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COMMENTARY

Reply to "Ichthyosaur embryos outside the mother body: not due to carcass explosion but to carcass implosion" by van Loon (2013)

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In his recent discussion on the taphonomy of ichthyosaurs, van Loon (2013) supported—at least partially—the view of Reisdorf et al. (2012) and emphasized that explosion of vertebrate carcasses on the sea floor should not be considered as a taphonomically reasonable scenario. Carcass explosion is thus not a process that can be used to explain both the disarticulation of certain ichthyosaur skeletons and the displacement of their bones in the geological record. Van Loon (2013), however, did suggest that, as an alternative hypothesis, implosion could have led to the displacement of bones on the sea floor.

Van Loon (2013) focussed his explanation of the implosion hypothesis on the example of a maternal ichthyosaur having embryonic ichthyosaurs around and within its body cavity (Staatliches Museum für Naturkunde Stuttgart, specimen number SMNS 50 007). Reisdorf et al. (2012) outlined that

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this maternal specimen is just one example of many similar cases. In fact, Reisdorf et al. (2012) challenged the hypothesis of carcass explosion based on numerous ichthyosaur finds, which are preserved in the Lower Jurassic (Toarcian) Posidonienschiefer Formation in SW Germany; however, most of these are specimens without embryos. The generalised taphonomic model suggested by Reisdorf et al. (2012) can also be applied to other vertebrates if their anatomical peculiarities are taken into account (Reisdorf and Wuttke 2013). Therefore, in the following assessment and discussion, the focus is not on this specific specimen SMNS 50 007 but on the question of whether vertebrate carcasses can implode after having settled to the sea floor as well as on the related physical and physiological aspects.

The hypothesis of van Loon (2013) is based on three main assumptions: (1) bodies of ichthyosaur should have had a lower density than seawater *in vivo* (van Loon 2013: p. 105); (2) putrefaction gases could have filled some (connected) cavities within the carcass even at hydrostatic pressures of 5–15 bar (= water depth 50–150 m; van Loon 2013: p. 107); (3) on the sea floor at a water depth of 50–150 m, an underpressure has developed/maintained within the ichthyosaur carcass (van Loon 2013: 107); van Loon invoked a submarine as analogue (van Loon 2013: 107). These three assumptions are discussed in detail in the following text.

(1) Van Loon (2013) provides no explanation as to how a vertebrate carcass having a lower density than the ambient fluid may have settled to the sea floor, in particular as putrefaction gases may accumulate in some body cavities during the time when the carcass floated at the sea surface. The latter process lowers the mean density of the carcass. A low body density would have resulted in a prolonged floating interval of the carcass at the sea surface. During that time, the carcass is subjected to biogenic and physical destruction, with all its taphonomic consequences (i.e. loss of soft tissue and possibly even bones due to decomposition processes, scavenging and wave action). In contrast, a large number of the Early Toarcian ichthyosaurs of SW Germany are preserved as more or less complete skeletons (e.g. Hofmann 1958; Heller 1966; Keller 1992; Martill 1993) and thus, they must have sunk *in toto* to the sea floor immediately after death (Reisdorf et al. 2012). Settling of an ichthyosaur carcass to the sea floor would have required a body density higher than that of seawater as explained by Reisdorf et al. (2012: pp 72, 75 and references therein).

(2) Putrefaction gases forming in subaquatic settings mainly consist of CO_2, H_2 and N_2, (Mallach and Schmidt 1980; Kelly 1990; Bernaldo de Quirós et al. 2013), which have a considerable solubility in water under hydrostatic pressures of >5 bar (Weiss 1970, 1974; Wiesenburg and Guinasso 1979; Reisdorf et al. 2012). Accordingly, these gases are soluble within the carcass bodily fluids, and soft tissues that become increasingly fluidized during autolytical processes and putrefaction (e.g. Teather 1994). Therefore, the volume of undissolved putrefaction gases is low in carcasses located at water depths of 50–150 m (compare Figs. 1 and 2; see explanation and references in Reisdorf et al. 2012: p. 72; Reisdorf and Wuttke 2012: p. 155). During residence on the sea floor, fluidization of soft tissues leads to an increasingly plastic consistency of the carcass which, in combination with the necessarily small volumes of putrefaction gas within the carcass, if ever present, rules out the implosion scenario invoked by van Loon (2013). Nevertheless, a simple gravitational collapse of the body due to soft-tissue fluidization and the loss of connectivity of the skeletal elements is highly likely (e.g. Hofmann 1958; Kauffman 1981; Keller 1992; Martill 1993), but this process does not represent an ‘implosion’. It is physiologically and physically impossible to generate or to maintain an underpressured cavity within a vertebrate carcass on the sea floor at water pressures ranging from 5 to 15 bar. Unfortunately, van Loon (2013) provides neither a physical explanation nor experimental evidence as to how such an underpressure might have developed or have been maintained within a vertebrate carcass on the sea floor. His comparison of a submerged carcass with a submarine is not valid because a submarine has a rigid outer shell (e.g. Polmar 2004; in terms of palaeontology this corresponds to a rigid exoskeleton, which is the case for certain cephalopods; e.g. Hewitt and Westermann 1987; Kanie and Hattori 1983). In contrast, ichthyosaurs have an endoskeleton covered by flexible skin and multiple openings that allow for the exchange of gases and fluids with the ambient seawater and also for a certain degree of deformation of the rib cage (Taylor 1987, 2000; Hänggi and Reisdorf 2007: p. 13). Therefore,

Fig. 1 Bloated pig carcass in shallow waters (water depth 7–15 m) in Howe Sound, British Columbia. Bloat lasted 3–10 days (G.S. Anderson; see also Anderson 2010; Kelly 1990). (Photograph by J. Haywood)

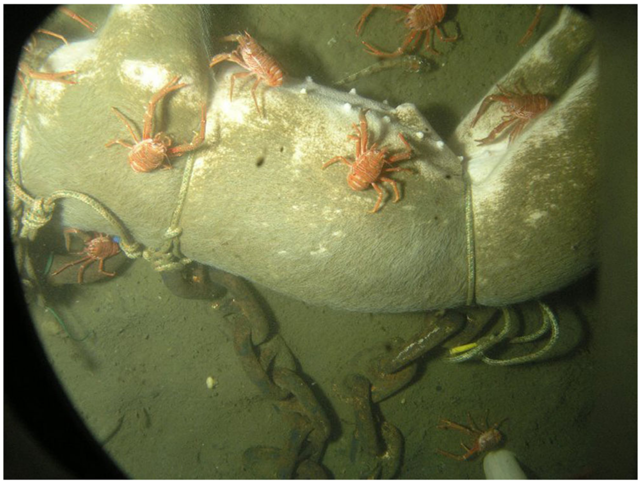


Fig. 2 Pig carcass at a water depth of 99 m, 5 days after placement in Saanich Inlet, British Columbia (water temperature 9.2 °C). No evidence of bloat (for detailed information as well as faunal colonization, see Anderson 2010; Anderson and Bell 2010). [Photograph by VENUS Project (Victoria Experimental Network Under the Sea), G.S. Anderson and L.S. Bell]

van Loon's (2013) implosion hypothesis has no physical basis. At the most, a carcass may gravitationally collapse on the sea floor.

(3) Referring to the example of the above-mentioned gravid female, van Loon (2013) proposes that its implosion led to the dissemination of embryo bones. The power of an implosion, of course, depends on the total *connected* volume being underpressured, the underpressure relative to the ambient setting and the speed of pressure equilibration. Is it possible that a large gas-filled, but sufficiently underpressured cavity to implode could develop at the sea floor? At the hydrostatic pressure present at a considerable water depth, putrefaction gases become dissolved in the surrounding liquids and tissues, forming numerous, small-sized bubbles (= 'gas crepitation'; e.g. Dumser and Türkay 2008), or they are maintained in small pockets of the decaying body (e.g. Anderson 2010). They do not accumulate to form a large balloon-like volume (compare Figs. 1 and 2; e.g. Anderson 2010). Therefore, putrefaction gases are unlikely to be available for an implosion. Furthermore, there is currently no experimental observation or theory that explains how to develop an underpressure in a newly formed or persisting gas- or liquid-filled cavity within a vertebrate carcass at the sea floor. Van Loon (2013) did neither provide an explanation that is physically and physiologically sound nor did he obtain experimental evidence or provide an explanation about how, where and why the 'implosion centre' developed. To our knowledge, it is highly unlikely that a reasonably large, underpressured gas-filled volume develops in a carcass on the sea floor without a sufficiently rigid frame to physically explain an implosion. In contrast, the most common and plausible scenario for a carcass on the sea floor would appear to be a gradual gravitational collapse of the skeleton due to decaying soft-tissues and the loss of connectivity of the skeletal elements.

From the physical point of view, there has to be a spatial relation between the location of the underpressured cavity, the area of skin damage through which pressure equilibration took place and the dissemination of bones. However, van Loon (2013) did not provide any evidence or other arguments in support of the implosion hypothesis; for instance, he did not state where such underpressured volumes might have been located within the carcass and how the implosion of the carcass would have been expressed taphonomically. The anatomy of (extant) viviparous reptiles does not show any peculiarity that would lead to the implosion of a carcass under natural conditions at a considerable water depth (e.g. Gans and Parsons 1977; cf. Böttcher 1990; Blackburn et al. 2003; Maxwell and Caldwell 2003; Kear and Zammit 2014; Motani et al. 2014). In fact, to date, there has been no published report about the implosion of a vertebrate carcass on the sea floor. In contrast, the physiology of extant lung-breathing vertebrates clearly illustrates that the body with its endoskeleton and lungs passively responds to an increase in hydrostatic pressure (e.g. Hui 1975; Ridgway et al. 1969; Kooyman 1989). For example, the body is compressed within the anatomically possible range if external pressure increases during (deep) diving (see conclusions and references in Reisdorf et al. 2012: p. 76). The same is true for extant dolphins, which have been suggested to represent a modern analogue to ichthyosaurs with respect to adaptation to the marine habitat (e.g. Ridgway et al. 1969; Hui 1975; McGhee 2011; Zammit et al. 2014). Ichthyosaur thoraxes were adapted to dive to reasonably great depths similar to those of extant Cetaceans (e.g. Taylor 1987, 2000). In addition, even the fairly rigid thorax of terrestrial mammals (including humans) has some flexibility and becomes compressed at water depths of >10 m (e.g. Kelly 1990). In other words, if dead lung-breathing vertebrates sink to the sea floor, their density increases due to the compression of the gas-filled spaces in the body as well as compression and dissolution of the gas inside the respiratory tract (see Reisdorf et al. 2012, and references therein). In such cases, no underpressure can develop. Modern observations support this view: Smith and Baco (2003) demonstrated that cetacean carcasses bloated by putrefaction gases settled to the sea floor as deep as 1,900 m (substantial amounts of ballast, up to 2.7 t, were used to sink them), but they did not implode, even if they were attacked by scavengers at this depth. These examples illustrate again that submarines do not

> represent suitable analogues for ichthyosaurs, neither for living or for dead ones. To conclude, van Loon's (2013) scenario of a carcass implosion has neither a physical nor a physiological base. Therefore, we disagree with van Loon's hypothesis of carcass implosion.

Additionally, carcass implosion does not provide an explanation for the dissemination of (ichthyosaur) bones on the sea floor [in, for example, a stagnant basin *sensu* Seilacher (1982), like that of the Early Toarcian epicontinental sea]. In contrast, the fluidization of the soft tissues during decomposition and the effects of bottom currents on the carcass may lead to the translocation of anatomic units and thus disarticulation as well as dislocation of bones. Fluidization may have allowed an effluence of a viscous mass carrying disarticulated bones when the skin becomes locally damaged (e.g. by scavengers) or partly degraded (Wuttke and Reisdorf, in preparation).

In fact, there are many indicators of bottom-current activity in the epicontinental sea covering Central Europe during the Toarcian, although this was doubted by van Loon (2013). The Mesozoic Central European Epicontinental Sea (Wetzel et al. 2013) was partly surrounded by landmasses and shallow seaways to the open oceans, to the Arctic Sea to the north and to the Tethys to the SW, while in the SE between the Alemannic Island a shallow shoal existed (e.g. Ziegler 1990; Cope et al. 1992; Röhl and Schmid-Röhl 2005; Suan et al. 2013). While located roughly around 35° N in a warm climate, terrigenous clastics form the major proportion of the sediment of the Posidonienschiefer Formation, implying a considerable influx of river water, mainly from Scandinavia and the Bohemian Massif (e.g. Prauss et al. 1991; Cope et al. 1992; Bour et al. 2007; cf. Harazim et al. 2013). The high amount of organic matter and the fine-lamination and dark colour of the sediment are seen as evidence for temporary anaerobic conditions at the sea floor and a stratified water body (e.g. Röhl et al. 2001; Bour et al. 2007).

Since this epicontinental basin was connected to the world ocean at different sides by fairly wide gateways, storms and similar events probably introduced dense ocean water into the Posidonienschiefer basin (cf. Bour et al. 2007; Harazim et al. 2013). Depending on the sea floor topography and the power of the (storm-) events current-reworked layers extend more or less far into the basin. The influx of dense ocean water was often followed by short-term oxygenation at the sea floor (e.g. Bour et al. 2007). Less intense events might have resulted in sediment reworking only. It is also possible that a continuous flow of dense oceanic water existed for short periods of time that share some similarities with contour current deposits outlined by van Loon (2013: p. 106); we fully agree with this statement. During times of enhanced precipitation it is most likely that an estuarine circulation was established within the basin, whereas during periods of prevailing evaporation, dense saline downwelling water would have initiated an anti-estuarine circulation (e.g. Röhl 1998; Röhl et al. 2001).

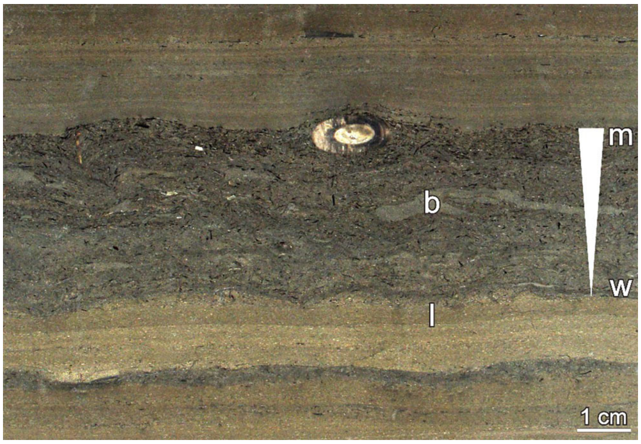


Fig. 3 Current reworking of sediment by the bottom current that increased in flow velocity as indicated by the inverse grading. Prior to the main episode (*m*), weaker reworking (*w*) occurred; the onset of the latter is marked by the absence of lamination (*l*). During the main event the sea floor was oxygenated, as indicated by the burrows (*b*). (Temporary exposure at Pädagogische Hochschule Reutlingen/Germany, lower commune subzone, above the limestone bed 'Inoceramenbank'; Photograph by A. Wetzel)

It is not the purpose of this commentary to explain how the bottom currents within the Posidonienschiefer basin would have been initiated; rather, our aim is to provide evidence for their existence and effects. Many studies describe the effects of such bottom currents; for example, current-related sedimentary structures and alignment of fossil hard parts have been documented by Bour et al. (2007), Kauffman (1979, 1981), Martill (1993), Röhl (1998), Seilacher (1982, and references therein) and Schieber et al. (2007). For ichthyosaurs, Brenner

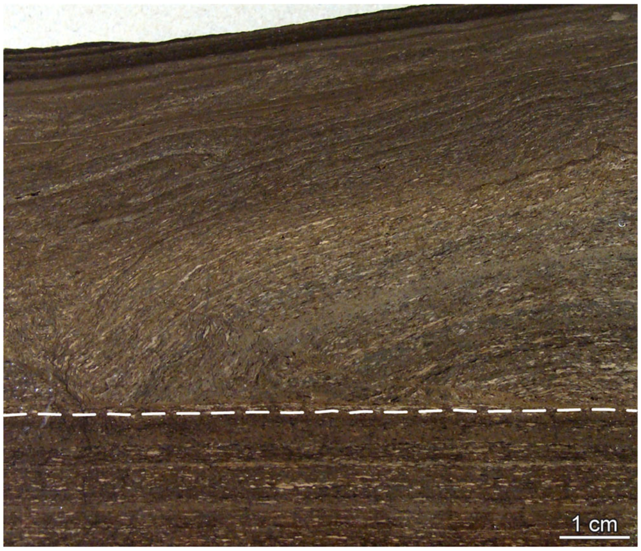


Fig. 4 Mass movement within the Posidonia-Shale; base marked by *broken line*. Note folding. (Temporary exposure at Pädagogische Hochschule Reutlingen/Germany, lower commune subzone, above the limestone bed 'Inoceramenbank'; Photograph by A. Wetzel)

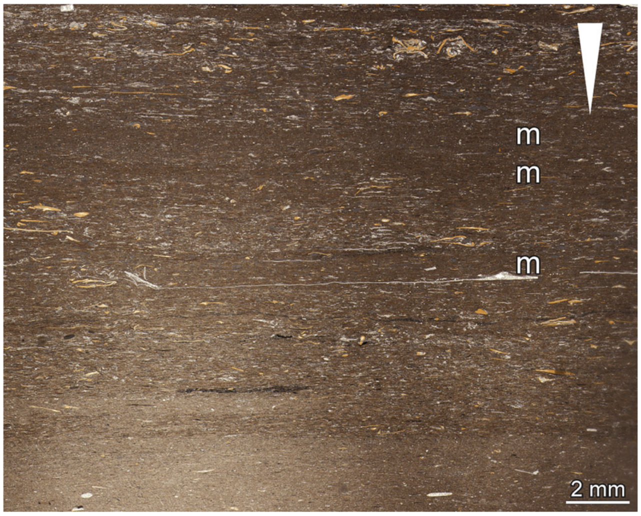


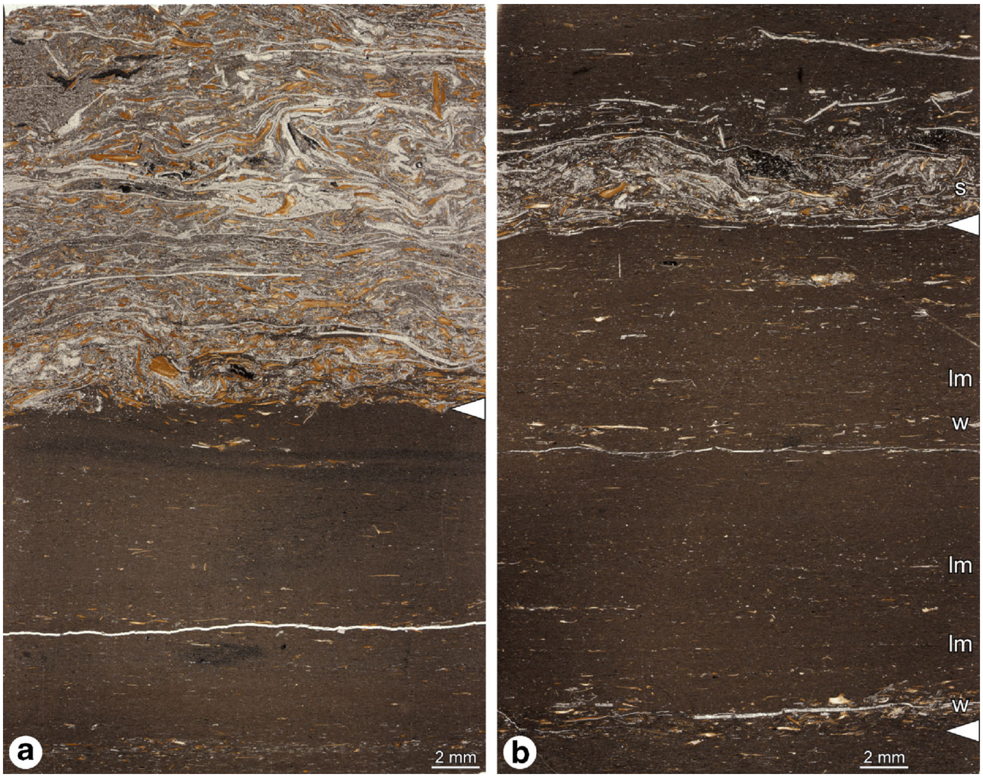
Fig. 5 Thin section of an interval with fluctuating bottom current activity as evidenced by subtle inverse grading and enrichment of fossil debris and layerwise enrichment of mud (*m*). Inversely graded interval with upward increasing content of coarse material is marked by a white arrowhead. (Temporary exposure at Pädagogische Hochschule Reutlingen/Germany, lower commune subzone, above the limestone bed 'Inoceramenbank'; Photograph by A. Wetzel)

(1976a, b), Brenner and Seilacher (1979), Hofmann (1958) and Osborn (1905) have provided examples supporting the hypothesis of bottom currents that affected the sea floor of the Posidonienschiefer basin.

A variety of primary sedimentary structures and bioturbation structures occur in the Toarcian Posidonienschiefer Formation of SW Germany. They include centimetres-thick, partly bioturbated layers consisting of reworked sediment (Fig. 3), mass flow deposits (Fig. 4), reworked sediment layers characterised by oriented sediment components (Fig. 5) and thin layers indicating moderate to weak currents (Fig. 6). Such layers are more frequent than has been commonly assumed, although only very few such examples have been published (Figs. 3, 4 and 5) or they are somewhat hidden in the literature (Riegraf et al. 1984; Riegraf 1985; Wetzel and Uchman 1998). Nonetheless, careful observations led Kauffman (1979, 1981) to question the stagnant basin model. It is not the purpose of this commentary to continue this debate on Seilacher's (1982) model; rather, we wish to draw the reader's attention to the frequent occurrence of current indicators.

Given the vertical extent of a dead adult ichthyosaur sinking to the sea floor, it is highly likely that due to the low average net sedimentation rate [4 mm/kyr (compacted), equivalent to 40 mm/kyr in a decompacted state at approx. 90 % porosity; see Einsele and Mosebach 1955 as well as Hofmann 1958, for an estimate) the elevated parts of the carcass are exposed to currents for a considerably long time span. This rate is as low as today in the deep-sea (20–60 mm/kyr; e.g. Scholle et al. 1983). As long as a carcass is not completely embedded within the sediment it can be affected by currents. Theoretically, it would take 20 kyr to fully cover a ichthyosaur carcass of a diameter of 80 cm with sediment at the given sedimentation rates and under conditions of the absence of carcass collapse (see also Martill 1993), but it is an extremely

Fig. 6 Thin sections of layers indicating bottom current activity. **a** Layers exhibit a sharp base (*white arrowhead*) that is enriched in fossil debris due to condensation and winnowing ('Schlacken'); note the considerable proportion of fish scales and other phosphatic debris (*brownish* in colour). **b** Several thin layers (*s, w*) with condensed debris and bivalve shells indicate benthic colonization events according to Röhl et al. (2001), some of them with a sharp base (*white arrowhead*) laminated mud (*lm*) in between meets the criteria given by Schieber et al. (2007) for deposition by currents. (Temporary exposure at Pädagogische Hochschule Reutlingen/Germany, lower commune subzone, above the limestone bed 'Inoceramenbank'; Photographs by A. Wetzel)



dubious assumption that a carcass prevails over thousands of years without being effected by decay. As van Loon (2013) outlined, degradation of a carcass, however, might have affected the soft parts within a relatively short time. Even then, the articulated bones still form elevations on the sea floor for some time and could have been affected more easily by currents than the adjacent sea floor according to Bernoulli's principle (e.g. Vogel 1994). Furthermore, ichthyosaur bones consist mostly of spongiosa, and hence they have a relatively low density (and thus a small hydraulically equivalent diameter) that facilitates their displacement by currents (see explanation by Reisdorf et al. 2012 and references therein).

Van Loon doubts that some ichthyosaur carcasses sunk—at least partly—into the sea floor sediment, which most likely had a soupy consistency (Hofmann 1958; Martill 1993; Schmid-Röhl and Röhl 2003) that would have allowed their articulated preservation (some of them even with a preserved body outline = so-called 'soft tissue preservation'; e.g. Heller 1966; Hauff and Hauff 1981; Martill 1993; Lindgren et al. 2014). Unfortunately, van Loon (2013) did not provide an alternative embedding mechanism for such ichthyosaurs. Van Loon (2013) argued that, for example, empty extant shells with a considerably higher density do not sink into soupy mud. However, some ichthyosaurs carcasses did sink into the sediment of the Posidonienschiefer Formation, as evidenced by their mode of preservation; normally the lower surface of the specimens is prepared and exposed in museums because the upper side is preserved at a considerable lower quality, as described in detail by Heller (1966), Hofmann (1958) and Martill (1993). In this context it has to be taken into account that the density of ichthyosaurs became higher during the sinking process to the sea bottom due to compression of the thorax and, therefore, the carcasses achieved a certain acceleration as they sank through the water column to the sea bottom (Reisdorf 2007; Reisdorf et al. 2012; in contrast to the benthonic fauna, e.g. shells). As shown by Fröbisch et al. (2006), Hänggi and Reisdorf (2007), Hofmann (1958), Martill (1993), Reisdorf (2007), Wahl 2009 as well as Wetzel and Reisdorf (2007), this high settling speed is corroborated by many excellent ichthyosaurs specimens all over the world, which landed head-first on the sea floor with the snout penetrating several decimetres into the uncompacted sediment.

Some stratigraphic intervals contain almost only isolated bones of ichthyosaurs, whereas others contain more or less completely preserved, but disarticulated ichthyosaur skeletons in relatively high abundance. The latter horizons correspond to episodes of rising or high sea-level, whereas isolated bones occur more frequently in deposits that formed during falling or low sea-level [based on the sea-level charts of Haq et al. (1988) and Hallam (1988, 2001)]. Reisdorf et al. (2012) explained this coincidence by their taphonomic hypothesis. Van Loon criticised this explanation without comprehensive reasoning or alternative hypotheses. In the absence of alternative hypotheses and a convincing falsification, we still favour our hypothesis of the relationship between sea-level fluctuations and preservation of ichthyosaurs.

In any case, the discussion of van Loon is most welcome because each critical examination of existing sedimentological and palaeontological models and hypotheses represents a further step towards our better understanding of the processes involved.

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