

Float, explode or sink: postmortem fate of lung-breathing marine vertebrates

Achim G. Reisdorf · Roman Bux · Daniel Wyler ·
Mark Benecke · Christian Klug · Michael W. Maisch ·
Peter Fornaro · Andreas Wetzel

Received: 20 October 2011 / Revised: 16 December 2011 / Accepted: 22 December 2011 / Published online: 1 February 2012
© Senckenberg Gesellschaft für Naturforschung and Springer 2012

Abstract What happens after the death of a marine tetrapod in seawater? Palaeontologists and neontologists have claimed that large lung-breathing marine tetrapods such as ichthyosaurs had a lower density than seawater, implying that their carcasses floated at the surface after death and sank subsequently after leakage of putrefaction gases (or “carcass explosions”). Such explosions would thus account for the skeletal disarticulation observed frequently in the fossil record. We examined the taphonomy and sedimentary environment of numerous ichthyosaur skeletons and compared them to living marine tetrapods, principally cetaceans, and measured abdominal pressures in human carcasses. Our data and a review of the literature demonstrate that carcasses sink and do not explode (and spread skeletal elements). We argue that the normally

slightly negatively buoyant carcasses of ichthyosaurs would have sunk to the sea floor and risen to the surface only when they remained in shallow water above a certain temperature and at a low scavenging rate. Once surfaced, prolonged floating may have occurred and a carcass have decomposed gradually. Our conclusions are of significance to the understanding of the inclusion of carcasses of lung-breathing vertebrates in marine nutrient recycling. The postmortem fate has essential implications for the interpretation of vertebrate fossil preservation (the existence of complete, disarticulated fossil skeletons is not explained by previous hypotheses), palaeobathymetry, the physiology of modern marine lung-breathing tetrapods and their conservation, and the recovery of human bodies from seawater.

This article is a contribution to the special issue "Taphonomic processes in terrestrial and marine environments"

A. G. Reisdorf (✉) · A. Wetzel
Geologisch-Paläontologisches Institut, Universität Basel,
Bernoullistrasse 32,
4056 Basel, Switzerland
e-mail: Achim.Reisdorf@unibas.ch

R. Bux
Institut für Rechtsmedizin und Verkehrsmedizin,
Universitätsklinikum Heidelberg,
Voßstrasse 2, Gebäude 4420,
69115 Heidelberg, Germany

D. Wyler
Pathologie und Rechtsmedizin, Kantonsspital,
Loëstrasse 170,
7000 Chur, Switzerland

M. Benecke
Internatinal Forensic Research & Consulting,
Postfach 250411,
50520 Köln, Germany

C. Klug
Paläontologisches Institut und Museum,
Universität Zürich,
Karl Schmid-Strasse 4,
8006 Zürich, Switzerland

M. W. Maisch
Institut für Geowissenschaften,
Eberhard Karls-Universität Tübingen,
Hölderlinstr. 12,
72074 Tübingen, Germany

P. Fornaro
Imaging and Media Lab, Universität Basel,
Bernoullistrasse 32,
4056 Basel, Switzerland

Keywords Ichthyosaur · Nekton falls · Taphonomy · Fossilagerstätten · Early Jurassic sea-level · Forensic sciences · Whales

Introduction

Large vertebrate fossils such as ichthyosaurs are spectacular documents of earth history, but uniformitarian studies of the fate of large vertebrate carcasses in shallow marine environments before fossilization are rare (Britton and Morton 1994; Dahlgren et al. 2006; Glover et al. 2005; Liebig et al. 2007; Schäfer 1972; Smith 2007a). Recent studies have mainly dealt with decomposition of vertebrate carcasses in the deep sea (e.g., Glover et al. 2008; Kemp et al. 2006; King et al. 2006; Smith and Baco 2003). Because of the usual lack of food at the deep-sea floor, the scavenging rate on carcasses can be much higher than in shallow marine habitats (Bozzano and Sardà 2002; Janßen et al. 2000; Kemp et al. 2006). Consequently, direct comparisons between deep and shallow marine habitats are of only limited value (e.g., Fujiwara et al. 2007; Martill et al. 1995; Smith 2007a), since physical, chemical, and microbial decomposition are significantly more important than scavenging in the shallow-water (Anderson and Hobischak 2004; Kahana et al. 1999; Mosebach 1952; Petrik et al. 2004; Smith and Baco 2003).

We thus examined peri- and postmortem processes concerning carcasses of lung-breathing vertebrates in a shallow marine regime by applying palaeontological, sedimentological, forensic, anthropological, archaeological, veterinary, marine biological, and trophological methods. This integrative approach enabled us to falsify several previously applied hypotheses to explain taphonomic phenomena. It is our aim to portray the processes involved in the stratinomy of lung-breathing vertebrates, to falsify some old hypotheses, and to discuss possible applications.

Ichthyosaurs represent a diverse group of extinct marine reptiles which were almost cosmopolitan during most of the Mesozoic [245–90 million years ago (Ma); Gradstein et al. 2004; McGowan and Motani 2003]. Although these fossil lung-breathing tetrapods exhibit a whole set of morphological characters which evolved convergently to the Odontoceti (cetaceans), it has been assumed that ichthyosaur bodies had a lower density than seawater (e.g., McGowan 1992; McGowan and Motani 2003; Taylor 1987, 2001). The prevailing interpretation implies that ichthyosaurs drifted after death for a while at the sea surface and the preservation quality decreased with the floating duration (e.g., Fröbisch et al. 2006; Long et al. 2006; Martill 1986, 1993). The carcasses sank finally to the sea-floor only after leakage of the putrefaction gas, often by bursting (e.g., Cruickshank and Fordyce 2002; Kuhn-Schnyder 1974; Long et al. 2006; Martill 1993; commonly called “carcass explosion”).

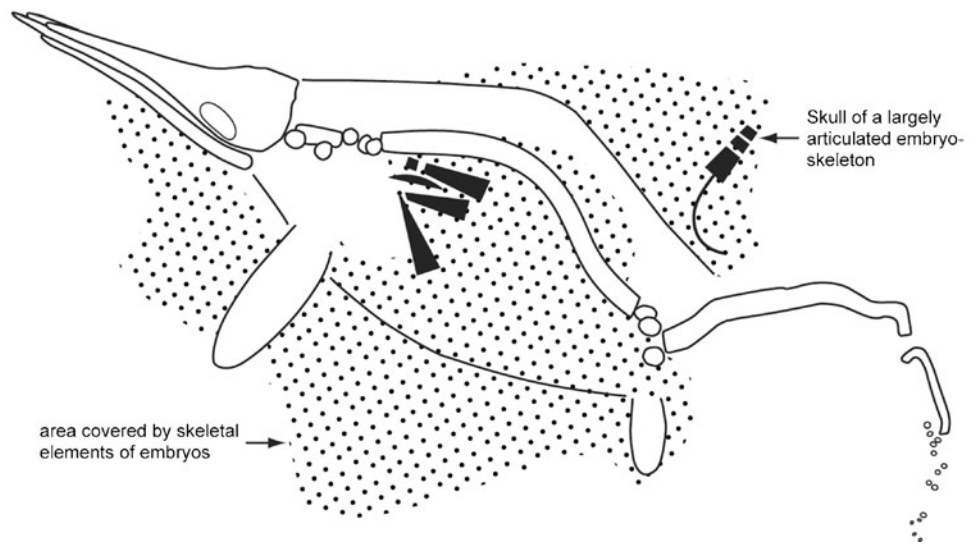
Ichthyosaurs were probably able to dive to depths exceeding 500 m (Dollo 1907; Humphries and Ruxton 2002; McGowan and Motani 2003). This inference can be drawn from the absence of ossified tracheas in fossil ichthyosaurs, which can otherwise be preserved in great detail in marine crocodiles of the same age and localities as the ichthyosaur finds (e.g., Westphal 1962). A more or less ossified trachea limits diving depth (Mason and Macdonald 1986; Tarasoff and Kooyman 1973), and the tracheas of Recent, deep-diving lung-breathers are cartilaginous (Kooyman 1989). Such cartilaginous tracheas are usually not preserved in the fossil record.

Exploding the myth: can carcasses explode?

“Carcass explosion” was first discussed among palaeontologists and geologists 32 years ago (Keller 1976), when studying the Early Jurassic Posidonienschiefer Formation (Bloos et al. 2005; ca. 183–181 Ma) of Germany. These black shales were deposited at depths between 50–150 m (Röhl et al. 2001) and contain exceptionally well-preserved remains of ichthyosaurs and other marine tetrapods (Hauff 1921; Hofmann 1958; Martill 1993). The excellent fossil preservation within finely laminated, unbioturbated black shales was explained with the widely accepted classic “stagnant basin model” (Keller 1976; Pompeckj 1901). The ichthyosaur skeletons are usually complete but disarticulated to varying degrees (Hauff 1921; Hofmann 1958). Therefore, “carcass explosion” appeared to be a reasonable explanation. It was assumed that carcasses which lie on the sea-floor might have exploded or internal organs and bones erupted, and that in so doing, bones as well as fetuses were ejected and ribs were fractured (Fig. 1; e.g., Böttcher 1989; Hofmann 1958; Keller 1976; Martill 1993). In spite of the lack of (direct) evidence for these processes, these ideas have never been questioned.

These classic models rely on the observation that beached Cetacean carcasses can get inflated impressively by putrefaction gases within hours (=bloated stage; Malakoff 2001; Schäfer 1972; Smith and Baco 2003; Stede et al. 1996; Tønnessen and Johnsen 1982). This process is mainly initiated by the activity of intestinal bacteria (=intrinsic flora; Daldrup and Huckenbeck 1984; Fiedler and Graw 2003; Mallach and Schmidt 1980; Robinson et al. 1953; Stevens and Hume 1998). Postmortem bacterial activity is highly variable because it depends on numerous factors such as the type of bacteria involved, the cause of death, injuries, and composition and amount of ingested food, as well as environmental conditions (Bajanowski et al. 1998; Daldrup and Huckenbeck 1984; Keil et al. 1980; Mallach and Schmidt 1980; Pedal et al. 1987; Pierucci and Gherson 1968; Rodriguez 1997; Sakata et al. 1980). Putrefaction rates decelerate with decreasing (water) temperature (Bonhotal et al. 2006; Dickson et al. 2011; Haberda 1895; Padosch et al.

Fig. 1 Ichthyosaur skeleton with approximately 10 embryos, Holzmaden (Germany), Posidonienschiefer Formation (*Stenopterygius*, specimen SMNS 50007; drawing modified after Böttcher 1990; image by courtesy of Staatliches Museum für Naturkunde Stuttgart). In contrast to the skeleton of the mother, most of the embryonal skeletons are largely disarticulated. Many embryonal bones are scattered far beyond the body limits of the mother. Böttcher (1990) explained this arrangement by a displacement of already disarticulated embryos during the expulsion of putrefaction gases through the ruptured body wall of the mother. Osborn (1905) explained such phenomena by currents



2005; Petrik et al. 2004; Robinson et al. 1953). Decay by intestinal bacteria (e.g., *Clostridia*, *Escherichia*) all but halts below 4°C, while enzymes (=autolysis) remain active until -5°C (Jauniaux et al. 1998; Keil et al. 1980; Lochner et al. 1980; Robinson et al. 1953; Sharp and Marsh 1953; Vass et al. 2002; compare Rollo et al. 2007). In aquatic environments, putrefaction and autolysis progresses most rapidly at low hydrostatic pressures within an intact, large, cylindrical and well-insulated carcass (e.g., a whale; Hood et al. 2003; Innes 1986; McLellan et al. 1995; Robinson et al. 1953; Worthy and Edwards 1990), independent of oxygen availability. When an inflated carcass experiences mechanical stress such as inappropriate transport or dissection, body liquids and internal organs may be ejected from the carcass (Fig. 2; Anonymous 2004; Stede 1997; Tigress Productions 2008; Tønnessen and Johnsen 1982). There is no evidence for skeletal elements being included in such “eruptions”.

During the Toarcian, the conditions in the European epeiric sea were favourable for putrefaction and autolytical processes,

because the sea surface temperature has been estimated to have varied between 25 and 30°C (Röhl et al. 2001).

In spite of the adaptations to the marine habitat, it is still probable that sometime after death seawater containing anaerobic or aerobic bacteria intruded both digestive and respiratory tracts of ichthyosaurs because of the hydrostatic pressure (=exogenous bacteria; e.g., Eisele 1969; Hänggi and Reisdorf 2007; Kakizaki et al. 2008; Siebert et al. 2001; Sims et al. 1983). Onset of putrefaction processes due to exogenous bacteria is thus conceivable (as in human carcasses; Davis 1986; Dickson et al. 2011; Lunetta et al. 2002; Mallach and Schmidt 1980; Padosch et al. 2005; Tomita 1975, 1976). The putrefaction gases produced by the intrinsic bacteria but probably also by exogenous bacteria comprise CO₂, H₂, N₂, to a lesser amount CH₄, H₂S, and even O₂ (Keil et al. 1980; Mallach and Schmidt 1980; see also Ettwig et al. 2010). To obtain data for the pressure that builds up in carcasses in different stages of bloating, intra-abdominal pressures were measured in 100 human corpses at the Institut

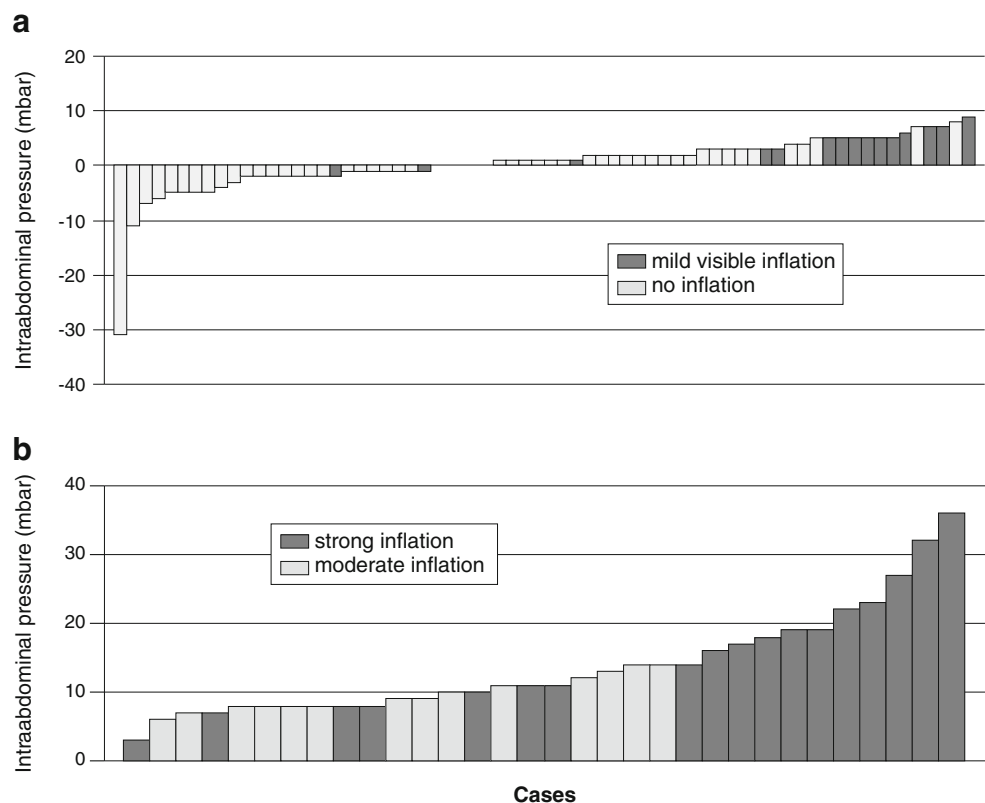


Fig. 2 Improper sectioning of a stranded whale carcass bloated by putrefaction gases at the beach of Nymindegab/ Denmark; body liquids and parts of the intestinal tract erupt violently from the body cavity (Krarup 1990; image by courtesy of TV/Midt-Vest)

für Forensische Medizin Frankfurt am Main in 2004 (Bux et al. 2004). The manometer (C9557 Pressure Meter; Comark, Hertfordshire, UK) was introduced into the abdominal cavity

in the vicinity of the umbilicus by means of an anasarca trocar. The intraabdominal pressures did not exceed 0.035 bar (Fig. 3). This agrees with the pressures which were measured

Fig. 3 Relationship between effective intra-abdominal pressures and bloated stages in 100 human corpses (measured between January 1 and August 30, 2004). **a** Intraabdominal pressures at no (light grey bars) or mild (dark grey bars) visible inflation. Intra-abdominal pressures lower than atmospheric pressures are due to postmortem cooling of the corpses. **b** Intraabdominal pressures at moderate (light grey bars) or strong (dark grey bars) visible inflation. The range of intraabdominal pressures due to bloating by putrefaction gas is comparable to the pressures used in laparoscopic surgery (Abu-Rafea et al. 2006)



by Fallani (1961) in human dead bodies. In goat carcasses, however, pressures up to 0.079 bar have been recorded (Li et al. 2003). These pressure values correspond to submersion depth in water of 0.35 and 0.79 m. In the case of ichthyosaur carcasses that sank to the bottom of the Toarcian epeiric sea in Europe, potential hydrostatic pressures corresponding to a water depth of 50–150 m would reach 5–15 bar (Boyle's law; e.g., Haglund and Sorg 2002; Toklu et al. 2006; Tomita 1975). It is highly unlikely that intraabdominal pressures in the most common European ichthyosaur *Stenopterygius quadriscissus* (which usually attained 1.5–2.9 m in length; e.g., von Huene 1922; McGowan and Motani 2003) exceeded these values, and therefore, “carcass explosion” was impossible in greater water depths, close to or at the water surface. This appears even more unlikely because ichthyosaur fetuses are commonly found directly adjacent to the carcass of their mother in calculated water depths of 50–150 m (Fig. 1; Böttcher 1990; Hofmann 1958; Röhl et al. 2001), where such explosions are physically impossible.

Subsequently, we present two models explaining disarticulation of ichthyosaur skeletons of the Posidonienschiefer Formation. The burial depth of the carcass (0–100% covered by sediment) plays an important role. This is especially true since the palaeoenvironment of the Posidonienschiefer Formation was neither entirely nor continuously anoxic (e.g., Kauffman 1981; Röhl et al. 2001; Röhl and Schmid-Röhl 2005).

Effects of sediment compaction and currents

Even in an oxygen-deficient environment, preservation potential of carcasses of marine tetrapods depends on burial depth (Hofmann 1958; Martill 1993). Organic-rich mudrocks such as the Early Jurassic Posidonienschiefer Formation exhibit a high initial porosity. During some time intervals, the topmost decimetres of the sediment were probably nearly fluid (“soupy substrate”; Hofmann 1958; Martill 1993; Röhl et al. 2001). The physical properties of such “soupy substrates” enabled ichthyosaur carcasses to sink into the sediment partially or entirely [e.g., Hofmann 1958; Martill 1993; Schimmelman et al. 1994; Smith and Wuttke (2012, this issue), however, critically evaluate this taphonomic scenario of embedding of ichthyosaur carcasses]. Afterwards, the sediment was compacted by over 90% due to burial, causing intense brittle and “plastic” deformation of the skeleton parts (Einsele and Mosebach 1955; Hofmann 1958; Martill 1993) unless embedded in early diagenetic concretions (Keller 1992; Wetzel and Reisdorf 2007). The most intense deformation during compaction occurred in the thorax, causing the ribs to depart from their original arrangement and, as documented in some ichthyosaur fossils, from phosphatized or pyritized soft part remains (e.g., the stomach) near the abdominal and cloacal regions (Hofmann 1958; Keller

1976). These phenomena resemble injuries of an originally intact body characteristic of “crush/traumatic asphyxia” (e.g., Byard et al. 2006; Machel 1996), and this type of preservation contradicts explosion.

Organic-rich, muddy sediments like the Posidonienschiefer Formation are stated to accumulate mainly under prevailing tranquil conditions (e.g., Seilacher 1982). Evidence for weak to moderate currents, however, can be encountered in nearly all levels of the Posidonienschiefer Formation, indicating fluctuations in the depositional environment (Kauffman 1981; Röhl and Schmid-Röhl 2005; Schieber et al. 2007). Indeed, recent experiments show that such mud can be deposited from currents moving at 0.1–0.26 m/s (Schieber et al. 2007). The erosion of such cohesive sediments requires high current velocities, depending on the degree of consolidation because of the electrostatic forces between particles (Sundborg 1956). Bacteria–particle interactions at the sediment surface might also increase the resistance against erosion (Black et al. 2003; Röhl et al. 2001; Widdel 1988). The low net sedimentation rate of the Posidonienschiefer Formation of 4 mm/1,000 years (calculated for compacted sediments; Röhl et al. 2001) and the high compressibility of such sediments might have favored dewatering of an initially “soupy substrate” (e.g., Bernhard et al. 2003; Wetzel 1990). Flume-experiments with human and animal bones (density of dry and wet bones is usually below 2.65; Blob 1997; de Ricqlès and de Buffrénil 2001; Lam et al. 2003) revealed that bones of the thorax and the appendages begin to move at current velocities as low as 0.2–0.4 m/s (e.g., Blob 1997; Boaz and Behrensmeier 1976; Coard 1999; Fernández-Jalvo and Andrews 2003). Such currents have been postulated for the shallow marine Early Toarcian epeiric sea (e.g., Hofmann 1958; Kauffman 1981; Martill 1993; Röhl and Schmid-Röhl 2005). The histology of ichthyosaur bones displays some convergences to Recent cetacean bones, which possess a lower density than land tetrapods (de Buffrénil et al. 1986; de Ricqlès and de Buffrénil 2001; Maas 2002). A further density decrease might have been caused by decay, microbial activity, and bone diagenesis (Arnaud et al. 1980; Fujiwara et al. 2007; Glover et al. 2005; Kiel 2008; Meyer 1991; Smith and Baco 2003). Thus, there was a real potential for transport of ichthyosaur bones by water currents.

All these factors make it highly probable that currents moved bones on the seafloor without eroding mud. This deduction is supported by the fact that 90% of all ichthyosaur specimens are disarticulated (Hauff 1921). The arrangement of ichthyosaur skeletal remains documents that the carcass was not or incompletely embedded in sediment for a considerable time (physical properties of the topmost decimetres of the seabottom prevented carcasses from being embedded entirely). Under these conditions, soft-tissues initially decomposed, causing the loss of connectivity of the skeletal elements, and the carcass eventually collapsed gravitationally (Hofmann

1958; Martill 1993; Reisdorf and Wuttke 2012, this issue). Thoracic elements were most strongly affected by currents because they were usually exposed furthest above the ground and experienced highest current velocities. It is also conceivable that larger Metazoan scavengers played an additional role in the disarticulation and transport of skeletal elements (e.g., Kauffman 1981; Martill 1993; von Huene 1922), but the processes discussed above are of greater importance in a predominantly oxygen-deficient environment.

Sink or float?

The density of the ichthyosaur body and other aquatic lung-breathing tetrapods plays a crucial role in the potential to sink or float. Today, no Recent reptiles are known which can be considered as closely related to ichthyosaurs, especially with respect to anatomical and physiological characteristics. Therefore, Recent (facultatively) aquatic reptiles are only of limited use for such comparisons (e.g., Wade 1984). By contrast, Recent cetaceans (e.g., de Ricqlès and de Buffrénil 2001; Ridgway 2002; Sekiguchi and Kohshima 2003; Staunton 2005; Taylor 2000; Williams et al. 2000) may serve as a morphological and ecological model to reconstruct the postmortem fate of ichthyosaurs. With the exception of the species *Eubalaena glacialis* and *Physeter macrocephalus*, cetaceans have a density slightly higher than that of seawater (e.g., Butterworth 2005; Schäfer 1972; Shevill et al. 1967; Smith 2007a, b; Tønnessen and Johnsen 1982). *E. glacialis* and *P. macrocephalus* are relatively slow-swimming whales and the only species which usually does not sink after having been shot by whalers (Braham and Rice 1984; Gosho et al. 1984; Nowacek et al. 2001). [Jurassic Ichthyosaurs are usually considered to have been the fastest sustained swimmers of the Mesozoic seas (e.g., Lingham-Soliar and Wesley-Smith 2008) and thus seem also likely to have been negatively buoyant.] The low density of the bodies of these species, the so-called “right whales”, is caused by an extraordinarily high content of oil and fat (e.g., Glover et al. 2008; Gosho et al. 1984; Kemp et al. 2006; Slijper 1962). Other “right whales” (e.g. *Balaenoptera musculus*) may float after death only when caught by “Electrical Whaling”; paralyzed thoracic musculature apparently accounts for this phenomenon (Øen 1983).

Odontoceti might also become positively buoyant when the lungs are almost completely or entirely filled by air (e.g., Ridgway et al. 1969; Slijper 1962). Among living and etiologically unconditioned cetaceans, the lung volume never gets used exhaustively (Wartzok 2002). The respiration physiology of mammals, however, is significantly different from that of Recent reptiles; most of the latter exhale actively and inhale passively (Carrier and Farmer 2000; Perry 1983).

This line of reasoning suggests that even if inhalation in ichthyosaurs was passive as in Recent reptiles, they would still have been negatively buoyant (e.g., Hogler 1992; Wade 1984) and sunk immediately after death, unless the lungs were filled with air to an abnormal degree (e.g., pulmonary emphysema; Siebert et al. 2001; Slijper 1962; Ridgway et al. 1969; Fig. 4).

Incipient decomposition at the seafloor causes a reduction in carcass density. How far gaseous putrefaction products develop in the carcass, and whether they are dissolved or bound within the soft-tissues and body liquids, depends mainly on the local hydrostatic pressure and temperature (Allison et al. 1991; Dickson et al. 2011; Hofmann 1958; Lucas et al. 2002; McLellan et al. 1995; Smith and Baco 2003; Tomita 1975, 1976; Wasmund 1935; Zangerl and Richardson 1963). All main components of the putrefaction gas (N_2 , H_2 , O_2 ; possibly also CH_4) except for the CO_2 share a low solubility at temperatures below 4°C and moderate pressures ($O_2 > N_2 > CH_4 > H_2$; Ashcroft 2002: 59; Mallach and Schmidt 1980; Ramsey 1962; Shafer and Zare 1991; Weiss and Price 1989) and tend to increase buoyancy by forming bubbles (Dumser and Türkay 2008; Mueller 1953; Tomita 1975). It depends on the integrity of the skin and the digestive tract whether these gases can accumulate inside the carcass (beneath the skin and in the body cavities; Anderson and Hobischak 2004; Dumser and Türkay 2008; Haglund 1993; Schäfer 1972; Smith and Baco 2003; Thali et al. 2003).

In shallow water and at temperatures above 4°C, it is very likely that putrefaction gases would cause carcasses to surface and drift (presuming that they are not covered by sediment; Haberda 1895; Hofmann 1958; Moreno et al. 1992; Petrik et al. 2004; Sorg et al. 1997; Tomita 1975, 1976; Wasmund 1935). Drifting at the water surface, sometimes over months and long distances, carcasses decompose gradually (Giertsen and Morild 1989; Haglund 1993; Schäfer 1972; Smith 2007a; Tomita 1975, 1976; Wild 1978).

Empirical data on the hydrostatic pressure needed to keep a carcass at the sediment surface are available for cetaceans, various terrestrial tetrapods such as humans, mice, and domestic pigs, and different freshwater fish (e.g., Allison et al. 1991; Anderson and Hobischak 2004; Berg 2004; Elder and Smith 1988; Esperante et al. 2008; Moreno et al. 1992; Smith 2007a; Tomita 1975, 1976; Tønnessen and Johnsen 1982). These studies reveal that higher hydrostatic pressures are required to suppress the rise of carcasses of larger dimensions compared to smaller carcasses (e.g., Barton and Wilson 2005; Tomita 1975, 1976; see also Kemp 2001). Apparently, taxonomy does not play a major role in this respect, but physics does (Tomita 1975).

In marine environments, Recent cetaceans and human carcasses may rise from water depths up to 50 m, but never from below 100 m (Tomita 1975, 1976; Tønnessen and Johnsen 1982). The above-mentioned water depth estimate

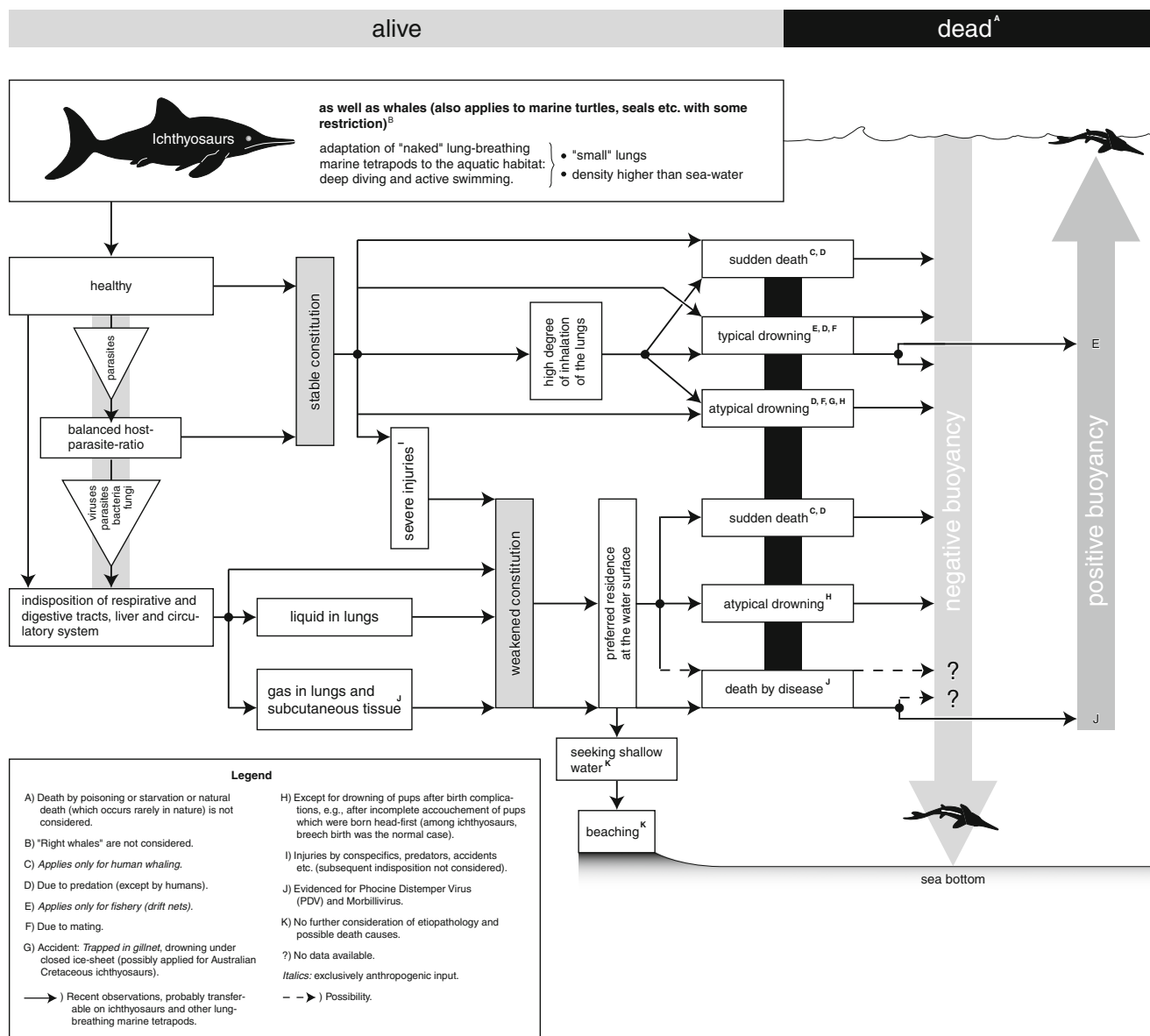


Fig. 4 Peri- and postmortem behavior of marine tetrapods without buoyancy-increasing body fat, oil, hair or feathers in the pelagic realm (modified after Hänggi and Reisdorf 2007; references in Reisdorf 2007)

of the "Posidonienschiefer Formation sea" in southern Germany of 50–150 m (Röhl et al. 2001) matches the physical requirements to keep an ichthyosaur carcass on the seafloor. In the case of nearly complete ichthyosaur skeletons, it is very likely that the carcass was entombed close to the place of death because of the short settling time.

Skeleton preservation as a sea-level proxy?

The taphonomy of lung-breathing tetrapods depends on water depth and, thus, can be used as palaeobathymetrical proxy (cf. Allison et al. 1991). Early Jurassic ichthyosaur remains

display recurring taphonomic patterns which can be grouped into three preservation categories: (1) articulated skeletons, (2) disarticulated skeletons, and (3) isolated bones (e.g., Martill 1986, 1993; isolated body parts of predated animals which sank towards the seafloor are not considered in the subsequent discussion; e.g., Böttcher 1989; Martill 1993; Taylor 2001).

Articulated skeletons are equally abundant and well-documented throughout the Early Toarcian; for instance, >3000 more or less articulated specimens are known just from the Holzmaden area in Germany (Martill 1993; McGowan and Motani 2003). These articulated skeletons are not included in this analysis because these carcasses were apparently largely or completely embedded

in the sediment immediately after grounding while sinking into the “soupy substrate” (Hofmann 1958; Martill 1993; but see Smith and Wuttke 2012, this issue). Adhesion and sediment weight prevented the carcass from surfacing even when putrefaction gases developed sufficiently to lift the carcass (Hofmann 1958; see also Piccard 1961). Additionally, they were protected against Metazoan scavengers (Hofmann 1958) or bottom currents, i.e. the carcasses could not be realigned after their deposition.

Disarticulated skeletons are mainly found in sediments deposited during times of eustatic sea-level rise (=transgressive cycles; e.g., de Graciansky et al. 1998; Hallam 2001) under oxygen-depleted conditions (Hauff 1921; Röhl et al. 2001). Such skeletons were probably not or not completely covered by sediment for a prolonged timespan or they were secondarily exhumed (e.g., Hofmann 1958; Kauffman 1981; Martill 1993). Apparently, rising of the carcasses was prevented by hydrostatic pressure and/or partial sediment cover (Allison et al. 1991; Hofmann 1958; Tomita 1975, 1976). Speculatively, an overgrowth by microbial mats or other organisms might have

had the potential to prevent the carcass from refloatation to the water surface. However, the remarkable completeness of isolated parts of a skeleton found in spatial proximity rules out strong bottom currents.

Isolated bones, scarcity or absence of ichthyosaur fragments result from times of eustatic sea-level fall (=regressive cycles; e.g., de Graciansky et al. 1998; Hallam 2001). Many carcasses surfaced because of the low hydrostatic pressure which allowed putrefaction gases to develop. These skeletons disintegrated while floating (e.g., Hofmann 1958; Martill 1986, 1993). Such isolated bones possibly underwent a further maceration up to complete disintegration.

The “Ichthyosaur Corpse Curve” (ICC; Fig. 5) summarizes the frequency of different modes of ichthyosaur preservation in Central Europe during the Lower Jurassic. The poor correlation of the ichthyosaur record of the Hettangian with the sea-level curve of Hallam (1988, 2001) may be explained by the generally still low sea-level of this interval. The “Ichthyosaur Corpse Curves” are based on data from England, Germany, and Switzerland for which a reasonable amount of well-

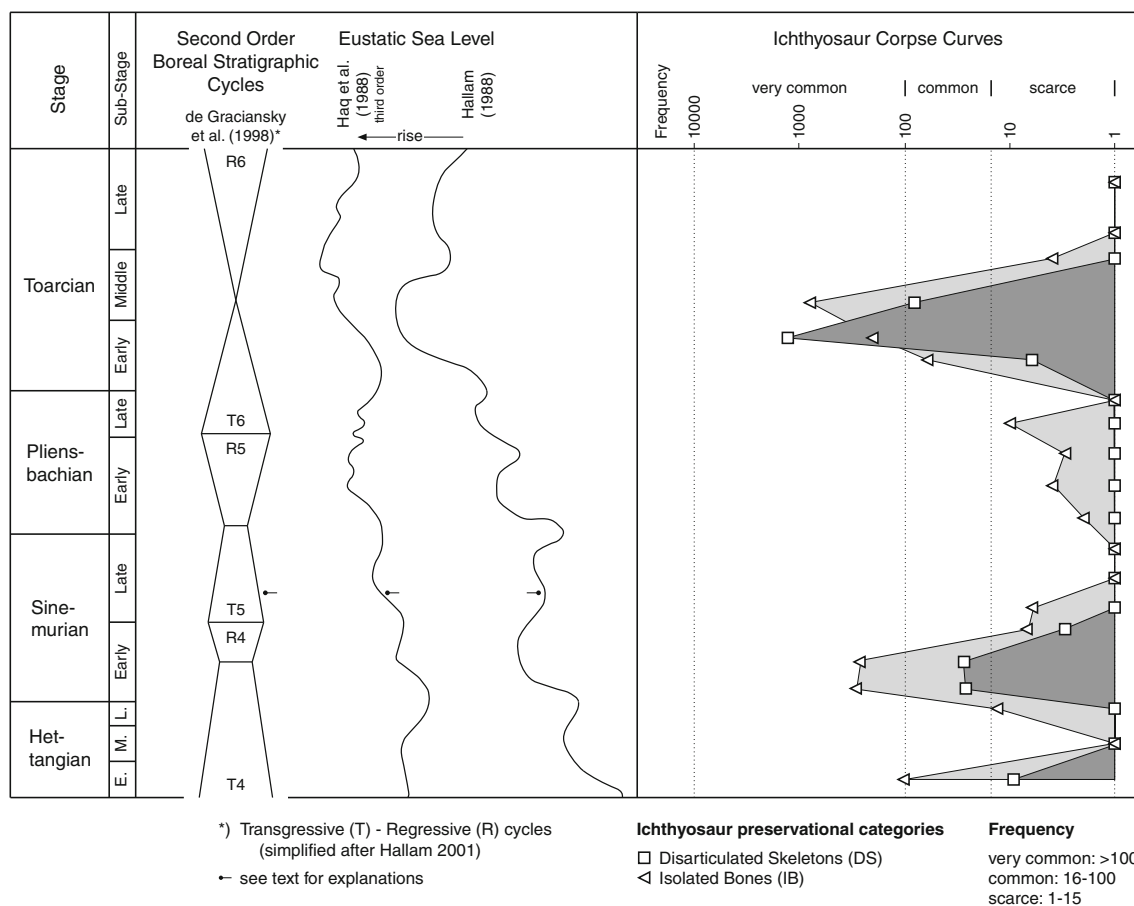


Fig. 5 Taphonomy of Early Jurassic ichthyosaurs from northwestern and central Europe compared to eustatic sea-level curves. Ichthyosaur taphonomy appears to reflect eustatic sea-level changes. A rising or relatively high eustatic sea-level sensu Hallam (2001) appears to favor

rich occurrences of ichthyosaurs (literature data and estimates; see Table 1). At times of low or falling sea-level or low-amplitude rise, ichthyosaur remains are scarce, and preservation of single bones prevails (see Table 1 and main text; see also Hesselbo and Palmer 1992)

documented ichthyosaur remains over a longer time interval is available. These occurrences are plotted on a logarithmic scale to give an impression of the three abundance categories. Absence of fossils was set to one occurrence to make them displayable on the logarithmic scale. Due to the unsatisfying documentation of ichthyosaur finds especially in the nineteenth century, partially caused by a focus on articulated skeletons, we had to guess the number of occurrences in several cases, especially since we chose a temporal resolution on ammonite-zone level. The numbers of disarticulated skeletons (DS) and isolated bones (IB) of the “Ichthyosaur Corpse Curves” represent an estimate of the minimum unless precise numbers from the literature or collections were available. In some cases, we estimated some numbers of IB based on the usual ratio of DS to IB of 1:10 to 1:100. Accordingly, the amount of DS in British fossilagerstätten is based on the number of occurrences of articulated skeletons. The abundance of disarticulated ichthyosaur-remains as shown by the DS:IB ratio thus reflects the fossil record in the Lower Jurassic ammonite zones of Great Britain, southern Germany and northern Switzerland (Table 1).

Table 1 These data on the occurrences and abundances of preservational modes (disarticulated skeletons *DS*; and isolated bones *IB*) were obtained from museum collection counts (Paläontologische Forschungs-, Lehr- und Schausammlung am Institut für Geowissenschaften Universität Tübingen, Sammlung am Staatlichen Museum für Naturkunde Stuttgart) and from the literature (Altmann 1965; Benton and Taylor 1984; Benton

and Spencer 1995; Berckhemer 1938; Dean et al. 1961; Delair 1960; Fraas 1891; Hauff 1921; von Huene 1922, 1931; Knitter and Ohmert 1983; Maisch 1999; Maisch and Reisdorf 2006; Maisch et al. 2008; Martin et al. 1986; McGowan 1978; McGowan and Motani 2003; Meyer and Furrer 1995; Pratje 1922; Quenstedt 1858; Reiff 1935; Reisdorf et al. 2011; Schieber 1936); for a comment of the quality of the data, see text

Conclusions and significance

1. According to our measurements and deductions, it is impossible that skeletons of vertebrates become disarticulated with their bones being scattered over a certain area exclusively by the release of putrefaction gases under hydrostatic or atmospheric pressures.
2. There is ample evidence that ichthyosaurs and most other lung-breathing marine tetrapods of comparable mode of life were negatively buoyant. This is

Ammonite zonation sensu Dean et al. (1961)	Stages	Great Britain		Germany		Switzerland		Sum DS	Sum IB
		DS	IB	DS	IB	DS	IB		
<i>levesquei</i>	Toarcian	0	0	0	1	0	0	0	1
<i>thouarsense</i>		0	1	0	0	0	0	0	1
<i>variabilis</i>		0	0	0	4	0	0	0	4
<i>bifrons</i>		61	610	18	180	0	0	79	790
<i>falcifer</i>		6	60	1,295	130	2	11	1,303	201
<i>tenuicostatum</i>		0	0	6	60	0	0	6	60
<i>spinatum</i>	Pliensbachian	0	0	0	1	0	0	0	1
<i>margaritatus</i>		0	0	0	10	0	0	0	10
<i>davoei</i>		0	0	0	3	0	0	0	3
<i>ibex</i>		0	0	1	4	0	0	1	4
<i>jamesoni</i>		0	1	0	0	0	1	0	2
<i>raricostatum</i>	Sinemurian	0	1	0	0	0	0	0	1
<i>oxynotum</i>		0	0	0	0	0	0	0	0
<i>obtusum</i>		1	6	0	0	0	0	1	6
<i>turneri</i>		0	1	3	6	0	0	3	7
<i>semicostatum</i>		25	250	1	6	1	11	27	267
<i>bucklandi</i>		25	250	1	35	0	0	26	285
<i>angulata</i>	Hettangian	0	0	0	11	0	2	0	13
<i>liasicus</i>		0	0	0	1	0	0	0	1
<i>planorbis</i>		9	90	0	12	0	0	9	102

corroborated by the fact that even the density of some of the lightest Recent cetaceans (e.g., harbor porpoise *Phocoena phocoena*) is higher than that previously assumed for the most common European ichthyosaur *Stenopterygius* (Kemp et al. 2006; McLellan et al. 2002; Motani 2001; Reisdorf 2007). Therefore, previous body mass calculations of ichthyosaur bodies, which presume a seawater density of the ichthyosaurs, are too low (Reisdorf 2007).

3. If an ichthyosaur body is assumed to have been negatively buoyant, locomotion models which assume that ichthyosaurs needed to overcome positive buoyancy when diving (e.g., Taylor 1987; McGowan 1992) require re-evaluation. Sleep behavior must also have been adapted for negative buoyancy: ichthyosaurs had to actively surface to respire, as do Cetaceans (e.g., Lyamin et al. 2006; Ridgway 2002; Staunton 2005; Wade 1984).
4. Most of the ichthyosaurs that were not killed by external forces died by drowning when rendered unable to surface, due to diseases, complications during pregnancy and the birth process, or old age (Kastelein et al. 1995; Knieriem and García Hartmann 2001; Reisdorf 2007; Shevill et al. 1967; Slijper 1962; Smith 2007a; Fig. 4). They subsequently sank. This theoretically opens the possibility to apply the “diatom-test” (e.g., Hürliemann et al. 2000) to ichthyosaurs, especially to Cretaceous representatives. These algae and other small particles (e.g., Knieriem and García Hartmann 2001; Möttönen and Nuutila 1977; Yoshimura et al. 1995) can be deposited in bones when lung-breathing vertebrates inhale water when drowning (but see also Kan 1973, and Koseki 1968). However, the possible occurrence of such a “fossil trap” has yet to be analysed.
5. Ichthyosaurs usually settled on the sea-floor without any density increase or buoyancy decrease except for the compression of the body as well as the compression (e.g., Hui 1975) and the dissolution of gas contained in the carcass (e.g., Haglund and Sorg 2002; Kemp 2001; Smith 2007a).
6. Buoyancy-increasing formation of putrefaction gases plays a crucial role with respect to the drift behaviour and fossilization of vertebrate carcasses in shallow marine (and lacustrine) depositional environments. A disarticulated skeleton with bones preserved in spatial proximity helps to estimate palaeobathymetry, because the hydrostatic pressure had to be sufficient to counteract the effects of gas formed by putrefaction (=“Cartesian Diver Effect”). This is also important for the interpretation of marine (and lacustrine) fossilagerstätten (e.g., Beardmore et al. 2012, this issue; Buffetaut 1994; Elder and Smith 1988; Esperante et al. 2008; Hofmann 1958; Hogler 1992; Mancuso and Marsicano 2008; Reisdorf and Wuttke 2012, this issue; Sander 1989; Smith and Wuttke 2012, this issue; Zangerl and Richardson 1963).
7. We suggest the use of the term “ichthyosaur fall” for more or less completely preserved ichthyosaur skeletons. This is in accordance with the established marine biological terms “nekton fall” and “whale fall” (e.g., Smith and Baco 2003), which describe carcasses or skeletons of nektonic organisms which sank through the water column to the seafloor.
8. We found that our newly constructed “Ichthyosaur Corpse Curves” for England, south-western Germany and Switzerland (Fig. 5) correlate well with the global sea-level curve of the Early Jurassic by Hallam (e.g., Hallam 2001), but do not match that of Haq et al. (1988) or de Graciansky et al. (1998). Additional uniformitarian taphonomic studies of modern marine lung-breathing vertebrates are necessary to improve “nekton falls” as a useful palaeobathymetric proxy.
9. Most of the outlined factors and mechanisms affecting the density and maceration of Recent cetaceans and ichthyosaurs in water can be generalised with respect to most lung-breathing marine vertebrates and various land-living tetrapods such as humans, at least with some minor modifications (e.g., Donoghue and Minnigerode 1977; Gray et al. 2007; Tomita 1975, 1976).
10. Our findings have implications for a number of today’s environmental problems and the protection of species: The carcasses of many lung-breathing marine vertebrates, such as those of whales, cannot be observed because most of them will never surface or strand (e.g., Cassoff et al. 2011; Ford et al. 2000; Kirkwood et al. 1997; Moreno et al. 1992; Smith 2007a). Knowledge of postmortem hydrostatic pressure, temperature and scavenging rate conditions in Recent cetaceans and ichthyosaurs can serve as a model for human carcasses (Anderson and Hobischak 2004; Haglund 1993; Hood et al. 2003; Kahana et al. 1999; Moreno et al. 1992; Petrik et al. 2004; Schäfer 1972) and thus be applied to the retrieval of missing humans after disasters (e.g., tsunamis, heavy flooding, cyclones) and crimes from bodies of water (e.g., Blanco Pampin and Lopez-Abajo Rodriguez 2001; Tomita 1975, 1976; Tsokos and Byard 2011).

Acknowledgements We thank R. Allenbach, H. Benke, R. Böttcher, J.K. Broadrick, D. Flentje, M.C. Haff, J. Hermann, J. Hürliemann, T. Keller, F. Lörcher, S. Lutter, J.H. Modell, M.D. Pirie, K. Schneider, R. Schoch, Y. Song, B. Springmann, M. Stede, D. Trottenberg, M. Wuttke, J. Zopfi, Institut für Rechtsmedizin der Universität Basel and WWF Bremen for their input. D.M. Martill and an anonymous reviewer critically read the manuscript and made helpful suggestions. Two anonymous colleagues kindly reviewed an earlier

version of this article. This research was supported by a grant from the Swiss National Science Foundation (to A.G.R. and A.W.) and Freiwillige Akademische Gesellschaft Basel (A.G.R.). All these contributions are gratefully acknowledged.

References

- Abu-Rafea B, Vilos GA, Vilos AG, Hollett-Caines J, Al-Omran M (2006) Effect of body habitus and parity on insufflated CO₂ volume at various intraabdominal pressures during laparoscopic access in women. *J Mini Invas Gynecol* 13:205–210
- Allison PA, Smith CR, Kukert H, Deming JW, Bennett BA (1991) Deep-water taphonomy of vertebrate carcasses. a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology* 17:78–89
- Altmann HJ (1965) Beiträge zur Kenntnis des Rhät-Lias-Grenzbereichs in Südwest-Deutschland. Dissertation, University of Tübingen
- Anderson GS, Hobischak NR (2004) Decomposition of carrion in the marine environment in British Columbia, Canada. *Int J Leg Med* 118:206–209
- Anonymous (2004) Rotting sperm whale spills its guts. *Nature* 427:478
- Arnaud G, Arnaud S, Ascenzi A, Bonucci E, Graziani G (1980) On the problem of the preservation of human bone in sea-water. *Int J Naut Archaeol Underw Expl* 9:53–65
- Ashcroft F (2002) Life at the extremes: the science of survival. University of California Press, Berkeley
- Bajanowski T, West A, Brinkmann B (1998) Proof of fatal air embolism. *Int J Leg Med* 111:208–211
- Barton DG, Wilson MVH (2005) Taphonomic variations in Eocene fish-bearing varves at Horsefly, British Columbia, reveal 10 000 years of environmental change. *Can J Earth Sci* 42:137–149
- Beardmore SR, Orr PJ, Furrer H (2012) Float or sink: modelling the taphonomic pathway of marine crocodiles (Mesoeucrocodylia, Thalattosuchia) during the death-burial interval. In: Wuttke M, Reisdorf AG (eds) Taphonomic processes in terrestrial and marine environments. *Palaeobio Palaeoenviron* 92(1). doi:10.1007/s12549-011-0066-0
- Benton MJ, Taylor MA (1984) Marine reptiles from the Upper Lias (Lower Toarcian, Lower Jurassic) of the Yorkshire coast. *Proc Yorkshire Geol Soc* 44:399–429
- Benton MJ, Spencer PS (1995) Fossil Reptiles of Great Britain. *Geol Conserv Rev Ser No. 10*, Chapman and Hall, London
- Berckhemer F (1938) Das Gebiß von *Leptopterygius platyodon* CONYB. *Paleobiology* 6:150–163
- Berg S (2004) Todeszeitbestimmung in der spätpostmortalen Phase. In: Brinkmann B, Madea B (eds) *Handbuch gerichtliche Medizin, Band 1*. Springer, Berlin, pp 91–204
- Bernhard JM, Visscher PT, Bowser SS (2003) Submillimeter life positions of bacteria, protists, and metazoans in laminated sediments of the Santa Barbara Basin. *Limnol Oceanogr* 48:813–828
- Black KS, Peppe C, Gust G (2003) Erodibility of pelagic carbonate ooze in the northeast Atlantic. *J Exp Mar Biol Ecol* 285–286:143–163
- Blanco Pampin J, Lopez-Abajo Rodriguez BA (2001) Surprising drifting of bodies along the coast of Portugal and Spain. *Leg Med (Tokyo)* 3:177–182
- Blob RW (1997) Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates. *Palaios* 12:151–164
- Boaz NT, Behrensmeier AK (1976) Hominid taphonomy: transport of human skeletal parts in an artificial fluvial environment. *Am J Phys Anthropol* 45:53–60
- Bonhotat J, Harrison E, Schwarz M (2006) Evaluating Pathogen Destruction in Road Kill Composting. *Biocycle* 47:49–51
- Bloos G, Dietl G, Schweigert G (2005) Der Jura Süddeutschlands in der Stratigraphischen Tabelle von Deutschland 2002. *Newslett Stratigr* 41:263–277
- Böttcher R (1989) Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier. *Stuttg Beitr Naturkd B* 155:1–19
- Böttcher R (1990) Neue Erkenntnisse über die Fortpflanzungsbiologie der Ichthyosaurier. *Stuttg Beitr Naturkd B* 164:1–51
- Bozzano A, Sardà F (2002) Fishery discard consumption rate and scavenging activity in the northwestern Mediterranean Sea. *ICES J Mar Sci* 59:15–28
- Braham HW, Rice DW (1984) The Right Whale, *Balaena glacialis*. *Mar Fish Rev* 46:38–44
- Britton JC, Morton B (1994) Marine carrion and scavengers. *Oceanogr Mar Biol* 32:369–434
- Buffetaut E (1994) The significance of dinosaur remains in marine sediments: an investigation based on the French record. *Berliner Geowiss Abh E* 13:125–133
- de Buffrénil V, Sire J-Y, Schoevaert D (1986) Comparaison de la structure et du volume squelettiques entre un delphinidé (*Delphinus delphis* L.) et un mammifère terrestre (*Panthera leo* L.). *Can J Zool* 64:1750–1756
- Butterworth A (2005) Death at sea - when is a whale dead? *Vet J* 169:5–6
- Bux R, Reisdorf A, Ramsthaler F (2004) Did the Ichthyosaurs explode? – A forensic-medical contribution to the Taphonomy of Ichthyosaurs in Bituminous Shales. *Baltic Medico-Legal Association, Abstracts of the 5th BMLA Congress, October 6.-9. 2004, Saint-Petersburg*, p 69
- Byard RW, Wick R, Simpson E, Gilbert JD (2006) The pathological features and circumstances of death of lethal crush/traumatic asphyxia in adults – a 25-year study. *Forensic Sci Int* 159:200–205
- Cassoff RM, Moore KM, McLellan WA, Barco SG, Rotstein DS, Moore MJ (2011) Lethal entanglement in baleen whales. *Diseas Aquat Org* 96:175–185
- Carrier DR, Farmer CG (2000) The Integration of Ventilation and Locomotion in Archosaurs. *Am Zool* 40:87–100
- Coard R (1999) One bone, two bones, wet bones, dry bones: transport potentials under experimental conditions. *J Archaeol Sci* 26:1369–1375
- Cruikshank ARI, Fordyce RE (2002) A new marine reptile (Sauropterygia) from New Zealand: Further evidence for a Late Cretaceous austral radiation of cryptoclidid plesiosaurs. *Palaeontol J* 45:557–575
- Daldrup T, Huckenbeck W (1984) Bedeutung des Fäulnisbakteriums *Clostridium sordellii* für die Leichenaltersbestimmung. *Z Rechtsmed* 92:121–125
- Dahlgren TG, Wiklund H, Källström B, Lundälv T, Smith CR, Glover AG (2006) A shallow-water whale-fall experiment in the north Atlantic. *Cah Biol Mar* 47:385–389
- Davis JH (1986) Bodies found in the water: an investigate approach. *Am J Forensic Med Pathol* 7:291–297
- Dean WT, Donovan DT, Howarth MK (1961) The Liassic ammonite zones and subzones of the north-west European province. *Bull Br Mus Nat Hist Geol* 4:435–505
- Delair JB (1960) The Mesozoic reptiles of Dorset: Part Three – Conclusion. *Proc Dorset Nat Hist Archaeol Soc* 1959(79):59–85
- Dickson GC, Poulter RTM, Maas EW, Probert PK, Kieser JA (2011) Marine bacterial succession as a potential indicator of postmortem submersion interval. *Forensic Sci Int* 209:1–10
- Dollo L (1907) L'Audition chez les Ichthyosauriens. *Bull Soc Belge Géol Paléontol Hydrol* 21:157–163
- Donoghue ER, Minnigerode SC (1977) Human body buoyancy: a study of 98 men. *J Forensic Sci* 22:573–579

- Dumser TK, Türkay M (2008) Postmortem Changes of Human Bodies on the Bathyal Sea Floor – Two Cases of Aircraft Accidents Above the Open Sea. *J Forensic Sci* 53:1049–1052
- Einsele G, Mosebach R (1955) Zur Petrographie, Fossilhaltung und Entstehung der Gesteine des Posidonienschiefers im Schwäbischen Jura. *N Jb Geol Paläont Abh* 101:319–430
- Eisele R (1969) Das postmortale Eindringen von Flüssigkeit in die Lungen und den Magen-Darmkanal beim Aufenthalt unter Wasser. Dissertation, University of Düsseldorf
- Elder RL, Smith GR (1988) Fish taphonomy and environmental inference in paleolimnology. *Palaeogeogr Palaeoclimatol Palaeoecol* 62: 577–592
- Esperante R, Brand L, Nick KE, Poma O, Urbina M (2008) Exceptional occurrence of fossil baleen in shallow marine sediments of the Neogene Pisco Formation, Southern Peru. *Palaeogeogr Palaeoclimatol Palaeoecol* 257:344–360
- Ettwig KF, Butler MK, Le Paslier D et al (2010) Nitrite-driven anaerobic methane oxidation by oxygenic bacteria. *Nature* 464: 543–548
- Fallani M (1961) Contributo allo studio della circolazione ematica post-mortale. *Minerva Medicoleg (Torino)* 81:108–115
- Fernández-Jalvo Y, Andrews P (2003) Experimental Effects of Water Abrasion on Bone Fragments. *J Taph* 1:145–161
- Fiedler S, Graw M (2003) Decomposition of buried corpses, with special reference to the formation of adipocere. *Naturwiss* 90:291–300
- Ford JKB, Ellis GM, Balcomb KC (2000) Killer whales: the natural history and genealogy of *Orcinus orca* in British Columbia and Washington, 2nd edn. UBC Press, Vancouver
- Fraas E (1891) Die Ichthyosaurier der süddeutschen Trias- und Jura-Ablagerungen. Laupp, Tübingen
- Fröbisch NB, Sander M, Rieppel O (2006) A new species of *Cymbospondylus* (Diapsida, Ichthyosauria) from the Middle Triassic of Nevada and a re-evaluation of the skull osteology of the genus. *Zool J Linn Soc* 147:515–538
- Fujiwara Y, Kawato M, Yamamoto T, Yamanaka T, Sato-Okoshi W, Noda C, Tsuchida S, Komai T, Cubelio SS, Sasaki T, Jacobsen K, Kubokawa K, Fujikura K, Maruyama T, Furushima Y, Okoshi K, Miyake H, Miyazaki M, Nogi Y, Yatabe A, Okutani T (2007) Three-year investigations into sperm whale-fall ecosystems in Japan. *Mar Ecol* 28:219–232
- Giertsen JC, Morild I (1989) Seafaring bodies. *Am J Forensic Med Pathol* 10:25–27
- Glover AG, Källström B, Smith CR, Dahlgren TG (2005) World-wide whale worms? A new species of *Osedax* from the shallow north Atlantic. *Proc R Soc Lond B* 272:2587–2592
- Glover AG, Kemp KM, Smith CR, Dahlgren TG (2008) Comment “On the role of bone-eating worms in the degradation of marine vertebrate remains”. *Proc R Soc Lond B* 275:1959–1961
- Gosho ME, Rice DW, Breiwick JM (1984) The Sperm Whale, *Physeter macrocephalus*. *Mar Fish Rev* 46:54–64
- de Graciansky PC, Dardeau G, Dommergues JL, Durlot C, Marchand D, Dumont T, Hesselbo SP, Jacquin T, Goggin V, Meister C, Mouterde R, Rey J, Vail PR (1998) Ammonite Biostratigraphic Correlation and Early Jurassic Sequence Stratigraphy in France: Comparisons with some U.K. Section. *SEPM Soc Sed Geol Spec Publ* 60:583–622
- Gradstein F, Ogg J, Smith A (2004) A Geologic Time Scale 2004. Cambridge University Press, Cambridge
- Gray N-M, Kainec K, Madar S, Tomko L, Wolfe S (2007) Sink or swim? Bone density as a mechanism for buoyancy control in early cetaceans: The Anatomical Record. *Adv Integr Anat Evol Biol* 290:638–653
- Haberda A (1895) Einiges über Wasserleichen. *Vierteljahresschr gerichtl Med öff Sanitätsw (Dritte Folge)* 9:95–110
- Haglund WD (1993) Disappearance of soft tissue and the disarticulation of human remains from aqueous environments. *J Forensic Sci* 8:806–815
- Haglund WD, Sorg MH (2002) Human remains in water environments. In: Haglund WD, Sorg MH (eds) *Advances in forensic taphonomy method, theory and archeological perspectives*. CRC Press, Boca Raton, pp 201–218
- Hallam A (1988) A re-evaluation of the Jurassic eustasy in the light of new data and the revised Exxon curve. *SEPM Soc Sed Geol Spec Publ* 42:261–273
- Hallam A (2001) A review of the broad pattern of Jurassic sea-level changes and their possible causes in the light of current knowledge. *Palaeogeogr Palaeoclimatol Palaeoecol* 167:23–37
- Hänggi H, Reisdorf AG (2007) Der Ichthyosaurier vom Hauensteiner Nebelmeer - Wie eine Kopflandung die Wissenschaft Kopf stehen lässt. *Mitt Natforsch Ges Kanton Solothurn* 40:7–22
- Haq BU, Hardenbol J, Vail PR (1988) Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level change. *SEPM Spec Publ* 42:71–108
- Hauff B (1921) Untersuchungen der Fossilfundstätten von Holzmaden im Posidonienschiefer des oberen Lias Württembergs. *Palaeontographica* 64:1–42
- Hesselbo SP, Palmer TJ (1992) Reworked early diagenetic concretions and the bioerosional origin of a regional discontinuity within marine mudstones. *Sedimentology* 39:1045–1065
- Hofmann J (1958) Einbettung und Zerfall der Ichthyosaurier im Lias von Holzmaden. *Meyniana* 6:10–55
- Hogler JA (1992) Taphonomy and paleoecology of *Shonisaurus popularis* (Reptilia: Ichthyosauria). *Palaios* 7:108–117
- Hood C, Daoust P, Lien J, Richter C (2003) An experimental study of postmortem ocular fluid and core temperature analysis in incidentally captured harbour porpoise (*Phocoena phocoena*). North Atlantic Marine Mammal Commission (NAMMCO). *Sci Publ* 5:229–242
- von Huene F (1922) Die Ichthyosaurier des Lias und ihre Zusammenhänge. Gebrüder Bornträger, Berlin
- von Huene F (1931) Neue Ichthyosaurier aus Württemberg. *N Jb Min Geol Paläont Abt B* 65:305–320
- Hui CA (1975) Thoracic collapse as affected by the *retia thoracica* in the dolphin. *Respir Physiol* 25:63–70
- Humphries S, Ruxton GD (2002) Why did some ichthyosaurs have such large eyes? *J Exp Biol* 205:439–441
- Hürlimann J, Feer P, Elber F, Niederberger K, Dirnhofer R, Wyler D (2000) Diatom detection in the diagnosis of death by drowning. *Int J Leg Med* 114:6–14
- Innes S (1986) How fast should a dead whale cool? *Can J Zool* 64:2064–2065
- Janßen F, Treude T, Witte U (2000) Scavenger assemblages under differing trophic conditions: a case study in the deep Arabian Sea. *Deep-Sea Res Part II* 47:2999–3026
- Jauniaux T, Brosens L, Jacquinet E, Lambrigts D, Addink M, Smeenk C, Coignoul F (1998) Postmortem investigations on winter stranded sperm whales from the coasts of Belgium and the Netherlands. *J Wildl Dis* 34:99–109
- Kahana T, Almog J, Levy J, Shmeltzer E, Spier Y, Hiss J (1999) Marine taphonomy: adipocere formation in a series of bodies recovered from a single shipwreck. *J Forensic Sci* 44:897–901
- Kakizaki E, Takahama K, Seo Y, Kozawa S, Sakai M, Yukawa N (2008) Marine bacteria comprise a possible indicator of drowning in seawater. *Forensic Sci Int* 176:236–247
- Kan T (1973) Studies on the determination of drowning from bones. *Jpn J Leg Med* 27:68–76
- Kastelein RA, Dokter T, Hilgenkamp J (1995) A swimming support for dolphins undergoing veterinary care. *Aquat Mamm* 21:155–159
- Kauffman EG (1981) Ecological Reappraisal of the German Posidonienschiefer and the Stagnant Basin Model. In: Gray J, Boucot AJ, Berry WBN (eds) *Communities of the Past*. Hutchinson Ross, Stroudsburg, pp 311–381

- Keil W, Bretschneider K, Patzelt D, Behning I, Lignitz E, Matz J (1980) Luftembolie oder Fäulnisgas? Zur Diagnostik der cardialen Luftembolie an der Leiche. *Beitr Gerichtl Med* 38:395–408
- Keller T (1976) Magen- und Darminhalte von Ichthyosauriern des süd-deutschen Posidonienschiefers. *N Jb Geol Paläont Mh* 5:266–283
- Keller T (1992) “Weichteil-Erhaltung” bei großen Vertebraten (Ichthyosauriern) des Posidonienschiefers Holzmadens (Oberer Lias, Mesozoikum Süddeutschlands). *Kaupia – Darmstädter Beitr Naturgesch* 1:23–62
- Kemp KM, Jamieson AJ, Bagley PM, McGrath H, Bailey DM, Collins MA, Priede IG (2006) Consumption of large bathyal food fall, a six month study in the NE Atlantic. *Mar Ecol Progr Ser* 310:65–76
- Kemp RA (2001) Generation of the Solnhofen tetrapod accumulation. *Archaeopteryx* 19:11–28
- Kiel S (2008) Fossil evidence for micro- and macrofaunal utilization of large nekton-falls: Examples from early Cenozoic deep-water sediments in Washington State, USA. *Palaeogeogr Palaeoclimatol Palaeoecol* 267:161–174
- King NJ, Bagley PM, Priede IG (2006) Depth zonation and latitudinal distribution of deep-sea scavenging demersal fishes of the Mid-Atlantic Ridge, 42 to 53°N. *Mar Ecol Progr Seri* 19:263–274
- Kirkwood JK, Bennett PM, Jepson PD, Kuiken T, Simpson VR, Baker JR (1997) Entanglement in fishing gear and other causes of death in cetaceans stranded on the coasts of England and Wales. *Vet Rec* 141:94–98
- Knieriem A, García Hartmann M (2001) Comparative histopathology of lungs from by-caught Atlantic white-sided dolphins (*Leucopleurus acutus*). *Aquat Mamm* 27:73–81
- Knitter H, Ohmert W (1983) Das Toarcium der Schwärze bei Badenweiler (Oberrheingebiet S Freiburg). *Jahresh geol L-A Baden Württemberg* 25:233–281
- Kooyman GL (1989) Diverse divers. Springer-Verlag, Berlin, Heidelberg
- Koseki T (1968) Fundamental examinations of experimental materials and control animals on the diagnosis of death from drowning by the diatom method. *Acta Med Biol* 15:207–219
- Krarp NT (1990) Hval. 19th November 1990, TV/ Midt-Vest, Holstebro, Denmark [video footage]
- Kuhn-Schnyder E (1974) Die Triasfauna der Tessiner Kalkalpen. *Neujahrsbl Natforsch Ges Zürich* 176:1–119
- Lam YM, Pearson OM, Mearns CW, Chen X (2003) Bone density studies in zooarchaeology. *J Archaeol Sci* 30:1701–1708
- Li ZH, Qin GM, Zhao YC, Li XL, Dong XT, Ma WX (2003) The development and changes of pressure of putrefactive gas in cadaveric enterocelia in spring and its forensic application. *Fa Yi Xue Za Zhi [J Forensic Med]* 19:72–75, in Chinese
- Liebig PM, Flessa KW, Taylor T-SA (2007) Taphonomic Variation Despite Catastrophic Mortality: Analysis of a Mass Stranding of False Killer Whales (*Pseudorca crassidens*), Gulf of California, Mexico. *Palaios* 22:384–391
- Lingham-Soliar T, Wesley-Smith J (2008) First investigation of the collagen D-band ultrastructure in fossilized vertebrate integument. *Proc Roy Soc Lond B* 275:2207–2212
- Lochner JV, Kauffman RG, Marsh BB (1980) Early-Postmortem Cooling Rate and Beef Tenderness. *Meat Sci* 4:227–241
- Long C, Wings O, Xiaohong C, Sander M (2006) Gastroliths in the Triassic Ichthyosaur *Panjiangsaurus* from China. *J Paleontol* 80:583–588
- Lucas J, Goldfeder LB, Gill JR (2002) Bodies found in the waterways of New York City. *J Forensic Sci* 47:137–141
- Lunetta P, Penttilä A, Sajantila A (2002) Circumstances and macro-pathologic findings in 1590 consecutive cases of bodies found in water. *Am J Forensic Med Pathol* 23:371–376
- Lyamin O, Pryslova J, Lance V, Siegel J (2006) Sleep Behaviour Lyamin et al. reply. *Nature* 441:E11
- Maas MC (2002) Histology of Bones and Teeth. In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of Marine Mammals*. Academic Press, San Diego, pp 116–122
- Machel HG (1996) Roadkill as teaching aids in historical geology and paleontology. *J Geosci Educ* 44:270–276
- Maisch MW (1999) Leptonectiden und Temnodontosauriden aus dem Alpha-Ölschiefer (Sinemurium) von Baden-Württemberg (SW-Deutschland). *N Jb Geol Paläont Mh* 1999(8):490–512
- Maisch MW, Reisdorf AG (2006) Erratum to the article “Evidence for the longest stratigraphic range of a post-Triassic Ichthyosauria *Leptonectes tenuirostris* from the Pliensbachian (Lower Jurassic) of Switzerland”. *Geobios* 39:743–746
- Maisch MW, Reisdorf AG, Schlatter R, Wetzel A (2008) A large skull of *Ichthyosaurus* (Reptilia: Ichthyosauria) from the Lower Sinemurian (Lower Jurassic) of Frick (NW Switzerland). *Swiss J Geosci* 101:617–627
- Mallach HJ, Schmidt WK (1980) Über ein quantitatives und qualitatives Verfahren zum Nachweis der Luft- oder Gasembolie. *Beitr Gerichtl Med* 38:409–419
- Malakoff D (2001) Marine mammals: Scientists use strandings to bring species to life. *Science* 293:1754–1757
- Mancuso AC, Marsicano CA (2008) Paleoenvironments and taphonomy of a Triassic lacustrine system (Los Rastros Formation, central-western Argentina). *Palaios* 23:535–547
- Martill DM (1986) The stratigraphic distribution and preservation of fossil vertebrates in the Oxford Clay of England. *Mercian Geol* 10:161–188
- Martill DM (1993) Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia – Darmstädter Beitr Natgesch* 2:77–97
- Martill DM, Cruickshank ARI, Taylor MA (1995) Speculations on the role of marine reptile deadfalls in Mesozoic deep-sea paleoecology; comment. *Palaios* 10:96–97
- Martin J, Frey E, Riess J (1986) Soft tissue preservation in ichthyosaurs and a stratigraphic review of the Lower Hettangian of Barrow-upon-Soar, Leicestershire. *Trans Leic Lit Phil Soc* 80:58–72
- Mason CF, Macdonald SM (1986) Otters. Cambridge University Press, Cambridge
- McGowan C (1978) Further evidence for the wide geographical distribution of ichthyosaur taxa (Reptilia: Ichthyosauria). *J Paleont* 52:1155–1162
- McGowan C (1992) The ichthyosaurian tail: sharks do not provide an appropriate analogue. *Palaeontology* 35:555–570
- McGowan C, Motani R (2003) Ichthyopterygia. In: Sues H-D (ed) *Handbook of Paleoherpitology*, Part 8, Verlag Dr. Friedrich Pfeil, München
- McLellan WA, Papst DA, Westgate AJ, Koopman HN, Read AJ (1995) Post mortem cooling rates of harbor porpoise, *Phocoena phocoena*. International Whaling Commission Meeting 1995, SC/47/SM21 (unpublished), Dublin, Ireland
- McLellan WA, Koopman HN, Rommel SA, Read AJ, Potter CW, Nicolas JR, Westgate AJ, Pabst DA (2002) Ontogenetic allometry and body composition of harbour porpoises (*Phocoena phocoena*, L.) from the western North Atlantic. *J Zool Lond* 257:457–471
- Meyer CA (1991) Burial experiments with marine turtle carcasses and their paleoecological significance. *Palaios* 6:89–96
- Meyer CA, Furrer H (1995) Taphonomie und paläoökologische Rekonstruktionen: Beispiele aus dem Mesozoikum des Jura. *Eclog Geol Helv* 88:711–720
- Moreno P, Benke H, Lutter S (1992) Behaviour of Harbour (*Phocoena phocoena*) carcasses in the German Bight: surfacing rate, decomposition and drift routes. In: Bohlken H, Benke H (eds) *Untersuchungen über Bestand, Gesundheitszustand und Wanderungen der Kleinwalpopulationen (Cetacea) in deutschen Gewässern*, unpublished Interim Report, WWF Fachbereich Wattenmeer & Nordseeschutz und Forschungs- und Technologiezentrum Westküste, Außenstelle der Universität Kiel, Kiel, pp 1–4
- Mosebach R (1952) Wässrige H₂S-Lösungen und das Verschwinden kalkiger tierischer Hartteile aus werdenden Sedimenten. *Senckenbergiana* 33:13–22

- Motani R (2001) Body mass estimation from silhouettes: testing the assumption of elliptical body cross-sections. *Paleobiol* 27: 735–750
- Möttönen M, Nuutila M (1977) Post mortem injury caused by domestic animals, crustaceans, and fish. In: Tedeschi CG, Eckert WG, Tedeschi LG (eds) *Forensic medicine: a study in trauma and environmental hazards*, vol II, Physical Trauma. Saunders, Philadelphia, pp 1096–1098
- Mueller B (1953) *Gerichtliche Medizin*. Springer, Berlin
- Nowacek DP, Johnson MP, Tyack PL, Shorter KA, McLellan WA, Pabst DA (2001) Buoyant balaenids: the ups and downs of buoyancy in right whales. *Proc Roy Soc Lond B* 268:1811–1816
- Øen EO (1983) Electrical Whaling: A Review. *Nordisk Veterinaarmed* 35:319–323
- Osborn HF (1905) Ichthyosaurs. The evolution of fitness in ichthyosaurs (Fossil wonders of the West). *Cent Mag* 69:414–422
- Padosch SA, Dettmeyer RB, Kröner LU, Preuss J, Madea B (2005) An unusual occupational accident: fall into a sewage plant tank with lethal outcome. *Forensic Sci Int* 149:39–45
- Pedal I, Moosmayer A, Mallach HJ, Oehmichen M (1987) Luftembolie oder Fäulnis? Gasanalytische Befunde und ihre Interpretation. *Z Rechtsmed* 99:151–167
- Perry SF (1983) *Reptilian lungs: functional anatomy and evolution*. Springer, Berlin
- Petrik MS, Hobischak NR, Anderson GS (2004) Examination of factors surrounding freshwater decomposition in death investigations: a review of body recoveries and coroner cases in British Columbia. *Can Soc Forensic Scie J* 37:9–17
- Piccard A (1961) In den Tiefen der Weltmeere. In: Wenzel H (ed) *Das Meer*. Kümmerly & Frey, Geographischer Verlag, Bern, pp 105–126
- Pierucci G, Gherson G (1968) Studio sperimentale sull'embolia gassosa con particolare riguardo alla differenziazione fra gas embolico e gas putrefattivo. *Zaccia* 43:347–373
- Pompeckj JF (1901) Der Jura zwischen Regensburg und Regenstauf. *Geogn Jahresh* 14:139–220
- Pratje O (1922) Lias und Rhät im Breisgau (Erster Teil). *Mitt Großherzogl Bad Geol L-anstalt IX:277–352*
- Quenstedt FA (1858) *Der Jura*. Laupp & Siebeck, Tübingen
- Ramsay WL (1962) Bubble growth from dissolved oxygen near the sea surface. *Limnol Oceanogr* 7:1–7
- Reiff W (1935) Saurierreste des Lias alpha der Langenbrückener Senke. *Zbl Min Geol Paläont in Verbindung mit dem N Jb Min Geol Paläont Abt B, Jg 1935:227–253*
- Reisdorf AG (2007) No Joke Movement: Mehr über den Hauensteiner Ichthyosaurier und rezente marine Lungenatmer. Textnoten zur Physiologie, Pathologie und Taphonomie; weiterführende Literatur. *Mitt Natforsch Ges Kanton Solothurn* 40:23–49
- Reisdorf AG, Maisch MW, Wetzel A (2011) First record of the leptonecid ichthyosaur *Eurhinosaurus longirostris* from the Early Jurassic of Switzerland and its stratigraphic framework. *Swiss J Geosci* 104:211–224
- Reisdorf AG, Wuttke M (2012) Re-evaluating Moodie's Opisthotonic-Posture Hypothesis in Fossil Vertebrates Part I: Reptiles – the taphonomy of the bipedal dinosaurs *Compsognathus longipes* and *Juravenator starki* from the Solnhofen Archipelago (Jurassic, Germany). In: Wuttke M, Reisdorf AG (eds) *Taphonomic processes in terrestrial and marine environments*. *Palaeobio Palaeoenv* 92(1). doi:10.1007/s12549-011-0068-y
- de Ricqlès A, de Buffrénil V (2001) Bone histology, heterochronies and the return of Tetrapods to life in water: were are we. In: Mazin J-M, de Buffrénil V (eds) *Secondary adaptation of tetrapods to life in water*. Friedrich Pfeil, München, pp 289–310
- Ridgway SH, Scronce BL, Kanwisher J (1969) Respiration and deep diving in the bottlenose porpoise. *Science* 166:1651–1654
- Ridgway SH (2002) Asymmetry and symmetry in brain waves from dolphin left and right hemispheres: some observations after anaesthesia during quiescent hanging behavior, and during visual obstruction. *Brain Behav Evol* 60:265–274
- Robinson RHM, Ingram M, Case RAM, Benstead JG (1953) *Whalemeat: Bacteriology and Hygiene*. Department of Scientific and Industrial Research, Food Investigation: Spec Rep 59:1–56
- Rodriguez WC (1997) Decomposition of buried and submerged bodies. In: Haglund WD, Sorg MH (eds) *Forensic taphonomy – The post-mortem fate of human remains*. CRC Press, Boca Raton, pp 459–467
- Röhl H-J, Schmid-Röhl A, Oschmann W, Frimmel A, Schwark L (2001) Erratum to “The Posidonia Shale (Lower Toarcian) of SW-Germany: an oxygen-depleted ecosystem controlled by sea level and palaeoclimate”. *Palaeogeogr Palaeoclimatol Palaeoecol* 169:273–299
- Röhl H-J, Schmid-Röhl A (2005) Lower Toarcian (Upper Liassic) Black Shales of the Central European Epicontinental Basin: A Sequence Stratigraphic Case Study from the SW German Posidonia Shale. *SEPM Soc Sed Geol Spec Publ* 82:165–189
- Rollo F, Luciani S, Marota I, Olivieri C, Ermini L (2007) Persistence and decay of the intestinal microbiota's DNA in glacier mummies from the Alps. *J Archaeol Sci* 34:1294–1305
- Sakata M, Miki A, Kazama H, Morita M, Yasoshima S (1980) Studies on the composition of gases in the post-mortem body: animal experiments and two autopsy cases. *J Forensic Sci* 15:19–29
- Sander PM (1989) The Pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the Description of a New Species. *Philos Trans Roy Soc Lond B* 325:561–666
- Schäfer W (1972) *Ecology and Palaeoecology of marine environments*. University of Chicago Press, Chicago
- Schieber W (1936) *Der Untere und Mittlere Lias im württembergisch-bayerischen Grenzgebiet (Aalen-Wassertrüdingen)*. Dissertation, University of Tübingen
- Schieber J, Southard J, Thaisen K (2007) Accretion of mudstone beds from migrating floccule ripples. *Science* 318:1760–1763
- Schimmelmann A, Schuffert JD, Venkatesan MI, Leather J, Lange CB, Baturin GN, Simon A (1994) Biogeochemistry and origin of a phosphoritized coprolite from anoxic sediment of the Santa Barbara Basin. *J Sed Res* A64:771–777
- Seilacher A (1982) Posidonia Shale (Toarcian, S. Germany) – Stagnate basin model revalidated. In: Gallitelli EM (ed) *Palaeontology, essential of historical geology*. STEM Mucchi, Modena, pp 25–55
- Sekiguchi Y, Kohshima S (2003) Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). *Physiol Behav* 79:643–653
- Shafer NE, Zare RN (1991) Through a beer glass darkly. *Phys Today* 44:48–52
- Sharp JG, Marsh BB (1953) *Whalemeat: Production and Preservation*. Department of Scientific and Industrial Research, Food Inv Spe Rep 58:1–47
- Shevill WE, Ray C, Kenyon KW, Orr RT, Van Gelder RG (1967) Immobilizing Drugs Lethal to Swimming Mammals. *Science* 157:630–631
- Siebert U, Wünschmann A, Weiss R, Frank H, Benke H, Frese K (2001) Post-mortem findings in harbour porpoises (*Phocoena phocoena*) from the German North and Baltic Seas. *J Comp Pathol* 124:102–114
- Sims JK, Enomoto PI, Frankel RI, Wong LMF (1983) Marine bacteria complicating seawater near-drowning and marine wounds: a hypothesis. *Ann Emerg Med* 12:212–216
- Slijper EJ (1962) *Whales*. Hutchinson, London
- Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. *Oceanogr Mar Biol Ann Rev* 41:311–354
- Smith CR (2007a) Bigger is better: the role of whales as detritus in marine ecosystems. In: Estes JA, DeMaster DP, Doak DF, Williams TM, Brownell RL (eds) *Whales, whaling and marine ecosystems*. University of California Press, Berkeley, pp 286–300

- Smith CR (2007b) A Whale's End is the Beginning of Life at the Deep Seafloor. In: Nouvian C (ed) *The Deep*. University of Chicago Press, Chicago, pp 234–239
- Smith K, Wuttke M (2012) From tree to shining sea: Taphonomy of the arboreal lizard *Geiseltaliellus maarius* from Messel, Germany. In: Wuttke M, Reisdorf AG (eds) *Taphonomic processes in terrestrial and marine environments*. *Palaeobio Palaeoenviron* 92(1). doi:10.1007/s12549-011-0064-2
- Sorg MH, Dearborn JH, Monahan EI, Ryan HF, Sweeney KG, David E (1997) Forensic taphonomy in marine contexts. In: Haglund WD, Sorg MH (eds) *Forensic taphonomy – The postmortem fate of human remains*. CRC Press, Boca Raton, pp 567–604
- Staunton H (2005) Mammalian sleep. *Naturwiss* 92:203–220
- Stede M, Lick R, Benke H (1996) Buckel- und Pottwale vor der ostfriesischen Küste: Probleme der Bergung und wissenschaftlichen Bearbeitung von Strandungen großer Walarten. *Oldenb Jb* 96:251–261
- Stede M (1997) Probleme bei der Entsorgung von verendeten Meeressäugern. *Dtsch Tierarztl Wochenschr* 104:245–247
- Stevens CE, Hume ID (1998) Contributions of Microbes in Vertebrate Gastrointestinal Tract to Production and Conservation of Nutrients. *Physiol Rev* 78:393–427
- Sundborg Å (1956) The river Klaraelven. A study of fluvial processes. *Geograf Ann* 38:125–131
- Tarasoff FJ, Kooyman GL (1973) Observations on the anatomy of the river otter, sea otter, and harp seal. – II. The trachea and bronchial tree. *Can J Zool* 51:163–170
- Taylor MA (1987) Reinterpretation of ichthyosaurs swimming and buoyancy. *Palaeontology* 30:531–535
- Taylor MA (2000) Functional significance of bone ballastin in the evolution of buoyancy control strategies by aquatic tetrapods. *Hist Biol* 14:15–31
- Taylor MA (2001) Locomotion in Mesozoic Marine Reptiles. In: Briggs DEG, Crowther PR (eds) *Palaeobiology II*. Blackwell, Oxford, pp 404–407
- Thali MJ, Yen K, Schweitzer W, Vock P, Ozdoba C, Dimhofer R (2003) Into the decomposed body-forensic digital autopsy using multislice-computed tomography. *Forensic Sci Int* 134:109–114
- Tigress Productions (2008) *The Whale That Blew Up In The Street*. – Nature Shock. Tigress Productions Ltd, Bristol [video footage]
- Toklu AS, Alkan N, Gürel A, Cimsit M, Haktanır D, Körpınar S, Purisa S (2006) Comparison of pulmonary autopsy findings of the rats drowned at surface and 50 ft depth. *Forensic Sci Int* 164:122–125
- Tomita K (1975) On putrefactions and floatations of dead bodies under water. *Hirosh J Med Sci* 24:117–152
- Tomita K (1976) On putrefactions and floatations of dead bodies under water (supplement). *Hiroshima J Med Sci* 25:155–174
- Tønnessen JN, Johnsen AO (1982) *The History of Modern Whaling*. University of California Press, Berkeley
- Tsokos M, Byard RW (2011) Putrefactive “rigor mortis”. *Forensic Sci Med Pathol* [Epub ahead of print]. doi:10.1007/s12024-011-9232-y
- Vass AA, Barshick SA, Sega G, Caton J, Skeen JT, Love JC, Synstelién JA (2002) Decomposition chemistry of human remains: a new methodology for determining the postmortem interval. *J Forensic Sci* 47:542–553
- Wade M (1984) *Platypterygius australis*, an Australian Cretaceous ichthyosaur. *Lethaia* 17:99–113
- Wartzok D (2002) Breathing. In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of Marine Mammals*. Academic Press, San Diego, pp 164–169
- Wasmund E (1935) Die Bildung von anabitaminösem Leichenwachs unter Wasser. *Schr Brennstoffgeol* 10:1–70
- Weiss RF, Price BA (1989) Dead Sea gas solubilities. *Earth Planet Sci Lett* 92:7–10
- Westphal F (1962) Die Krokodilier des deutschen und englischen Oberen Lias. *Palaeontographica A* 118:23–118
- Wetzel A (1990) Interrelationships between porosity and other geotechnical properties of slowly deposited, fine-grained marine surface sediments. *Mar Geol* 92:105–113
- Wetzel A, Reisdorf AG (2007) Ichnofabrics elucidate the accumulation history of a condensed interval containing a vertically emplaced ichthyosaur skull. *SEPM Soc Sed Geol Spec Publ* 88:241–251
- Widdel F (1988) Microbiology and ecology of sulfate- and sulfurreducing bacteria. In: Zehnder ABJ (ed) *Biology of Anaerobic Microorganisms*. Wiley, New York, pp 469–585
- Wild R (1978) Ein Sauropoden-Rest (Reptilia, Saurischia) aus dem Posidonienschiefer (Lias, Toarcium) von Holzmaden. *Stuttg Beitr Natkd Ser B* 41:1–15
- Williams TM, Davis RW, Fuiman LA, Francis J, Le Boeuf BJ, Horning M, Calambokidis J, Croll DA (2000) Sink or swim: Strategies for cost-efficient diving by marine mammals. *Science* 288:133–136
- Worthy GAJ, Edwards EF (1990) Morphometric and Biochemical Factors Affecting Heat Loss in a Small Temperate Cetacean (*Phocoena phocoena*) and a Small Tropical Cetacean (*Stenella attenuata*). *Physiol Zool* 63:1012–1024
- Yoshimura S, Yoshida M, Okii Y, Tokiyasu T, Watabiki T, Akane A (1995) Detection of green algae (Chlorophyceae) for the diagnosis of drowning. *Int J Leg Med* 108:39–42
- Zangerl R, Richardson ES (1963) The paleoecological history of two Pennsylvanian black shales. *Fieldiana-Geol Mem* 4:1–352