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Coláiste na hOllscoile Corcaigh

1  "Stick 'n' peel": explaining unusual patterns of disarticulation and loss of completeness in fossil

2  vertebrates.

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16

17  **Few fossil vertebrate skeletons are complete and fully articulated.  Various taphonomic processes**

18  **reduce the skeletal fidelity of decaying carcasses, the effects of most of which are reasonably well**

19  **understood.  Some fossil vertebrates, however, exhibit patterns of disarticulation and loss of**

20  **completeness that are difficult to explain. Such skeletons are one of two variants. They are**

21  **incomplete, often markedly so, but the preserved parts are highly articulated. Alternatively, they**

22  **are complete, or nearly so, but articulation varies markedly between parts of the body. A**

23  **characteristic feature is the absence of skeletal elements that, on the basis of their larger size**

24  **and/or greater density, would be predicted to be present. Here we erect a model, termed "stick**

25  **'n' peel", that explains how these distinctive patterns originate.  The model emphasizes the role of**

26  **decay products, especially fluids released from the carcass while resting on the sediment surface.**

27  **These fluids permeate the sediment below and around the carcass. As a result, skeletal elements**

28  **on the downward facing side of the carcass become adhered to the sediment surface, and are less**

29  **likely to be remobilized as a result of current activity than others.  The pattern of articulation and,**

30  **especially, completeness is thus not what would be predicted on the basis of the size, shape and**

31  **density of the skeletal elements. The effects of stick 'n' peel are difficult to predict *a priori*. Stick**

**32** **'n' peel has been identified in vertebrate fossils in lacustrine and marine settings and is likely to be**

**33** **a common feature of the taphonomic history of many vertebrate assemblages. Specimens**

**34** **becoming adhered to the substrate may also explain the preservation *in situ* of the multi-element**

**35** **skeletons of invertebrates such as echinoderms, and integumentary structures such as hair and**

**36** **feathers in exceptionally preserved fossils.**

**39** **1. Introduction**

**40**        As a vertebrate carcass decays loss of skeletal fidelity is almost inevitable.  As a result, most

**41** fossil vertebrate skeletons exhibit some combination of disarticulation and loss of completeness, as

**42** bones separate from, and are then removed from, the remainder of the carcass.  The extent of any

**43** disarticulation and loss of completeness can be described qualitatively (Soares 2003) or using semi-

**44** quantitative (Beardmore et al. 2012a, b) or more fully quantitative methods (McNamara et al. 2011).

**45**        Disarticulation of individual bones or a series of co-joined bones (a unit such as a limb) is a

**46** pre-requisite for, but does not always result in, loss of completeness. Other that this basic tenet, it

**47** can be difficult to identify the specific processes that were responsible for loss of skeletal fidelity in a

**48** vertebrate fossil.  Some processes, for example scavenging of carcasses, may leave distinctive

**49** taphonomic signatures (see Madgwick and Mulville 2015, and references therein), but many do not.

**50** The taphonomic history of a carcass after death and before final burial can be extremely complex.

**51** Carcasses may be subjected to multiple taphonomic processes acting in tandem or in sequence.

**52** Even subtle variations in external environmental parameters can impact on whether, and how,

**53** disarticulation and loss of completeness occurs.  For example, variables such as water temperature

**54** and hydrostatic pressure impact on whether a carcass floats before settling to the sediment-water

**55** interface, and/or refloats after the build up of decay gases internally (see review by Reisdorf et al.

**56** 2012).

**57**        Hydrodynamic sorting of bones due to water current activity is a common cause of the

**58** disarticulation and loss of completeness the skeletons of vertebrate carcasses can experience before

**59** burial. This process occurs in both continental and marine environments. Continental environments

**60** include terrestrial land surfaces, fluvial systems and lakes that may be permanent or temporary. The

**61** carcass may be transported by the current, or currents pass over a carcass that remains *in situ.*

**62** Tidal, fluvial, floodplain and marginal lacustrine settings may experience regular or episodic changes

63    in water level that leave carcasses alternately resting on the sediment-water, and sediment-air,
64    interface on various timescales.

65    In the past few decades, substantial progress has been made in understanding how current
66    activity reduces the completeness and articulation of skeletons.  It has long been recognised (Boaz
67    and Behrensmeyer 1976) that field (Nasti 2005) and laboratory based experiments are invaluable in
68    resolving how the skeletal fidelity of a carcass can be reduced by current activity (see Peterson and
69    Bigalke 2013). The scenario that has been investigated most frequently is how isolated bones are
70    transported by water currents.  Experimental studies repeatedly confirm that the processes involved
71    are not just complex, but even unpredictable.  Size, shape, mass and density are key variables that
72    can be quantified for individual bones.  The interaction of such variables makes it difficult to predict
73    *a priori* exactly how individual bones will behave in a current (Voorhies 1969; Boaz and
74    Behrensmeyer 1976; Blob 1997, Trapani 1998, Peterson and Bigalke 2013).

75    Skeletons need not be reduced first to individual bones then transported. Transport of a
76    freshly killed carcass tends not to result in its disarticulation and loss of completeness, i.e., during
77    the first of the three unit-phases of fluvial transport defined by Nawrocki et al. (1997).  As noted by
78    Haglund and Sorg (2002) relatively few experimental studies have attempted to simulate scenarios
79    between the end member conditions of 'freshly killed' and 'reduced to isolated skeletal elements':
80    i.e. how current activity impacts carcasses at different stages during progressive decay of their non-
81    biomineralised tissues (the non-skeletonised tissues).  Attempts include the simulation of the
82    transport of defleshed but articulated limbs (reconstructed by wiring together bones that would
83    have been juxtaposed in life (e.g. Coard and Dennell 1995)).   Forensic studies including experiments
84    with analogues, and the study of human remains recovered from aquatic settings, have provided
85    information on the various variables, including transport, that act in concert to reduce skeletal
86    fidelity (Anderson and Bell 2014, and references therein). The taphonomy of carcasses in fluvial
87    systems has been reviewed by Evans (2013).

88    In this study, we identify and demonstrate the significance of another variable: how
89    disarticulation and loss of completeness of the skeleton is influenced by whether the carcass
90    becomes adhered to the substrate in advance of being exposed to current activity. Aspects of this
91    phenomenon, which we term "stick 'n' peel", have been noted by previous authors, for example
92    Bickart (1984), Trewin and Davidson (1996) and Mayr (2001). A generalised model that considers the
93    mechanisms by which stick 'n' peel forms has, however, not been developed.  We present this first,
94    then use a series of existing and new examples to define a series of criteria by which the presence of
95    stick 'n' peel can be tested for in fossil material. These examples demonstrate that stick 'n' peel

96 occurs in a wide range of fossil taxa preserved in various different environmental settings. This

97 indicates that it is likely to be a recurrent feature of the taphonomic history of vertebrate fossils, and

98 merits further study.  Problematically, some of the features produced in vertebrate skeletons as a

99 result of stick 'n' peel can also be produced by other taphonomic processes.

**2. Mechanisms for the genesis of stick 'n' peel textures**

101         It has long been recognised that carcasses can become adhered to microbial mats coating

102 the sediment-water interface (see Hellawell and Orr 2012, and references therein).  A classic

103 example of how this can influence disarticulation and loss of completeness is the fish illustrated by

104 Viohl (1990, fig. 2; see also Mayr 1967 and Seilacher et al. 1985). The vertebral column of the fish

105 recurved dorsally while it lay on the sediment surface in response to the osmotic effects of the

106 hypersaline water. Before it did so, the carcass had adhered to the microbial mat. The tail thus

107 remained *in situ* and fully articulated, when the vertebral column ripped free from the carcass and

108 curved into its new position.  Chellouche et al. (2012) mooted the possibility that a similar process

109 could explain the occurrence of isolated caudal fins of fish in the Wattendorf Plattenkalk (Upper

110 Kimmeridgian, southern Germany); the fin had been "overgrown by a microbial mat or was sticking

111 to the sediment for other reasons" (op cit. p. 111).  If only part of the caracass becomes adhered

112 other parts can lift off the surface and disarticulate *in situ* (see Hellawell and Orr, 2012).  Peñalver et

113 al. (2002) attributed the unusual patterns of completeness and articulation exhibited by insects

114 preserved in Miocene lacustrine sediments to parts of the carcasses having become adhered to

115 microbial mats on the lake floor. Subsequently, currents removed or displaced those parts not

116 adhering to the mat, leaving the fossils incomplete but with the remaining parts preserved in life

117 position.

118         The former presence of microbial mats is relatively easy to identify in carbonate successions.

119 In vertical section there may be thin organic laminae that anastomose and interconnect over short

120 vertical distances; other biosedimentary structures include roll-up structures (see for example

121 Simonson and Carney 1999, figs 3A-B, 4, 5).  Even if degradation of the organic matter is complete,

122 (typical of siliciclastic settings) the former presence of microbial mats is often revealed by various

123 sedimentary features.  Bedding surfaces often exhibit distinctive textures (microbially induced

124 sedimentary structures (MISS)) (Noffke 2010; Noffke and Chafetz 2012).

125         Some of the fossil examples examined in the course of this study show no obvious indication

126 that the surface of the sediment was covered in a microbial mat. Examples of stick 'n' peel originate

127 via various other mechanisms. During decay, carcasses may become covered by a localised microbial

128  biofilm that may extend beyond the periphery of the carcass (see Borkow and Babcock 2003, figs 1

129  and 2). In other examples, non-biomineralised tissues such as the integument may be infested, even

130  pseudomorphed, by microbes (Redelstorff and Orr 2015). Potentially, the microbes in such biofilms

131  may play a role in stick 'n' peel, for example via the production of extracellular polymeric substances

132  (More et al., 2014) that locally coat the organism's tissues and the substrate and bind each to the

133  other.

134       The localised growth of this microbial population will be facilitated by the decay products

135  generated by autolysis and putrefaction of the carcass (purge fluids) leaking downwards and

136  outwards from the carcass into the substrate. This is analogous to the cadaver decomposition island

137  (CDI) of Carter et al. (2007, p. 12), a "highly concentrated island of fertility" centred below, and

138  extending lateral to, a decaying carcass.  The CDI originates in two steps. In the first (the "bloated"

139  phase *sensu* Carter et al. 2007) purge fluids exit via orifices (mouth, nose, anus). In the following

140  stage, "active decay", substantial release of cadaveric fluids connects the isolated islands that

141  formed previously, and the CDI becomes established. These fluids may also serve to bind the carcass

142  to the substrate. There is conclusive evidence that such fluids can bind a carcass to the substrate in

143  subaerial settings.  Bickart (1984, p. 527) attributed the adhesion of bird carcasses to the substrate

144  to "possibly a combination of body fluids and ground moisture"; floodwaters passing over these

145  carcasses subsequently failed to change the position of most. The escape of fluids from the interior

146  of decaying carcasses is extremely common, suggesting stick 'n' peel is potentially a recurrent

147  taphonomic feature of vertebrate fossils.

148       There is also evidence that non-biomineralised tissues decaying in permanently subaqueous

149  settings can become stuck to the surface on which they are lying, at least under experimental

150  conditions. The examples in Figure 1 are experimentally decayed specimens of the medusa *Aurelia*

151  *aurita* (Adler 2013; see also Hertweck 1966).The specimens are right-way up, with the exumbrellar

152  surface upwards. In the specimen in Figure 1A the ventral parts of the lower surface (the oral arms)

153  are in contact with and have become stuck to the floor of the experimental vessel.  The umbrella

154  remains free-floating in the experimental tank; it is positioned centrally above the oral arms (Figure

155  1A, upper image). As decay progresses minimal disturbance of the experimental vessel is sufficient

156  to tear the umbrella (the circular outline indicated by an arrow in Figure 1B) from the remainder of

157  the body and offset it laterally.  Other experimental studies have also recorded that carcasses

158  decaying in fluids can become adhered to surfaces inside the experimental vessel. Freidman (1999,

159  p. 37-38, Figures 16 and 17) experimentally decayed specimens of the hagfish *Myxine glutinosa* in

160  containers filled with water; a number of the decayed specimens stuck to the floor of the vessels

161  either locally or along most of their body surface.

162      How the distribution of the decay fluids are affected by continuous current activity and a

163  sediment substrate (as opposed to the solid floor of an experimental vessel) are unknown, but

164  amenable to experimental testing. Decay fluids will settle downwards inside the specimen and from

165  there leak into the underlying substrate. The effects of current activity may therefore be limited and

166  the decay products not dispersed into the overlying water column. The binding effects of the decay

167  fluids would presumably be influenced by the porosity and permeability of the sediment.

168  **3. Indicators of stick 'n' peel in fossils**

169      We have identified a series of features indicative of stick 'n' peel, one or more of which a

170  vertebrate fossil will exhibit if its disarticulation and loss of completeness was controlled, at least in

171  part, by this mechanism. Schematic illustrations of these features using generalised vertebrate

172  bodyplans are shown in Figure 2, and candidate examples of fossil taxa in Figure 3.

173  *3.1 Displacement of an articulated part of the skeleton beyond the body outline*

174      In many exceptional biotas the body outline of vertebrate fossils is preserved, often as a

175  dark-coloured carbonaceous stain or a thin film that represents the degraded remains of the non-

176  biomineralised tissues. Part of the skeleton, for example a limb or the tail, may be articulated and

177  connected with the remainder of the skeleton but occur outside the body outline (Figure 2A, 3A).

178  While lying on the substrate, this part of the skeleton moved into a position other than that in which

179  it came to rest initially. Before it did so, the body became sealed to the substrate and thus remained

180  *in situ*.  In examples where the tail is moved to a new position, current activity or contraction of the

181  tissues connecting successive vertebrae (see Seilacher *et al.* 1985) could produce the same result.

182  As there is no disarticulation, stick 'n' peel that occurs via this process is only apparent if the body

183  outline is preserved (as in the example in Figure 3A). If the body outline is not preserved the process

184  can only be identified if it results in disarticulation at a joint, for example, if the distal part of an

185  appendage such as the tail or a limb remains *in situ* and the part proximal to it moves to a new

186  position (Figure 2B; see also Viohl 1990, fig. 2).  In such cases, the original continuity of the

187  appendage should be recovered if the displaced part is moved back to its original position.

188  *3.2 Localised variations in disarticulation and loss of completeness within a skeleton*

189      In this scenario, part of the skeleton shows extensive disarticulation (but not necessarily loss

190  of completeness) and the remainder is complete and fully articulated.

191    In the example in Figures 2C and 3D, the anterior and posterior halves of the skeleton are
192    juxtaposed; in the fossil frog (Figure 3D) the body outline of each half is also juxtaposed. In each
193    example, the anterior half of the skeleton is in life position, complete, and fully articulated.  The
194    posterior part is complete, out of position, and extensively disarticulated. If decay has progressed
195    sufficiently, the effects of gravity can force bones out of their in-vivo position when a carcass settles
196    passively onto the substrate (Syme and Salisbury 2014). In the case of the example in Figure 2C and
197    3D, disarticulation did not occur when the carcass came to rest on the substrate (or both the
198    anterior and posterior parts would have disarticulated to the same extent).  Thus disarticulation
199    occurred later, after decay had progressed sufficiently to weaken or remove the tissues (muscles,
200    ligaments and tendons) connecting the bones. The process responsible must explain two
201    phenomena: disarticulation of only the posterior half of the specimen, although the anterior half
202    would have been decayed to the same extent; the movement of the posterior half as a unit, plus
203    retention of all its skeletal elements. The second feature would be easiest while the skeleton was
204    enclosed inside the integument (as seems likely to have occurred in the fossil example in which the
205    body outline is preserved).  The posterior half either rotated laterally, or flipped vertically, over the
206    anterior half during current activity.  Definitive evidence for it having flipped would be if the
207    opposite surfaces of two skeletal elements were exposed on the same bedding plane; for example,
208    the dorsal side of the skull and the ventral face of the pelvis. Only the anterior of the specimen may
209    have been fixed to the substrate before the posterior half was moved to its new position.
210    Alternatively, the carcass may have also have been fixed locally at other points, but ripped free.  This
211    possibility cannot be rejected on the evidence presented in the specimens in Figure 2C and 3D. It
212    would be the preferred option if any of the skeletal elements from the posterior of the skeleton
213    were still in their original position. This scenario is shown in the theoretical example in Figure 2D in
214    which the articulated distal part of the left hindlimb has remained behind in life position.

215    Figure 3B is of the skeleton of the holotype of the bird *Primotrogon wintersteini* described by
216    Mayr (1999, p. 430) who noted its unusual taphonomy. There are marked discrepancies in the
217    degree of completeness and articulation between different parts of the body.   Both forelimbs are
218    fairly complete (the phalanges are absent) and articulated. They, plus the left hindlimb are in life
219    position relative to each other.  In contrast, other parts of the skeleton are either incomplete (e.g.
220    the vertebral column) or absent (the right hindlimb and tail).  Mayr (2001) described a second
221    specimen of *Primotrogon wintersteini* noting the unusual combination of its feet being articulated
222    and preserved in life position, but the absence of the tibiotarsi, femora and caudal part of the trunk
223    (Figure 2C).  The vertebral column is present but disarticulated.  The proximal parts of the forelimbs
224    are articulated and in life position; the distal parts are truncated by the edge of the slab.

225    Both specimens exhibit the combination of (1) moderate to high completeness, (2) extensive

226    disarticulation of specific parts of the body, plus (3) limited, or no, disarticulation of those parts of

227    the skeleton that remain in life position relative to each other. Many of the bones present but

228    displaced from life position did not disarticulate when the carcass settled to the sediment surface;

229    for example, the more distal parts of the forelimbs would have been unlikely  to remain in life

230    position if elements such as the coracoid and scapulae were extensively displaced at the time of

231    deposition.  Skeletal elements that are absent were not lost while the carcass floated in the water

232    column, i.e. in the interval between death and coming to rest on the sediment surface; most

233    obviously, it would not be possible to retain the distal part of the hindlimbs but not the proximal

234    parts. The specimens settled onto the sediment surface shortly after death before decay had

235    progressed significantly; most, perhaps all, of the disarticulation and loss of completeness they

236    experienced happened subsequently. Mayr (2001) concluded that current activity might have

237    removed the bones of the pelvic region and the proximal part of the legs of the specimen in Figure

238    3C; he (op cit.) envisaged that the distal part of the hindlimbs remained *in situ* as they had become

239    adhered to the sediment. This conclusion is supported here and also suggested as the reason why

240    the wings are articulated and complete in both specimens.

241    The taphonomy of each specimen would have differed in detail, but a general model can be

242    erected.  In the first step each bird came to rest with one forelimb either side of the body. This

243    would have presented the bones of these limbs close to the sediment surface. Other parts of the

244    skeleton would have been more elevated above the substrate, especially if the body was oriented

245    ventral side downwards. These bones would only have moved adjacent to, and eventually onto, the

246    substrate after a period of decay during which the skeleton collapsed.  Therefore, if the carcass

247    became stuck to the substrate and disturbed by a current before any such collapse, those parts of

248    the skeleton closest to the substrate at the time of deposition would experience least disarticulation

249    and loss of completeness.   The high degree of articulation and completeness of the wings is thus

250    interpreted to indicate their having being stuck to the substrate when the carcass was disturbed.

251    The two specimens differ as to which bones of the hindlimbs are present. In the specimen in Figure

252    3B, the left hindlimb is complete and articulated and the right hindlimb absent; only minimal tilting

253    of the posterior of the specimen at the time of deposition would be required to leave one limb

254    resting on, and the other above, the substrate (see section 3.4).  In the specimen in Figure 3C the

255    distal parts of the limbs are present, articulated and but their proximal parts are absent.  This may

256    imply that the legs were flexed vertically along their length while the specimen rested on the

257    substrate. The podotheca may have increased the likelihood of the distal parts of the hindlimbs

258    remaining an articulated unit (see Casal et al. 2013), but alone would not have ensured they

259    remained in life position. The right limb is in life position.

260    *3.3 Unpredicted loss of skeletal elements*

261    It may not always be possible to predict *definitively* which elements of any skeleton would

262    be affected preferentially by current activity (see section 1). Nonetheless, on the basis of their

263    shape, density and, especially, size, it is possible to suggest which elements would be more likely to

264    be affected than others  For example, the smaller bones of a carcass (such as vertebrae and

265    phalanges), should be transported preferentially compared to larger elements (e.g. the femora and

266    humeri). Stick 'n' peel may, however, 'trump' this general rule, and should be suspected when

267    elements considered more likely to have remained *in situ* and in life position are those that are

268    displaced and removed. The example in Figure 2E is of a limb in which the distal part, including the

269    phalanges, is articulated, complete and in life position relative to the remainder of the carcass; the

270    humerus is missing.  It is difficult to envisage a scenario where current winnowing would selectively

271    remove the humerus, yet leave the phalanges not just present, but fully articulated.   It is therefore

272    envisaged that the distal part of the forelimb, but not the humerus, was adhered to the substrate.

273    This theoretical example is similar to the example of *Primotrogon wintersteini* in Figure 3C, in which

274    the distal parts of the left hindlimb, including the phalanges, are present and articulated, but more

275    proximal bones, including the relatively large tibiotarsi and femora, are missing.

276    Trewin and Davidson (1996) observed rare examples of the acanthodians *Climatius* and

277    *Ischnacanthus* in which the fin spines, notably the pectorals, are in life position, but the body scales

278    almost totally absent.  The spines are among the larger individual elements. They would be unlikely

279    to be removed preferentially.  It is also unlikely that their mass alone would result in their remaining

280    precisely in life position while every other element was removed or displaced. It is more likely that,

281    as Trewin and Davisdon (1996) suggest, the spines became stuck to the substrate; the build-up of

282    gas inside the decaying carcass may have lifted the remainder above the substrate and it was

283    removed by weak currents.

284    3.4 *Higher fidelity preservation of the lower facing side of a specimen*

285    Taxa that are strongly laterally compressed often come to rest on the sediment surface in

286    lateral aspect (many fish, for example). This orientation presents the sagittal plane through the body

287    parallel to the substrate.  Vertebrates are bilaterally symmetrical either side of this plane. The

288    taphonomy of paired elements that are identical in size, shape and density can be compared

289    directly.  The stick 'n' peel model predicts that the side in contact with the substrate will become

290    adhered to it and is the more likely to retain skeletal fidelity when the specimen is subjected to

291    current activity.

292        In specimens preserved in lateral aspect stick 'n' peel could result in differences in the

293    fidelity of preservation between the left and right sides of the body, for example in the

294    completeness and articulation of the limbs and/or ribs (Figure 2F). In the example in Figure 2G (see

295    also Figure 3E), the head of the fish is disarticulated completely, but otherwise, it is almost

296    exclusively the relatively large, deepened, flank scales from one side of the body only that are

297    displaced or absent. The tail of the fish in Figures 2G and 3E is entire. The tail comprises some of the

298    smallest skeletal elements that should be among the easiest to transport; note their size relative to

299    that of the flank scales and operculum in Figure 3E. Furthermore, the tail is at the distal end of the

300    animal and fully exposed to any currents. The latter observation falsifies the possibility that the side

301    in contact with the substrate is more articulate and complete simply because it was protected from

302    the effects of current activity by the scales from the opposite side of the body without being stuck

303    down.

304    **4. Discussion**

305        The theoretical models and fossil examples reviewed above suggest that stick 'n'peel could

306    potentially be recognised in fossils by a number of diagnostic taphonomic features. These features

307    include loss of completeness and articulation in certain areas of the body, although other parts of

308    the skeleton remain complete and fully articulated. This is most apparent when the left and right

309    hand sides of a body in lateral aspect are preserved differently. Differences in completeness and

310    articulation can occur over short distances and be subtle, for example, the displacement or absence

311    of a single bone either side of which the adjacent bones are present and in life position. The

312    argument that this is due to stick 'n' peel is strengthened if the absent skeletal element would be

313    predicted to be present on the basis of its (larger) size, (greater) density, or shape.

314        The criteria for recognising stick 'n' peel should, however, be used with caution.

315    Problematically, some of the patterns of disarticulation and completeness characteristic of stick 'n'

316    peel can also originate via other processes. Unusual patterns of disarticulation and loss of

317    completeness do not automatically imply that the carcass became adhered to the substrate.

318        For any carcass resting on a substrate, the bones on the lower facing side will be more

319    difficult to dislodge from life position. As a carcass decays and collapses skeletal elements on the

320    lower facing side will rotate *in situ* to more stable orientations than those at which they came to

321    rest. These elements may separate from each other, but any displacement is likely to minimal.

322 Elements on the upper side of a carcass are more likely to be displaced. This displacement can occur
323 as bones slide downwards under gravity into more stable orientations.  Gravitational sliding has
324 been documented in elephant carcasses decaying subaerially (Haynes 1988), and can result in
325 marked differences in articulation between the left and right sides of a carcass lying in lateral aspect.
326 On its own the process should not result in loss of completeness.

327 The animal's anatomy, in combination with the orientation in which the specimen comes to
328 rest, can impact on the extent of disarticulation.  Bones that are at a high angle to bedding when the
329 carcass comes to rest may become disarticulated as the skeleton collapses downwards as it decays.
330 For example, articulated skeletons of anurans are preserved almost exclusively in dorso-ventral
331 aspect (although unless the way up of the specimens is known the specific orientation cannot be
332 determined (McNamara *et al.* 2012)); often each limb is lateral to the body. In these postures most
333 of the skeletal elements are presented parallel to bedding and close to the sediment surface in
334 highly stable orientations.  If there is no disturbance after deposition, anuran skeletons routinely
335 show a high degree of articulation. The urostyle, ilia, and sacral vertebra, however, are often an
336 exception. These form a three-dimensional, prism-like structure at the core of the body; these bones
337 invariably disarticulate from each other as each rotates parallel to bedding in response to decay-
338 induced collapse and sediment loading during burial. There are criteria by which disarticulation due
339 to decay-induced collapse can be distinguished from stick 'n' peel. Decay-induced collapse results in
340 limited displacement (as each element is likely to remain inside the body outline) and does not result
341 in any loss of completeness. Stick 'n' peel is most obvious if it involves loss of completeness and
342 displacement of elements is over larger distances. Decay-induced collapse will affect specific joints
343 and the effects will be the same for all specimens in the same posture. The same need not be the
344 case for disarticulation resulting from stick 'n' peel; this depends on the timing of current activity
345 relative to how far decay has progressed.  The taphonomic features produced via stick 'n' peel need
346 not therefore be consistent between specimens within an assemblage, even those of the same
347 taxon.

348 One of the distinctive features of stick 'n' peel is that there are highly localised differences in
349 completeness and articulation within a specimen. A limited number of other processes can produce
350 spatial variation in the fidelity of preservation within a single specimen, for example abdominal
351 rupture, as a result of the explosive release of decay gases. This will reduce the skeletal fidelity of
352 the thorax and abdomen; other parts of the skeleton are less likely to be affected.

353 Not all skeletal elements in a vertebrate carcass have equal fossilisation potential.  Less well-
354 ossified elements are likely to dissolve preferentially during early diagenesis. Complete decay or

355    dissolution of a skeletal element before sediment lithification would result in no mould to indicate

356    its former presence. Skeletal completeness can therefore be strongly sensitive to developmental

357    stage and the pattern of ossification during ontogeny.  Alternatively, decay microenvironments that

358    are conducive to the dissolution of bone may develop locally within a carcass, for example, inside

359    the body cavity (see McNamara et al. 2009). As a result, the fossilization potential of skeletal

360    elements may differ between parts of the body. The specimen of the bat *Palaeochiropteryx*

361    *tupaiodon* illustrated by Franzen (1990, fig. 2) lacks any bones in the body cavity, but is otherwise

362    complete and highly articulated (limited disarticulation of the tail has occurred). The absence of

363    bones inside the body was attributed to their having dissolved during diagenesis.

364    **5. Stick 'n' peel: limitations of a predictive model**

365    Whether stick 'n' peel occurs depends on when skeletal elements become stuck to the substrate

366    relative to the timing of the current activity responsible for their displacement and removal.  When

367    skeletal elements become stuck to the substrate depends on the interaction of two variables: rate of

368    collapse of the carcass; rate at which the CDI builds up, then dissipates (Figure 4). Firstly, as decay

369    progresses, the muscles, ligaments and tendons that hold the skeleton together lose mass and

370    strength; the skeleton will progressively collapse downwards under its own weight. Individual bones

371    will rotate into more stable positions than those in which they were originally deposited, presenting

372    more of their length or surface area parallel to the substrate. Over time, therefore, progressively

373    more bones move closer to, and, ultimately, rest on, the substrate. Secondly, the areal extent and

374    volume of the CDI will initially increase, but then decrease as the decay purge is metabolised and

375    disperses. Three fields can be defined over time (Figure 4). In stage 1, during the initial stages of

376    decay, the volume of the CDI is limited and collapse of the skeleton minimal. Current activity will

377    either transport the entire carcass or have limited impact on the skeletal fidelity of a carcass that

378    remains *in situ*.  In stage 3 the extent of the CDI will be limited and the carcass will have been

379    reduced to individual, or co-joined, bones.  Which skeletal elements are displaced and removed will

380    be governed largely, possibly exclusively, by their hydrodynamic properties.  The effects of stick 'n'

381    peel on skeletal fidelity will be most pronounced during Stage 2. During Stage 2 the volume of the

382    CDI will change and collapse of the skeleton will be on-going. Differences in completeness and

383    articulation will result depending on the timing of current activity.

384            It is difficult to model what may happen in any more detail, as a number of other variables

385    are involved. How the skeleton collapses will reflect the animal's anatomy and the orientation of the

386    carcass. The rate at which decay progresses and, linked to it, the rate at which purge fluids are

387    generated and metabolised, will be controlled by environmental conditions (including temperature

388  and oxygen levels). The geometry of the CDI and how long it will persist are both difficult to predict.

389  There is no reason to assume the CDI will retreat from its periphery inwards, and persist longest

390  centrally. It is likely that it would be most dense and persist longer in proximity to the orifices such

391  as the mouth and anus and other sites (wounds) via which the decay purge exited the body. The

392  geometry of the CDI will also be sensitive to the orientation the carcass came to rest in. The nature

393  of the substrate is potentially important. Carcasses would presumably be more likely to adhere if the

394  substrate has some, but limited, permeability, as this will inhibit the diffusion of the purge fluids

395  downwards.

396  **6. Wider Implications**

397  The various fossil examples presented indicate the phenomenon of stick 'n' peel is likely to

398  be a common feature of the taphonomic history of vertebrate fossils deposited on either a subaerial

399  or subaqueous substrate.  There are implications for various other aspects of vertebrate taphonomy.

400  Inferences as to the extent of bottom water current activity based on the degree of completeness

401  and articulation of fossils should be made with caution. Limited disarticulation and near full

402  completeness need not imply that bottom water currents were absent. Instead, specimens that

403  adhered to the substrate may have been resistant to the winnowing effects of currents.

404  Carcasses that become buoyed up by decay gases may refloat after initially sinking. The

405  reasons whether they refloat or do not are complex; the biology of the organism, and the

406  temperature, density and depth of the water (and thus the hydrostatic pressure) are important

407  variables (see review by Reisdorf et al. 2012).  The preservation of complete, fully articulated,

408  skeletons is often attributed to environmental conditions that inhibited scavenging, and the water

409  pressure having been high enough to have prevented refloating. Refloating could  also be inhibited if

410  a carcass became stuck to the sediment-water interface.   Problematically, in the absence of any

411  disarticulation and loss of completeness (i.e. if the 'stick' component occurs but not the 'peel') there

412  may be no evidence in the fossil that the carcass had adhered to the substrate.

413  It is likely that stick 'n' peel is also an important part of the taphonomy of invertebrate

414  fossils. The effects of stick 'n' peel will be most apparent in invertebrates with multi-element

415  skeletons, for example echinoderms. Possible examples occur in assemblages of the crinoid

416  *Uintacrinus* described by Meyer and Milsom (2001). The assemblages represent *in situ* mass

417  mortalities of opportunistic taxa that colonised persistently low-oxygen to anoxic environments

418  during brief episodes of oxygenation.  Mortality occurred as a result of anoxia not obrution.

419  Carcasses were therefore exposed on the seafloor after death and buried subsequently.  Meyer and

420      Milsom (2001) observed that the downward-facing side of an individual calyx can be highly-

421      articulated and complete, yet the opposite side extensively disarticulated.  At a larger scale, an

422      *Uintacrinus* layer routinely comprises disarticulated crinoidal material on its upper surface, but

423      crinoids with articulated calyxes and arms on its lower side.  Meyer and Milsom (2001) attributed

424      this unusual combination of preservational states to a microbial mat of necrolytic origin having

425      grown over the crinoids early in the decay process.  The cohesive properties of this mat held

426      disarticulated ossicles in place on the upper surface of a layer and prevented their being dispersed

427      by bottom currents. The occurrence of the latter is indicated by the parallel alignment of *Uintacrinus*

428      arms and baculites on some slabs. There is now no evidence for such a microbial mat on the upper

429      surface of the crinoid layer; Meyer and Milson (2001) suggested it degraded before being covered by

430      sediment.  Remnants of organic matter persist within the crinoid layer as thin organic laminae.

431      Meyer and Milson (2001) suggested these represented microbial mats, or organic matter exuded

432      from the compressed calyxes.  If the latter, the decay products would presumably have leaked

433      downward under gravity, and may have 'glued' skeletal elements in position inside the layer. This

434      would have enhanced the likelihood of these parts of skeletons remaining articulated and,

435      contributed to the discrepancy in the fidelity of preservation between the opposite faces of both

436      single specimens and a layer of crinoids as a whole.

437      The body outline of the specimen of *Apateon pedestris* in Figure 3A remained entire and *in*

438      *situ* when the vertebral column rotated into its new position. More generally, it is not uncommon for

439      integumentary structures such as hair and feathers to be retained in life position in exceptionally

440      preserved fossils; the inset in Figure 3B shows the outline of the feathers of the holotype of

441      *Primotrogon wintersteini*. Fossils can exhibit these features even though their skeletons

442      disarticulated and lost completeness while resting on the sediment-water interface. It is conceivable

443      that the integumentary structures are retained in life position because they became adhered to the

444      sediment surface they were lying on. The possible role of this in the taphonomic history of

445      exceptionally preserved fossils merits further investigation.

446      **7. Conclusions**

447      Stick 'n' peel refers to the distinctive patterns of disarticulation and loss of completeness

448      that result if vertebrate carcasses become adhered to the substrate in the initial stages of decay and

449      are then disturbed by water currents.  It has long been known that carcasses can adhere to microbial

450      mats on the surface of the sediment (Mayr 1967, Viohl 1990, Seilacher et al. 1985). However, many

451      fossil examples occur in sedimentary contexts that show no evidence for such mats having been

452      present. The degraded tissues of the carcass, the associated microbiota, and especially, the decay

453     purge released from inside the decaying carcass, are alternative mechanisms by which carcasses can

454     become locally adhered to the substrate. Field and laboratory experiments confirm that this occurs

455     in both subaerial and subaqueous settings.

456     Retrospective identification in fossils that stick 'n' peel occurred is not straightforward. Two unusual

457     features of the skeletal taphonomy of vertebrates may be indicative:

458     (1) in disarticulated and incomplete skeletons the presence of bones that, on the basis of size, shape

459     and/or density, would be expected to have been displaced and removed, and the absence of bones

460     that would have been predicted to be present;

461     (2) those parts of the carcass that can be shown on independent criteria (by knowing the way up of

462     the specimen) to have been in contact with the substrate will be more fully articulated and complete

463     than those that were not in contact with the substrate.

464     Stick 'n' peel can result in various different patterns in fossil skeletons. Problematically some of

465     these can also originate via other mechanisms.  There is sufficient evidence to confirm that the

466     phenomenon recurs in fossil assemblages preserved in both marine and freshwater systems. Field

467     observations confirm that it can also develop on land (Bickart 1984). Stick 'n'peel is likely to be a

468     common feature in vertebrate fossil assemblages in which caracsses experienced an extended

469     residence time at the sediment-water or sediment-air interface as part of their taphonomic history.

470     The phenomenon is also likely to have affected invertebrate taxa with similar taphonomic histories

471     preserved in the same environments.  Finally, stick 'n' peel offers a potential mechanism by which

472     the body outline, and integumentary structures such as feathers and hair, can be retained in life

473     position in exceptionally preserved vertebrate fossils in which the skeleton is disarticulated and

474     incomplete.

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598

599    FIGURE CAPTIONS

600    Figure 1. Stick 'n' peel exhibited by experimentally decayed examples of the moon jellyfish *Aurelia*

601    *aurita.* (A) Those parts of decaying specimens that come into contact with the bottom of the

602    experimental vessel can become stuck to it. (B) Even minimal disturbance of the experimental vessel

603    is sufficient to tear the floating umbrella from those body parts stuck to the floor of the

604    experimental vessel. When the umbrella settles to the floor of the vessel it can be laterally offset

605    from the adhered parts. Upper and lower images show corresponding planar and lateral views of the

606    same experimental vessel. The arrow in the upper image in part B indicates the margin of the

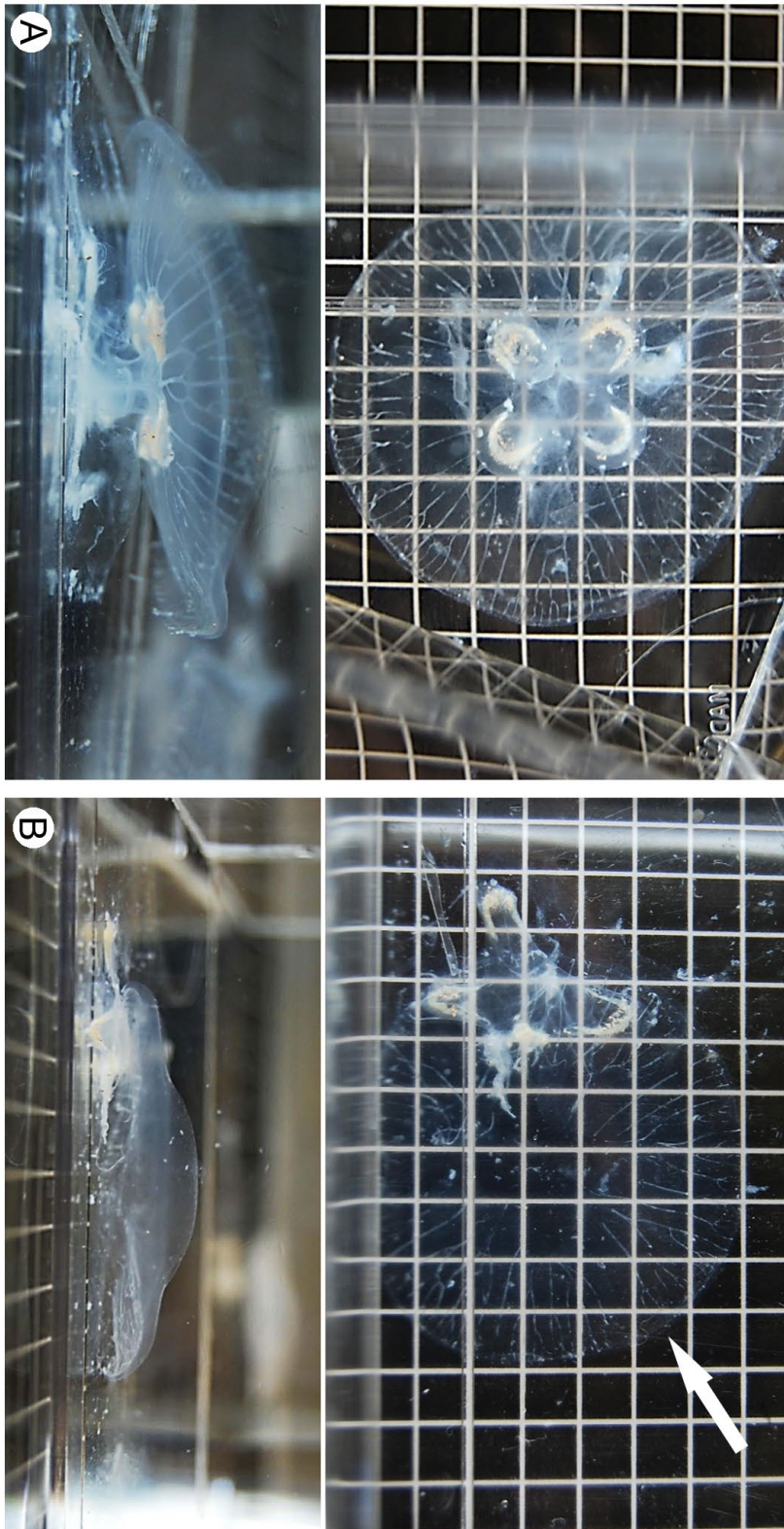607    umbrella (Adler 2013).

608    Figure 2. Schematic illustrations of taphonomic features that form via stick 'n' peel.  (A) The

609    vertebral column of the tetrapod is intact but curves outside the body outline. The integument has

610    adhered to the substrate and remained *in situ* when the vertebral column of the tail rotated into its

611    new position.  This evidence for stick 'n' peel requires the body outline to be preserved. (B) The

612    skeleton is entire and fully articulated except for one point of separation within the tail (at arrow).

613    The carcass came to rest on the substrate and the distal part of the tail (and possibly other parts of

614    the skeleton) became adhered to it.  The distal part of the tail remained *in situ* when part of the

615    vertebral column rotated into a new position.  The alignment of successive vertebrae was retained in

616    both parts of the tail. Note that in contrast to the example in Figure 2A, evidence for stick 'n' peel

617    does not require that the body outline is preserved.  (C) The anterior half of the skeleton is complete

618    and fully articulated. The posterior half is complete, but extensively disarticulated and out of life

619    position.  The carcass came to rest on the substrate fully articulated and complete; subsequently,

620    after an extended period of decay, the posterior part either flipped over, or rotated anticlockwise

621    onto, the anterior part. In doing so, it disarticulated.  Completeness and articulation of the anterior

622    half was unaffected. On the evidence available it cannot be proven whether the anterior was the

623    only part that adhered to the substrate, or whether the specimen was also adhered elsewhere and

624    the posterior half preferentially tore free (contrast with the scenario in Figure 2D). (D) The only

625    difference in the distribution of this skeleton and that in Figure 2C is that the distal part of the left

626    hindlimb is in life position. This implies that the carcass first adhered to the surface at both the

627    anterior and at the distal part of the left hindlimb; when the posterior part tore free the latter

628    remained *in situ*.    (E) The skeleton is fully articulated and, except for loss of a single humerus (at

629    arrow), complete. All elements are in life position. The isolated limb is separated from the remainder

630    of the carcass by exactly the length of the humerus; i.e. the limb did not separate from the

631 remainder of the carcass as a unit. The distal part of the limb (and presumably other parts of the

632 skeleton) adhered to the substrate and remained *in situ* while the humerus was selectively removed.

633 (F) and (G) The carcass came to rest in right lateral aspect. Only the left side of the skeleton is

634 extensively disarticulated. Elements displaced significantly from life position include some of the

635 largest bones, for example the left femur and humerus in F and the chevron-shaped flank scales in G.

636 The skeletal elements that remained *in situ* share two features. Firstly, they would have been in

637 contact with the substrate after the carcasses came to rest. Secondly, not all would have been

638 shielded from the effects of currents by being concealed on the lower-facing side of the carcass.

639 Those that would have been exposed include some of the smallest bones, for example the phalanges

640 of the limbs from the right hand side of the body and the distal vertebrae of the tail in F, and the

641 bones of the caudal fin ray in G.

642 Figure 3. Examples of fossil taxa interpreted to show taphonomic features derived via stick 'n' peel.

643 (A) Specimen of the amphibian *Apateon pedestris* (Museum für Naturkunde Berlin: Institut für

644 Palaontologie, MB Am1300). (B) and (C) Specimens of the early Oligocene bird *Primotrogon*

645 *wintersteini.* Inset in B shows distribution of feathers. Line drawings based on Figures 1 and 2 in

646 Mayr (2001). (B, Bayerische Staatssammlung für Paläontologie und Historiche Geologie, BSP1997I38.

647 C, Forschungsinstitut Senckenberg Frankfurt am Main, Germany SMFAv423). c, coracoid; f, furcular;

648 h, humerus; r, radius; s, scapula; tm, tarsometatarsus; tt, tibiotarsus; u, ulna; ub, unidentified bone;

649 v, vertebrae; prefix l and r indicate left and right hand side of the body, respectively. (D)

650 *Palaeobatrachus sp.* from the Late Eocene - Oligocene Ústí Formation (36.1-25.5 Ma) of North

651 Bohemia (Czech Republic) (Natural History Museum Prague Specimen Pb684). (E) Specimen of the

652 fish *Habroichthys minimus* from the Prosanto Formation, Early Ladinian, southeastern Switzerland

653 (Paläontologisches Institut und Museum der Universität, Zürich, PIMUZ A/I 3733). fs, flank scales, o,

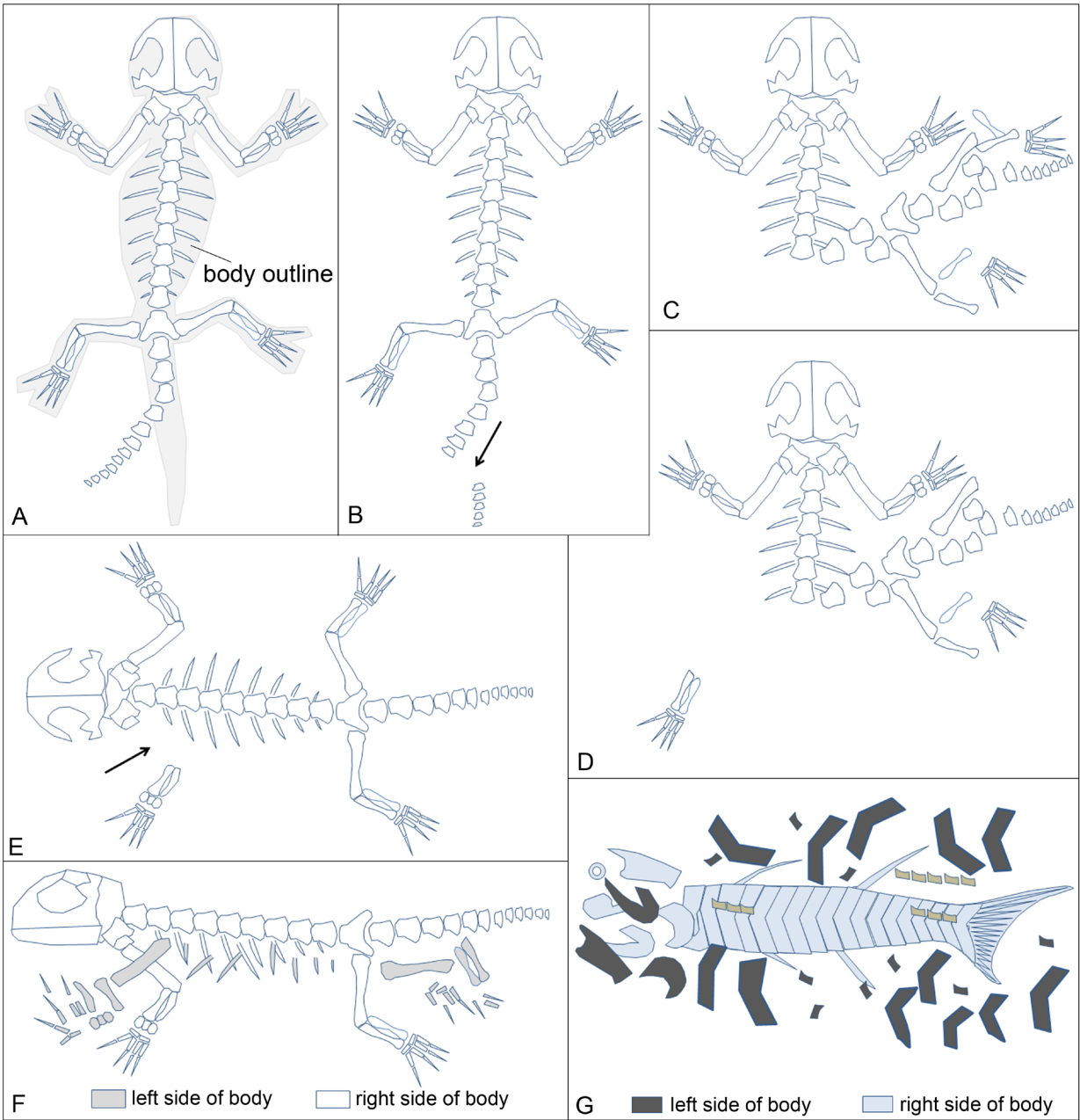654 operculum; pf pectoral fin; so, suboperculum. All scale bars 10mm.

655 Figure 4. Model for the formation of stick 'n' peel textures, indicating the potentially complex

656 interplay of the three principal factors: (1) progressive, decay-induced, collapse of the skeleton; (2)

657 development and then loss of the cadaver decay island; (3) the timing of any disturbance of the

658 carcass by current activity. Factors 1 and 2 allow three fields to be defined in each of which the

659 impact of current activity on the taphonomy of the skeleton will be different. A-E represent

660 schematic illustrations of a generalised tetrapod showing the changes in posture, extent of collapse

661 of the skeleton (see transverse sections through body) and the areal extent of the CDI at different

662 times.

663

665

Figure 1

A

B

body outline

C

D

E

F  ■ left side of body  □ right side of body

G  ■ left side of body  □ right side of body

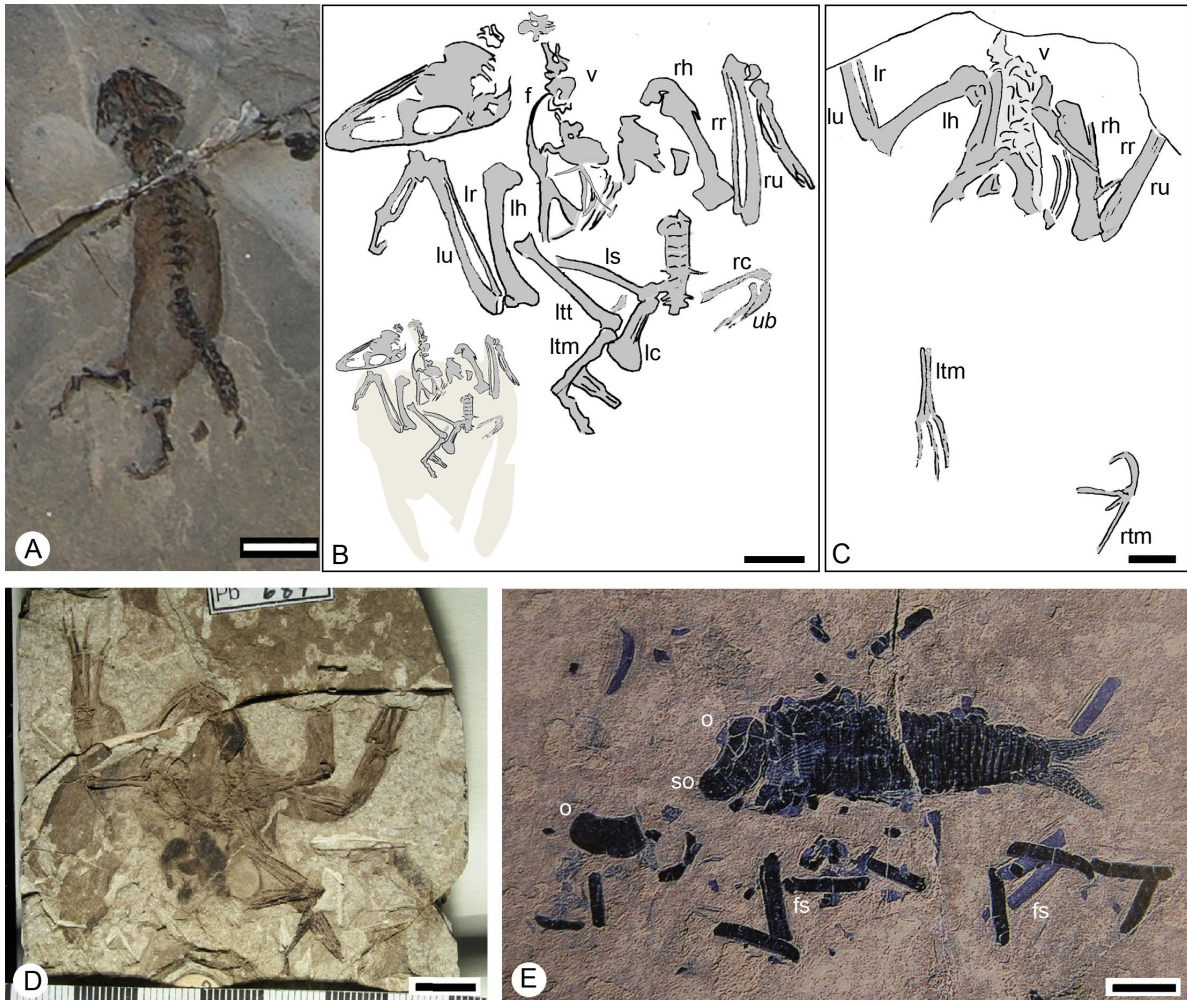667

668    Figure 2
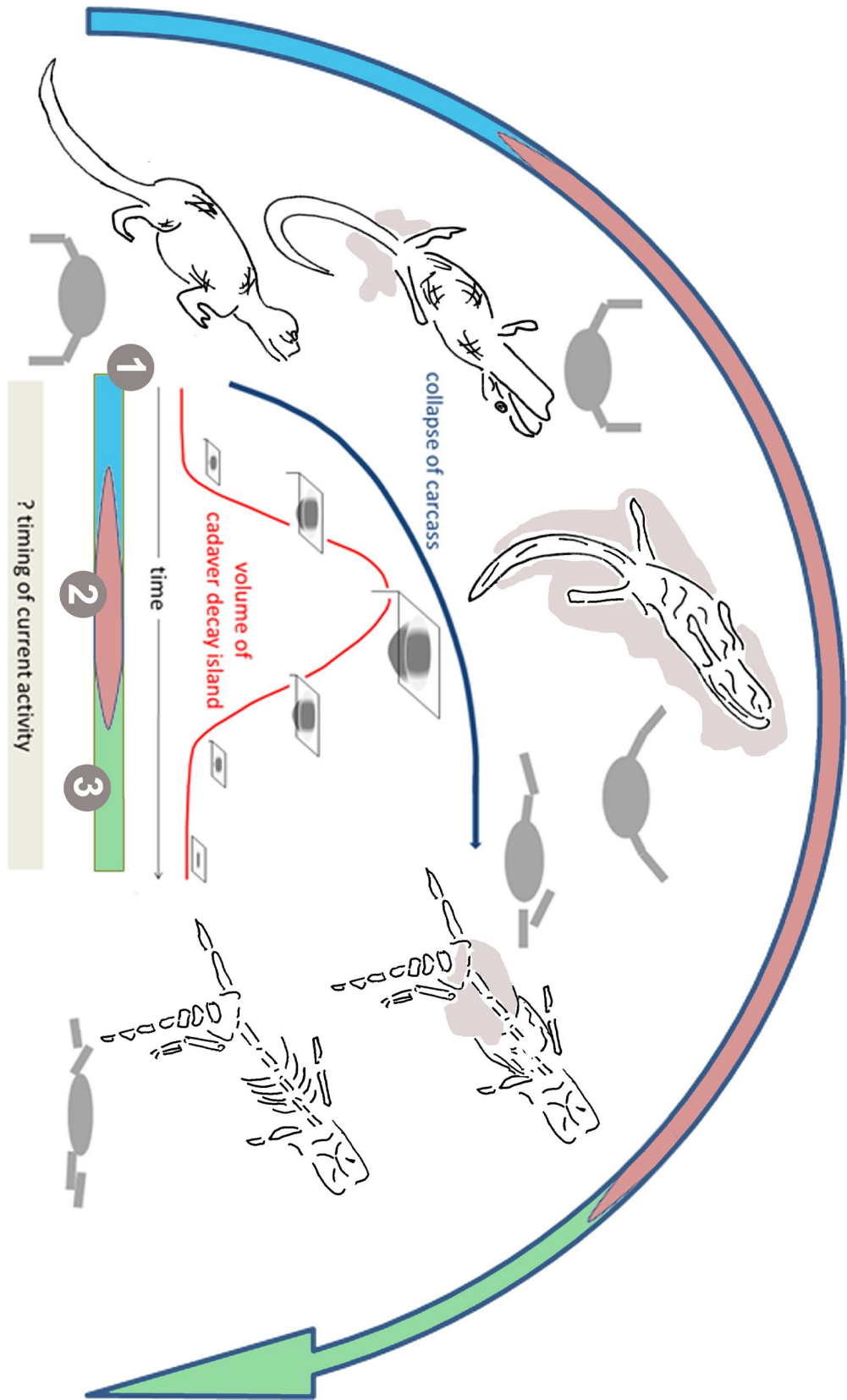
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676    Figure 3

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687    Figure 4