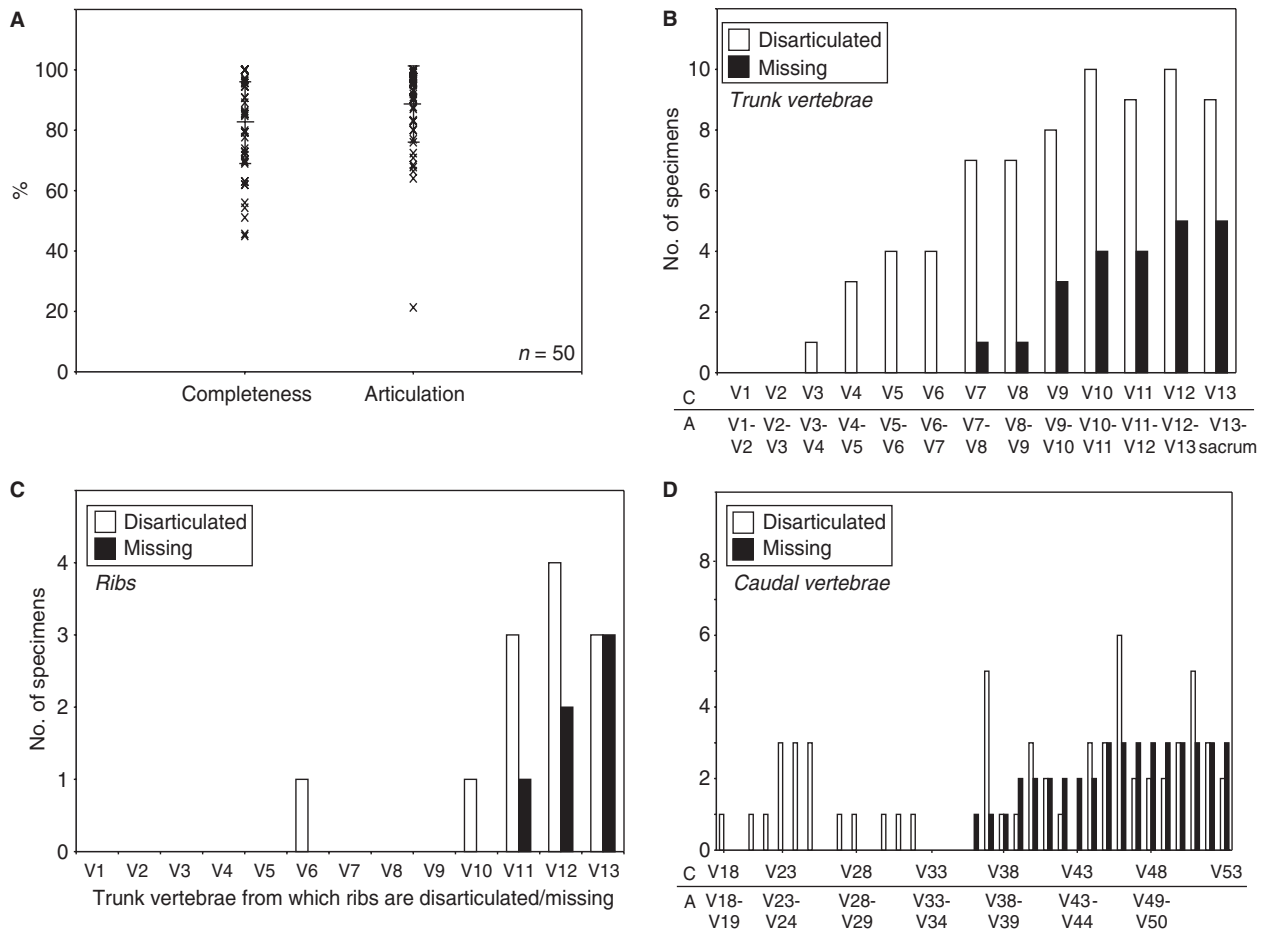


Fig. 4. Completeness and articulation. A, plot of the percentage completeness and articulation of specimens. Horizontal and vertical bars indicate mean and standard deviation respectively. B–D, plots of the number of specimens in which each of the trunk vertebrae (B), ribs (C) and caudal vertebrae (D) are missing and disarticulated.

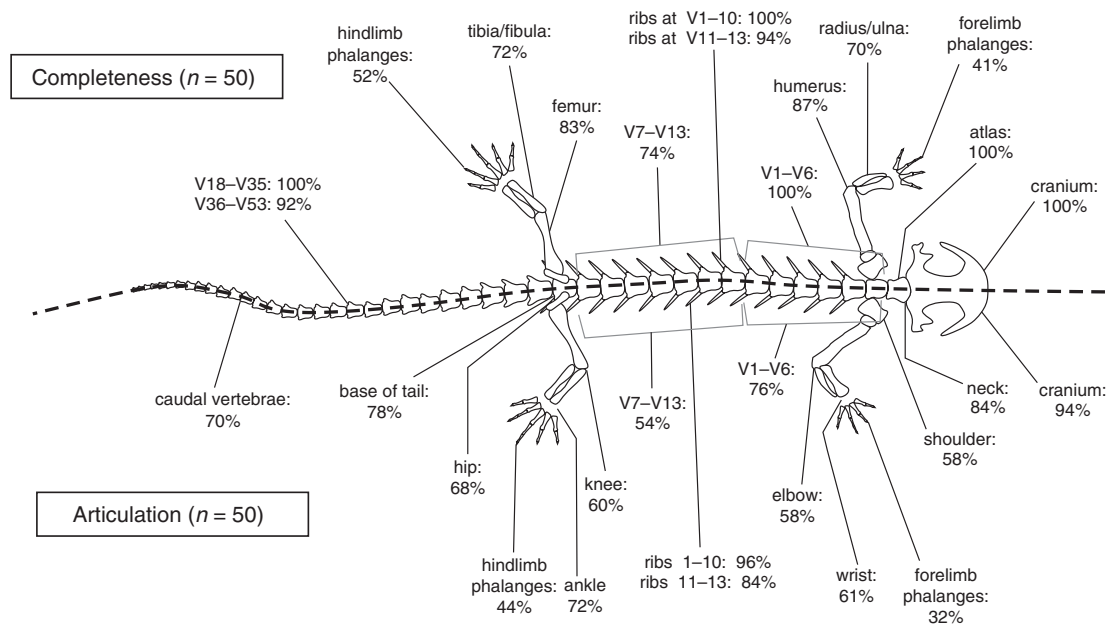


Fig. 5. Outline drawing of a salamander skeleton indicating the percentage of specimens in which each of the major bones (or bone groups, e.g. phalanges) is complete, and in which the bones at the major joints (or joint groups) are articulated.

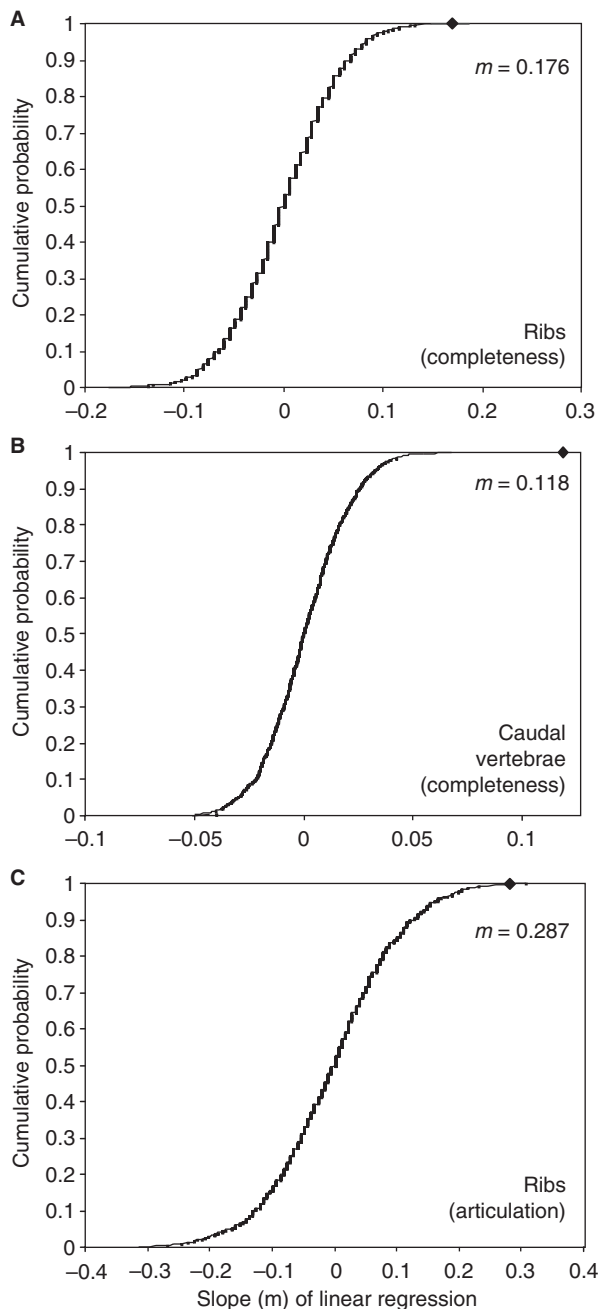


Fig. 6. Probability distributions of the slope of 1000 realisations of the number of specimens in which each of the ribs (A) and caudal vertebrae (B) are absent, and in which each of the ribs is disarticulated (C). The slope of the observed data (m) approximates to a cumulative probability of one in each case, indicating that the observed data in each are non-random (see Data S1 Supporting information for details of this trend analysis).

polygonal texture (Fig. 2K) similar to that in fossil anurans, where it defines the former positions of dermal glands (McNamara *et al.* 2009). The preserved soft tissues in the Rubielos de Mora salamanders are therefore considered to represent the degraded remains of the skin. When visible, the extent of soft

tissues was assessed using the following qualitative terms: extensive (all or most of the former outline of the body and tail is preserved); moderately extensive (the body outline is not preserved, but general body shape is apparent); rare (the soft tissues comprise discontinuous patches of limited extent); and absent. Specimens were coded according to these 'soft tissue extent categories'.

Analysis of the relationships among the taphonomic variables

The existence of any systematic relationships among the taphonomic variables was tested as follows:

- (1) Percentage completeness (ranked in descending order) was plotted against type of skeletal element absent (Fig. 9A).
- (2) Percentage completeness was plotted against percentage articulation (Fig. 9B).
- (3) Percentage completeness and articulation were plotted for each orientation (Fig. 9C).
- (4) Percentage completeness and articulation were plotted for each soft tissue extent category (Fig. 9D).
- (5) The following were calculated: (a) the percentage of specimens in which the bones at each of the major limb joints are disarticulated *and* the bone(s) immediately distal of that joint is (are) missing; (b) the percentage of specimens in which any of the trunk vertebrae is disarticulated *and* any vertebra at that joint is missing; and (c) the percentage of specimens in which the bones at the neck joint are disarticulated and any elements at that joint missing (Table 1).
- (6) For each completeness and articulation category, the number of specimens in each orientation (Table 2A, B) and in each soft tissue extent category (Table 2C, D) was recorded. Differences in the frequency of specimens among categories were tested statistically using Fisher's exact test.

Results

Lithological context of specimens

Comparison of the vertical faces of fossil-bearing slabs reveals few lithological correlations among them. Most (81 specimens; $n = 98$) specimens are from different horizons. Five horizons contain more than one salamander: two horizons contain two salamanders, two contain five, and a single horizon contains three.

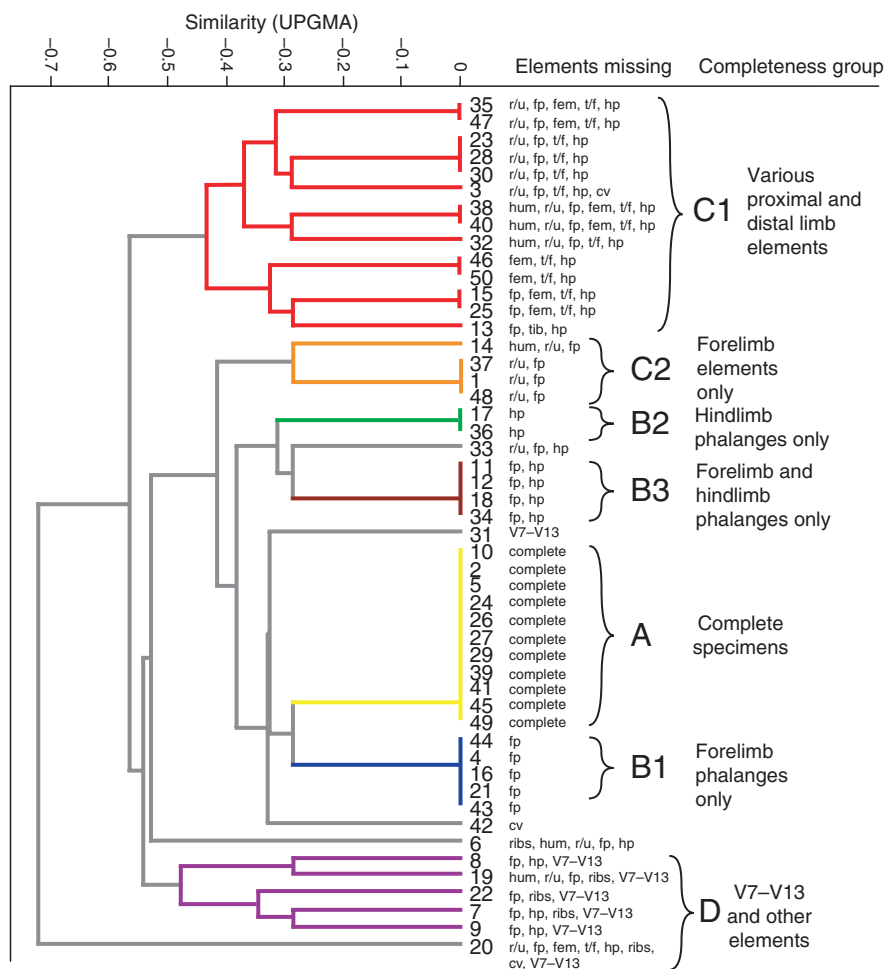


Fig. 7. Dendrogram based on cluster analysis (using the Euclidean UPGMA algorithm) of completeness (i.e. the type of skeletal element missing from each specimen). Coloured lines and letters A–D at right of dendrogram, denote major groupings of specimens. cv, caudal vertebrae; fem, femur; fp, forelimb phalanges; hp, hindlimb phalanges; hum, humerus; r/u, radius/ulna; t/f, tibia/fibula; v, trunk vertebra. Numbers 1–50 correspond to individual specimens.

Orientation

All specimens are orientated with the anterior-posterior axis of the body and tail parallel to bedding; this suggests that the lake floor was firm and cohesive at the time of deposition. In 61 ($n = 75$) specimens, the three major skeletal units (i.e. cranium, trunk and tail) are similarly orientated: 55 of these specimens are orientated dorso-ventrally, and six, laterally (Fig. 3). The predominance of dorso-ventral orientations implies that this was the most hydrodynamically stable orientation: it positions the femora, humeri and phalanges in the horizontal plane. This control was occasionally overridden, as the near-cylindrical morphology of the body allowed carcasses to be deposited in (or re-orientated after deposition into) lateral orientations.

In 14 ($n = 75$) specimens, different parts of the body are orientated differently. In eight of these, the tail is orientated laterally, and the rest of the body,

dorso-ventrally (Fig. 2I at arrow; compare with Fig. 2C). This phenomenon occurs in other fossil salamanders (Roček 1996), and is thought to reflect the geometry of caudal vertebrae, and the capacity for tail autotomy. Each caudal vertebra bears a high, broad, transversely flattened neural spine contained in the sagittal plane. In a dorso-ventrally orientated carcass, the neural spines would be initially perpendicular to bedding, and (after decay of the surrounding soft tissues), prone to reorientating into a more stable position, i.e. lateral to bedding. Many salamanders possess a weak articulation between the last caudosacral and first caudal vertebra to facilitate tail autotomy (Duellman & Trueb 1986). In salamanders that autotome the entire tail, the anterior caudal vertebrae possess characteristic anterolateral transverse processes (Babcock & Blais 2001). These structures are present in the Rubielos de Mora salamanders, which strongly suggests that they had the capacity for tail autotomy.

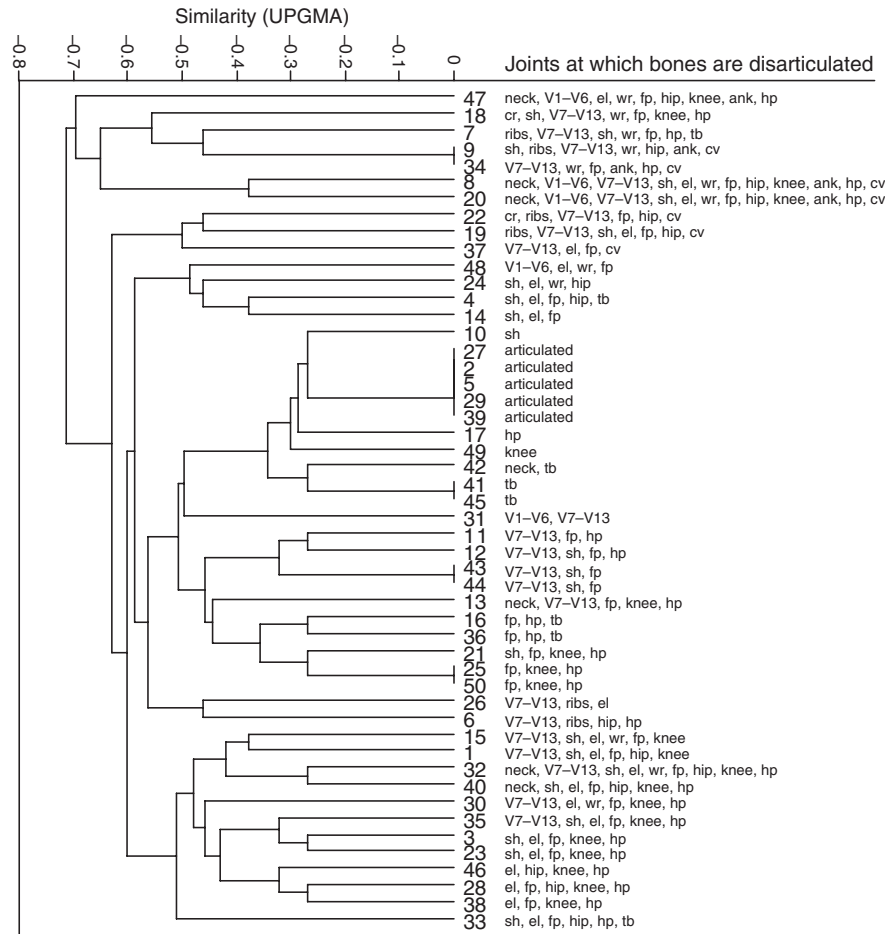


Fig. 8. Dendrogram based on cluster analysis (using the Euclidean UPGMA algorithm) of articulation (i.e. the joints in each specimen at which bones are disarticulated). ank, ankle; cr, cranium; cv, caudal vertebrae; el, elbow; fp, forelimb phalanges; hp, hindlimb phalanges, sh, shoulder; tb, tail base; V, trunk vertebra; wr, wrist. Numbers 1–50 correspond to individual specimens.

Reorientation of the entire tail in the fossil salamanders deposited in dorso-ventral orientations would be consistent with a weak articulation between the first caudal and the last caudosacral, vertebra.

In six specimens, the cranium is orientated dorso-ventrally and the remainder of the body is lateral (Fig. 2G), i.e. one part, almost certainly the entire cranium, has re-orientated as a unit. *In vivo*, most cranial bones are orientated with their largest surface area in the horizontal plane. Deposition of a carcass in a lateral orientation would orientate these bones perpendicular to bedding; disarticulation at the cranium-atlas joint would allow reorientation of the cranium as a unit into a more stable orientation, i.e. parallel to bedding. Unlike other amphibians, salamanders lack specialised trunk musculature to stabilise the head on the axial skeleton (Duellman & Trueb 1986). Reorientation of the cranium in fossil specimens that came to rest in lateral aspect reflects the weak articulation between cranium and atlas, explaining why it occurs without any disarticulation of the cranium itself.

Completeness

Percentage completeness of specimens values vary widely (45–100% (average 83.06%)) ($n = 50$) (Fig. 4A). Eleven specimens are complete (e.g. Fig. 2C, F). The cranium and atlas are present in all specimens (Fig. 5). Trunk vertebrae V1–V6 are present in all specimens; the number of specimens in which V7–V13 are absent increases progressively for V7 to V13 (Fig. 4B). Similarly, the ribs that articulate with V1–V10 are present in all specimens; the number of specimens lacking ribs increases progressively from V11 to V13 (Fig. 4C). Loss of vertebrae between V11 and V13 can be, but is not always, associated with loss of the corresponding ribs. The caudal vertebrae, V18–V35, are present in all specimens; the number of specimens lacking V36–V53 increases from V36 to V53 in a step-like manner (Fig. 4D). Trend analyses indicate that each of these distributions is statistically significant (Data S1 Supporting information, Fig. 1F; Figs. 6A, B). The following skeletal units are recognised: V1–V6, V7–V13 (trunk vertebrae), ribs at

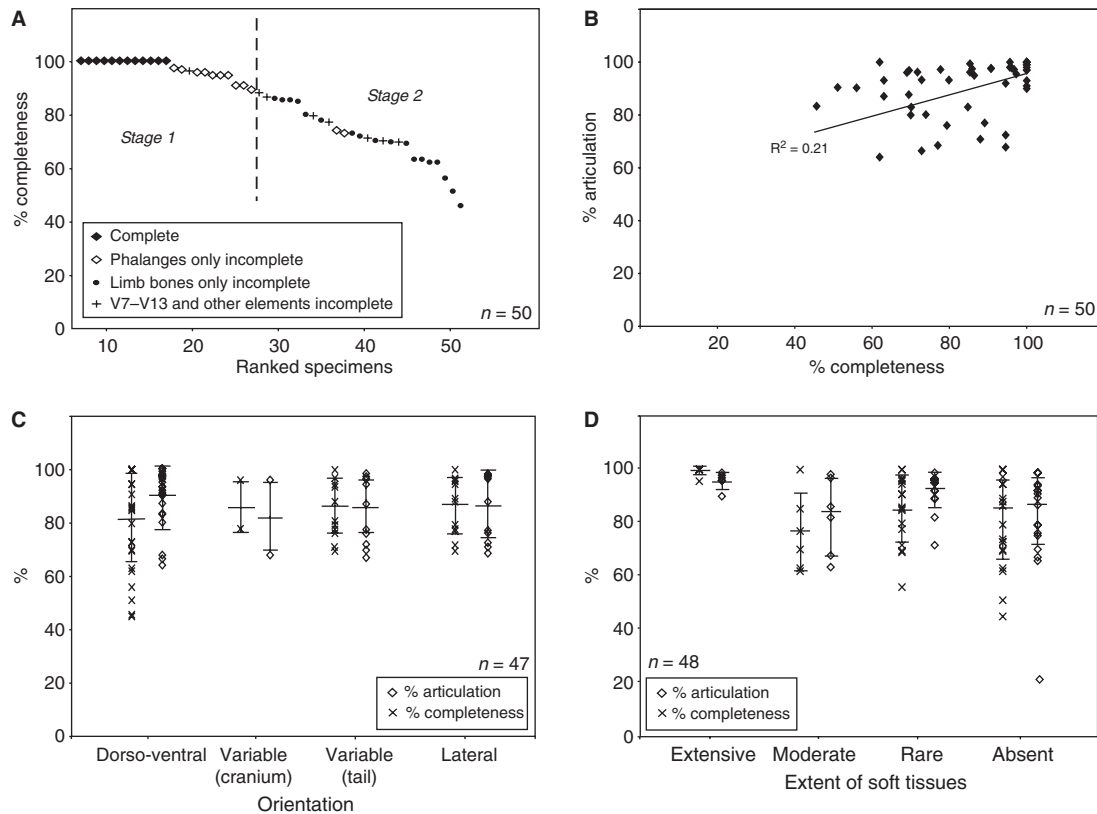


Fig. 9. Analyses of the relationships between completeness, articulation, orientation and the extent of soft tissues. A, percentage completeness versus skeletal elements that are absent (if any). B, percentage articulation of specimens versus percentage completeness. C, percentage completeness and percentage articulation of specimens in each orientation category. Horizontal and vertical bars denote mean and standard deviation respectively. The terms ‘variable (cranium)’ and ‘variable (tail)’ denote specimens in which these skeletal units are orientated differently to the rest of the body. D, percentage completeness and articulation of specimens in each soft tissue category.

Table 1. Percentage of specimens in which disarticulation of skeletal elements at specific joints is accompanied by loss of the more distal (upper box) and any (lower box) bone(s) at the joint.

Type of joint disarticulated	n	% specimens in which disarticulation at the joint is accompanied by loss of the more distal element(s) at the joint	
Wrist	34	94.2	Distal
Elbow	21	76.2	↓
Shoulder	16	56.3	Proximal
Ankle	28	92.3	Distal
Knee	20	75	↓
Hip	21	33.3	Proximal

Type of joint disarticulated	n	% specimens in which disarticulation at the joint is accompanied by loss of any of the relevant elements	
Trunk vertebrae	21	21.7	
Neck	8	0	

V1–V10, ribs at V11–13, V18–V35 and V36–V53 (caudal vertebrae).

Completeness decreases systematically towards the distal part of each limb. The phalanges are complete

in the forelimbs of only 41% of specimens, and in the hindlimbs of 52% (Fig. 5). All other elements are complete in $\geq 70\%$ of specimens. Notably, phalanges are always incomplete in cases where other limb elements are absent; the radius and ulna, and tibia and fibula are absent in all specimens in which the humerus and femur, respectively, are absent.

Approximately 92% of specimens ($n = 50$) are resolved into the following completeness groups, each of which exhibit moderate to high similarity (Fig. 7): A, complete specimens; B₁, specimens lacking only forelimb phalanges; B₂, specimens lacking only hindlimb phalanges; B₃, specimens lacking phalanges from both forelimbs and hindlimbs; C₁, specimens lacking only elements from the forelimbs; C₂, specimens lacking only elements from both forelimbs and hindlimbs; and, D, specimens lacking at least one trunk vertebra, in addition to other elements. Categories C₁ and D exhibit the lowest similarity values, as various different elements are lost in each; the types of element absent are, however, different in each and, especially, the other categories. Amalgamation of B₁, B₂ and B₃, and C₁ and C₂, produces the following major categories: A, complete specimens; B, specimens lacking

Table 2. Observed (obs) and expected (exp) frequency matrices for the number of specimens for each completeness (A) and articulation (B) category against specimen orientation and for each completeness (C) and articulation category against the extent of soft tissues in each specimen.

A

Obs	Specimen orientation				Exp	Specimen orientation			
	Dorso-ventral	Lateral	Variable (cranium)	Variable (tail)		Dorso-ventral	Lateral	Variable (cranium)	Variable (tail)
Completeness					Complete	5.85	0.23	1.8	1.12
Complete	8	0	1	0	Complete	5.85	0.23	1.8	1.12
Lacking phalanges only	4	1	1	3	Lacking phalanges only	9.1	0.35	2.8	1.75
Lacking limb elements only	11	0	2	1	Lacking limb elements only	5.2	0.2	1.6	1.0
Lacking axial elements (in addition to limb elements)	3	0	4	1	Lacking axial elements (in addition to limb elements)				

Disartic., disarticulated; vert., vertebra.

The terms ‘variable (cranium)’ and ‘variable (tail)’ denote specimens in which these skeletal units are orientated differently to the rest of the body.

B

Obs	Specimen orientation				Exp	Specimen orientation			
	Dorso-ventral	Lateral	Variable (cranium)	Variable (tail)		Dorso-ventral	Lateral	Variable (cranium)	Variable (tail)
Articulation					Fully articulated	1.89	0.222	0.278	0.611
Fully articulated	3	0	0	0	Fully articulated	8.81	1.04	1.3	2.85
Shoulder disartic.	9	1	1	3	Shoulder disartic.	10.1	1.19	1.48	3.26
Hip disartic.	8	2	1	5	Hip disartic.	13.2	1.56	1.94	4.28
Posterior trunk vert. Disartic.	14	1	3	3	Posterior trunk vert. Disartic.				

C

Obs	Extent of soft tissues				Exp	Extent of soft tissues			
	Extensive	Moderate	Rare	Absent		Extensive	Moderate	Rare	Absent
Completeness					Complete	1.28	1.28	3.62	3.83
Complete	5	1	2	2	Complete	1.53	1.53	4.34	4.60
Lacking phalanges only	1	0	5	6	Lacking phalanges only	2.17	2.17	6.15	6.51
Lacking limb elements only	0	4	9	4	Lacking limb elements only	1.02	1.02	2.89	3.06
Lacking axial elements (in addition to limb elements)	0	1	1	6	Lacking axial elements (in addition to limb elements)				

D

Obs	Extent of soft tissues				Exp	Extent of soft tissues			
	Extensive	Moderate	Rare	Absent		Extensive	Moderate	Rare	Absent
Articulation					Fully articulated	0.39	0.58	2.13	2.90
Fully articulated	1	0	1	3	Fully articulated	0.58	0.87	3.19	4.35
Shoulder disartic.	1	1	3	4	Shoulder disartic.	1.10	1.65	6.03	8.23
Hip disartic.	1	3	6	7	Hip disartic.	1.35	2.03	7.45	10.16
Posterior trunk vert. Disartic.	1	1	8	11	Posterior trunk vert. Disartic.				

phalanges only; C, specimens lacking limb elements only; and D, specimens lacking at least one of the trunk vertebrae V7–V13 (in addition to other elements).

Articulation

Percentage articulation of specimens values vary widely (64–100% (average 88.9%)) (n = 50)

(Fig. 4A). Six are fully articulated, only one of which is complete. Variation in disarticulation of the trunk vertebrae (Fig. 4B) is significant (30.4; $d = 12$; $\chi^2_{12} = 26.22$; $P < 0.01$). The anterior vertebrae (V1–V6) are rarely disarticulated, and the posterior vertebrae (V7–V13) are frequently disarticulated. The skeletal units V1–V6 and V7–V13 are thus treated separately herein. The ribs that articulate with V1–V10 are articulated in most specimens; the number of specimens in which the ribs at V11–V13 are disarticulated is high (Fig. 4C). Trend analysis (Fig. 6C) indicates that this distribution is statistically significant and thus the ribs at V1–V10 and V11–V13, respectively, are treated separately herein. Variation in disarticulation of the caudal vertebral joints (Fig. 4D) is not significant (47.5; $d = 34$; $\chi^2_{34} = 56.06$; $P < 0.01$); these joints are thus treated collectively herein.

Articulation is lowest for the phalanges: forelimb and hindlimb phalanges are articulated in 32% and 44% of specimens respectively ($n = 50$) (Fig. 5). Bones at more proximal joints in the limbs have higher articulation values (ranging between 58% and 72%), as are the ribs (84–96%) and the bones at the neck joint (84%) and V1–V6 (76%). In general, and similar to the loss of completeness, disarticulation followed a general distal to proximal trend; peripheral parts of the skeleton were affected first, and more often.

Several features are contrary to this trend:

1. *Poor articulation of V7–V13*: Articulation of trunk vertebrae V7–V13 is unexpectedly low (54% of specimens compared with 76% for V1–V6), given their location in the centre of the specimen. The trunk vertebrae affected are typically displaced by 3–8 mm and scattered in various directions (Fig. 2D). This is not consistent with dispersal of skeletal elements by a unidirectional current. With one exception, disarticulation of ribs occurs exclusively between V7 and V13; loss of ribs occurs where only the corresponding vertebrae are disarticulated. In most specimens in which V7–V13 are disarticulated, the cranium, V1–V6, tail and even the phalanges are well articulated (e.g. Fig. 2B, D). In extreme cases, a gap of up to 16 mm long may be generated between the anterior and posterior parts of the body, each of which remains well-articulated (Fig. 2B, D). The length of these gaps often exceeds the cumulative length of the missing vertebrae. Collectively, the observations indicate that the most likely cause of this localised disarticulation is abdominal rupture, i.e. the sudden release of decay gases generated during the decay process. This phenomenon was occasionally and sufficiently violent to displace the anterior and/or posterior halves of the body, and has been identified in other vertebrate fossils (Elder & Smith 1988).

2. *Anomalous disarticulation patterns in limbs*: Articulation of the bones at the shoulder (58% of

specimens) and hip joints (68%) is equal to, and only marginally better than that at the elbow (58%) and knee (60%) joints, respectively, and less than that at the wrist and ankle joints (61% and 72% of specimens respectively) (Fig. 5). Eleven (20%, $n = 54$) specimens lack one or more entire limbs; three specimens comprise isolated, articulated forelimbs. The bones at the hip and shoulder joints are therefore particularly prone to disarticulation. This feature could originate *via* one of two mechanisms (that are not necessarily mutually exclusive). The pectoral and pelvic girdles are ‘neither well developed nor especially firmly attached [to the axial skeleton]’ *in vivo* (Duellman & Trueb 1986, p. 364). The articulation of the bones at the hip joint is stronger than that at the shoulder joint (Duellman & Trueb 1986); this may explain the better articulation of the bones at the hip joint in the fossil material. Disarticulation of the bones at the hip joint may also reflect their proximity to the abdomen: 69% of specimens in which these elements are disarticulated exhibit evidence for abdominal rupture.

Articulation of bones at the elbow and knee joints (58% and 60% of specimens respectively) is less than that at the wrist and, especially, ankle joints (61% and 72% of specimens respectively). *In vivo*, the humerus and femur are orientated approximately horizontally, and the tibia, fibula, radius and ulna, vertically (although the angle between the upper and lower parts of each limb could alter somewhat when the carcass returns to a flaccid state following rigor mortis). Deposition of carcasses in a dorso-ventral attitude (the most common orientation) would present the latter set of bones steeply inclined to bedding. Decay-induced collapse of the soft tissues would result in the preferential reorientation of these bones, thus promoting disarticulation at the elbow and knee joints.

3. *Poor articulation at the base of the tail*: Articulation between the last caudosacral and first caudal vertebrae is lower than that between any successive two caudal vertebrae (78% and $\geq 94\%$ of specimens respectively). This reflects the weakness *in vivo* between the last caudosacral and first caudal vertebra, in salamanders that autotome the entire tail (see above).

Cluster analysis of disarticulation (Fig. 8) does not resolve specimens into well-supported categories (other than to identify fully articulated specimens). This is not unexpected, given the various processes by which disarticulation occurred; several processes may have occurred in a single specimen.

Extent of soft tissues

Soft tissues are extensive, moderately extensive, rare and absent in six, six, 17 and 19 specimens ($n = 48$) respectively.

Relationships among taphonomic variables

The phalanges comprise 44.5% of skeletal elements; loss of many, or most, of the phalanges would generate specimen completeness values of ca. 60%. Most (11 specimens, $n = 12$) specimens in which only the phalanges are missing, however, exhibit percentage completeness values of at least 90% (Fig. 9A), indicating that only some of the phalanges have been lost. Initial loss of a small number of phalanges ('Stage 1') therefore preceded a second stage ('Stage 2'), in which additional phalanges and, in some cases, more proximal limb elements are lost.

There is no obvious correlation between percentage completeness and articulation ($R^2 = 0.21$) (Fig. 9B). There is, however, a clear relationship between the location of disarticulated joints and which skeletal elements are missing (Table 1). Disarticulation at joints in the distal parts of the limbs (i.e. at the wrist and ankle joints) was almost invariably followed by the loss of the bone(s) distal to those joints. Disarticulation at joints in the proximal parts of limbs (i.e. at the shoulder and hip joints) and between trunk vertebrae was rarely accompanied by loss of the relevant skeletal elements. Disarticulation at a particular joint does not therefore automatically result in the removal of the relevant bones from the carcass. The critical variable is location within the skeleton: loss of skeletal elements at disarticulated joints occurs preferentially at peripheral parts of the carcass.

None of the following vary systematically between specimens in different orientations: percentage completeness and articulation (Fig. 9C), and which skeletal elements are lost (Table 2A; $P(\text{rand}) = 0.078$) and disarticulated (Table 2B; $P(\text{rand}) = 0.394$). Similarly, neither percentage articulation (Fig. 9D) nor which skeletal elements are disarticulated (Table 2D; $P(\text{rand}) = 0.06$) correlate with the extent to which the original outline of the soft tissues is preserved. There is, however, a correlation between completeness and the extent of soft tissues: (1) the standard deviation calculated for percentage completeness of specimens in which soft tissues that are extensive does not overlap that of any other category (Fig. 9D); and (2) the type of skeletal element lost correlates with the extent of soft tissues (Table 2C; $P(\text{rand}) = 1.8e^{-8}$). Two cells in the observed data matrix (Table 2C) yield values that are notably higher than expected: these are the number of complete specimens with extensive soft tissues, and the number of specimens lacking soft tissues and axial skeletal elements. The presence of extensive soft tissues, although not integral to the specimen remaining articulated, significantly enhances completeness. In particular, specimens in which soft tissues are extensive are more likely to retain peripheral skeletal elements; the

absence of soft tissues renders axial skeletal elements more likely to be removed. Decay experiments on amphibians have demonstrated that disarticulated skeletal elements may remain in close proximity to each another within the envelope of the degraded skin, which persists during decay (Wuttke 1983). Loss of distal skeletal elements in the Rubielos de Mora salamanders is therefore likely to have required degradation of the skin in the peripheral parts of the body.

Discussion

Taphonomic model: controls on physical taphonomy

The precise cause of death of the salamanders cannot be determined; the occurrence of most specimens as isolated individuals on separate horizons, however, demonstrates that carcasses were supplied to the site of deposition on a continual basis. Articulation and completeness values are generally high; this, combined with the preservation of soft tissues, indicates that most carcasses did not experience significant decay prior to transport. Carcasses would therefore have probably been sourced from either the lake itself or from streams or rivers in the immediate hinterland, and deposited in profundal lake zones shortly after death. The absence of fish in the lake would have eliminated scavenging of carcasses in the period between death and deposition; after deposition, prevailing hypolimnetic anoxia precluded disturbance of carcasses by bioturbators or scavengers.

Abdominal rupture is characteristic of partial flotation of a carcass (Smith & Elder 1985; Elder & Smith 1988), whereby the pressure generated by abdominal gases is sufficient to raise the abdomen of a carcass above the sediment-water interface, but not to allow the entire carcass to refloat (Smith & Elder 1985). There is no evidence for refloating and disarticulation of carcasses in surficial lake waters, which would result in wide scattering of partial carcasses; these processes could have been inhibited by low hypolimnetic temperatures and by the pressure of the overlying water column (Smith & Elder 1985; Barton & Wilson 2005). Variation in the physical taphonomy of the Rubielos de Mora salamanders therefore originated while specimens rested on the sediment-water interface.

Abdominal rupture resulted in disarticulation and, to a lesser extent, facilitated loss of posterior trunk vertebrae and ribs; it may also have contributed to disarticulation at the hip joint. The likelihood of abdominal rupture could have been influenced by various intrinsic and extrinsic factors including (but not restricted to) the temperature and depth of the lake

waters (Smith & Elder 1985; Ferber & Wells 1995; Barton & Wilson 2005), the amount of decay prior to carcass deposition, the rate of decay, salamander diet and the composition of the intestinal flora. The other patterns of completeness and disarticulation identified in the Rubielos de Mora salamanders reflect a suite of intrinsic, i.e. biological factors.

Skeletal elements in peripheral parts of the body (notably the limbs, especially their distal parts) are most likely to be incomplete. This occurred in tandem with loss of the protective envelope formed by the soft tissues (especially the skin); as this envelope progressively retreated from the periphery of the carcass during decay, the likelihood of exposed skeletal elements being removed (presumably by weak, possibly episodic, bottom currents) was increased.

There is a weak trend of increasing disarticulation towards the periphery of the skeleton. However, as indicated by the lower support for the categories identified for articulation than completeness in cluster analysis, patterns of disarticulation are more complex than those of completeness. Instead, the patterns are modelled best as a series of localised features that reflect the orientation of bones with respect to bedding and the relative strength of specific joints. Although dorso-ventral orientations dominate, the general cylindrical shape also allowed specimens to come to rest in lateral orientations. Disarticulation at the neck joint and at the base of the tail resulted in the rotation of either the cranium (if the remainder of the specimen is in lateral aspect) or tail (if the remainder of the skeleton is in dorso-ventral aspect) as a unit into a more stable position. Higher than expected values for disarticulation of the bones at the shoulder and hip joints is explained best by the weakness of these joints *in vivo* (although, in the case of the hip, may have been exacerbated by abdominal rupture). Salamanders use a sprawling posture; in specimens in

dorso-ventral aspect (or those now in variable orientation that would have come to rest with the abdomen in dorso-ventral aspect), the middle part of each limb would have been oriented at a high angle to bedding and prone to disarticulation at the knee and ankle.

Comparison with salamanders from the Libros biota

The preservation of salamanders in the late Miocene lacustrine-hosted Libros biota affords an opportunity to test the taphonomic model developed using the Rubielos de Mora salamanders and using a fauna from the same geographic area (Teruel province, Spain) of similar (Miocene) age, and also from a lacustrine depositional setting (Table 3).

The Libros biota includes 16 salamanders. All specimens are from organic-rich, finely laminated mudstones of the Libros Gypsum Unit, which were deposited in profundal lake zones beneath an anoxic, sulphidic monimolimnion (Ortí *et al.* 2003). Specimens were recovered during commercial exploitation of oil shales and sulphur deposits within the unit during the early part of the 20th century and are known only from museum collections; it is impossible to confirm whether the curated specimens are representative of the fossil assemblage. Specimens are typically preserved as articulated skeletons; the outline of the soft tissues can be defined by a brown carbonaceous layer (Fig. 10A–C). All specimens occur on separate horizons. Six specimens are assigned to *Oligosemia spinosa* (Salamandridae) (although this assignment is uncertain (Sanchiz 1977)); the affinities of the remainder are unknown. Taphonomic data for two specimens could not be assessed.

As with the Rubielos de Mora specimens, most of those from Libros ($n = 14$) are orientated consistently throughout the body and tail: twelve are orientated

Table 3. Comparison of the Libros and Rubielos de Mora sites, and fossil salamander data.

	Rubielos de Mora	Libros
Geological background		
Age	Early-middle miocene	Late miocene
Climate	warm humid	cool humid
Palaeolake alkalinity	low	high
Palaeolake depth	up to 20–30 m	up to 100 m
Host sediments	organic-rich laminated mudstones	organic-rich laminated mudstones
Salamander data		
n	160	16
Orientation	Most specimens dorso-ventral, some lateral; some variably orientated	Most specimens dorso-ventral, one lateral; one variably orientated
Completeness	64–100% high for axial bones except in posterior abdomen; decreases towards distal parts of the limbs and tail	85–100% high for axial bones; decreases towards distal parts of the limbs and tail
Articulation	45–100% high for axial bones except in posterior abdomen; lowest for phalanges	60–100% high for axial bones lowest for phalanges
Evidence for abdominal rupture?	Yes	No

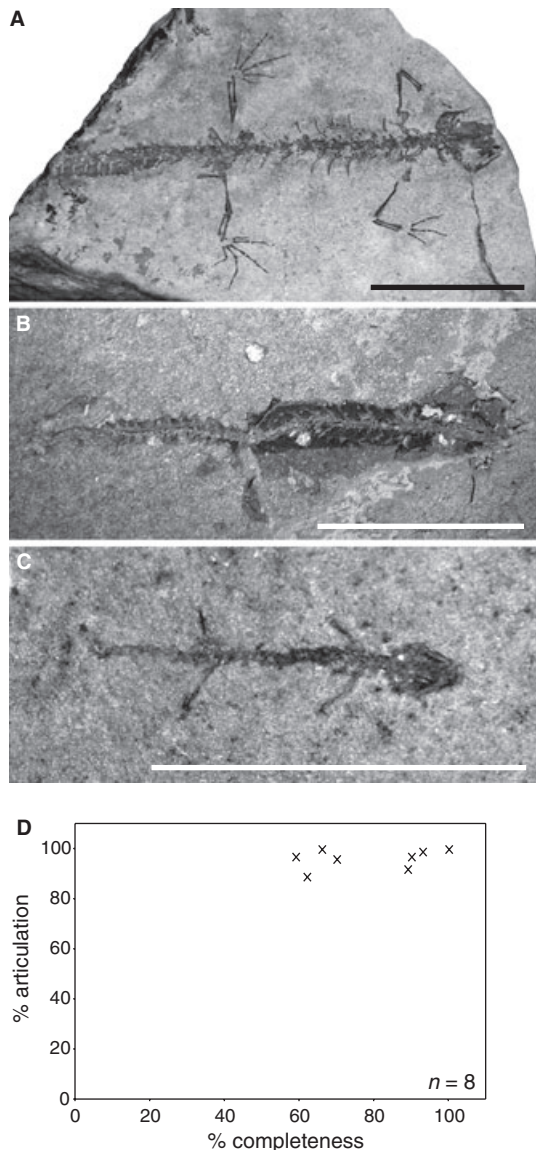


Fig. 10. Salamanders from the Late Miocene Libros biota. A–C: Specimens showing variation in completeness, articulation and the extent of soft tissues. Specimens in A and C are representatives of *Oligosemia spinosa*. A, FNS-A579. Tail laterally orientated, rest of body dorso-ventrally orientated, complete, fully articulated, rare soft tissues. B, MCS-615b. Dorso-ventrally orientated, moderate degrees of completeness and articulation of extensive soft tissues. C, MGB-27145. Dorso-ventrally orientated, moderate degrees of completeness and articulation of rare soft tissues. Scale for A–C = 20 mm. D, plot of percentage completeness versus percentage articulation for each specimen.

dorso-ventrally, and one laterally. One Libros specimen exhibits variable orientation: the tail is orientated laterally and the rest of the specimen, dorso-ventrally (Fig. 10A).

The Libros specimens consistently exhibit high percentage values for specimen completeness and articulation (Fig. 10D). The cranium, trunk vertebrae, humerus, femur and the anterior two-thirds of the caudal vertebrae are complete in all specimens. The

radius, ulna, tibia, fibula and caudal vertebrae in the proximal third of the tail are present in at least 50% of specimens. The forelimb and hindlimb phalanges, however, are present in only 25% and 37.5% of specimens respectively (Table 4). Articulation is lowest for the forelimb and hindlimb phalanges (each 25% of specimens), and higher for the bones at the knee, elbow, ankle and wrist joints (50%, 50%, 75% and 100% of specimens respectively) (Table 4). Patterns of completeness and articulation of specimens from Libros therefore closely resemble those of specimens from Rubielos de Mora.

The limited nature of the dataset for the Libros salamanders precludes systematic analysis of the relationship between completeness, articulation and the extent of soft tissues. Specimens with extensive soft tissues, however, are typically (near-) complete; soft tissues are absent in specimens with the lowest completeness values. These observations are consistent with the data for the Rubielos de Mora salamanders and suggest that a positive correlation between completeness and the extent of soft tissues is characteristic of fossil salamanders, in general.

Unlike specimens from Rubielos de Mora, there is no evidence for abdominal rupture in any specimen from Libros. This cannot be explained by the smaller size of the Libros dataset: abdominal rupture is evident in almost half of the specimens from Rubielos de Mora, on which basis it should occur in eight specimens from Libros. The absence of this taphonomic feature in the Libros salamanders probably reflects environmental factors. Cool lake temperatures (Barton & Wilson 2005), a high lake level and dense lake waters (i.e. containing high concentrations of ions (Ferber & Wells 1995)) can each inhibit the generation of decay gases in carcasses at the sediment-water interface. Climatic conditions were cool and humid during deposition of the Libros laminated mudstones (Van Dam & Weltje 1999), i.e. cooler than those prevailing during deposition in the Rubielos de Mora palaeolake. More significantly, however, the Rubielos de Mora palaeolake was characterised by low alkalinity and was not a locus for evaporite deposition, whereas the Libros lakefloor was the site of extensive deposition of primary gypsum. Furthermore, with a maximum depth of a few tens of metres (Anadón *et al.* 1988), the Rubielos de Mora palaeolake was considerably shallower than the Libros palaeolake (up to 100 m deep (Ortí *et al.* 2003)). The high frequency of abdominal rupture in salamanders from Rubielos de Mora, and its absence in salamanders from Libros, is therefore attributed to differences in palaeolake depth and alkalinity.

In summary, the physical taphonomy of salamanders from Rubielos de Mora and Libros is broadly

Table 4. Percentage of salamander specimens from Libros, in which each of the major skeletal elements (or element groups, e.g. phalanges) is complete and the bones at specific joints (or joint groups) are articulated.

Completeness		Articulation	
Skeletal element	% of specimens ($n = 8$)	Joint at which bones are disarticulated	% of specimens ($n = 8$)
Cranium	100	Cranium	87.5
Atlas	100	Neck	100
Humerus	100	Shoulder	75
Radius/ulna	50	Elbow	50
Forelimb phalanges	25	Wrist	100
Trunk vertebrae	100	Forelimb phalanges	25
Ribs	100	Trunk vertebrae	100
Femur	100	Ribs	100
Tibia/fibula	50	Hip	87.5
Hindlimb phalanges	37.5	Knee	50
Anterior caudal vertebrae	100	Ankle	75
Posterior caudal vertebrae	50	Hindlimb phalanges	25
–	–	Anterior caudal vertebrae	87.5
–	–	Posterior caudal vertebrae	62.5

similar and reflects the prevalence of intrinsic, biological, taphonomic controls. Foremost among such controls are the geometry of the skeleton and of individual skeletal elements, the inherent strength of individual joints and the extent to which soft tissues persist during decay. The effects of the above biological controls upon the physical taphonomy of the salamanders are superimposed by an environmentally controlled process (abdominal rupture). The overall result, subtle taphonomic differences between the salamander faunas, reflects differences in limnology.

Wider implications

This study uses quantitative taphonomic techniques that are broadly applicable to other vertebrate taxa, including exceptionally preserved specimens, and those preserved as well-articulated skeletons. Trend- and cluster analyses are useful to define, and assess statistical support for, groupings based upon articulation and completeness data. Previous quantitative taphonomic studies on exceptionally preserved vertebrates have emphasised the impact of different depositional regimes on physical taphonomy (e.g. Kemp & Unwin 1997; Casey *et al.* 2007). Herein, we have shown how quantitative techniques can also identify various subtle biological factors that influence patterns of physical taphonomy. Furthermore, there is a clear link between patterns of physical taphonomy in fossil salamanders and the biology of their modern relatives (e.g. posture and relative joint strength). The methods used herein therefore have the potential to shed light on similar aspects of the biology and functional anatomy of other fossil tetrapods with a similar skeletal configuration and body plan, i.e. a roughly cylindrical, slender, body with a long tail, and limbs held at right angles to the sagittal axis. Examples of

such fossils deposited in similar environmental settings to that of the Rubielos de Mora and Libros biotas (i.e. anoxic, with few or no bottom currents and low sedimentation rates) should exhibit similar taphonomic patterns to the salamanders studied herein. The accuracy of our taphonomic model is also amenable to experimental testing *via* controlled laboratory degradation of extant analogues.

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Data S1. Trend analysis.

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