

# 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)

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Received: 24 October 2011 / Revised: 19 December 2011 / Accepted: 22 December 2011 / Published online: 8 February 2012  
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**Abstract** More or less complete and articulated skeletons of fossil air-breathing vertebrates with a long neck and tail often exhibit a body posture in which the head and neck are recurved over the back of the animal. Additionally, the tail is typically drawn over the body, while the limbs have a rigid appearance. In palaeontological literature, this “opisthotonic posture” of such fossils still requires a causal interpretation in an etiological context. According to this hypothesis, there is a presumption of a cerebral disorder generating perimortem muscle spasms that are preserved by rapid burial or other sequestration of a skeleton in the fossil record. We re-evaluate this “opisthotonic posture hypothesis” by analysing the non-avian theropods *Compsognathus longipes* and *Juravenator starki* from the famous South Franconian plattenkalks of the Upper Jurassic Solnhofen Archipelago. Decay experiments with the extant domestic fowl *Gallus gallus* L. and analysis of the theropods' constructional morphological

constraints reveal that the opisthotonic posture is not a perimortem but a postmortem phenomenon. By analysing the timeline of decomposition, it is possible to recognise different stages of decay, depending on the varying decay resistance of soft tissues. Adipocere formation must have blocked further decay until embedding was completed by minimal sedimentation. Analyses of the palaeoenvironment of the basins of the Solnhofen Archipelago show that the conditions of deposition of individual basins cannot be considered to be similar, even inside the same time frame. Therefore, a generalised approach of looking at the depositional setting must be excluded. Assumptions by Faux and Padian (2007) that the accepted palaeoenvironmental reconstruction of the Solnhofen Fossilagerstätte has to be questioned in the light of the opisthotonic posture hypothesis enforce the need for a review of palaeoecological factors of the Franconian Plattenkalks from a taphonomic perspective.

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

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**Electronic supplementary material** The online version of this article (doi:10.1007/s12549-011-0068-y) contains supplementary material, which is available to authorized users.

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**Keywords** Taphonomy · Opisthotonic posture · Theropods · Palaeoecology · Plattenkalks · Bipedal trackway

“‘Opisthotonus’ [in vertebrates] is merely a physical phenomenon which causes the neck region of a macerating vertebral column to bend backward.”

Bashford Dean (1919)

## Introduction

More or less complete and articulated skeletons of fossil air-breathing vertebrates with a long neck and tail often exhibit a body posture in which the head and neck are recurved over

the back of the animal. Additionally, the tail is typically drawn over the body, while there is a rigid appearance of the limbs. This peculiar posture first received attention in the 19th century (e.g., Wagner 1859), and was to become the subject of interdisciplinary academic controversy in the first half of the 20th century (e.g., Anonymous 1919; Dean 1919; Huene 1925; Moodie 1923).

In terms of pathophysiology, this posture noticeably matches those of particular neurological illnesses or damage in extant vertebrates, leading to a spastic stiffening of the back musculature and the extremities, possibly resulting in opisthotonus. Opisthotonus (Gr.: *opistho*=behind, *tonos*=tightening, suggesting extreme extension) is a well-known topic in existing veterinary and medical literature (a PubMed literature survey resulted in 200 hits).

The similarity between the fossil record and pathophysiological phenomena prompted Williston (1890) to introduce the term *opisthotonic* into the palaeontological vocabulary to characterise this body posture of fossil vertebrates. Williston did not, however, propose any etiological interpretations. It was the medical professional Moodie (1918) who, with his *Studies to Paleopathology*, was the first to attempt a causal interpretation in an etiological sense in fossils with an “opisthotonic posture”. He came to the conclusion that “there can be, I think, little doubt that many of the opisthotonic attitudes assumed by fossil vertebrates are easily explained as a phenomenon accompanying the death throes, but whether all can be so explained on this basis is extremely doubtful.” In search of evidence of diseases in fossil vertebrates, it seemed probable to him “that some of the instances of opisthotonus and pleurothotonus among fossil vertebrates may be due to acute cerebrospinal infections.”

Moodie’s hypothesis did not remain unchallenged. The zoologist Dean (1919) based his refutation of this opisthotonus hypothesis on biomechanical considerations and the various resistances of muscle tissues and ligaments to decomposition, which he believed would necessarily lead to a recurvature of the neck in decomposing carcasses. Moodie (1919), in his response to Dean’s explanations, asserted that “the pull [backwards] is exerted by the muscles and tendons, and the reason why opisthotonos is the more commonly seen is that the muscles of the neck are strongest.” He considered the ligaments of the vertebral column to merely be “slightly elastic”. Therefore, “It would puzzle Dr. Dean to furnish examples of opisthotonos caused by the action of the ligaments.” At the same time, he presented numerous examples, where “sheep, cattle and horses are commonly seen dead in this position on the western plains ... while it is easily and daily proven that they died in a spastic condition, in opisthotonos.” He also cited an oral report on cats that died in the opisthotonus posture during the night and became fixed in this position by rigor mortis.

Moodie (1923) expanded his considerations through observations on fossil and extant vertebrates, and in

conclusion conceded to his critics only that “Not all vertebrates preserved in opisthotonus are necessarily regarded as victims of cerebrospinal disease but many of them suggest a strong neurotoxic condition and insofar are to be fairly regarded as ancient evidences of disease.”

Neither was the opisthotonus hypothesis to remain unchallenged from a palaeontological perspective. Weigelt (1927, 1989) agreed with the views of Huene (1925) that this posture comes about postmortem. Ironically, Huene used the same argument against Moodie’s opisthotonus hypothesis that Moodie used in support of his own hypothesis (see above): “[A] referee has seen, just recently, while travelling in the Patagonian steppes, many carcasses of guanacos and ostriches (*Rhea*) lying around and displaying this posture, without any exception. Generally, this posture is (even by the natives) attributed to postmortem desiccation, and therefore resulting in a constriction of the musculature.” [Translation by the authors.]

There have been many attempts to discover causes and explanations for the recurvature, but they have all ultimately been unsatisfying because they could neither be confirmed nor ruled out experimentally (Davis 1996; Davis and Briggs 1998; Faux and Padian 2007). Various explanatory models have been proposed to explain the hyperextended disposition of the vertebral column, with the most important of these being that this body posture can be explained as the consequences of (1) perimortem death throes as a result of affliction of the central nervous system (CNS; Faux and Padian 2007; Lingham-Soliar 2011; Moodie 1918, 1923); (2) elastic pull of the ligaments after relaxation of muscles after death (Wellnhofer 1991) and, as a variant, an antemortem sleeping posture with all muscles relaxed (Heinroth 1923) or an antemortem relaxed posture (Seemann 1933; Weigelt 1927); (3) the commencement of rigor mortis combined with various contractions of muscles (Gillette 1994; Laws 1996); (4) contraction of the ligaments (Heinroth 1923; Henning 1915; Ostrom 1978; Rayner 1989; Wild 1974); (5) a dangling head, neck and tail while drifting and sinking down through the water column and the arrival of the carcass at the seafloor (de Buissonjé 1985; Kemp 2001; Mäuser 1983; Rietschel 1976); (6) anchoring of the skull and movement of the trunk by current flow (“*schwoien*” of Quenstedt 1927; de Buissonjé 1985; Frey and Martill 1994; Schäfer 1962, 1972); (7) mummification (Barthel 1970; Davis 1996; Huene 1925; Müller 1951; Sander 1992; Weigelt 1927, 1989; Wellnhofer 1970) or osmotic desiccation in hypersaline environments (Davis 1996; Schäfer 1962, 1972; Seilacher et al. 1985; Viohl 1994; Wellnhofer 1991).

Compared with the desiccation and the “osmotic-shrinking in hypersaline environments” hypotheses, the opisthotonus hypothesis remained under-represented in palaeontological literature. Some 80 years later, however, the veterinarian Cynthia Marshall Faux and the vertebrate palaeontologist

Kevin Padian addressed Moodie's hypothesis in a publication that received much attention. Faux and Padian (2007) give a critical review of the state of knowledge about opisthotonus and the opisthotonic posture in fossil and extant vertebrates, enriched with a tremendous and convincing amount of veterinarian and medical literature dealing with "opisthotonus" [as a pathophysiological symptom] and the "opisthotonic posture" in the sense of a "hyperextended disposition of the vertebral column [that can be observed directly in fossil carcasses]" (Faux and Padian 2007). Faux and Padian (2007) moreover reflected the findings of forensic medicine: "Immediately after death, vertebrate skeletal muscles are relaxed and movable, and one can position a carcass in a variety of attitudes at this point."

The special contribution of Faux and Padian (2007) is to have submitted the various hypothetical explanatory models of opisthotonic posture to comprehensive testing. In a series of experiments using simulations of various environmental conditions, Faux and Padian (2007) tested such explanatory models of the postmortem shortening or shrinking of muscles, tendons and ligaments (elastic pull, desiccation, rigor mortis and osmotic shrinking in a hypersaline environment). With the exception of the hypersalinity tests, however, they limited their experiments to the subaerial domain. The results of these studies revealed flaws in the observations and experimental arrangements upon which the more or less established explanatory models were based.

In their conclusions, they asserted that ligaments, whose function is to be solid, stress- and strain-resistant bone-to-bone connections, merely play a subordinate, that is, a passive, role in the manifestation of movements: "The joints simply move in the direction of gravity, or in whatever direction the skeleton is being otherwise moved. Therefore, ligaments in their normal position are like unstretched rubber bands." Through actualistic taphonomic experiments, Faux and Padian (2007) were able to determine that the shortening of muscles, tendons and [not tested directly in extracted form] ligaments by desiccation or osmotic dehydration did not occur to the extent necessary for the creation of fossil opisthotonic postures in vertebrates with long necks and tails.

Taking into account the results of these experimental studies, practical veterinary experience, comprehensive research found in the literature of human and veterinary pathophysiological opisthotonus phenomena and theoretical considerations, Faux and Padian (2007) arrived at the following conclusions, which according to them also provide a new view of the circumstances of death and the palaeoenvironment of fossil vertebrate, and from which even a phylogenetic signal could be derived: (1) "It is not postmortem contraction but perimortem muscle spasms resulting from various afflictions of the central nervous system that cause these extreme postures", (2) "the opisthotonic posture is the

result of 'death throes', not postmortem processes, and individuals so afflicted assumed the posture before death, not afterwards", (3) "the subsequent onset of rigor mortis would (temporarily) fix the carcass in this position, if it is not previously disturbed, and burial would provide ultimate preservation", (4) "rapid burial or other sequestration must be presumed if an articulated skeleton is preserved", (5) "to test the opisthotonic hypothesis in any skeleton, the limbs as well as the vertebral column can provide important evidence", (6) "the opisthotonic posture tells us more about the circumstances surrounding death than about what happened after death ... and also revises interpretations of palaeoenvironmental conditions of many fossil deposits" and (7) "when some taxa appear consistently to show diagnostic criteria of the opisthotonic posture, whereas others do not, the consistent pattern allows a unified explanation of cause of death and a validation of a phylogenetic signal."

The conclusions of Faux and Padian (2007) have been for the most part accepted in recent palaeontological work (e.g. Eberth et al. 2010; Elgin et al. 2011; Georgi and Krause 2010; Lingham-Soliar 2011; Tweet et al. 2008). There has been criticism about their assumption of the rapid burial of carcasses, since this is not supported by sedimentological data (e.g. Beardmore et al. 2009; Benton et al. 2008), and about "the fact that some ... [small, non avian theropod dinosaurs] exhibit both flexed and unflexed limbs, necks, and tails argue against that ["opisthotony"] interpretation" (Eberth et al. 2010). Benton et al. (2008) and Beardmore et al. (2009) also point out the problem of postmortem transport of terrestrial fauna into aquatic depositional settings. In fact, all examples of fossil air-breathing vertebrates in Faux and Padian (2007) do indeed come from aquatic sediments and are thus to be classified as allochthonous faunal elements of an aquatic taphocoenosis. The majority of these embedding locations are marine, lacustrine and fluvial sediment environments, with only one (a terrace pool environment of the hot springs of Yellowstone National Park) being a small and shallow aquatic depositional environment (Channing et al. 2005).

Even Moodie (1918: fig. 3) used *Compsognathus longipes*, presented here, as superlative evidence for an etiological diagnosis of an opisthotonic posture ["tetanic spasm"], a view that Faux and Padian (2007: fig. 1b) concur with (see Figs. 3a, 4a). In this context, however, it is important to point out that Moodie's (1918, 1923) interpretations, which conflict with the most commonly held opinions today, originated at a time when the lithographic limestone of southern Germany ("Solnhofen Plattenkalk") was believed to be a sediment formed under mainland-to-shallow marine depositional conditions (Weigelt 1927, 1989; further citations in Mayr 1967). Particular sites of the depositional area were specified as beach or as periodically dried-up lagoons or sea basins. Such settings, according to Moodie's contemporaries,

were appropriate ones to (1) subject carcasses to little or no postmortem transport and (2) maintain the body posture achieved following death throes in vertebrates and invertebrates (Abel 1922; Rothpletz 1909; Wiman 1914). Thus, in the context of the history of science, Moodie's hypothesis still possesses a stringency that Faux and Padian's (2007) hypothesis is lacking in light of the paradigm change introduced by Barthel (1964, 1970) concerning the formation of the lithographic limestone.

The analysis of the positional relationships of the skeletal elements of the *C. longipes* specimen we have performed shows that the additional hypotheses and facts formulated and compiled by Faux and Padian (2007) do not conform to any of our taphonomic observations of the fossil record of the lithographic limestone. However, the faunal spectrum of terrestrial vertebrates of the Solnhofen Archipelago does confirm Faux and Padian's (2007) assertion that in many of the vertebrate sites they analysed, "some taxa appear consistently to show diagnostic criteria of the opisthotonic posture, whereas others do not." (see, for example, Kemp 2001). Chiappe and Göhlich (2010) have already critically examined this fact in their description of *Juravenator starki*. These inconsistencies make it necessary to re-evaluate the above-mentioned competing hypotheses with regard to their plausibility and testability in explaining the opisthotonic posture in *Compsognathus* and the non-opisthotonic posture in *Juravenator*.

The goals of our paper are (1) to describe the taphonomical phenomena of the specimens of the Jurassic bipedal dinosaurs *Compsognathus longipes* and *Juravenator starki*, (2) to find a morphologically and biomechanically grounded explanation for a postmortem opisthotonic and a non-opisthotonic posture, (3) to re-evaluate the diagnoses of Moodie (1918, 1923) and Faux and Padian (2007) that cerebral diseases are displayed by an opisthotonic posture in long-necked and long-tailed fossil vertebrates, (4) to test, by experiments of maceration, the hypothesis of Dean (1919) that "opisthotonus" is merely a physical phenomenon which causes the neck region of a macerating vertebral column to bend backward" and the hypothesis of Wellnhofer (1991) that ligaments exert an inherent elastic pull after death, thus drawing the head back, (5) to find a non-pathophysiological syndrome-induced functional morphological explanation for the "rigid limb" posture of Moodie (1918, 1923) and the limb postures caused by the *decerebrate rigidity* and *decerebellate rigidity* of Faux and Padian (2007) and (6) to resolve the inherent contradiction formulated by Faux and Padian (2007) that the opisthotonic posture (in fossil vertebrates) is the result of death throes, and the fact that immediately after death, vertebrate skeletal muscles are relaxed and movable—a postmortem physiological reaction that should loosen the opisthotonic spasm.

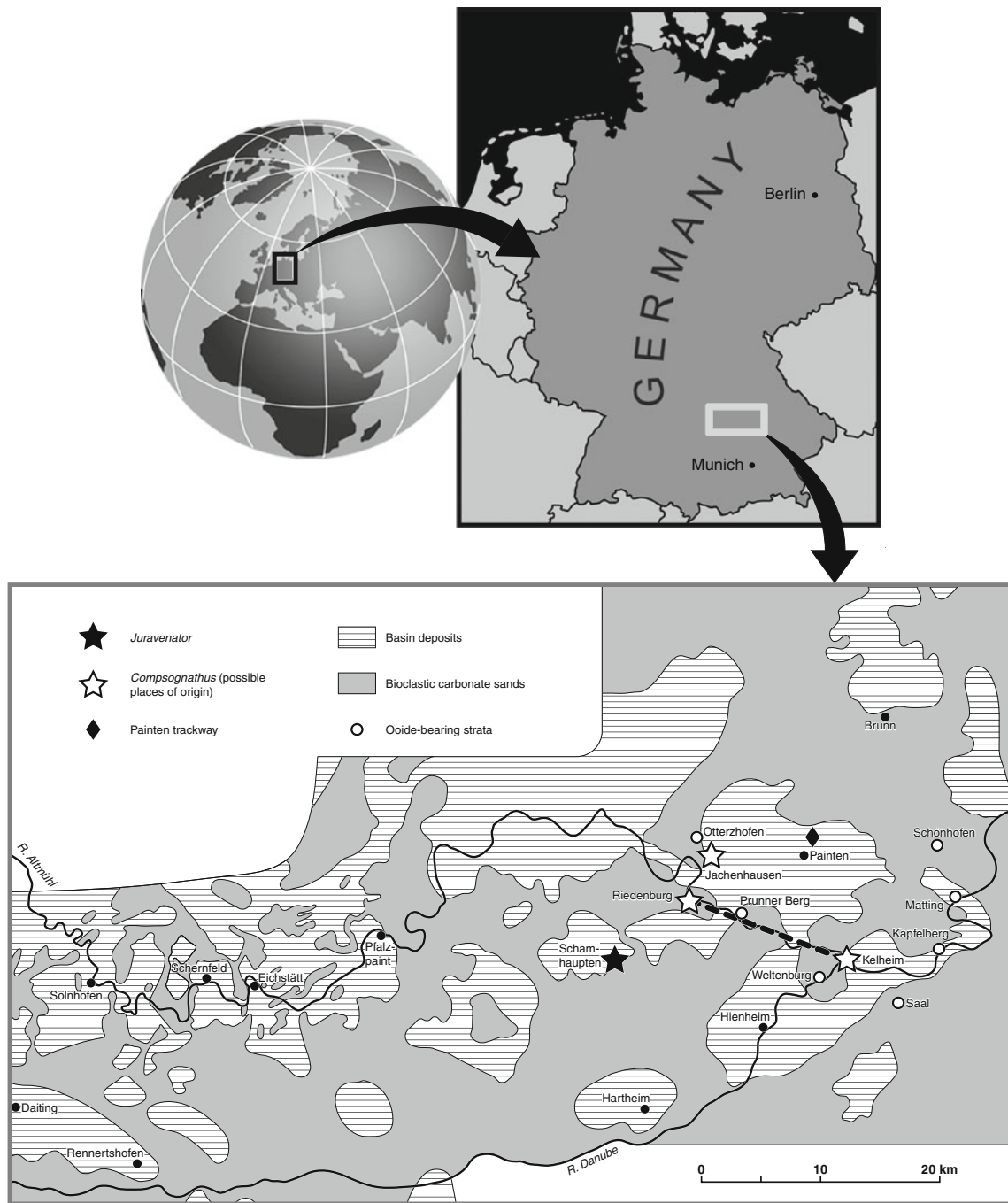
In Part II of our re-evaluation of Moodie's hypothesis (Wuttke and Reisdorf, in preparation) we will provide a rebuttal of the explanation for the hypothesis put forth by Faux and Padian (2007) about a connection between cause of death and the validation of a phylogenetic signal. Taphonomical literature on the vertebrates out of the Solnhofen Plattenkalks always reflects the contemporary perception about the depositional environment. Therefore, earlier assumptions cannot be understood and dignified without knowledge of this background. In our opinion, it seems necessary to give a summary of the extant state of knowledge, including the current debate about the depositional environment.

### Geological and stratigraphic framework

Both of the specimens investigated in this taphonomic study come from the Southern Franconian Alb (Fig. 1) (Chiappe and Göhlich 2010; Wellnhofer 1996). This classical Southern German fossil area has become world famous, particularly for its Upper Jurassic conservation lagerstätten (e.g. Schweigert 2007; Seilacher et al. 1985; Viohl 2000; Wellnhofer 2008).

According to the widely accepted palaeogeographical interpretation, these fossil lagerstätten were formed in marine basins ("Wannen" after Fesefeldt 1962) less than 10 km in diameter. These basins are considered to have been areas of deep bathymetries of a comparatively shallow epicontinental sea within the Franconian-Southern Bavarian carbonate platform (e.g. Keupp et al. 2007; Viohl 1998). Palaeoceanographically, this epicontinental sea belongs to the Northern Tethys (e.g. Keupp et al. 2007; Schweigert 1998). According to the traditional interpretation, the individual basins were enclosed by expansive buildups formed by sponges, cyanobacterial crusts and, locally, also by corals (known as *sponge-algal reefs*; for references see, for example, Keupp et al. 2007). Recent sedimentological and palaeontological studies, however, suggest that the areas surrounding the basins are composed less of true sponge-algal reefs and more of bioclastic carbonate sands (e.g. Keupp et al. 2007; Koch et al. 1994). Depending on the sea level, the basins were more or less connected to one another, and thus in more or less unrestricted contact to the open sea (the Tethys; e.g. de Buissonjé 1985; Oost and De Boer 1994; Röper 2005a; Schwark et al. 1998; Schweigert 1998; Viohl 2000; Viohl and Zapp 2007; Zügel 1997).

As the terrestrial flora and fauna of the conservation lagerstätten show in particular, the Franconian-Southern Bavarian carbonate platform apparently became periodically emerged during the Kimmeridgian and Tithonian (e.g. Fürsich et al. 2007b; Keupp et al. 2007; Röper 2005a; Viohl 1998). Today, it is generally accepted that some of the areas of bioclastic carbonate sands formed long-enduring islands



**Fig. 1** Geographic location of *Compsognathus longipes*, and *Juravenator starki* (Chiappe and Göhlich 2010, modified; courtesy of L. Chiappe and U. Göhlich) and palaeogeographic constellation during the Late Jurassic (Late Kimmeridgian; after Meyer and Schmidt-Kaler 1984; cf. Burnham 2007; Meyer and Schmidt-Kaler 1989, 1990; Schmid et al. 2005). The basins have a stratigraphical range from Late Kimmeridgian to Early Tithonian (e.g. Burnham 2007; Keupp et al.

2007; Schweigert 2007). Upper Jurassic ooide-bearing strata are after Meyer and Schmidt-Kaler (1984) and Streim (1961: p. 33; see also Mayr 1953, 1967: p. 28; Schairer 1968). *Thick black dashed line between white stars: Compsognathus* locality after Ostrom (1978: “Riedenburg–Kehlheim area”), *diamond* bipedal trackway of Painten (Lower Tithonian; Pöfrringer 2000)

(= “Solnhofen Archipelago”; e.g. Barthel et al. 1990; Röper 2005a; Viohl 1998). However, the exact locations, expanse and longevity of such islands are still unknown for the most part (e.g. Burnham 2007). There is yet no evidence for the expected soil formation and possible karst formation during

the palaeoclimatic scenario (see below) to be found, indicated by the sediments of the Kimmeridgian and Tithonian of the Southern and Northern Franconian Alb. The only published, direct (though allochthonic) evidence for any such actual terrestrial weathering process is one pebble-

bearing exotic lithoclast (“Geode”) that was found in sediments of the Lower Tithonian (Hybonotum Zone) in Solnhofen (Schweigert 1998). From its pebble composition, however, this spectacular find possesses only limited significance for the Franconian-Southern Bavarian carbonate platform, as its possible origin can only be a mainland—and not one of the questionable hypothetical islands (see Schweigert 1998). As the case may be, from the frequency, distribution and composition of the terrestrial flora and fauna of the late Jurassic conservation lagerstätten, it can be assumed that some of these islands had a sufficiently long subaerial exposure for them to have experienced at least a minimum of soil creation and accumulation of fresh water, and thus colonisation by terrestrial organisms (e.g. Burnham 2007; Etter 2002; Kemp 2001; Keupp et al. 2007; Röper et al. 2000; Viohl 2000; Viohl and Zapp 2007). Reflecting on the conceptions developed in the 1960s about the sedimentary environment of the eastern basins of the Franconian-Southern Bavarian carbonate platform, Gerhard (1992), Röper et al. (2000) and Röper (2005a) further propose a tidal to shallow lagoonal environment for some of the basins at particular times. Viohl (1998, 2000) and Tischlinger (2001) disagree with this hypothesis (see chapter *Palaeoenvironment and taphonomic landscape of *Compsognathus* and *Juravenator**). There is consensus today, however, that most neighbouring mainlands of the Franconian-Southern Bavarian carbonate platform are to be sought to the north (Rhenish Massif) and east (Bohemian Island) (e.g. Burnham 2007; Keupp et al. 2007; Schweigert 1998). Palaeogeographically, the Rhenish Massif is closest to the Late Jurassic conservation lagerstätten (possibly 30–50 km from the Solnhofen area; Viohl 2000). There is also agreement that the Late Jurassic lagerstätten of the Franconian-Southern Bavarian carbonate platform are temporally between the Kimmeridgian and Tithonian, and that they were causally connected with the formation of the plattenkalk to the north and east of the platform during the Late Kimmeridgian and then propagated westwards during the Early Tithonian (e.g. Keupp et al. 2007; Schweigert 2007).

Many of the researchers of the Franconian-Southern Bavarian carbonate platform focus—in more or less detail—on the facial peculiarities of the particular basins. The sediments and taphocoenoses of the basins do in fact exhibit a multifaceted spectrum (e.g. Bausch 1963; Meyer and Schmidt-Kaler 1993, 1994; Röper 1997, 2005a, b; Viohl 1998, 2000; Zeiss 1977). Yet not even all of the Franconian-Southern Bavarian carbonate platform basins can also be classified as fossil lagerstätten (e.g. Röper et al. 2000; Viohl 1998). Furthermore, certainly not all the conservation lagerstätten can be classified as having the facies of the often-cited Solnhofen Lithographic Plattenkalk (e.g. Barthel 1964; Bernier 1994; Link and Fürsich 2001; Meyer and Schmidt-Kaler 1984; Röper 2005a, b). For example, the specimens investigated in this

study were definitely not embedded in the sediments of the Lithographic Plattenkalk (see below; Griffiths 1993; Mäuser 1983; Ostrom 1978; Viohl and Zapp 2006, 2007; Wellnhöfer 1996). As well, not all of these lagerstätten are distinguished by carbonate with distinctive lamination (e.g. Link and Fürsich 2001; Mäuser 1984; Munnecke et al. 2008; Park and Fürsich 2003; Viohl 2000). This is the case for the slab of the *Compsognathus longipes* specimen (Mäuser 1983; Nopcsa 1903). Further, Viohl (1998), Röper et al. (2000: p. 119), and Röper (2005a) document deposits of finely laminated limestone in which profile sections with disturbed lamination textures occur. Excellently preserved vertebrates (fish) discovered over the bioturbation horizons are referred to by Röper et al. (1996: p. 90; 2000: p. 121).

Throughout the history of research on this subject, a great number of names for the lithostratigraphic units for the Late Jurassic strata of the Franconian-Southern Bavarian carbonate platform have been coined (e.g. Keupp et al. 2007; Meyer and Schmidt-Kaler 1994; Schweigert 2007; Zeiss 1977). Many of these terms are still in co-existing use today (e.g. Chiappe and Göhlich 2010; Keupp et al. 2007; Viohl and Zapp 2007). Specifically, these terms are associated with the classical subcategorisation in what is known as the Quenstedt alphabet, which was originally created for southwestern Germany and is now obsolete (e.g. Keupp et al. 2007; Schmid et al. 2008). The second, modern-day classification concept now being used was created by Zeiss (1977). Because of these circumstances, both of these stratigraphical classification concepts currently have a more or less informal character. Other lithostratigraphic units introduced into literature at later dates also have a somewhat informal character.

This is also the case with the stratigraphic sequence from which the *Juravenator starki* comes. Viohl and Zapp (2006, 2007) suggest a new lithostratigraphic unit for these strata, the “Schamhaupten Member”, which is classified as part of the Painten Formation (cf. Zeiss 1977). Schweigert (2007) and Chiappe and Göhlich (2010) assign it a Late Kimmeridgian age (Beckeri Zone, Ulmense Subzone; Fig. 2).

*Compsognathus longipes*, the other specimen discussed in this study, comes from the Eastern region of the Southern-Franconian Alb, either from Jachenhausen or from the Riedenburg–Kelheim area (Mäuser 1984; Ostrom 1978; Wellnhöfer 1996). Because of its uncertain origin, neither its biostratigraphical age nor its lithostratigraphic classification is considered certain (Fig. 2). If it originated in Jachenhausen, then it can be considered to be from the Painten Formation (Zandt Member; cf. Zeiss 1977), and thus of an assumed Early Tithonian age (Rueppellianus Zone, Riedense or Early Rueppellianus Subzone) (G. Schweigert, personal communication 2011). On the other hand, if it came from the Kelheim area, then it is either from the lithostratigraphic equivalent of the uppermost Kimmeridgian of the

Sub-stage	Zone	Subzone	<i>Compsognathus</i>	<i>Juravenator</i>
Early Tithonian	Hybonotum	Moersheimensis		
		Rueppellianus	↑ ? ↓	
		Riedense		
Late Kimmeridgian	Beckeri	Ulmense		

**Fig. 2** Biostratigraphic affiliation of *Compsognathus longipes* (from the Kelheim basin or Painten basin), and *Juravenator starki* (Schamhaupten basin). The biostratigraphic range for the specimens is shown in grey. Because of the arguable origin of *C. longipes*, its biostratigraphical age is considered uncertain. Biostratigraphical subdivision sensu Schweigert (2007)

Kapfelberg locality, or from the Lower Tithonian plattenkalks of the Goldberg locality (cf. Röper 2005a; Schweigert 2007). Since Kapfelberg has delivered a great quantity of reptile finds, it is the more probable locality (cf. Abel 1922; Kemp 2001). Whatever the case, both of these Plattenkalk deposits are considered part of the Painten Formation (G. Schweigert, personal communication 2011).

### Testing the opisthotonic posture hypothesis—perimortem or postmortem

As Faux and Padian (2007) demonstrated by way of their investigations, the shrinking of muscles and tendons during subaerial or osmotic desiccation occurred to such a small extent that it could not, for example, lead to an “opisthotonic recurvature” of a long neck (see chapter [Palaeobathymetry and salinity](#)). A possible influence of ligaments on recurvature in bird necks has thus far only been investigated by Heinroth (1923) and Davis (1996), with a positive result (see [Introduction](#)). This was not, however, accepted by Faux and Padian (2007).

After Moodie’s (1919) response to Dean’s physically founded hypothesis (1919), the latter was not addressed or re-assessed again in palaeontological literature.

In the following, we would like to further present and substantiate our hypothesis that the “opisthotonic posture” sensu Moodie (1918) in general, and its evaluation by Faux and Padian (2007) more specifically, represent nothing other than a fossilised postmortem artifact.

As already posited by Faux and Padian (2007), the complexity of the evidence makes it necessary to look more

closely at the variability of the taphonomic phenomena and factors that terrestrial reptiles could have been exposed to peri- and postmortem—in particular, sedimentary environments and climatic zones. The key aspect of our argumentation is based on what we consider to be the most crucial point in the scenario presented by Faux and Padian (2007) concerning the postmortem persistence of an opisthotonic posture, namely, the requirement for no substantial change of location of a carcass. Since the fossils presented by Faux and Padian (2007) are without exception from aquatic sediments, we place the focus of our re-evaluation on aquatic depositional environments. Our remarks here only minimally concern the problematic issues of a rapid burial, since we do not wish to anticipate the results of Patrick J. Orr’s (see Beardmore et al. 2009, 2011; Benton et al. 2008) work group.

### Abiotic factors influencing an opisthotonic posture

Faux and Padian (2007) suggest three fundamental factors for the postmortem persistence of an opisthotonic posture in a fresh carcass up through skeletonisation: (1) buried soon after death, (2) no substantial transport and (3) no extensive deterioration by currents or scavengers. These factors are without distinction required in both terrestrial and aquatic environments, and because of the qualitatively and quantitatively most common classification and discussion of the “Solnhofen deposits”, they are valid not just for depositional settings with obrution phenomena. Fossils that come from depositional settings with provably small sedimentation rates, such as the “Solnhofen deposits”, fit in smoothly with the hypothesis of Faux and Padian (2007)—as long as an appropriate embedding mechanism can actually be construed from the broader sense of the definition of a “burial”. If the geological definition of Bates and Jackson (1980) is followed—“covering up or concealing geologic features by the process of sedimentation”—then bacterial and fungal mats, for example, could be involved in a rapid burial without substantial quantities of clastic sediments having to be accumulated. In the case of the “Solnhofen deposits”, this requirement would be satisfied by a covering of the carcass by microbial mats (e.g. Röper et al. 2000; Seilacher 2008; Tischlinger 2001; see also Dahlgren et al. 2006) and, on occasion, by the biogenetically induced precipitation of calcium carbonate.

Faux and Padian (2007), however, did no further research on the plausibility of these hypotheses in regard to the fossil record. In Faux and Padian’s (2007) view, a rapid burial in life-sustaining and life-inimical environments would provide sufficient protection from extensive deterioration from currents and scavengers, an assumption that Benton et al. (2008) and Beardmore et al. (2009), among others, were skeptical of.

In our opinion, the critical point in the scenario proposed by Faux and Padian (2007) concerning the fossil preservation of an opisthotonic posture is the requirement that terrestrial vertebrates not be subjected to “substantial transport” (undefined by the authors) postmortem. As obligatory as this requirement for a fossilised opisthotonic posture that is preservationally possible is to be assessed, so little does this apply to all of the specimens presented by Faux and Padian (2007). The reason is that according to the latest findings, the entire individual finds and lagerstätten, both large and small, must be assigned to aquatic depositional settings (references in Faux and Padian 2007; see also Cutler et al. 2011). In this, it is immaterial whether, or to what extent, sediments of volcanic origin in a lake or opal-precipitation induced by microorganisms in a terraced pool, for example, are involved in embedding (e.g. Beardmore et al. 2009, 2011; Benton et al. 2008; Chaffee 1952; Channing et al. 2005). The commonly accepted present-day state of knowledge about the sedimentary environments of the fossil sites actually referred to or discussed by Faux and Padian (2007) is, in our opinion, also not touched on in their conclusion, whereby: “These and other examples suggest that re-evaluation may be in order for an untold number of palaeoenvironments whose story has been at least partly explained on the basis of the death positions of many of their fossil vertebrates.” (See also Lingham-Soliar 2011.)

The rather unspectacular reason why we evaluate the examples Faux and Padian (2007) presented in their argumentation not as fossilised “true opisthotonic posture” but rather as a postmortem artifact controlled by inherent anatomical structures *sensu* Dean (1919) is based on the scenario that Faux and Padian (2007) themselves developed as their prime example: the Solnhofen deposits. In their own words: “It raises anew the question whether the pterosaurs, birds, and terrestrial dinosaurs (who obviously did not live in the lagoon waters) died in the lagoon for some reason, or died very near it and were rapidly immersed and buried in it.”

In a depositional environment whose water column, according to the authors cited by Faux and Padian (2007), was at least 20 m deep, the requirement for a “rapid immersion” also necessarily means a “substantial transport”. If—as they themselves presented it—Faux and Padian (2007) now accept that “immediately after death, vertebrate skeletal muscles are relaxed and moveable”, then (along with the transport into the water after having “died very near” it) there is the distance the carcass covers from the water surface to the water bottom—a transport during which “one can position a carcass in a variety of attitudes at this point”.

By also not explicitly arguing for rigor mortis as the applicable principle for adequately rigidly freezing an opisthotonic posture maintained by sticking friction for transport

on land, Faux and Padian (2007) further deprive themselves of the speculative scenario of transporting, at least in a short window of time, a carcass to a sedimentation environment favourable to fossilisation. Forensic medicine has proved that bodies in the postmortem phase can develop rigor mortis of such strong rigidity that it can support the body’s own weight (e.g. Holzhausen et al. 1961; Perper 2006). As, for example, prey animals transported by birds presently demonstrate, it is entirely possible for terrestrial vertebrates many centimeters in length to be transported significant distances in toto while maintaining a particular death pose (e.g. Duncan et al. 2003).

The authors’ opisthotonic-posture hypothesis, unproven in this and in other respects, creates a vantage point for us, as does all of the veterinarian and medical literature cited by Faux and Padian (2007) dealing with opisthotonus, to verify accordingly whether concrete cases of individuals are documented in which an opisthotonic posture developed antemortem and perimortem and which persisted postmortem. Moodie (1919) cited the following observation: “Captain Weed told me that cats inoculated with cerebrospinal meningitis often died during the night in the opisthotonic position and were found fixed in this attitude by the rigor mortis.” Dewey (2008: p. 237) provides evidence for the accuracy of this case: “The animal [cat] suddenly loses consciousness and falls to its side in opisthotonus with the limbs extended.” In Faux and Padian (2007: p. 226) there is a note added in proof: “Liz Reed (University of Flinders, Australia) reports witnessing the adoption of the opisthotonic posture in kangaroos, just prior to death, for example after having been poached by hunters.” Aside from these two short reports, there are, surprisingly, no forensically or taphonomically usable data reported in any of the other numerous publications cited by Faux and Padian (2007). The results of our own research in literature were no different.

These meager research results can at least be attributed to the fact that the issues addressed in these publications are primarily of a medical and biological nature, and thus there was little reason to focus on (or to impart) forensically or taphonomically usable data. Therefore, further research is needed that also focuses on the questions surrounding the crucial conditions needed for a postmortem persistence of opisthotonic posture.

Even though we consider the observations of Reed in Faux and Padian (2007) and of Weed in Moodie (1919) to be thoroughly credible because of the phenomenon of sticking friction, it remains questionable to us in how far the uniformitarian findings presented by Faux and Padian (2007) as evidence are usable because they are, without exception, terrestrial fossils embedded in aquatic sediments. From our point of view, an opisthotonic posture in these vertebrates can only become fixed if it occurs at the point of



death on subaerial, solid ground. It is only under such circumstances that the sticking friction between the carcass and the ground is great enough to maintain, in spite of the relaxation of the musculature, an opisthotonic posture with etiological significance (Koenig 2007; Krienitz et al. 2003; Wernery et al. 1998: fig. 3). Even this seemingly simple and thus applicable assumption about all vertebrates preserved in an opisthotonic posture is subject to a great number of variables in different environments and climatic zones.

#### Biological factors influencing an opisthotonic posture

Faux and Padian (2007) regarded perimortem muscle spasms induced by neuronal disorders as the main cause of the extreme postures of an opisthotonus posture in fossil vertebrates. For such a hypothesis to be valid, the opisthotonic posture must be maintained postmortem as well.

In fact, muscle activity is controlled mainly by the activity of the CNS sending action potentials through the upper motor neurons to the spinal cord, which controls the lower motor neurons. From there, action potentials are sent, via the neuromuscular junction, to the motor end plates of the muscle fibers (Schünke et al. 2007; Sherwood 2003). The lower motor neurons receive additional information by way of the extrapyramidal system, which controls certain types of muscular contraction. Only during simultaneous damage of the extrapyramidal pathway do the muscles cramp; otherwise a paresis will occur. It logically follows that immediately after death; spastic constrictions will be terminated as a result of the failure of action potentials of the CNS. Even by extreme spastic exhaustion of the muscles antemortem, enough adenosine triphosphate remains in the muscle cells so that physiological reactions that relax the muscles can continue. This necessarily means that “immediately after death, vertebrate skeletal muscles are relaxed and movable” (Faux and Padian 2007; see also Perper 2006).

#### The dorsal ligaments of neck and tail

As Faux and Padian (2007) have demonstrated, in the creation of an opisthotonic posture in long necks and tails, drying processes and osmotic dehydration of muscles and ligaments can be ruled out. (However, the authors only investigated ligaments in their anatomical connection with muscles and tendons in desiccating birds, rather than investigating isolated, i.e. removed, ligaments alone, as it would be necessary to get significant results.).

Therefore, as an initiator of an opisthotonic posture with a recurved spine in long-necked and -tailed vertebrates, from an anatomical perspective only the epaxial ligaments in neck, trunk and tail can be considered, as was believed by Dean (1919) and Wellenhofer (1991).

Ligaments exert forces passively without energy expenditure (Dzemski 2006; Dzemski and Christian 2007; Provenzano and Vanderby 2006). However, in contrast to the views of Faux and Padian (2007) that “joints simply move in the direction of gravity, or in whatever direction the skeleton is being otherwise moved”, the primary role of ligaments in diarthrotic and amphiarthrotic joints is to constrain the range of motion and act as a brace against gravity. In this, the bony joint members can optimally glide over each other (Wagner 2009). Secondly, they are able to store elastic energy, the relative amount of energy depending on the percentage of elastin fibers of the ligament (Dzemski 2006; Dzemski and Christian 2007), and thus reduce the metabolic cost of movement (e.g. Ligamentum nuchae). Forces counteracting gravity are generated independently when ligaments are stretched antemortem or (before decay) postmortem. This means that each movement (e.g. by gravity) in a particular direction puts the ligaments involved under tension. This tension passively stores elastic energy in the ligament. The stored energy can be released afterwards by drawing the joint back into a maximally loose-packed position (“normal position” sensu Faux and Padian 2007) in an aquatic environment.

The *maximally loose-packed position* (MLPP) is defined as the position of a joint in which the articulating bones are in a loose-packed position (*status perlaxus*) and the ligamental apparatus of the joint capsule is relaxed to the greatest degree. The MLPP depends on the shape of the partners of articulation (bones) and the grade of tension of the articular capsule itself, including the ligaments that enforce the articular capsule (Schomacher 2001; Wagner 2009).

Only in a maximally loose-packed position of ligaments of joints are some ligaments—but not all (see below)—“like loose rubber bands” sensu Faux and Padian (2007). Additionally, the range of motion of a joint is confined by muscles and soft tissues, which also have a viscoelastic limiting and recoiling effect when they are stretched beyond their resting position (Kahle et al. 1976; Minajeva et al. 2002; Schünke et al. 2007; Wagner 2009; Wuttke 1983b). Muscle tissue is considered to form elastic springs which store elastic strain energy (Witte et al. 1997). As Witte et al. (1997) and Minajeva et al. (2002) and Linke (2000, review article) have demonstrated, it is the involvement of the macro-protein titin that especially determines the viscoelasticity of muscle fibres because it can recoil a muscle ‘passively’ by sarcomere shortening. So “titin functions as a molecular spring responsible for the development of a retractive force upon stretch of non-activated muscle” (Minajeva et al. 2002), which can retract muscles of a carcass into the resting position in an aquatic environment. The MLPP is specified for every joint in extant animals (“habitual resting position” [“*habituelle Ruhestellung*”], Dzemski 2006; Wagner 2009). This posture exists with the

qualification that either no or the least possible muscular demands are required to maintain the joint position (Dzemski and Christian 2007).

As already explained, ligaments and recoiling muscles in an aquatic milieu are able to bring joints, such as those of the neck, into a maximally loose-packed position postmortem, yet not into an opisthotonic posture with an overextended recurved neck, as personal observations and underwater experiments on freshly killed long-necked gray geese (*Anser anser*) and oystercatchers (*Haematopus ostralegus*) on the island of Amrum (Germany) and partly dissected domestic fowl (*Gallus gallus* L., see below) have shown. The experiments of Davis and Briggs (1998) also did not reveal an opisthotonic posture under aquatic conditions.

### Constructional morphology of dorsal ligaments

Of particular importance concerning the structure, roles and way of functioning of dorsal ligaments of the neck in birds are the investigations by Dzemski (2006) and Dzemski and Christian (2007) on the long-necked ostrich *Struthio camelus* and that by Tsuihiji (2004) on *Rhea americana*. These authors investigated (1) the Ligamentum intraspinale (Ligamentum nuchae in mammals), which covers or is fused with the tips of the spinal processes of the neck and the first thoracic vertebra, and (2) the Ligamentum elasticum interlaminae, which is composed of unpaired, narrow bundles that connect laminae of adjacent vertebrae between the spinal processes (Baumel and Raikow 1993) [in *Cyconia alba* it continuously stretches over the tips of the spinal processes between the ninth and twelfth cervical vertebrae—Boas 1929: table 19]. The Lig. intraspinale does not exist in domestic fowl (Yasuda 2002; personal observation) because its main role is the stabilisation of the neck (McGowan 1999) and the limitation of the ventral flexion of the neck (Dzemski 2006; Dzemski and Christian 2007). In addition, according to these authors, it stores a small amount of kinetic energy during ventral flexion that is released by a re-straightening of the neck. In *Gallus gallus domesticus*, the function of limiting ventralwards movement is taken on by bony restraints at the base of each vertebra.

In their considerations of the causes of the opisthotonic posture, Faux and Padian (2007) assume that “ligaments in their normal position [= MLPP] are like unstretched rubber bands”. As the investigations by Dzemski (2006), Dzemski and Christian (2007) and our own experiments have shown, this is not the case for the Lig. elasticum because it already is in a pre-stressed state between the dorsal vertebral processes. Only in an extracted state can it fully relax: that is, in living and even in dead animals that are not yet fully decayed, it constantly exerts a tensile stress between the counterpart vertebrae. We therefore consider the crucial point of our findings to be the completed dorsal recurvature

of the neck following an artificial removal of the long neck musculature as soon as it was exposed subaquatically. This complete re-straightening anticipates, so to speak, the end state of the decay experiment of the neck with a complete musculature tube. This was still underway when this manuscript was finished. The increasing recurvature of the neck from 90° at the start to 140° in progress shows that an increasing weakening of the muscular tissues against the tensile force of the Lig. elasticum occurred in correlation with the advancing decay of the musculature.

In *Struthio camelus*, the Lig. elasticum is already up to 100% pre-stressed in an extreme dorsal flexion (in this, approx. 3 newtons are artificially added), and then it can be stretched only another 90%. In the MLPP of the neck (= “normal position” sensu Dzemski 2006), there is already a stretching of 140% ( $\pm 10\%$ ) according to Dzemski (2006). According to Dzemski’s (2006: diagram 8) calculations, the Lig. elasticum pulls with a tension of approximately 15 Nm to approximately 20 Nm between the vertebrae.

If these results are applied to the experiments with the necks of domestic fowl, it can be concluded that the tensile forces of the Lig. elasticum are not sufficient to overcome the gravity and postmortem intra-musculature restraints to erect the neck by a compression and stretching of the long dorsal and ventral neck musculature under subaerial conditions. Under subaquatic conditions, however, the buoyancy of the soft parts and the bones is sufficient to allow the pre-stress of the Lig. elasticum to come into play and bring the neck into an upright position.

According to the principles of leverage, the longer the neck of the animal, the greater the pull of the Lig. elasticum. Therefore, without having to use muscle energy, the Lig. elasticum can maintain the MLP position, with the neck thus being supported by dorsal flexion during re-straightening. This also applies to subaquatic exposure.

### Flexed limb postures sensu Faux and Padian (2007)

As Faux and Padian (2007) report: “often associated with opisthotonus, though not necessarily present, are two syndromes that affect the posture of the limbs: *decerebrate rigidity* and *decerebellate rigidity*.” (These are the “rigid limbs” of Moodie 1923.) In *decerebrate rigidity*, “all the limbs are stiffly extended” and in *decerebellate rigidity*, “the forelimbs are extended while the hindlimbs are flexed. The differences in hindlimb posture reflect damage to separate but proximate areas of the cerebellar cortex (Bagley 2005)”.

This posture of the limbs in fossil vertebrates from subaquatic environments is well known in palaeontological literature (reviewed in Wuttke 1983b). Numerous documented in the classic works of forensic medicine (e.g. Baumann 1923; Reh 1968; Reuter 1923), this MLPP found its way as “passive posture” [*passive Haltung*] into palaeontology with Weigelt

(1927, 1989). This was identified by Wuttke (1983b, 1988a/1992a, 1988b/1992b) as the functional-morphologically determined “medial position of the joint” [“*Mittelstellung der Gelenke*”, the former German anatomical expression for the extant MLPP] and considered by von Koenigswald and Wuttke (1987) to be the typical water cadaver position [“*Wasserleichen-Haltung*”].

As Wuttke (1983b) has already stated, this posture (“*Mittelstellung der Gelenke*”) is triggered by ligamental and muscle forces which can act postmortem in an aquatic environment (for humans see, for example, Krause et al. 2006). This posture is well understood in medical, medico-legal and veterinary literature; therefore, we only present the modern definition for this resting posture of joints which is displayed by the specimens of *Compsognathus* and *Juravenator*. As stated before, the MLPP depends on the shape of the partners of articulation (bones) and the grade of tension of the articular capsule itself, including the ligaments that reinforce the articular capsule, as can, for example, be seen in chameleons. Their prehensile tail tends to adopt a curled MLPP, and the arms and legs in these upright walkers are extended (Peterson 1984). Further examples of specified MLPP postures of extant and fossil vertebrates [buried in a subaquatic environment] are shown by Kielan-Jaworowska and Hurum (2006) but also in several articles of this special issue (Richter and Wuttke 2012; Schwermann et al. 2012; Smith and Wuttke 2012, this issue). Each of the specified MLPP postures of these extant and fossil amphibians, reptiles, and mammals depends on the species-specific structure.

In the context of “passive exertion of forces by ligaments”, there are also the “decerebrate rigidity and decerebellate rigidity” that caused the flexed limb postures of reptiles placed in an aquatic environment sensu Faux and Padian (2007: figs. 1A–C, E–G, 2, 5) because these joints are also influenced postmortem by their particular ligamental apparatuses.

Even though the joint connections of the reptiles considered by Faux and Padian (2007: figs. 1A–C, E–G, 2) were disintegrated, the original joint positions can still be identified in our opinion. With the possible exception of the crurotarsal joints of the tyrannosaur *Albertosaurus* (fig. 1G in Faux and Padian 2007; intraspecific research is needed), all of the joint connections of the limbs lie in the area of the functionally substantiated MLPP of the particular species. The reptile finds presented by the authors likely arrived at the bottom of the water body before the onset of rigor mortis, or hovered shortly after the end of rigor mortis, so that all of the limb joints could attain the MLP posture by the passive exertion of forces of the ligaments, muscles and tissues. Decerebrate diseases are not necessary to generate these limb postures in an aquatic burial environment.

Constructional constraints must be preferred (per Ockham’s razor) over the opisthotonic posture hypothesis with its

numerous hypothetical exceptions and requirements (e.g. fixation by rigor, transport and rapid burial; see above).

### Rigor mortis

Under temperate and tropical climatic conditions, rigor mortis normally sets in between 2 and 6 h after death (Gill-King 1997; Gunn 2006; Janaway et al. 2009), but it can become noticeable as soon as 0.5 h after death (Perper 2006). Inner organs can also show evidence of rigor mortis in 0.5 h (Mueller 1953). In humans, this postmortem rigidity as a rule lasts 12–84 h (Gill-King 1997; Gunn 2006; Mueller 1953). Such data concerning humans, however, cannot per se be applied to other organisms.

Rigor mortis can affect the whole body or merely various parts of it (Kahana et al. 1999; Reh 1968; Straßmann 1931). The time of onset, duration and extent of rigor mortis are dependent on intrinsic and extrinsic factors. A so-called cataleptic rigor mortis (the only hypothetical possibility for freezing the opisthotonic posture) has been discounted by recent research (Pfäffli and Wyler 2010; Sauvageau et al. 2010), even if it is considered feasible in some recent publications (Gunn 2006; Mastrolorenzo et al. 2010 v.s. Prokop and Göhler 1976: p. 147; Perper 2006)—though without any physiological basis. Since biochemical processes of the musculature of an organism are responsible for rigor mortis alone, intrinsic factors are determined by species-specific anatomy (Beier et al. 1977; Dix and Graham 2000; Krompecher and Fryc 1978; Perper 2006; Schäfer 1997), physiology (body temperature and warmth isolation; Dix and Graham 2000; Robinson et al. 1953; Sharp and Marsh 1953) and the state of health (overall and nutritional state; Clark et al. 1997; Gill-King 1997; Mueller 1953; Schäfer 1997). On the other hand, the extent of physical activity and psychological stress before the onset of death, and the cause of death itself, can also have an effect on the point in time of the onset, dissipation and intensity of rigor mortis (Dix and Graham 2000; Krompecher et al. 1983; Perper 2006; Tornberg 1996). An increased strain on the muscles antemortem (whether illness or stress related, and whether in direct relation or without any relation to the cause of death) can, for example, accelerate the onset of rigor mortis (Aursand et al. 2009; Clark et al. 1997; Gill-King 1997; Kiessling et al. 2006; Krompecher et al. 1983; Robinson et al. 1953; Roth et al. 2006; Tornberg 1996).

The most fundamental extrinsic factor concerning rigor mortis is the environmental temperature that the body is exposed to after death (Dix and Graham 2000; Gill-King 1997; Krompecher 1981). A general guideline is that rigor mortis sets in earlier at higher temperatures (in humans, as early as approx. 0.5 h at 30–40°C; Mueller 1953) than at lower temperatures (Giertsen 1977; Perper 2006). Lower environmental temperatures, however, can significantly

extend the duration of rigor mortis (Gunn 2006: extending rigor mortis up to 16 days at 4°C, in parts up to 28 days; see also Krompecher 1981; Mueller 1953), while higher environmental temperatures can significantly shorten it or even suppress it in particular body areas (Brettel 1978; Gill-King 1997; Krompecher 1981; Mueller 1953; Perper 2006). In a carcass, external forces can cause anatomical locomotory units to experience powerfully induced excursions that can interrupt the rigor mortis in the muscle groups affected (Gunn 2006; Mueller 1953; Perper 2006). A renewed onset of rigor mortis is possible after this, though only to a limited extent (Krompecher et al. 2008; Mueller 1953; Perper 2006; Straßmann 1931). Such a sequence is of significance, for example, for carcasses in an aquatic depositional setting that are continually subjected to positional changes through wave action and water currents (e.g., Berg 1928; Boyle et al. 1997; Davis and Goff 2000; Kahana et al. 1999; Reuter 1923).

#### Subaerial environment of deposition and burial

As can be concluded from the explanations above, a persistent body position of a carcass lying on land can become fixed by rigor mortis only within the narrow time frame of a few hours to several days. In tropical to arid climates, as can, for example, be assumed for the Late Jurassic Solnhofen Archipelago (e.g. Billon-Bruyat et al. 2005; Keupp et al. 2007; Oost and De Boer 1994), taking the higher body temperature of the sauropods into consideration (Eagle et al. 2011), this time frame could be reduced to merely a few hours. In how far a particular body position fixed by rigor mortis can allow etiological as well as forensic conclusions to be drawn depends on whether the position remains stable within this short time frame, or whether rigor mortis is interrupted by external forces and then possibly reoccurring in a modified form. This issue is especially relevant in an allochthonic fauna that died in a particular environment and is of fundamental importance to the interpretations by Faux and Padian (2007) concerning their terrestrial reptilian fossils in an opisthotonic posture in aquatic sediments.

#### Aquatic environment of deposition and burial

In contrast to the facts of preservation of the opisthotonic posture in a subaerial environment, as presented above, frictional resistance plays a minor role in an aquatic environment.

The following presentation should make clear that the postmortem fates of terrestrial vertebrates in aquatic environments vary significantly from those in subaerial environments. Two fundamental physical conditions are responsible for this: (1) the specific gravity of a carcass in water and (2) the prevailing current. The first determines the transport potential of a carcass (i.e. susceptibility to sinking; e.g.

Dilen 1984; Donoghue and Minnigerode 1977; Haglund and Sorg 2002; Nawrocki et al. 1997): according to Archimedes' principle, the specific gravity (including the shape characteristics) of a lifeless object in a liquid or liquefied medium determines whether the object possesses a neutral, a negative or a positive buoyancy. As concerns our taphonomic inquiries, the specific gravity determines where in the water column particular terrestrial vertebrates possibly end up postmortem. Depending on their specific gravity, the carcasses will either float at the water's surface or somewhere in the water column, or sink to, or hover directly above, the bed of the body of water. Decisive in what sort of movement profile results from a particular transport potential, however, is the second physical force, namely the strength and the direction of the current the carcass is exposed to in an aquatic environment (e.g. Adelson 1974; Blanco Pampin and Lopez-Abajo Rodriguez 2001; Carniel et al. 2002; Haglund 1993; Lunetta and Modell 2005).

Recent terrestrial vertebrates generally possess a specific gravity that differs only slightly from fresh and normal saline water (e.g. Berg 1928; Haberdar 1895; Luciani 1904: p. 284; Parker 1925; Reuter 1923; Schoener and Schoener 1984; Slijper 1962: p. 69; Spennemann and Rapp 1988, 1989). Thus, even slight modifications in the specific gravity or in the characteristics of the currents affect the transport of the carcass (Adelson 1974; Blanco Pampin and Lopez-Abajo Rodriguez 2001; Carniel et al. 2002; Haglund 1993; Lunetta and Modell 2005). Depending on these two physical conditions and their variability, the possibilities of dramatic changes of location postmortem in air-breathing animals are quite diverse and thus occasionally result in unexpected findings. It is known from forensic medicine, for example, that terrestrial vertebrate carcasses are able to move large horizontal distances in short amounts of time by way of currents and can even be transported from terrestrial to open-ocean depositional environments (e.g. Blanco Pampin and Lopez-Abajo Rodriguez 2001; Mannucci et al. 1995).

For describing the postmortem descent through the water column as the initial substantial posture and spatial change of a carcass into the depths—aside from possible predation (e.g. Nielsen 1930 in Gewalt 2001)—the terms *nekton fall* and *food fall* have become established in marine biology (e.g. Britton and Morton 1994; Gooday and Turley 1990; Jones et al. 1998; Priede et al. 1991; Smith 1985; Smith et al. 1997; Soltwedel et al. 2003; Stockton and DeLaca 1982). As an extension of these comes the term *whale fall* (e.g. Allison et al. 1991; Deming et al. 1997; Feldman et al. 1998; Smith 1992) and, in palaeontology, such terms as *marine reptile deadfalls* and *saurian deadfalls* are used (Hogler 1994; Martill et al. 1995). This obvious, concomitant vertical component of postmortem transport, which is valid even for terrestrial aquatic depositional realms, as proven by the fossil record, was completely undervalued by Faux and

Padian (2007) in their opisthotonic posture hypothesis. For the preservation of more or less articulated terrestrial vertebrates in aquatic sediments, however, this vertical component is mandatory in a palaeontological and forensic sense, because only through this vertical component are the circumstances at all created for the settling of a vertebrate carcass onto the bed of the body of water, where through rapid burial it can be effectively protected from biotic and abiotic maceration and disarticulation.

Whatever the case, according to forensic observation, when fresh cadavers sink in a body of water, they usually do not settle in complete contact with the bed of the body of water, which is due in particular to breathed-in air remaining in the carcass. Fresh cadavers are often discovered floating freely in the water column (Adelson 1974; Blanco Pampin and Lopez-Abajo Rodriguez 2001; Haberda 1895; Hofmann 1927: p. 648). Many of the situations documented in forensic literature are examples of the phenomenon of a partly floating, easily movable cadaver (Adelson 1974: p. 563; Dix et al. 2000; Haberda 1895; Reuter 1923). This is especially the case when the hydrostatic pressures involved cannot lead to any substantial compression of the breathed-in air still enclosed in the body. It can be assumed that this is the case not only in human bodies but in other terrestrial vertebrates as well.

However, because of the fact that living terrestrial vertebrates demonstrate different floating behaviours depending on their species-specific anatomy (e.g. specific gravity and shape characteristics), physiology and thus their centre of gravity (Chanin 1985; Dilen 1984; Haberda 1895; Haglund and Sorg 2002; Rietchel and Storch 1974; Schoener and Schoener 1984; Slijper 1962; Spennemann and Rapp 1988, 1989; Tarasoff and Kooyman 1973a, b), it is to be expected that their fresh carcasses will exhibit differences in sinking behaviour and in the death posture assumed on the bed of the water body (e.g. Burnham 2007; Kielan-Jaworowska and Hurum 2006; Parker 1925; Rietchel and Storch 1974). Any differences in the bodily posture and location of such partly floating fresh carcasses can be explained by intrinsic and extrinsic factors, including (1) the anatomical bauplan (including the type of body covering, the length and flexibility of the extremities and neck and tail vertebrae and the position, relative size and biomechanics of the respiratory tract; e.g. Buffetaut 1994; Donoghue and Minnigerode 1977; Hobischak and Anderson 2002; Kooyman 1989; Kooyman et al. 1992; Sander 1989; Schäfer 1962, 1972; Slijper 1962); (2) the cause of death and the surrounding circumstances (= the problematic issues of competing causes of death; Haberda 1895; Mallach and Schmidt 1980; Schoon and Kikovic 1989; Straßmann 1931); (3) physical parameters (e.g. hydrostatic pressure, hydrodynamic currents, water temperature and salinity; Adelson 1974; Berg 2004; Kemp 2001; König 1892; Reisdorf et al. 2012, this issue; Sternberg 1970; Tomita 1975, 1976).

From the observations and deductions presented above on the buoyancy behaviour of fresh carcasses, it can be concluded that in an aquatic environment, neither the pure force of gravity nor frictional resistance come into play to a sufficient extent to allow a postmortem persistence of an opisthotonic posture. Instead, because of the predominant specific gravity and the buoyancy of a body at the time of death, in the open water column, the weak, joint-inherent elastic forces, such as those in the ligamental joint capsules and the joint-strengthening ligaments, the muscles and the soft tissues, come into effect in such a way that the joints will attain their resting positions. At the water floor, the only body parts limited in their freedom of movement are those lying directly on the water floor or those that are restricted in some other way, for example by submerged plants (e.g. Adelson 1974: p. 564). All other, unanchored locomotory units of the carcass will move into their appropriate MLP postures as determined by location and conditions of the water currents.

## Experiments

In the above-mentioned experiments performed by various authors investigating the phenomenon of opisthotonic posture in fossil vertebrates, the aquatic “physical phenomenon hypothesis” of Dean (1919) has thus far remained untested.

To test the hypothesis of Dean (1919) that the recurvature of the neck is merely a physical phenomenon that causes the neck region of a macerating vertebral column to bend backward, we studied the necks of six adult domestic fowl (*Gallus gallus* L.). These were obtained from a commercial butcher shortly after being slaughtered. Fully preserved but decapitated necks, together with the intact thoraxes, were taken from the birds immediately their slaughter; three of them were preserved by freezing. Maximum neck flexions in the dorsal and ventral directions were determined with the complete necks and trunks based on a study of full-scale pictures. Thereafter, the distal halves of the ribs were removed, as well as the vertebrae posterior of the notarium.

In the first step of the experiment, two of the necks were dissected in order to investigate any possible inhibiting effect of the skin or musculature on a passive dorsalwards recurvature of the necks. The long dorsal neck musculature was removed muscle by muscle, followed by the removal of the ventral musculature. The manipulated specimens were then investigated in subaerial and subaquatic testing setups for possible effects. In contrast to, for example, *Rhea americana* and *Struthio camelus* (Baumel and Raikow 1993; Boas 1929; Dzemski and Christian 2007; Tsuihiji 2004), domestic fowl do not possess a Ligamentum interspinale (= Ligamentum nuchae in mammals). Therefore, we focused in particular on the influence of the Ligamentum elasticum interlaminare between the spinal processes of the

cervical and the thoracic vertebrae. We also studied a third neck from which only the skin was removed. The first results of these experiments were presented at the TAPHOS meeting in June 2011 (Wuttke and Reisdorf 2011).

In the following, we use the anatomical nomenclature of the ligaments of Baumel and Raikow (1993), Baumel and Witmer (1993), Hogg (1982) and Vanden Berge and Zweers (1993) but shorten the term *Ligamentum elasticum interlaminare* to *Lig. elasticum*.

### Experimental results

The experimental results presented here are limited to those which are useful in elucidating the opisthotonic posture phenomenon of recurved necks and tails. The documentation of the whole pilot experiment with detailed descriptions of the decay stages and its further implications will be published elsewhere (Reisdorf and Wuttke, in preparation).

Flexibility of the neck—with musculature tube, subaerial exposure: (1) The neck is supported in a dorsal orientation at a maximum manual dorsal excursion with the atlas of the thoracic spine; recurvature approximately 180°; (2) the ventral flexion, of approximately 80°, occurs in the proximal section of the cervical spine, while the rest of the neck remains straight (bony restraint); a manual flexion is possible in the area of the second and third vertebrae.

Flexibility of the neck—dorsal and ventral musculature removed, subaerial exposure [Electronic Supplementary Material (ESM) Fig. 1a]: (1) The neck can be bent in a maximum manual dorsal excursion (engagement of bony restraint by the zygapophyses) beyond the plane of the thoracic vertebrae (bony restraint); the bending takes place mostly in the proximal area of the vertebral column, maximally 190°; (2) the ventral flexibility remains unchanged; during the fixation of the cervical spine in a ventral position, the thoracic part of the vertebral column is immediately lifted to an angle of 45° under the influence of the distal *Lig. elasticum*; (3) cutting completely through the proximal *Lig. elasticum* of the neck results in a lowering of the thoracic vertebrae.

Flexion of the neck—with musculature tube, subaquatic exposition (ESM Fig. 1b): The neck was fixed in a natural life position at the notarium in a container (70×40×50 cm). The container was then filled with drinking water and inoculated with pond water (T=9°C). The neck became immediately erect and took on an angle of approximately 90° relative to the notarium. The bend occurred in the proximal area of the cervical vertebral column. Only with pressure being put on the atlas after submersion by a weight of 20 g was there a bending towards the original position. Afterwards, the temperature was raised to approximately 20°C through sun exposure. After 3 days, there was a curvature of the neck to 110°; after approximately 3 months, with increasing degradation of the musculature, the curvature was approximately 140°.

Flexion of the neck—dorsal and ventral musculature removed, subaquatic exposure (ESM Fig. 1c): The neck was fixed in a life posture at the notarium in the container. The experiment was conducted under the same conditions as described above. After submersion, the neck immediately bent dorsally until the atlas finally arrived under the plane of the thoracic vertebrae (approx. 190° curvature). A further recurvature was prohibited by the bony restraint of the zygapophyses. The main curvature took place in the proximal area of the vertebral column. The recurvature stopped after 4 months by zygapophyseal blockage, and disarticulation started.

Cutler et al. (2011) independently performed experiments with dead domestic fowl to re-evaluate the opisthotonic posture hypothesis of Faux and Padian (2007). They report that “...once immersed, natural muscle tone of the epaxial muscles hyperextends the skull and neck resulting in the classic death pose almost instantly” (see chapter [Conclusions](#)).

## Taphonomical analysis of *Compsognathus* and *Juravenator*

### Case 1: *Compsognathus longipes*

#### *Current knowledge on the taphonomy of Compsognathus longipes*

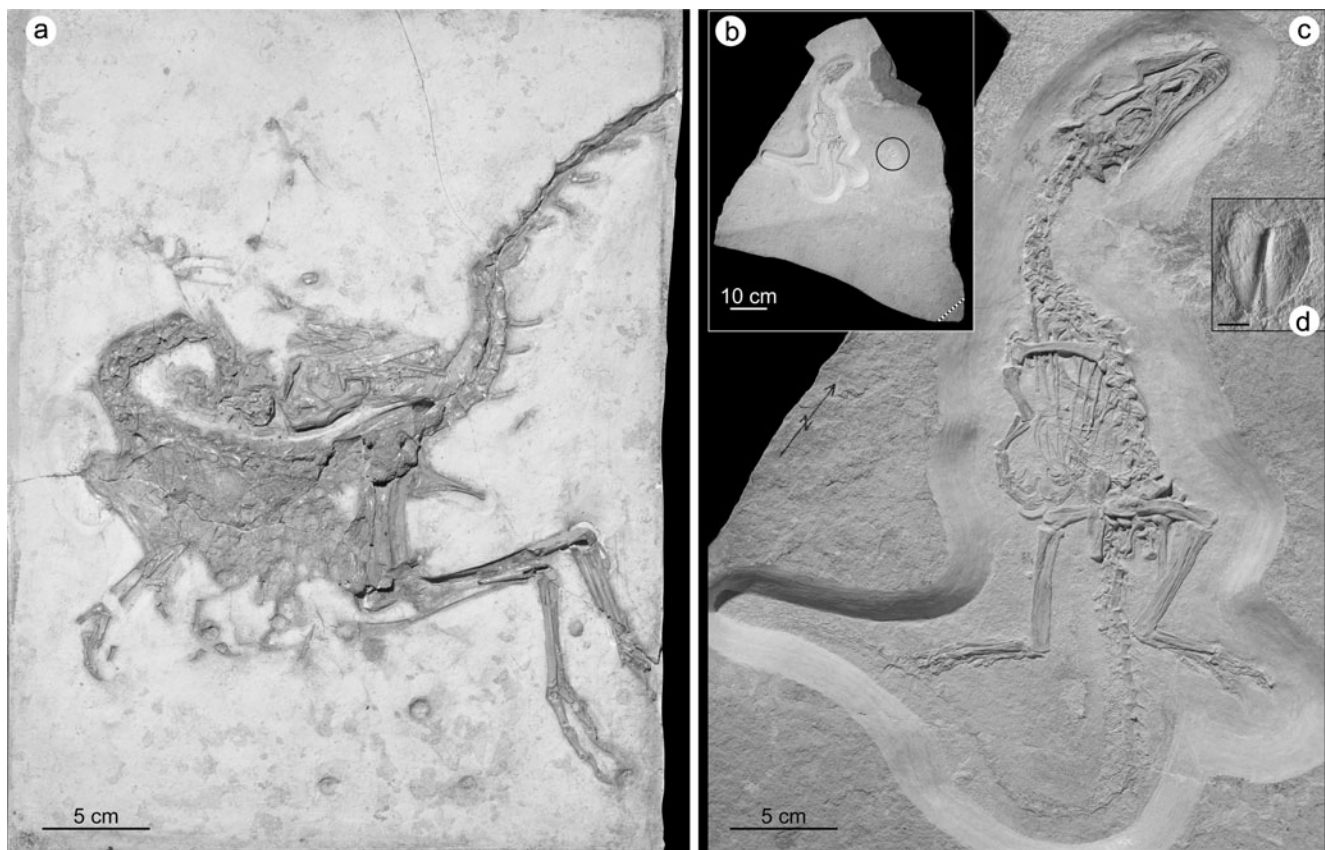
Some of the early researchers worked on taphonomical questions regarding the non-habitual bone positions of the neck and skull of *Compsognathus* (Fig. 3a). A review of classical literature reveals that until the paradigm change initiated by Barthel (1970), subaerial and subaquatic embedding scenarios for the *Compsognathus* specimen stood opposed to each other (subaerial: e.g. Abel 1919, 1922; Mayr 1967; Walther 1904; Weigelt 1927 vs. subaquatic: e.g. Barthel 1964; Moodie 1923). In addition to the more general comments by Moodie (1918, 1923), who assumed only an etiologically based opisthotonic posture of the recurved neck (see [Introduction](#)), a number of more detailed remarks were made by consecutive authors. Abel (1919: p. 582) misinterpreted Liesegang rings (consisting of iron hydroxide; personal observation, but see also Griffiths 1993) on the bedding plane as claw marks, scratched into the soft mud by the claws of the toes of the hind feet, when the heavily decayed carcass was stranded at the beach. He also mentioned the heavily bent back neck. Nopcea (1903) provided a more thorough analysis of the emerging taphonomic pattern of the *Compsognathus* specimen and concluded that “the base of the skull was torn off from the anterior-most cervical vertebrae, and from these displaced only through a parallel movement, therefore still maintaining a relatively

natural position, while the rest of the skull was twisted off, and perhaps washed away.” [Translation by the authors.]

Ostrom (1978) noted that *Compsognathus* displays a “death pose” like many other theropods in the “opisthotonic position”, with a “cervical column looped back on itself almost at 360° arc” (see also Nopcsa 1903). A reason for the backward distortion of the neck was, he assumed, “shrinking (due to drying) of the dorsal neck muscles and ligaments, particularly the Ligamentum nuchae”, but he also stated that “whether or not desiccation is involved, contraction of dorsal muscles and/or ligaments appears to be the most probable explanation of this opisthotonic state.” Ostrom (1978) could not account for the fact that the “braincase and skull, to which these ligaments [i.e. Ligamentum nuchae] and muscles were firmly attached are completely separated from the cervical column and each other” (Figs. 3, 4). For the entire skeletal elements, mainly the “posterior cervical ribs, the slightly displaced right fibula and the scattered phalanges of the hands”, Ostrom (1978) argued that they “may have been scattered by scavengers, but more likely they simply were drifted away from their original sites by gentle currents after connective tissues had

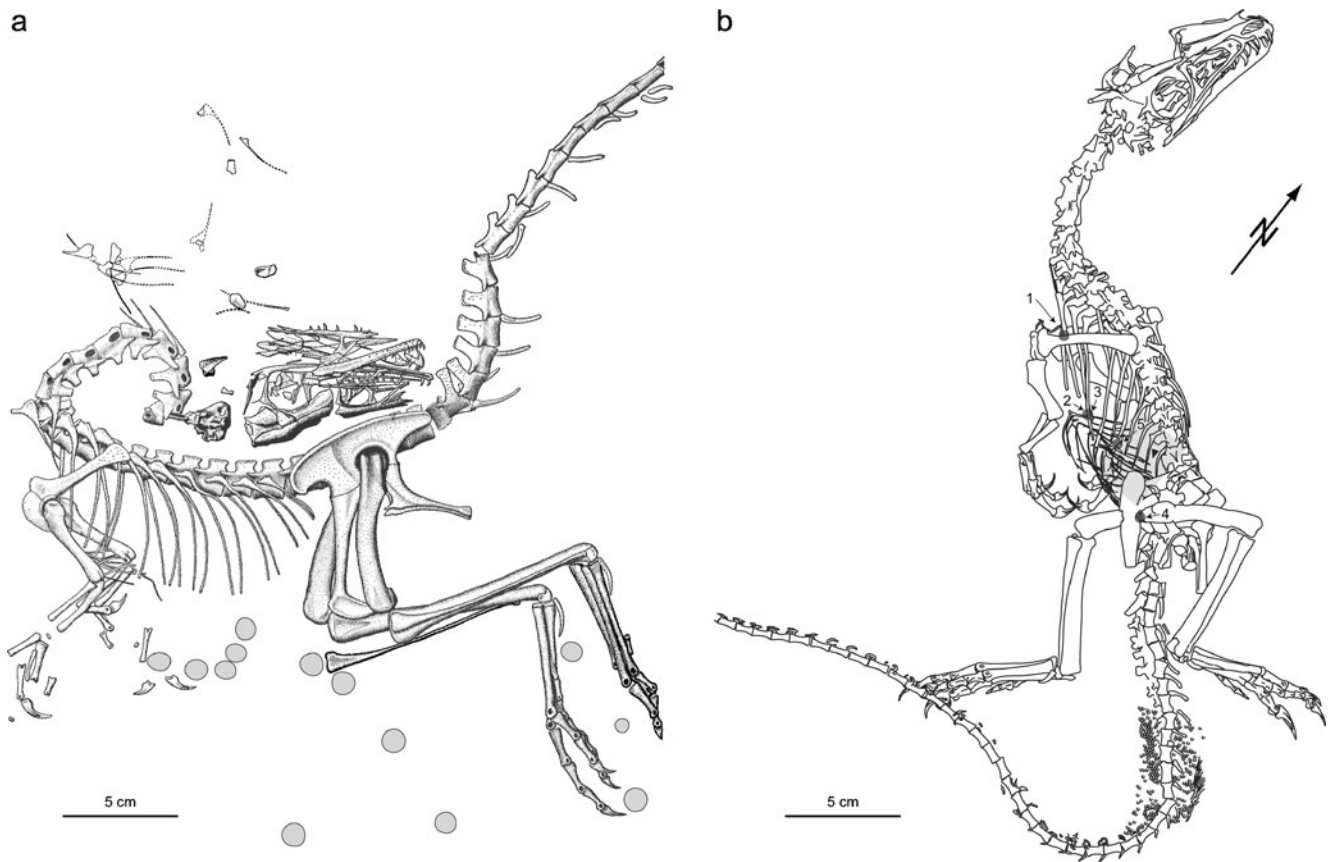
decomposed.” In the case of the gastralia, he noted that “there is some evidence that the stomach and body cavity were breached—perhaps due to build-up of gases generated within the rotting carcass” after the carcass came to be stabilised on the ground.

A number of authors also consider the weak currents on the seafloor (Barthels 1964; Kemp and Unwin 1997; Mäuser 1983) as an explanation for the dislocated skeletal elements of the *Compsognathus* (including the prey animal). In the literature, the ascertainable signs of decay of the *Compsognathus* specimen, however, have been seen primarily as slight maceration during a more or less short drifting time (cf. Barthel 1964; Kemp 2001; Wellnhofer 2008). Mäuser (1983) assumes that a bursting of the gas-swollen abdomen led to sinking. Evans (1993), Griffiths (1993) and Davis (1996) interpreted Ostrom’s subaquatic “breaching” of the body cavity due to the build-up of gases as “eruption of decomposition gases”. [Nopcsa (1903) and Barthel (1964) also discuss the interactions of the fluid and gaseous decay products with the sediment.] Davis (1996) further stated that the carcass of *Compsognathus* “reached the lagoonal floor well preserved”. Reporting the etiologically based view of



**Fig. 3** **a** *Compsognathus longipes* (AS I 1563) from the Kelheim basin or Painten basin (courtesy of G. Janßen, O. Rauhut). **b** *Juravenator starki* (general view; JME Sch 200) from Schamhaupten; circle location of aptychus (Fig. 3d), dotted line saw cut for thin section sample

(see Fig. 7). **c** *Juravenator starki* (general view; JME Sch 200) (**b**, **c** © LMU/ G. Janßen/Jura-Museum Eichstätt; courtesy of L. Chiappe, U. Göhlich). **d** Aptychus (scale bar: 1 cm)



**Fig. 4** **a** Three-dimensional (3D) drawing and interpretation of *Compsognathus longipes* by Ostrom (1978: figs. 1, 2; combined by the authors roundish “structures” [“eggs”] after Griffiths 1993 and Mäuser 1983; cf. Röper et al. 1999: fig. 10; see section [Speculations on the cause and location of death](#)). **b** Contour drawing of *Juravenator starki*

by Chiappe and Göhlich (2010; modified; courtesy of L. Chiappe, U. Göhlich). Grey circles Isopods finds (1–4 present, 5 removed; P. Völkl, personal communication 2011), triangle location of “ooids”, grey box location of Fig. 9)

Moodie (1923) of the recurved neck with articulated skull, he came to the conclusion that “it is more likely to be due to desiccation [of “tendons”] as Heinroth (1923) assumed [in his case study about the wing of *Archaeopteryx*].” The “bicycling pose” of the hindlimbs seemed to him be “due to osmotic desiccation”.

In their taphonomic analysis, Kemp and Unwin (1997) also focus on the recurvature. Unlike in Seilacher et al. (1985) and Davis (1996), hypersaline seafloor water is not seen by these authors as an indispensable explanation. According to Kemp and Unwin (1997) and also to Mäuser (1983) and Viohl (1990), the curvature phenomenon developed by the *Compsognathus* specimen can be considered to be the result of the sinking process through the water column and its settlement onto the seafloor. In this way, the carcass would arrive at its final embedding situation after its sinking to the seafloor. Wellnhofer (2008) for his part assumes a postmortem recurvature on land before the carcass made it to the aquatic site of deposition. With such an interpretation, Wellnhofer (2008) rules out drowning as a cause of death. According to Kemp (2001), however, there

is no evidence of mummification of the *Compsognathus* specimen before the subaquatic deposition. In the interpretation of the taphonomic pattern in the plattenkalks of the Southern Franconian Alb, drowning has been formulated as a potential cause of death for terrestrial vertebrates (Kemp 2001). According to this hypothesis, the animals arrived as fresh carcasses at the depositional sites as the result of catastrophic events (e.g. storms).

Faux and Padian (2007) repeated the opinion of Moodie (1923) that *Compsognathus* displays a typical “opisthotonic posture”, induced by a cerebral disorder. The authors did not analyse other bone positions of the specimen. Faux and Padian (2007) discuss some unknown toxicant in the environment (e.g. algal blooms or “red tides”; but compare Barthel 1976) as a cause for the cerebral disorder.

Our taphonomical analysis of *C. longipes* is reinforced by the detailed anatomical description and interpretations by Wagner (1861), Nopcsa (1903), Ostrom (1978) and Gishlick and Gauthier (2007), so we need not repeat them here. Nomenclature is in accordance with Ostrom (1978) and Baumel and Raikow (1993). We received specialised advice



about previously unknown anatomical details from Oliver Rauhut, Munich. In our opinion, the position of skeletal remains is one of the keys to understanding the decomposition behaviour of vertebrates (see Wuttke and Reisdorf, in preparation). Therefore, we analysed every single synarthrotic and syndesmotic bone connection and its state of decay at the moment of disarticulation to (1) obtain an overview of the timeline of the decomposition process and (2) to find out the intrinsic and extrinsic causes of the movement of bones. Each unique phenomenon must be in accordance with the others, and all phenomena together must be in accordance with the knowledge about the palaeoenvironment.

#### *General description of Compsognathus longipes*

The specimen displays its left side (Figs. 4a, 5a). It shows a high degree of articulation (Kemp and Unwin 1997). According to Ostrom (1978), the only regions that suffered some disarticulation are the skull, most of the cervical ribs, the hands and the posterior gastralia. A striking characteristic is the strongly recurved cervical column and the backwardly-separated braincase. Noteworthy are the slightly re-bent spine of the trunk and caudal vertebrae 1–7, which are dorsally contorted, a 90° rotation of the first caudal vertebra and a break between caudal vertebrae 7 and 8. Caudal vertebrae 8–16 are slightly flexed in a ventral direction.

**Skull:** Nearly all of the elements of the skull are disarticulated and slightly dislocated. Noteworthy are the separated articularia, lying on the surface of the slab in their anatomical context, whereas the posterior part of the skull, for example the removed and flipped braincase, is dislocated and rotated, displaying its left dorsolateral view. There is no sediment between overlapping bones.

**Cervical vertebrae:** The cervical series consists of ten vertebrae, including the atlas, which is separated from the other cervicals and the skull (Figs. 3, 4, 8). The atlas is situated between the skull, braincase and cervical vertebra 5. The third cervical vertebra is slightly removed from the fourth. The cervical spine is strongly bent backward. All cervical vertebrae, except cervicals 7 and 8, which are in a straight line, are maximally flexed in a dorsal direction; the flexion is limited by the vertebral zygapophyseal facets. It is possible that there was even slight hypertension, so that the joint surfaces of the centra gape slightly on their ventral side. The first break combined with a ventral gap of the centra is displayed between the tenth cervical and first dorsal vertebrae. All cervical neural spines are crushed and lost, or are on the non-preserved counter slab. Cervical ribs of cervical vertebrae 4 and 5 are nearly in their anatomical position; all others are separated and dislocated. All cervical vertebrae, except cervicals 7 and 8, which are in a straight line, are maximally flexed in a dorsal direction. A slight

hyperextension was possibly rendered by a slight ventral gap of the centra of the vertebrae. The first break combined with a ventral gap of the centra is displayed between the tenth cervical and first dorsal vertebrae.

**Dorsal vertebrae:** The dorsal spine is articulated entirely and slightly curved backwards to the point of zygapophyseal blockage. Ribs are inclined, as typical for theropods. The right rib of the first dorsal is disarticulated; the remaining ones are almost in anatomical position.

**Sacral vertebrae:** The sacrum is widely covered by the ilium and the left femur, only the last two co-ossified vertebrae are visible.

**Caudal vertebrae:** Sixteen segments are preserved in the caudal series; the elements become progressively longer distally, “this suggests a very long tail” (Ostrom 1978; Peyer 2006 hypothesises 60 elements). The first caudal vertebra is disarticulated; rotated 90° upward in the medial plane. Caudal vertebrae 2–7 display a maximal flexion in the dorsal direction with zygapophyseal blockage. Neural spines are taller than those of the dorsals (Ostrom 1978); spines of caudal vertebrae 8–10 slope progressively downwards. Caudal vertebrae 1–7 are separated from the 8th–16th by a kink; the latter are slightly flexed ventrally. The chevrons are elongated and rod-shaped throughout the tail. Chevrons of the first and third and of caudal vertebrae 6–9 and 12–14 are disarticulated.

**Shoulder girdle:** The shoulder girdle is in anatomical position.

**Pelvic girdle:** All bones are in anatomical position.

**Forelimbs:** Right arm—humerus twisted inwards in the longitudinal axis; elbow joint disarticulated, ulna and radius moved anteriorly; elements of the hand disarticulated and partly scattered. Left arm—humerus in resting position; radius and ulna articulated; metacarpals and phalanges nearly totally disarticulated, most elements shifted.

**Hindlimbs:** Bones in MLPP. Femora in anatomical position. Right tibia and fibula disarticulated, fibula has shifted. Left tibia and fibula in anatomical position. Elements of the right foot articulated, except the digits of the first toe. Elements of the left foot in anatomical position.

#### *Orientation of the slab of Compsognathus longipes*

Knowing the exact geographic and stratigraphic origin, as well as the original position of a fossil embedded in a rock unit is of utmost importance for its taphonomic analysis. A thorough documentation of the spatial orientation of a multi-component skeleton in the finding horizon provides information essential for the reconstruction of its taphonomic history. With respect to historic finds, however, these data are often rare and/or ambiguous. A retrospective reconstruction of the find spot and the embedment can thus often only

be accepted with some reservation. Such a background can consequently reduce the scientific value of a fossil.

The specimen *Compsognathus* investigated in the framework of this study is a historical find. The year of its discovery is unknown, but its first mention by Wagner dates back to 1859 (Wellnhofer 1996). In 1865, it was acquired by the palaeontological state collection in Munich. According to present-day standards, its documentation is vague and insufficient (Mäuser 1983; Wellnhofer 1996).

Historically undocumented but manifested by recent weathering phenomenon, the specimen *Compsognathus* is considered to be a waste rock pile find (Davis 1996; Mäuser 1983; Ostrom 1978; Wellnhofer 1996; regarding authigenic quartz; see also Streim 1961). However, neither its geographical origin nor the stratigraphic finding horizon are known (Figs. 1, 2). Respectively, the existence and the whereabouts of the counter slab remain unknown (e.g., Nopcsa 1903; Wellnhofer 1996). Knowing the palaeontological inventory and petrographic construction of this counter slab is not only of great palaeontological and scientific relevance, it also indirectly affects the interpretation of the original orientation of the fossil slab at hand.

The remarks of Griffiths (1993) imply that the present-day untraceable counter slab does not represent the counterpart of a more or less axially split carbonate bank (“Flinz”), but rather a discrete carbonate layer (“The fossils from the Solnhofen Plattenkalke are usually found at the lower surface of the overlying bed, often partially embedded in the matrix. The state of the specimen is consistent with this type of preservation [...]”). If this assumption complied with the facts, it would result in the original orientation of the slab as suggested by Griffiths: the fossil horizon of the specimen *Compsognathus* would correspond to the lower side of this plattenkalk bed. In contrast, Mäuser (1983) concluded that the specimen *Compsognathus* is located in the upper part of the slab, an interpretation that is based on sedimentary structures of the slab. Indicative geopetal structures were found by neither by these authors nor by ourselves.

Our decision-making regarding the original orientation of the slab is intimately connected to our taphonomic analysis of the specimen of *Compsognathus*. The results are largely based on the inventory of the degree of articulation as well as disarticulation phenomena of its anatomic units (a detailed description can be found in Ostrom 1978; Kemp and Unwin 1997). Due to its lateral death posture, we attribute the highest significance to the bilateral-symmetrical skeleton elements. In the present example, the extremities are particularly indicative. It is thereby important to note that the front and hind extremities on the left side are less strongly disarticulated and dislocated than the ones on the right side. Based on these findings, we formulate the working hypothesis that the specimen was left-laterally positioned on the seafloor. Such a basic assumption implies

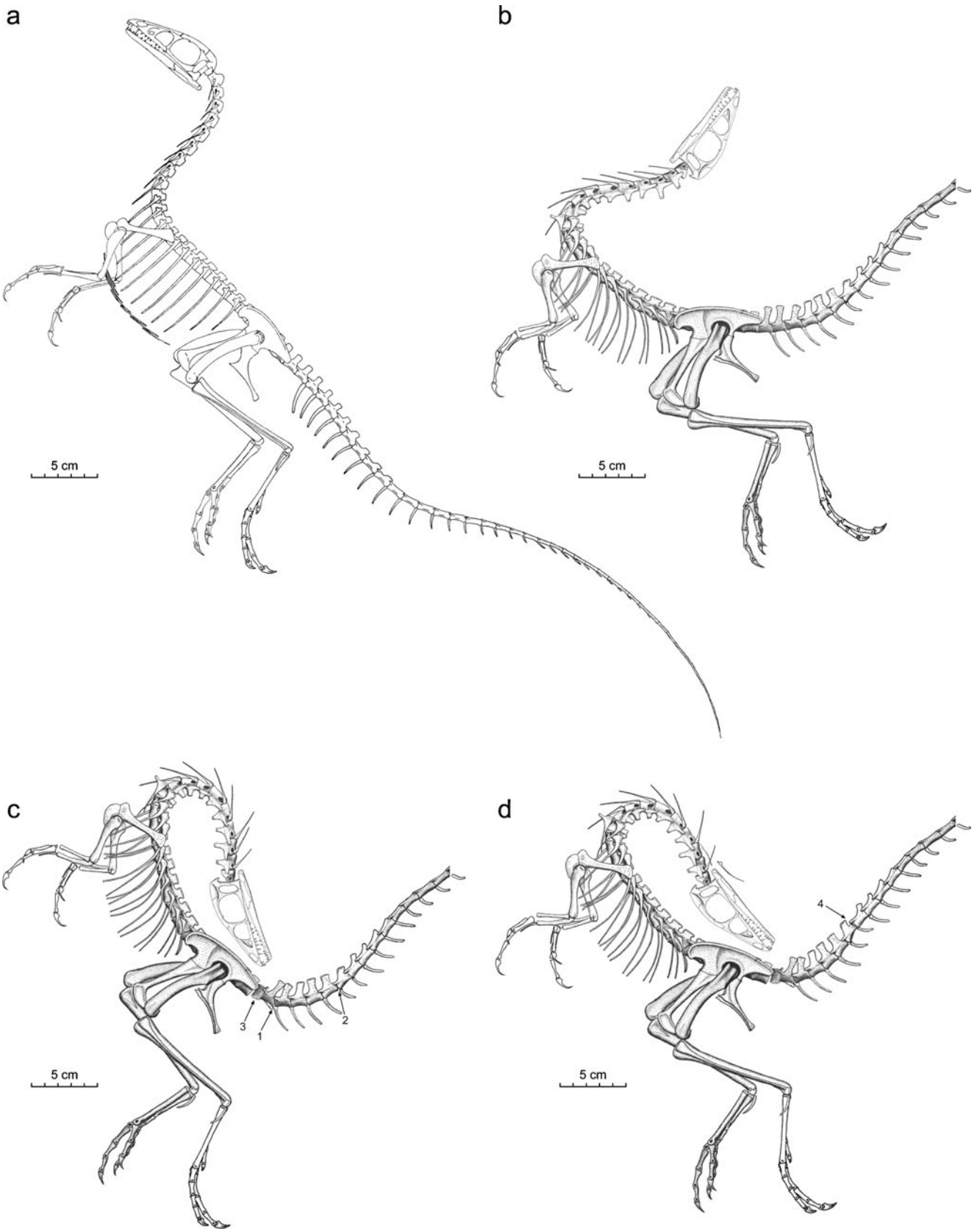
**Fig. 5 a** Specimen of *Compsognathus longipes* showing decay stage 1: specimen is lying on its left side, joints of head, neck, tail and extremities are in resting position [MLPP] (redrawn after Ostrom 1978: fig. 14, modified). **b** Specimen of *C. longipes* showing decay stage 2: muscles of the neck and tail are partly decayed, pre-stressed Ligamentum elasticum starts to bend neck and base of the tail backwards; disarticulation of the left Metacarpale I (1 Mc I) (after Ostrom 1978: figs. 1–3, and Gishlick and Gauthier 2007; modified). **c** Specimen of *C. longipes* showing decay stage 3: muscles of the neck and tail are partly decayed, pre-stressed Lig. elasticum further bending of neck and base of the tail backwards; (partial) rupture of connective tissue and ligaments of the first caudal; sequence: 2–3 (1), 6/7 (2), last lumbal–first caudal, and 1–2 (3), with rotation; from Ostrom 1978: fig. 1, modified. **d** Specimen of *C. longipes* showing decay stage 4: intensive backarching of the neck, disarticulation of cervical ribs; zygapophyseal blockage in the tail; rupture of connective tissue vertebrae 7/8 (4) (after Ostrom 1978: figs. 1–3, and Gishlick and Gauthier 2007: fig. 10; modified). **e** Specimen of *C. longipes* showing decay stage 5: jaw bones rest on the ground in anatomical position; required torsion of the neck is not illustrated; widening of the kink between vertebrae 7/8 (4); disarticulation of the articularia and of cervical ribs (after Ostrom 1978: combination of figs. 1, 2, and Gishlick and Gauthier 2007: fig. 10; modified). **f** Specimen of *C. longipes* showing decay stage 6: revertive rotation of the skull into anatomical position; further backarching of the neck; widening of the kink between vertebrae 7/8 (6); disarticulation of cervical ribs (after Ostrom 1978: combination of figs. 1–3, and Gishlick and Gauthier 2007: fig. 10; modified). **g** Specimen of *C. longipes* showing decay stage 7: further backarching of the neck until the skull is arrested by the trunk; decay of the skull starts (after Ostrom 1978: combination of figs 1–3, and Gishlick and Gauthier 2007: fig. 10; modified). **h** Specimen of *C. longipes* showing decay stage 8: cervical spine arches backwards, removing the braincase out of the skull; disarticulation of skull elements and atlas and partly of the forelimbs (after Ostrom 1978: combination of figs. 1, 2, and Gishlick and Gauthier 2007: fig. 10; modified)

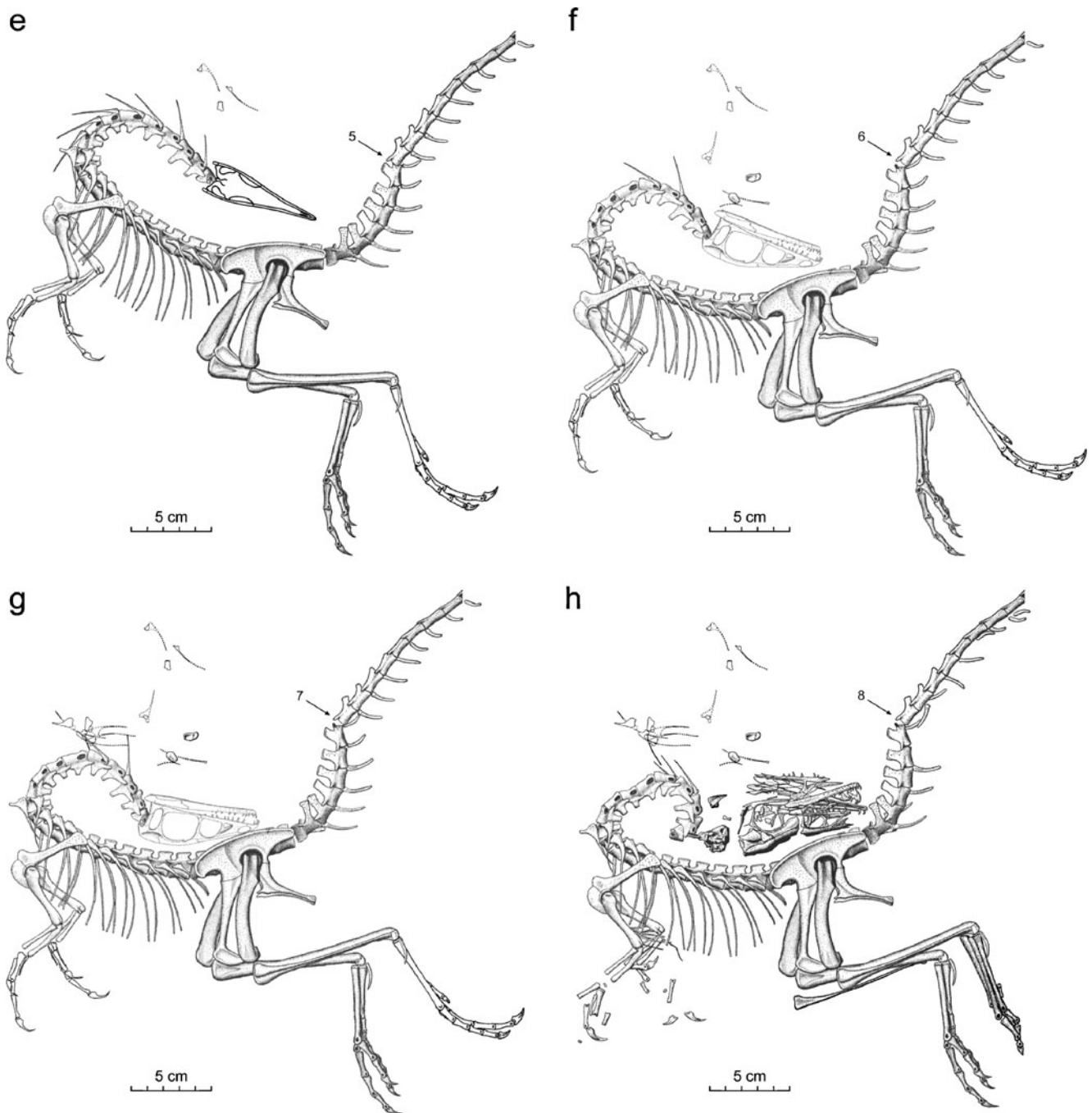
that the fossil horizon of the slab represents the basis of the slab. We related this working hypothesis to the other anatomic units of the specimen and developed a taphonomic scenario for the *Compsognathus* specimen (subdivision of the degradation process in single, consecutive decay stages).

The taphonomic phenomena (disarticulation, dislocation) that occur at the anatomic units of the cranial and postcranial skeleton were thereby used as validation. Balancing our reconstruction of the taphonomic scenarios and the individual findings, and furthermore considering our working hypothesis, we conclude that the specimen *Compsognathus* is exposed at the bottom side of the slab.

### Interpretation

By way of the positional relationships of the skeletal elements of *Compsognathus*, individual phases of the decompositional history of the specimen can be distinguished and, for the most part, reconstructed on the basis of our experiments. The starting point of the reconstruction of this taphonomic scenario is the nearly complete (minimal completeness 74%, according to Kemp and Unwin 1997) and mostly articulated skeleton (articulation degree 76%,





**Fig. 5** (continued)

according to Kemp and Unwin 1997). Missing elements likely became lost through incomplete recovery (parts of the tail) and through later handling, for example during the creation of the forms for molds (Wellnhofer 1996). The counter slab, which possibly contains some skeletal elements, has been lost (Wellnhofer 1996).

The time and distance of transport are speculative because the spatial relationships of the skeletal elements provide no evidence as to whether this *Compsognathus* was swept into the sea while alive or as a carcass (see Discussion).

Decay Stage 1 (Fig. 5a): The picture of *Compsognathus* after its arrival at the bottom of the lagoon can be analysed using constructional–morphological and forensic evidence and considerations. Based on these findings from these analyses, a multiple-stage decomposition scenario can be recreated.

*Compsognathus* reached the seafloor either antemortem or directly after it died, or, at the very latest, in a very early stage of decay, after a maximum of a few hours of drifting time (see Discussion). In the last case, it is likely that mainly

autolytic processes were occurring at that time. In spite of the assumed water temperature of 16.9–26°C (see [Palaeobathymetry and palaeo-water temperatures](#)), during the drifting time to the depositional location, bacterial gas-producing decay occurred—if at all—only to a small degree within the intestines and in the head. Otherwise, the decay process would have resulted in putrefactive bloating within a few hours, the consequence being a substantial decrease of the specific gravity and thereby a lengthy floating of the carcass at the water's surface.

At the time of deposition, all soft-part tissues that had an effect on the position of the joints were still intact. It is uncertain what position the extremity joints were in when they reached the seafloor. It is certain, however, that the *Compsognathus* specimen came to settle onto a firm surface which, though lacking evidence of higher organisms, was certainly inhabited by microbes (e.g. Briggs 2003). If the specimen reached the seafloor antemortem, then the death posture was transformed into an MLP position at the point of death at the latest. If, on the other hand, the specimen reached the seafloor pre-rigor mortis, then the MLP position was already established at that point in time in the fresh carcass. Then again, if this *Compsognathus* died on land and was then transferred to its place of deposition already in rigor mortis, then the strong extremity positions fixed by rigor mortis can no longer be reconstructed because following the passing of rigor mortis on the seafloor, the MLP position was achieved on the seafloor through the lack of sticky friction or through the floating of the carcass, as evidenced by the lack of settling and drag marks [the “drag marks” referred to by Abel (1919) are actually mineral precipitations on the surface: Liesegang rings).

Because of the tension and pressure distribution within the musculature and the ligamental system, the neck and tail of *Compsognathus* took on the typical resting position (= MLPP).

The following phases of advanced decomposition began to take place after the site of deposition was reached. Based on the lack of evidence for wave action effects on the seafloor (as far as can be interpreted from the fossil slab), it can be assumed that the water depth at the site of deposition exceeded the storm wavebase; therefore, the carcass (or pieces of it) was subjected to neither current-induced maceration nor current-induced transport in any substantial way. Apparently, conditions inhospitable to life dominated the seafloor, such that the carcass was protected from scavengers (see [Palaeoenvironment and taphonomic landscape of \*Compsognathus\* and \*Juravenator\*](#)). However, it can be assumed from the climatic conditions that the water temperature was such as to allow an early onset of decompositional processes (see [Palaeobathymetry and palaeo-water temperatures](#)). Even if not limited or prohibited a priori by chemical properties of the seawater, the hydrostatic pressure at the

depositional site alone would limit the expansion of substantial amounts of buoyancy-producing gases (Boyle's law), which in a shallower area would have led to the surfacing of the carcass (cf. Adelson 1974; Kemp 2001; König 1892; Krause 2004; Reisdorf et al. 2012, this issue; Tomita 1975, 1976).

Decay Stage 2 (Fig. 5b): At this point in time, the torso and the ventral neck and the ventral tail musculature in the area of caudal vertebrae 1–7 have been so extensively decomposed by microbes that there is an initial recurvature of the neck, trunk and tail (caudals 1–7) due to the pre-load of the Ligamentum elasticum (see chapter [Experimental results](#)). Through this, the tension on the ligament connections of the first caudal vertebra and on the ligaments between caudals 7 and 8 is increased.

Decay Stage 3 (Fig. 5c): Prograding decomposition damped the strength of the muscles along the spine so much that the cervical spine reached its maximum recurvature without decay of the intervertebral discs. Zygapophysal blockage stopped the recurvature along the whole spine. A sufficiently strong tension force exists only on the first to third caudal vertebra (Fig. 5c, 1) and on the connections between caudals 6 and 7 (Fig. 5c, 2), rotating the first caudal vertebra in the median plane (Fig. 5c, 3), and thus tearing the ligament connections between caudals 6 and 7.

Decay Stage 4 (Fig. 5d): Stage 4 is the first phase of decomposition that can be deduced directly through the distribution pattern of disarticulated and dislocated skeletal elements. Because of the partial decay of the skin of the neck area, the cervical ribs of cervical vertebra 6 become dislocated. The same applies to the left hand side, as the left metacarpale I becomes disarticulated and sinks to the sediment. From the position of scattered bones and the absence of drag marks, we assume that the trunk floated above the ground, anchored by more distal parts of the tail. The connection between caudal vertebrae 7 and 8 starts to disintegrate (Fig. 5d, 4).

A possible substantial sealing or fixing of the carcass by microbial mats (cf. Hecht 1933; Link and Fürsich 2001) is thus unlikely to occur at this time.

Decay Stage 5 (Fig. 5e): The trunk with its connected neck and skull and caudal vertebrae 1–7 start to rotate relative to the lower part of the slab, while the rest of the tail maintains the position it assumed in Stage 1. This relative movement is assumed to be the result of a weak, directed current—one so weak that it could not cause the dislocation of any skeletal elements. Connective tissue between caudal vertebrae 7 and 8 is so stressed by the movement of the trunk that it partly ruptures (Fig. 5e, 5).

The cervical column curves further, and cervical ribs 6–10 and 3 either start to become disarticulated and sink onto the sediment or, if they are partly touching the seafloor, remain connected. The skull finally comes to lie on the

sediment ventrally with its lower jaw, which is still articulated and thus anatomically connected. This is where the articularia finally become disarticulated, while still maintaining their former anatomical relationships. The left articular comes to rest on of the cervical ribs of cervical vertebra 3.

Decay Stage 6 (Fig. 5f): The torso with its connected neck and head rotate into its final position relative to the lower border of the slab, while the rest of the tail remains in position.

As a consequence of this, the kink in the tail at the connection between caudal vertebrae 7 and 8 becomes stronger (Fig. 5f, 6): caudal vertebrae 8 to probably 60 (Peyer 2006) remain in their original position, possibly as a result of adhesion forces. There is disintegration and displacement of some of the haemal arches within the integument.

Advancing decay of the musculature additionally releases pre-load forces of the Lig. elasticum. As a result, there is a strong curving of the neck, with the skull becoming pressed onto the torso in the pelvic area.

Decay Stage 7 (Fig. 5g): The curvature of the neck continues to increase. Owing to the still mostly intact ligament connections between the atlas, axis and occiput, the connected braincase and epipterygoids start to disintegrate from the rest of the skull and are dislocated caudally.

The ligamental connections between occiput, braincase, atlas and axis disintegrate. The atlas and braincase sink separately to the seafloor. The braincase with the anterior part arrives at the sediment first, rotates perpendicular 90° to its longitudinal axis, and finally tilts towards the parietal with its caudal rim.

While the torso is arriving at its final position, the first phalange of the first digit of the left foot and parts of the right hand become disarticulated.

Decay Stage 8 (Fig. 5h): The facial bones lie on the sediment slightly dorsolaterally tilted on the lower right side of the skull and disintegrate in situ. During movements via the trunk, the left maxilla becomes “glued” to the sediment and disintegrates. Other elements of the skull are pulled nearer to the trunk over the left dental to the sediment surface. The left and right mandibular rami become disarticulated. Fixed in place by connective tissue the interosseous connections of the right maxilla and the right lacrimal remain articulated with the nasals. The nasal–parietal connection decomposes. All elements lie bone on bone, without sediment between them.

Cervicals 2–5 curve even further, accompanied by the decay of the intervertebral discs (through a slight opening of the articulation surfaces of the centra). The neural arches of cervical vertebrae 2 and 3 become disarticulated and incline laterally.

Following the final, possibly current-induced oscillations, by which the right fibula and elements of the left and right hand are ripped off and fall onto the surface of the sediment, the torso finally also comes to rest on the

sediment surface. The integument breaks open in the posterior area of the torso. Decay fluids transport the disarticulated skull of the prey animal and the posterior gastralia of the *Compsognathus* outwards from the inside of the body and towards the knee joints.

### Conclusions

Based on the ligamental connections of the individual joints, a relative timeline can be determined of the sequence of decay, as well as for the relative resistance of particular types of tissue to decay under the conditions of a subaquatic decomposition. It should be noted here that the decomposition of a carcass floating at the surface of the water differs significantly from subaquatic decomposition, especially concerning the extremities and the lower jaw (cf. Haglund 1993; Schäfer 1962, 1972). Most vulnerable to decay were apparently the ligamental connections of the cervical ribs and those of the finger and toe joints compared with the other joint connections of the extremities. Ligamental connections closer to the torso began to decompose only when the carcass finally came to rest fully on the sediment surface. The dorsal ligaments of the spine the Lig. elasticum in particular were more resistant to decay than other intervertebral ligaments.

It is not possible to reconstruct whether the prey animal had been digested premortem, before the deposition of *Compsognathus*. Reptiles digest food more slowly than mammals (e.g. Secor and Phillips 1997). This, however might have been different if theropod dinosaurs had a bird-like metabolism (O. Rauhut, personal communication 2011). It seems probable that the decay of the skull is attributable to the decay process within the carcass of the *Compsognathus* and not to digestive processes, which also would have attacked the extremities and the vertebral column (see Nopcsa 1903: plate XVII).

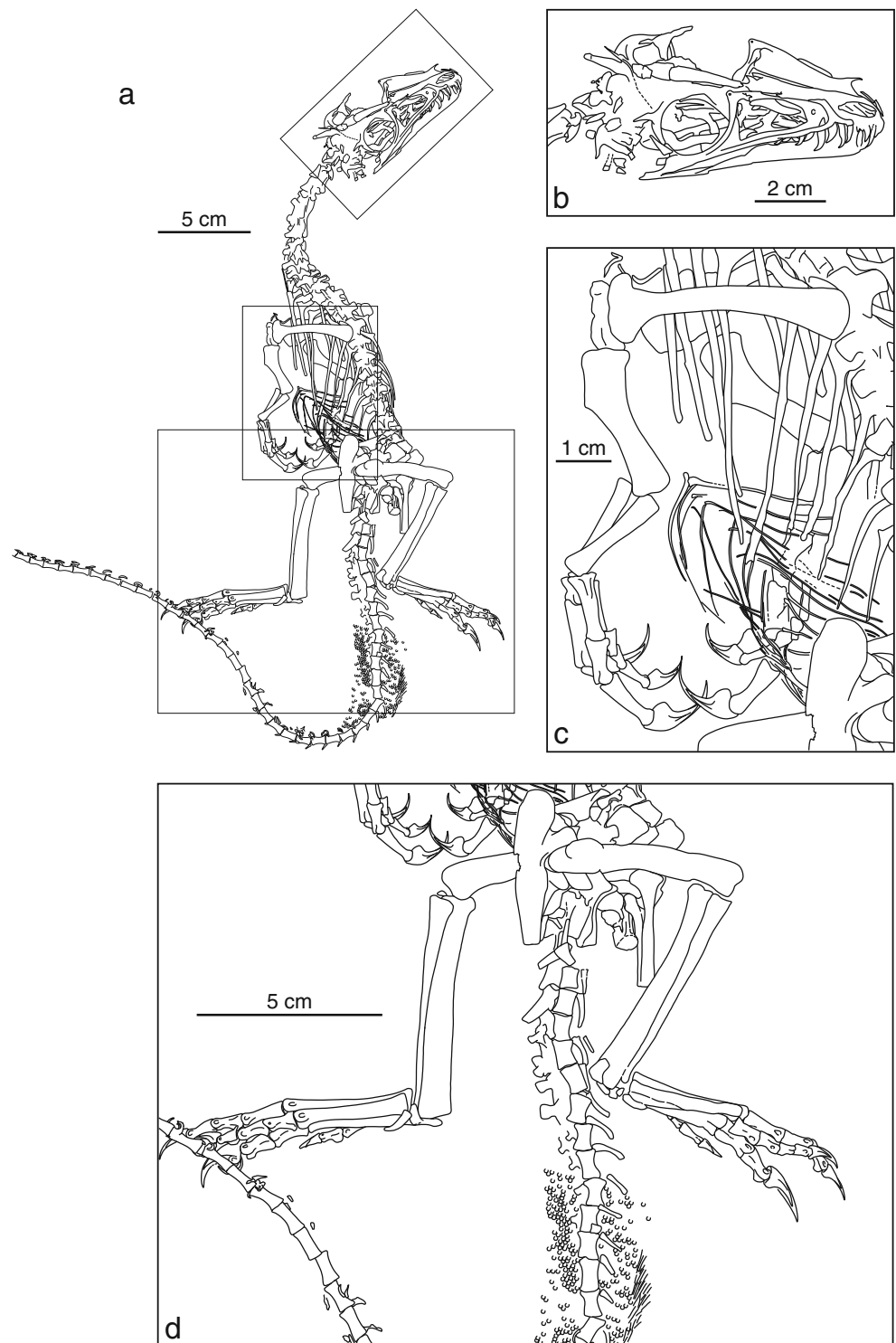
The lack of sediment between the skeletal elements of the skull, which are laying bones on bones, indicates that the carcass did not serve as a sediment trap up to the time of its complete skeletonisation (cf. Janicke and Schairer 1970; Viohl 1994: isolated scale armour of an *Aspidorhynchus* fish; Supplement Fig. 2). This itself suggests a low rate of sedimentation at the place of deposition during the weeks and months the decomposition of parts of the various soft tissues and the adipocere formation at the surface of the seafloor is likely to have lasted (see [Sedimentation rates and Subaquatic decomposition and adipocere](#)).

### Case 2: *Juravenator starki*

#### *Current knowledge on the taphonomy of Juravenator starki*

Viohl (1999) and Viohl and Zapp (2006, 2007) assume that this *Juravenator* (Figs. 3c, 4b, 6a, ) must have lived on a

**Fig. 6** **a** Contour drawing of *Juravenator starki* with mark-ups of close-ups. Close-ups: **b** skull, **c** shoulder girdle, forelimbs, gastralia, **d** pelvis, proximal caudal vertebrae, hindlimbs (after Chiappe and Göhlich 2010, modified; courtesy of L. Chiappe and U. Göhlich)



nearby island and, furthermore, that it was probably washed into the basin, where it drowned, by a flash flood during the monsoon season. The high degree of completeness and articulation of the specimen is explained by the very short period of time between death and emplacement on the seafloor (see also Kemp 2001). According to the model concept of a stratified water body and a seafloor subjected

to hypersaline, dysaerobic conditions, the fresh carcass became rapidly overgrown by bacterial mats (Viohl 1999; Viohl and Zapp 2006, 2007).

Göhlich et al. (2006) and Chiappe and Göhlich (2010) share the opinion that the features of the skeleton preservation and the accompanying soft-part conservation suggest a drifting into the Schamhaupten Basin shortly after death or

drowning near the place of deposition (because of the lack evidence, however, nothing concrete was stated here about the cause of death; cf. Dal Sasso and Maganuco 2011). While floating, the cadaver was colonised by isopods (see also Viohl and Zapp 2006, 2007), considered to have been carnivorous scavengers. Soft tissue of the *Juravenator* specimen presumably is preserved by microbial mats under hostile conditions (Chiappe and Göhlich 2010). Torsions within the carcass are explained—with or without reservations—by compaction during burial diagenesis (see *Orientation of the slab of *Juravenator starki**; Chiappe and Göhlich 2010; Viohl and Zapp 2006).

According to Riegraf (2007), however, the above hypotheses underestimate the transport potential of fully articulated terrestrial vertebrate carcasses in marine environments. In a review article, Riegraf (2007) conjectured that the *Juravenator* specimen did not come from a nearby island, but rather drifted from the Bohemian Massif (cf. Meyer and Schmidt-Kaler 1990; Schweigert 1998) into the Schamhaupten Basin.

#### *General description of *Juravenator starki**

The subadult specimen displays its left side (Fig. 4b), almost completely articulated. According to Göhlich et al. (2006) and Chiappe and Göhlich (2010) the only regions that have suffered some disarticulation are the skull, the pelvic girdle and the base of the tail.

**Skull:** Only some elements of the left side of the skull (Fig. 6b) are disarticulated; they have sunk down into the cavity of the inner skull. Only the left nasal, postorbital and squamosal are in near anatomical position. There is no sediment between overlapping bones.

**Cervical vertebrae:** The cervical column (Fig. 3c) is bent to the right; the vertebrae are exposed primarily in dorsal view. The cervicals are all articulated, but the region is not well-preserved, especially its cranial half. Most cervical ribs are missing, it is impossible to decide whether they are overlain by the cervical vertebrae, lost and scattered or lying in a deeper bedding plane.

**Dorsal vertebrae:** The dorsal spine (Fig. 3c) is entirely articulated, there are at least 13 dorsal vertebrae. Except the last one, which rotated 90° to the left, all of them are exposed dorsally.

Twelve pairs of thoracic ribs are preserved in near articulation, possibly representing the complete ribcage (Figs. 3, 4, 6).

**Gastralia:** A full set of partially articulated gastralia (Fig. 6c) is preserved in front of the pelvis. Disarticulations are displayed in the distal part of the row.

**Sacral vertebrae:** The sacrum was not fused (Chiappe and Göhlich 2010), and the vertebrae are disarticulated and disarranged (Fig. 6d); single vertebra cannot be identified, because they are partly covered by other bones.

**Caudal vertebrae:** The tail is curved to the left, all caudal vertebra, except the first one, are exposed in the right lateral view. The first caudal vertebra is disarticulated and contorted and presumably lies beneath the left ilium. Caudal vertebrae 2–10 experienced a compressive force, resulting in a zigzag-like evasion of the elements distally, and opening clefts between the single elements (Fig. 6d). This force was presumably performed by the contracting Ligamentum elasticum. Chevrons of caudal vertebrae 7 and 8 are disarticulated, but in near anatomical position.

**Shoulder girdle:** Both scapulae are preserved approximately in their anatomical position (Fig. 6c). The left coracoid is only partially articulating with the scapula; the right one is covered by the left scapula. The clavicals are preserved in disarticulation, lying at the cranioventral end of the left scapula. Chiappe and Göhlich's (2010) so-called clavicles actually represent fragments of the damaged furcula. The flexure of the central part is clearly visible (O. Rauhut, personal communication 2011).

**Pelvic girdle:** The pelvic bones are somewhat disarticulated—the ilia are displaced and exhibit their right sides. The heads of the femora are still in the acetabulum (Fig. 6d).

**Forelimbs:** The arms are in near MLPP (Fig. 6c). The humeri are slightly disarticulated and shifted some millimeters in ventral direction. The right forearm and the hand are fully articulated and in MLPP. In the left forearm the radius is disarticulated; the proximal end moved laterally.

**Hindlimbs:** The pelvic girdle has rotated with attached femora. The hindlimbs are still in near MLPP (Fig. 6d). The right knee joint is disarticulated; the proximal heads of the right tibia and fibula moved below the distal head of the femur. All other bones of the hindlimbs are in their anatomical position.

#### *Orientation of the slab of *Juravenator starki**

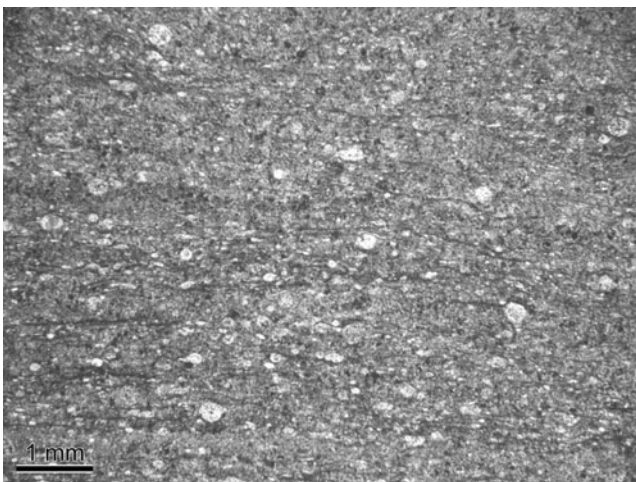
The *Juravenator starki* specimen was discovered in 1998 by two volunteer excavation assistants, Klaus-Dieter Weiß and Hans-Joachim Weiß, during an excavation campaign of the Jura-Museum Eichstätt (e.g., Viohl 1999). It was found in the “Stark” quarry located close to Schamhaupten (e.g., Göhlich et al. 2006; Viohl 1999). The find locality and the circumstances of the specimen's discovery are thoroughly documented (e.g., in Chiappe and Göhlich 2010; Göhlich et al. 2006; Viohl and Zapp 2006, 2007). During the excavation, performed by Klaus-Dieter Weiß and Hans-Joachim Weiß, the spatial orientation of the specimen was thoroughly documented (the N–S orientation was marked on the bottom as well as on the upper side of the slab; K.-D. Weiß, personal communication 2011). One of the two original north arrows, which are no longer visible, was documented photographically (see Fig. 3c; Chiappe and Göhlich 2010: figs. 3, 4; Göhlich et al. 2006: plate 1 and 2). The



photographs, which show the prepared specimen, reveal that the axial skeleton is cranially oriented northwards by approximately  $310^\circ$ . From the taphonomy chapter of Chiappe and Göhlich (2010), it can be deduced that the north arrow, photographically conveyed, apparently served as point of reference for the up–down orientation of the slab (thereby, the prepared surface was considered to be the upper side of the slab). Furthermore, we assume that the second north arrow was removed prior to the scientific investigation of the piece (and thus was not recognised by the processors). Given this background and considering the general wide acceptance of the deposition model of the Schamhaupten basin (see Röper 1997, 2005a; Viohl and Zapp 2006, 2007), the taphonomic analysis presented by Chiappe and Göhlich (2010) revealed an inconsistency with respect to the death posture of the specimen (assuming that the cadaver was oriented in a ventral position on the seafloor). This issue was addressed by Chiappe and Göhlich (2010).

The problem was thus how the *Juravenator* specimen in his ventral position could have performed a torsion in front of the pelvis in a hostile, low-energy environment. A strong compaction of the embedding material during burial diagenesis is considered to be one explanation, albeit with reservation (cf. Chiappe and Göhlich 2010; see also Viohl and Zapp 2006).

Similarly to the *Compsognathus* specimen, we formulated two hypotheses regarding the original orientation of the slab (hypothesis 1: preparation was performed from the upper side of the slab; hypothesis 2: preparation was performed from the lower side of the slab). To verify the two scenarios, macro-invertebrates found on the slab were tested for their potential as upside–downside indicators (e.g. preferential orientation of specific fossil groups, geopetal structures; cf. Barthel et al. 1990/1994; Schweigert 2009).



**Fig. 7** Microfacies of the *Juravenator* slab. Bindstone (thin section JME Sch 200-1). According to Viohl and Zapp (2006, 2007), dark filaments can be interpreted as trichomes of cyanobacteria

Additionally, two thin sections of the slab were made and investigated by light microscopy (see Fig. 7). The number of invertebrate fossils actually visible anywhere on the slab is low. Neither the macro-fossils nor the thin sections revealed any signs of the existence of geopetal structures. However, an aptychus, located on the slab surface and oriented towards the *Juravenator* specimen, showed promising indications of being statistically significant with respect to a preferential spatial orientation (Fig. 3b, d). According to Janicke (1969: p. 152), Viohl (1985) and Barthel et al. (1990/1994), aptychi found in the plattenkalks of the Southern Franconian Alb are almost exclusively embedded in a position with the concave side up. Janicke's statistics are based on field data of 103 aptychi of which only five show features of the convex side being up. If we apply this statistically preferred orientation to the only aptychus found on the *J. starki* slab, it would render its orientation consistent with the slab orientation proposed by Chiappe and Göhlich (2010) (i.e. working hypothesis 1).

However, considering the two working hypotheses, we came to the conclusion that the taphonomic scenario of hypothesis 2 is less restrictive when compared to the model proposed by Chiappe and Göhlich (2010) (see [Current knowledge on the taphonomy of \*Juravenator starki\*](#)). K.-D. Weiß, the discoverer of the *J. starki*, readily confirms our view that the specimen is in fact exposed on the bottom side of the slab (K.-D. Weiß, personal communication 2011).

### Interpretation

The skeleton of *Juravenator* is preserved nearly complete and profoundly articulated; the incompleteness of the preserved tail is seen as an artefact of recovery. Through the altered spatial relationships of the skeletal sections, particular phases of the decompositional history of the specimen can be distinguished and reconstructed.

Only very limited statements about the transport history can be made, since from the spatial relationships of the skeletal elements, it cannot be determined with certainty whether this *Juravenator* found its way to the Schamhaupten basin while still alive (drowning there) or already dead (Chiappe and Göhlich 2010; Göhlich et al. 2006; Viohl 1999; see [Discussion](#)).

Decay Stage 1 (Fig. 3): Constructional–morphological and forensic evidence make it possible to reconstruct the posture in which *Juravenator* came to rest on the sediment–water interface and, based on reconstruction, to understand the multiple-stage decomposition history.

Similar to the *Compsognathus*, which was found in one of the neighbouring basins to the east, the *Juravenator* specimen reached the seafloor either antemortem or directly after death, or at least as a fresh carcass. In the last case, it was only the autolytic processes that had had a substantial effect at that

time. Here, in spite of the water temperature of 16.9–26°C (see [Palaeobathymetry and palaeo-water temperatures](#)) bacterial gas-producing decay occurred only minimally—if at all—while the carcass was drifting to the depositional site.

All the joints of the *Juravenator* were fully flexible when they reached the seafloor, as is evidenced by the curvature and condition of the tail.

The carcass reached the seafloor with its ventral side up (see [Orientation of the slab of \*Juravenator starki\*](#)). The head came to lie on its right side. The laterally compressed tail was curved to the left (Göhlich et al. 2006) with its right side up. The impact onto the seafloor apparently created a slight deformation of the sediment surface or a slight sinking into the sediment. This conclusion was drawn from the articulated preservation of the right side of the skull and the right side of the skullcap, which would have become disarticulated had they been only partially resting on the seafloor. Under the conditions of quasi-stagnating environment on the seafloor, the head and tail in this position enabled stabilisation of the torso in a ventral-side-up position (making the extremities point upwards into the water column). In this scenario, the MLP position of the extremities also became established in the fresh carcass.

The stages of advanced decay first started to take place at the site of deposition of the specimen. From the lack of evidence of wave-action effects on the seafloor, it can be assumed that the water depth at the site of deposition exceeded that of the wavebase, so that the carcass (or parts of it) was not exposed either to current-induced maceration or to current-influenced transport in any substantial way (see [Palaeobathymetry and palaeo-water temperatures](#)). The fine laminated bindstone is evidence of a colonisation of the sediment by microbial mats (e.g., Viohl and Zapp 2006, 2007; Fig. 7). Otherwise, conditions on the seafloor were apparently unfavourable to higher organisms, and so scavengers did not have access to the carcass (see [Palaeobathymetry and oxygen availability](#)). From the climatic conditions, it can be further assumed that the water temperature at the seafloor was in a range that allowed an early onset of decompositional processes (see [Palaeobathymetry and palaeo-water temperatures](#)). Even if the chemical properties of the seawater had not a priori limited or prohibited the decay processes, at least the hydrostatic pressure at the depositional site hindered the accumulation and expansion of buoyancy-producing decompositional gases in the carcass (e.g. Kemp 2001; Reisdorf et al. 2012, this issue).

Decay Stage 2 (Fig. 3): This stage can be reconstructed by way of the anatomical units that were the first to experience disarticulation and dislocation. Owing to the assumed only slightly fused cranial sutures of a sub-adult (Chiappe and Göhlich 2010), the elements of the left skull half were nearly completely disarticulated; many of these sank into the right half before there was an accumulation of sediment in

the cranium (Fig. 6a). At this time, the decomposition of the muscles and ligaments of the hindlimbs was so advanced that excursions of the joints beyond their natural degree of mobility were possible; it is also possible that the medial tendons became partly torn. As a result, the hindlimbs at the hip joints leaned outward, though while still remaining, as did the forelimbs, within the anatomical association of the skeleton.

Decay Stage 3: The intercostal muscles and connective tissue membranes became decomposed. The rib cartilage, yet to be ossified, was also so far decayed that the intercostal distances could be altered through passive movements (e.g. those of a gravitational nature).

The only slight shiftings of specific syndesmotomic connections of the gastralia are evidence that, although they were still an anatomical unit, the connective tissue connections between the gastralia were so far decayed that the spatial relationships between them were altered. At this point (Fig. 6c), the connective tissues attaching the gastralia to the rib cartilage and the pelvis were partially decomposed. The torso and the forelimbs lost integrity between each other, and because of their potentially imbalanced weight distribution due to the dorsal position of the carcass, they rotated, due to gravitation, onto the left side. During this movement, the cervical and thoracic vertebrae mostly maintained their original positions. The forelimbs and the pectoral girdles remained in anatomical association in the MLP position. The cervical ribs continued to nestle on the cervical vertebrae because of the unchanged ventral-up position of the torso and its axial skeleton. The heads of the ribs were free to move, yet the ligaments and tendons still held them in situ. During the rotation, the distal ends of the right-sided ribs moved caudally, strongly overlapping and nearing one another. The pelvis rotated as a moveable unit along with its articulated femora (cf. [Orientation of the slab of \*Juravenator starki\*](#)), meaning that all of the bands of the extremity joints were still stable enough to withstand the stresses of the rotation. The gravitationally induced movement resulted in a position that was unnaturally sprawling for bipedal vertebrates (cf. Kielan-Jaworowska and Hurum 2006). The tail remained on its right side, resulting in a disarticulation between the last sacral vertebra and the first tail vertebra. Caudal vertebrae 2–10 experienced the compressive force of the contracting Ligamentum elasticum, resulting in a zigzag like dislocation of these skeletal elements.

### Conclusions

The lack of peri-depositional sedimentary structures (e.g. settling marks, “life activities immediately prior to death” [cf. de Buissonjé 1985; Kemp 2001; Schairer 1968: fig. 9] and drag marks next to the specimen) and the dislocation of skeletal elements are indications that the specimen did not move from its initial position on the seafloor. The skull and

tail stabilised the fresh carcass in a ventral-up position. Subsequent spatial changes of skeletal elements occurred only during the advanced stages of decomposition within the carcass, resulting in gravitational movements of individual anatomical elements and functional units. This site-oriented decomposition speaks for extremely calm-water conditions and nearly abiotic, life-inimical conditions on the seafloor.

During the various stages of decomposition of the soft parts of the carcass, there was no—or only minimal—sedimentation, but one that could not be directly deduced from the prepared *Juravenator* specimen. This can also be said for any possible covering by microbial mats (Viohl and Zapp 2006, 2007; Fig. 7). From the uniformity of the finely laminated sediment (“*Kieselplattenkalk*” sensu Röper 1997) of the fossil’s slab (as well as the layers above the *Juravenator*), it can be concluded that before, during and after the decomposition of the carcass there were consistent depositional conditions on the seafloor, which manifested in a slow rate of sedimentation (see [Sedimentation rates](#)).

The rotation of the torso was a consequence of the taphonomic constellation, that is, the landing position and the initial resting position of the carcass. Therefore, it is not an artefact of the burial diagenesis (compare in this respect the perspective in Chiappe and Göhlich 2010; see also Viohl and Zapp 2006)—in other words, not the result of a compaction of the sediment and the animal closed within it (see [Orientation of the slab of \*Juravenator starki\*](#)). The absence of an “opisthotonic posture” sensu Faux and Padian (2007) in the *Juravenator* specimen (Chiappe and Göhlich 2010) can be explained by the assumed stabile dorsal placement of the carcass from the initial stage (due to a slight deformation of the surface sediment at the sea bottom=impact of the carcass onto the seafloor) and up through the advanced stages of decomposition (with possible support from adhesive forces and, possibly, by bacterial exopolymer “gluey” substances and/or overgrowth): the (still relatively) weakly developed Ligamentum elasticum (as shown by the flat spinal processes of the neck, torso and proximal tail vertebrae as well as the short neck) of this sub-adult were incapable, after the maceration of the neck musculature, of releasing the pre-load bound energy in such a way as to support the carcass in a lateral position and to give free rein to the backwards-curving of the neck (for the taphonomic mechanism of neck recurvature, see [Experimental results](#)).

## Discussion

### Palaeoenvironment and taphonomic landscape of *Compsognathus* and *Juravenator*

With respect to the interpretation of the sedimentological and palaeontological inventory of the Late Jurassic

lagerstätten, there are at the present time fundamentally varying models of the palaeoenvironment that strongly invoke Barthel’s publications (see below). Karl Werner Barthel can be seen as one of the most important pioneers in modern plattenkalk research. His name is linked with a paradigm change in the interpretation of fossil lagerstätten, leaving behind the notion of episodically flooded or emerged areas (cf. Barthel 1964) and embracing the idea of a depositional setting dominated by an enduring epicontinental sea (Barthel 1970, 1972, 1978; Barthel et al. 1990/1994). In the history of research of the plattenkalk deposits and lagerstätten, there are currently two palaeogeographical hypotheses existing in opposition to one another: (1) a marine environment permanently submerged and (2) an at least episodically recurring subaerial exposure of areas near the coast (“*Trockenlegungs-Hypothese*” [“drying-out hypothesis”], Barthel 1964). The first adherents of constant subaquatic formation conditions included Gumbel (1891) and Krumbeck (1928), while those first adherents of the “drying-out hypotheses” included Abel (1922, 1935) and Mayr (1967), as well as Weigelt (1927: pp. 97, 106, 206) and Schäfer (1941, 1962, 1972), with the last two being most certainly the most prominent pioneers of taphonomic research. The paradigm change initiated by Barthel (1970) appears especially remarkable in this light. These facts of the history of science are of a fundamental importance for the plausibility and stringency of the “opisthotonic posture” hypothesis of Moodie (1923) and Faux and Padian (2007) (in terms of the terrestrial fauna of the Late Jurassic Solnhofen Archipelago they analysed: *Archaeopteryx*, pterosaurs, *Compsognathus*). This is especially so because both Moodie (1923) and Faux and Padian (2007) accepted an aquatic-embedding scenario. [Moodie (1923: p. 324) stated: “There are however a great number of vertebrate skeletons known in a fossil condition whose positions we are assured have not suffered a change since the interment of the body; such skeletons are commonly seen in aquatic deposits, such as the prolific Solnhofen slates, wherein we feel confident that the conditions represented are indications of what took place when death occurred.” Faux and Padian (2007: p. 223) stated: “It raises anew the question whether the pterosaurs, birds, and terrestrial dinosaurs (who obviously did not live in the lagoon waters) died in the lagoon for some reason, or died very near it and were rapidly immersed and buried in it.”]

We also are of the opinion that the embedding of the “Solnhofen specimens” used as evidence by Moodie (1918, 1923) and Faux and Padian (2007) took place subaquatically. This consensus more or less forms the context of the following examinations of the palaeoenvironment and the taphonomic scenarios linked to it. In this section, we focus on the environmental settings from which derive both specimens examined in this study: for *Juravenator starki*, this is

the Schamhaupten Basin, and for *Compsognathus longipes*, the Painten Basin (Jachenhausen locality) or the Kelheim Basin (Riedenburg–Kelheim region). In the following analysis, we view the overall rare finds of terrestrial vertebrates in these plattenkalks (e.g. Kemp 2001; Viohl and Zapp 2007; Wellnhöfer 2008) as taphonomic snapshots of the actual find areas rather than—as explained below—as a generalised genesis model of all the basins of the Late Jurassic Solnhofen Archipelago (cf. Ebert and Kölbl-Ebert 2010; Röper et al. 2000; Viohl 1998).

### Palaeoclimate

According to the palaeolatitude (29–35°N; Billon-Bruyat et al. 2005; Munnecke et al. 2008; Oost and De Boer 1994), fossil finds (e.g. xerophytic plants), isotope geochemistry, clay mineralogy and a subtropical to tropical as well as a semiarid to arid climate can be reconstructed for the Solnhofen Archipelago during the Late Kimmeridgian and Early Tithonian (e.g. Barthel 1964; Barthel et al. 1990/1994; Bausch 2006; Billon-Bruyat et al. 2005; de Buissonjé 1985; Oost and De Boer 1994; Röper et al. 1999; Viohl 2000; Viohl and Zapp 2006). de Buissonjé (1985) determined the palaeotemperature on land to be approximately 28–30°C (with an annual and daily variation of <5°C). A vertebrate carcass on land today decomposes significantly faster under such climatic conditions than in a temperate or polar climate (e.g. Micozzi 1991, 1997; Notman et al. 1987; Richards and Goff 1997; Tullis and Goff 1987; see also Ambach et al. 1991; Benecke 2008; Rollo et al. 2007). A fundamental extrinsic factor controlling decomposition is the environmental temperature (Galloway et al. 1989; Pinheiro 2006; Sledzik 1990; Tsokos and Byard 2011), and this is also true for aquatic environments (e.g. Anderson and Hobischak 2004; Brettel 1978; Davis and Goff 2000; Haglund and Sorg 2002; Kahana et al. 1999; Smith and Elder 1985).

### Palaeobathymetry and palaeo-water temperatures

Using stable isotopes, calculations of the seawater temperature of the Solnhofen Archipelago have been made for the Solnhofen Basin (= *Wanne*) (Billon-Bruyat et al. 2005) but not for the Schamhaupten, Painten or Kelheim Basins. The Solnhofen Basin is approximately 45–65 km west of the other basins (cf. Barthel et al. 1990/1994; Röper et al. 2000; Viohl 2000). Billon-Bruyat et al. (2005) investigated the oxygen isotope compositions of fish (Osteichthyes) and reptile (Crocodylia, Chelonia) finds of the Early Tithonian age in the plattenkalk of the Solnhofen Basin (late Hybonotum Zone; cf. Groupe Français d'Étude du Jurassique 1997: p. 100). The calculated palaeo-water temperature ranged from 16.9 to 22.9°C. From a biological perspective, “these temperatures seem to be very low: According to Markwick

(1998), in recent crocodiles, longer spells of temperatures below 18°C can result in organ malfunction, and feeding is already restricted at temperatures below 22°C. If these conditions applied to marine crocodiles, which represent the most common marine reptiles in the plattenkalks (together with turtles), the temperature probably did not drop below 20°C for longer periods of time” (O. Rauhut, personal communication 2011; see also Volkheimer et al. 2008).

The assumed water temperatures using only the Solnhofen fishes are 16.9–21.8°C (18.8±2.6°C). These palaeo-water temperatures are relatively low considering the generally deduced tropical palaeolatitudes for the Late Jurassic Solnhofen Archipelago and thus are barely compatible with the corals that appear in the broader Solnhofen area. These corals were considered by de Buissonjé (1985) and Barthel et al. (1990/1994) to be indicators for relatively warm water (conjectured surface temperature between 26° and 28°C; cf. Billon-Bruyat et al. 2005). If these temperatures from Billon-Bruyat et al. (2005) are accepted, the question then arises whether the fauna found and investigated in Solnhofen is actually endemic, or whether the water temperatures based on the existence of the corals are too high; possible evidence for the latter is the only occasional appearance of the tropical radiolarian *Vallupus hopsoni* (cf. Joyce 2000; Matsuoka 1996; Zügel 1997). Nevertheless, the temperatures calculated by Billon-Bruyat et al. (2005) are significantly lower than the oft-cited water-surface temperature of 26°C in the plattenkalk literature of the last decades by Engst (Engst 1961; calculated using oxygen isotope compositions of calcite belemnite guards of the Eichstätt area; cf. Barthel et al. 1990/1994; Mayr 1964). However, to use Engst's (1961) temperature value in general for the lagerstätten of the Late Kimmeridgian and Early Tithonian—regardless of the critical evaluation of isotope measurements taken from belemnite rostrums for this time (Veizer 1977; Veizer and Fritz 1976)—is in own view questionable considering the time frame, because this value was determined by Middle Kimmeridgian specimens of the Treuchtlingen Formation (cf. Barthel 1964; Mayr 1964; Schmid et al. 2005, 2008). Moreover, during the Middle Kimmeridgian, the plattenkalks were not yet being deposited in the area of the present-day Southern Franconian Alb (e.g., Keupp et al. 2007). An appropriate facies for the Middle Kimmeridgian is so far known only from the Northern Franconian Alb (Fürsich et al. 2007a, b). Concerning the two specimens investigated in the context of this study, the palaeotemperature values published by Billon-Bruyat et al. (2005) can be best applied, with respect to age, to two possible places of origin and stratigraphic levels for *Compsognathus longipes*: Jachenhausen (Painten Basin) and Goldberg (Kelheim Basin).

The degree to which the palaeotemperature values calculated by Billon-Bruyat et al. (2005) tend to be adapted to

taphonomic scenarios in a three-dimensional (3D) space of a basin (with a lagerstätte in the making) depends not least on which of the two competing models for the palaeoenvironment of the “Plattenkalk-Wannen” is preferred. This question will also naturally have to address the problem of the temperature at the seafloor, one of the crucial extrinsic factors influencing the decomposition of a sunken carcass.

As mentioned above, both of these models are based on Barthel (1964, 1970, 1972, 1978; Barthel et al. 1990/1994). The two hypotheses derived from these models differ from each other in their bathymetry.

Model 1 (e.g., Keupp et al. 2007; Viohl 1998, 2000): This model is based on a practically permanent, more than 20-m-deep water column, which in more or less generalised form is applied to the areas where the plattenkalk facies occur. It is currently assumed that, for typically developed plattenkalk, water depths were approximately 60 m (de Buisonjé 1985; Schwark et al. 1998; Viohl and Zapp 2007). Plattenkalks with ichnofabrics could indicate depositional conditions at shallower water depths (Viohl 2000; see also Etter 2002). The advocates of this hypothesis divide the water column into an oxygenated, hospitable surface zone with more or less normal salinity, and a mostly hostile, probably dysoxic or anoxic, deep zone (e.g. de Buisonjé 1985; Keupp et al. 2007; Viohl 1994). Schwark et al. (1998) propose that photic zone anoxia was probably at least an intermittent occurrence. A mostly stagnating water body is expected for the seafloor, which would mean an extremely low-energy environment (e.g. Keupp et al. 2007; Viohl 1998). Possible indicators for directional currents at the seafloor are attributed to turbidities or the presence of a channel connecting two basins (Barthel et al. 1990/1994; cf. Röper et al. 1999; Viohl 1998, 2000). Viohl (1985, 1998, 2000) and Tischlinger (2001), for example, make the case for a salinity stratification of the water column (with a chemocline), which would result in hypersaline conditions in the bottom water (salinity <117 ppt, averaging between 40 and 80 ppt; compare also Kemp and Trueman 2003). For the Schamhaupten Basin (the find site of *Juravenator starki*), Viohl and Zapp (2006, 2007) speak of saline values at the seafloor lower than those claimed for the Solnhofen Basin, for example.

Model 2 (e.g. Röper 2005a, b; Röper et al. 2000): This model fundamentally asserts, and to a greater extent than Model 1, significantly different depositional environments for the individual basins. Along with the varying sea levels, Model 2 posits the individual palaeo-oceanic positions and seafloor morphology of the basins as fundamental causes for the sedimentary differentiation both temporally and spatially (e.g. Röper et al. 1998, 1999). Sea levels of 20 m down to very much shallower levels were common for many of the basins of the Solnhofen Archipelago and episodic at least for some. Given such conditions, Röper (1997) and Röper et al. (2000) envision not only depositional settings that are

influenced by the hydrodynamic regime of storm and fair-weather wave-bases, but also ones where tides could have their effect (for example, in the form of bottom currents). A bathymetry of approximately 20 m is in a range where the usual hospitable conditions down to the seafloor can be expected. This scenario is taken into account especially in terms of the biotopes of benthos. On the other hand, it is less the single finds and more the mass occurrences of marine invertebrates and vertebrates that provide evidence of a dramatic deterioration of the conditions favourable to life of such biotopes. For such scenarios, Janicke (1969), Röper (1997) and Röper et al. (1999, 2000) see episodic oxygen deprivation and hypersalinity from water warming and evaporation as possible causes, especially when, at low sea level, part of a morphologically more strongly subdivided basin becomes separated (salinity variability through freshwater inflow is discussed further in Röper et al. 1998, 2000).

From this short outline, it emerges that only the second of the two models provides enduring hospitable conditions at the seafloor. Accordingly, only in the second model could the deepest area of the water column be colonised regularly by nekton (cf. Mayr 1967: plate 7/2; Röper et al. 1998). These two models, so different in their bathymetry, thus have far-reaching consequences for speculations about the water temperature at the seafloor. In this regard, if the isotope studies of the nekton sediment are considered (cf. Billon-Bruyat et al. 2005; Engst 1961), then the calculated temperature values can theoretically apply only to the seafloor water of the second model. Nevertheless, neither of the two models rules out decay processes that are temperature-determined. de Buisonjé (1985) assumes in this context relatively low temperatures for the stagnant bottom water. Kemp (2001) also speaks about a reduced water temperature. This would at least imply a water temperature higher than 4°C (cf. Berg et al. 1969; Elder and Smith 1984; Mueller 1953; Reh 1968), whereby in Model 2 these temperatures are estimated to be clearly higher because of the significantly decreased bathymetry (cf. Keupp et al. 2007; Mayr 1964; Röper et al. 2000).

#### *Palaeobathymetry and oxygen availability*

As has already been remarked upon, hypotheses concerning oxygen availability at the seafloor are naturally closely associated with the bathymetry of the depositional environment. Advocates for a water depth of approximately 60 m are at least in agreement that a body of water close to the bottom in most cases experienced no direct hydrodynamic turbulence from meteorological phenomena. Storm-induced seafloor currents and bottom-affecting waves occurred in this scenario only episodically and seldom led to a significant mixing of the water body. Quasi-stagnating bottom water can be concluded from the regular fine sedimentation,

the associated fossils with settling marks and “marginal sulcus”, the extraordinarily high percentage of fossils distinguished by a high degree of completeness and articulation and the organism remains decayed in situ and only insignificantly dislocated (e.g. de Buissonjé 1985; Janicke 1970; Keupp et al. 2007; Rau 1969; cf. Röper et al. 1999; Tischlinger 2001; Viohl 2000). In contrast, finds that represent food falls attacked by scavengers at the site of deposition are extremely rare (Mayr 1967; Viohl 1998, 2000; specimen JME-SOS8323 of the Jura-Museum Eichstätt; for the term *food fall* see, for example, Kemp et al. 2006; Sorg et al. 1997). The rarity of such specimens is considered to be a definite indicator for hostile conditions in the stagnant environment. While referencing the typical Solnhofen Plattenkalks (according to the definition, created in nearly bioturbation-free layers), such a life-inimical habitat is often applied to other plattenkalk deposits and, ultimately, in the sense of Barthel (1970, 1972, 1978; Barthel et al. 1990/1994), conceived of as anaerobic or dysaerobic environments (e.g. Keupp et al. 2007; Röper et al. 2000; Viohl 1998, 2000; but see also Kemp and Trueman 2003). Bioturbation horizons—especially those in association with preserved benthic and epibenthic life forms—are considered to be indicators for a renewal of the bottom water, occurring only partially and episodically, which would entail life-conducive environmental conditions. This explanation is considered to apply to stratigraphic horizons as well in which autochthonous benthic foraminifera, ostracods and gastropods occur (e.g. Viohl 2000 and references therein; see also Janicke and Schairer 1970: p. 460).

Röper et al. (1998, 1999, 2000) also agree in principle with the possibility of stagnation conditions at the seafloor—especially when, in the plattenkalks, restrictive conditions are evidenced by bituminous sediment layers or when particular stratigraphically levels exist that are characterised by mass occurrences of marine fauna (Barthel 1964, 1976; Keupp et al. 2010; Link and Fürsich 2001; Meyer and Schmidt-Kaler 1993; Röper et al. 1998; Schwark et al. 1998; cf. Walther 1904). Röper et al. (1999, 2000), however, refute the hypothesis that in the depositional settings the plattenkalk still-water environments can generally establish themselves only underneath the storm-wave base and only at the bottom of a stabile stratified water body. Röper (1997) and Röper et al. (1999, 2000) discuss the scenario of still-water conditions at low water that lead to significant enrichment of oxygen dissolved in the water. According to the model, the hostile or lethal environmental conditions could even occasionally develop in a subtidal or intertidal bathymetry, which could lead to dying events as well as contribute to a preservation of the marine fauna that died there—a scenario that in other models is considered possible only beneath the storm-wave base (cf. Viohl 1998, 2000).

### *Palaeobathymetry and salinity*

In the two opposing formation models, the question of a possible differentiated salinity of seawater takes on a more or less greater significance. Its relevance and consequences are fundamentally linked with the view of whether or not every deposit of the plattenkalks (along with their lagerstätten) should necessarily have occurred in a stratified water body approximately 60 m deep. Competing conceptions of the bathymetry of particular basins are thus coincident with opposing hypotheses about palaeosalinity, which can only be indirectly deduced.

Statements concerning the palaeosalinity of the marine ecosystems are traditionally determined by way of the stratigraphic distribution, frequency and composition of stenohaline life forms. In general, in the plattenkalks, the nektonic and planktonic faunas predominant (e.g. echinoderms, ammonites, and fishes, along with their trace fossils: e.g. coprolites; Janicke 1970; Viohl 1998, 2000) over autochthonous benthic faunas (e.g. pelecypods, gastropods; e.g. Röper et al. 1998, 1999, 2000; Viohl 2000). Bioturbation is rare in the typical Solnhofen Plattenkalks (Viohl 1998, 2000), but it can be significantly more common in other plattenkalk types (even in the same locality; cf. Röper et al. 1999; Viohl 1998, 2000). Such fauna and trace fossils are considered to be related with more or less normal salinity. From the salinity values that vary from the normal seawater composition, however, it can be concluded from plattenkalks which ones are either (1) free of biotracers and higher benthic organisms or (2) distinguished by the mass occurrences of marine vertebrates and invertebrates associated with particular stratigraphic horizons. In the first case, such finds are regarded as long-term hostile conditions; in the second case, they are indications of a dramatic deterioration and ultimately lethal environmental conditions for stenohaline organisms. Against this background, the two opposing models present a difference in the marine environments under question in two respects: a decrease in salinity (as a result of an increase in the inflow of fresh water), and an increase in salinity (as a result of the evaporation of a significant amount of seawater).

In the model of Röper et al. (1999, 2000), an episodic layering of seawater with fresh water (and occasionally also mixing) as a result of an increased amount of precipitation is considered. This is also implicated by Viohl (1998, 2000) and Viohl and Zapp (2007). Such scenarios are mentioned in both models with regard to terrestrial flora and fauna transported into the marine environment (e.g. for *Juravenator starki*, Viohl 1999; Viohl and Zapp 2007). In a strong presentation of their hypothesis that some of the plattenkalks in restrictive basins were deposited under shallow-water conditions, Röper et al. (1996, 1998, 1999, 2000) also discuss questions of etiology of the particular marine fossil

groups (namely, monospecific mass occurrences of nekton, e.g. medusae, echinoderms [*Saccocoma*], and fishes). Röper et al. (1999, 2000) do not insist, however, on a freshening of shallow water bodies cut off from the main basin, but rather see as an alternative to this a clearly increased salinity resulting from the evaporation of significant amounts of seawater. This hypothesis is used in turn as a counter-argument in the controversy about whether all plattenkalks of the Southern Franconian Alb and their lagerstätten were necessarily created in stratified bodies of water (for some of the basins the latter were not ruled out; e.g. Röper 1997; Röper et al. 1999, 2000).

Two extraordinary finds from the plattenkalk deposits of the Painten Basin support this, so far unchallenged, view. The first find is an Early Tithonian coral stock about 1 m high and over 1.5 m broad of the genus *Thecosmilia* (Meyer 1977). It comes from Jachenhausen and, therefore, from an area of origin considered possible for *Compsognathus*. This coral stock was transported by a subaquatic slide from the basin rim into the inner basin. It is concluded that this specimen not only lived on for an unknown time but also continued to grow (cf. Ali 1984; Meyer 1977; Nose and Leinfelder 1997; Viohl 1998). The long-standing life-friendly conditions at the seafloor reflected in this vitality are further proven by this coral stock having been bored into by at least two groups of organisms, at least one of them while the coral was already dead (Meyer 1977). Because a salinity of >40‰ is detrimental to reef organisms (e.g. Schwark et al. 1998), normal salinity at the seafloor can be assumed to have existed during the time these organisms were growing (Meyer 1977). An acceptance of this scenario is therefore in contradistinction to an increased salinity of a stratified water body and an anaerobic environment, at least until the termination of bioerosion at the coral stock.

The second find, which clearly does not indicate a stratified water body, is represented by dinosaur tracks. A 5-m-long trackway with 12 tridactyl tracks was reported from a quarry near Painten by Pfürringer (2000) in a horizon belonging stratigraphically to the Lower Tithonian. Pfürringer (2000) described the tracks as clearly tridactyl, the best-preserved track being 11 cm long and 7 cm wide, with some of the tracks having a sort of imprint of the “heel” at the rear of the print. The latter could be a (partial) impression of the metatarsus because the animal was sinking relatively deep into the sediment (D. Marty, personal communication 2011). Pfürringer (2000) also noted marked differences in morphology between the left and right tracks.

Unfortunately, none of the tracks was preserved, and the only documentation available are seven photographs, some of which are illustrated in Pfürringer (2000). On one photograph of Pfürringer (2000: table 5–fig. 1), the tracks are regularly aligned in a narrow trackway with a quite high pace angulation angle of around 170°. Two other photographs of

Pfürringer (2000: table 5–figs. 2, 3) show close-ups of some of the tracks. Based on these photographs some of the tracks have a tridactyl aspect, but because of the rather poor quality of the photographs and without any of the original tracks having been preserved, it is not possible to unambiguously confirm that these are tridactyl tracks (D. Marty, personal communication 2011). Judging from the same photographs, the tracks seem to overprint the wave ripple marks, and the track morphology is highly variable. The tracks look as if they were left on the level on which they were found, i.e. they are true tracks rather than undertracks or overtracks. Most likely, they were left in water-saturated mud and (partially) collapsed after foot withdrawal, rather than being modified by water run-off on an intertidal flat, as suggested by Pfürringer (2000) and Röper et al. (2000; D. Marty, personal communication 2011). The latter event possibly happened prior to track formation and is testified to by the numerous scour and flute casts (“Strömungsmarken”) on many different levels within the quarry, which actually were the main interest of the studies carried out by Pfürringer (cf. Barthel 1964; Janicke 1969; Meyer and Schmidt-Kaler 1983, 1984). However, from the descriptions and photographs of Pfürringer (2000), it is unclear if the scour and flute marks also occur on the level with the trackway or only on other levels.

To conclude, the tracks reported by Pfürringer (2000) may be considered as “poorly-preserved” true tracks or “deep tracks” sensu Marty et al. (2009), making any ichnotaxonomical and trackmaker identification difficult or impossible. The size of these tracks are clearly larger than tracks that would have been left by the two known, very small theropod specimens from Bavaria (Germany) *Compsognathus longipes* (Ostrom 1978; Wagner 1861) and *Juravenator starki* (Göhlich and Chiappe 2006; Göhlich et al. 2006). However, the *Compsognathus* specimen from Canjuers (SE France) is “some 50% larger than the original (Solnhofen) specimen”, as stated by Norman (1990), and the length of digit III can be estimated at about 6–8 cm judging from fig. 11 in Peyer (2006: 893). A similar sized tridactyl bipedal dinosaur is likely to be the producer of the Painten trackway, and this also does—of course—not exclude a small ornithischian dinosaur as possible trackmaker (Burnham 2007; D. Marty, personal communication 2011). A closer identification is not possible because none of the Painten tracks exhibited sufficient anatomical details (number of phalanges, claws) allowing comparisons with known foot skeletons of small Late Jurassic bipedal tridactyl dinosaurs (D. Marty, personal communication 2011).

The trackway has the typical fashion of a trackway left by a small biped dinosaur walking on land, similar to many other similar trackways reported from the Late Jurassic of Europe (e.g. Mazin et al. 1997; Marty 2008; Diedrich 2011), and there is no evidence to suggest that this trackway was left by a swimming or partially buoyant animal (e.g.

Ezquerro et al. 2007; Milner and Lockley 2006). It is suggested that the animal was walking at an exceptionally low tide (or water level if the basin was not affected by normal tides) over a (higher) intertidal flat, and the tracks and wave ripples may have been stabilised by desiccation and due to the presence of a coherent microbial mat, which may also explain the lack of desiccation cracks. The level was subsequently covered over during the next water high stand, preserving the tracks (D. Marty, personal communication 2011).

The bathymetry values from underneath the storm wave base are considered by Röper et al. (2000) to be acceptable within particular ranges of time (e.g. for the Solnhofen Basin), and these authors discuss the establishment and persistence of chemically and physically determined stratified water bodies against this background (e.g. the scenario of a salinity and density stratification). From this perspective, Röper et al. (2000) created a deposition model for plattenkalks that requires more of an individual than a generalised bathymetry for every basin under consideration. According to this model, the sea levels are ordered into a spectrum that ranges from well underneath the fair-weather wave-base to a few meters above the storm wave-base (Röper et al. 1996, 1998, 1999, 2000).

For advocates of a palaeoenvironment with a water depth of only approximately 60 m, these types of hypotheses are naturally questionable (e.g. Keupp et al. 2007; Viohl 2000). In their conceptual model, these sea levels (at least those underneath any wave base) are necessary preconditions for generating a stratified water body in all of the basins in question. Viohl (1998, 2000) and Keupp et al. (2007), for example, are of the generally accepted view that this stratification is causally associated with a differentiation of the salinity in the basins. The increased salinity in the deeper levels of the water body (hypersaline brines) is considered to be the result of an influx of hypersaline seawater. It is assumed that this in itself is the result of a high evaporation rate in the semi-arid climate (e.g. Keupp et al. 2007; Meyer and Schmidt-Kaler 1990; Oost and De Boer 1994; Viohl 1998, 2000). The conceptual model of a water body stratified initially by salinity or density stratification further indicates that stagnant, dysoxic to anoxic conditions developed underneath a chemocline (Barthel et al. 1990; Keupp et al. 2007; Meyer and Schmidt-Kaler 1993; Viohl 1998, 2000). Such a low-energy, hostile environment is then part of the taphonomic scenario at the seafloor of all the basins where plattenkalk was deposited.

Viohl (1998, 2000) and Tischlinger (2001) specify the salinity of the hypersaline brines with certainty at <117 ppt and on average between 40 and 80 ppt (salinity values close to 117 ppt are discussed in relation to the pore water of the seafloor). Schwark et al. (1998) came up with similar values for the water body underneath the chemocline (40–80 ppt,

episodic maximum of 100 ppt), yet classified the salinity as mesosaline. Veizer (1977) also did not support a hypersaline environment for the deposition of plattenkalk in the Southern Franconian Alb.

These statements about the palaeosalinity of the seafloor water have been without exception determined by indirect evidence. They are based on sedimentological data (e.g. Schwark et al. 1998; Viohl 1998, 2000; Viohl and Zapp 2007), geochemical and biochemical analyses (Kemp and Trueman 2003; Schwark et al. 1998; Veizer 1977) and palaeontological and uniformitarian data (Barthel 1970; Viohl 1998). Their informative values and validity vary, particularly because any evidence for salinities above the critical saturation level of 117 ppt—at which gypsum precipitates—is nearly completely lacking (Bausch 2005; Mayr 1967; Oost and De Boer 1994; Viohl 1998). Such indicators for hypersaline conditions as well as questionable halite pseudomorphoses (e.g. Janicke 1969; Münch 1955; Röper et al. 1999; Seilacher 1991; Walther 1904; see also Llewellyn 1968), however, are associated less with bottom water and more with the pore water of the seafloor (e.g. Barthel et al. 1990/1994; Viohl 1998; see also Haude 1970). There is also the fact that the precipitation of gypsum can be brought about under normal salinity conditions by sulfur-oxidising bacteria (e.g. Hecht 1933; Schmid et al. 2008; see also Hoareau et al. 2011), whereas in waters with a high carbonate productivity this process will be inhibited (Oost and De Boer 1994).

The least resilient argumentation, in our view, is that on hypersalinity proposed by Seilacher et al. (1985): “A dorsal bend of the vertebral column, comparable to post mortem deformations of drying modern carcasses (Schäfer 1955), is a familiar feature in Solnhofen *Archaeopteryx*, *Pterodactylus* and *Compsognathus*, but occurs also in fishes. In the latter case it cannot be a desiccation feature, because associated belly-up landing marks and tail fins disrupted during the bending of the vertebral column [...] clearly show that the deformation took place only after the carcass had sunk to the bottom. Therefore, it may be assumed that the bottom water was hypersaline to effect the necessary dehydration.” Since being adapted for many animal groups and even raised to the rank of hypothesis, this idea has currently gained wide acceptance in the palaeontological community (e.g. Barthel et al. 1990/1994; Griffiths 1993; Viohl 1994, 1998, 2000; Viohl and Zapp 2007). For most of the animal groups (e.g. cnidarians, echinoderms, crustaceans, reptiles), however, there is a lack of experimental taphonomic evidence for postmortem contortions occurring exclusively in hypersaline water. On the contrary, uniformitarian experiments prove that in fish, postmortem contortions occur regularly in seawater of normal salinity as well (e.g. Eberle 1929; Hecht 1933; Weiler 1929). It is further remarkable that Hecht (1933) recorded no postmortem curvature in his



experiments with seawater of a high salt content (cf. also Elder 1985: p. 34; MacDonald 1992); forensic data on human corpses stored in high-salinity mine water convincingly confirm this phenomenon (König 1892).

If salinity is seen as a singular factor, then these actuo-palaeontological results and forensic findings are in accord with the recently published laboratory experiments of Faux and Padian (2007). Faux and Padian (2007) tested the hypothesis of Seilacher et al. (1985) in a simulation of a marine environment with a salinity that was considered sufficient by Barthel et al. (1990) for postmortem contractions and contortions. For their taphonomic study, Faux and Padian (2007) used beef tendons and birds (in toto). In the course of the experiment, however, the specimen material did not experience any modification that the originators and advocates of this hypothesis could use in their support (Barthel et al. 1990; Keupp et al. 2007; Seilacher et al. 1985; Viohl 1998, 2000). Even though we also emphatically believe that such salinities as these are in fact not the cause of postmortem contractions and contortions, we are of the opinion that the experimental arrangement and duration of the experiments by Faux and Padian (2007) did not reflect the conceptual models of Seilacher et al. (1985) and Barthel et al. (1990) in fundamental ways. Even if temperatures of 4–18°C might perhaps fit the depositional model above (cf. de Buissonjé 1985), this is the case neither for the experimental setting (a non-stratified water body) nor for the duration of the experiment (maximum 2 weeks). According to Viohl (1998) and Keupp et al. (2007), a carcass on the seafloor is exposed to hypersaline brine typically for many weeks to months, perhaps even years. As we later demonstrate, it is indeed important that a carcass be completely submerged *for a long time* in water, a scenario demanded by Seilacher et al. (1985) and Barthel et al. (1990), yet one that Faux and Padian (2007) did not fulfill in their experiments. From the observations above, we conclude that an increased palaeosalinity in the seawater cannot be proven merely by the fact that recurvature is frequently found in vertebrates in the Late Jurassic South Franconian plattenkalks (cf. Kemp 2001; Kemp and Unwin 1997). Also, the lack of recurvature does not imply low salinity levels, because such recurvature phenomena have been documented actuo-palaeontologically in seawater of normal salinity as well (Eberle 1929; Hecht 1933; Weiler 1929; cf. Viohl and Zapp 2006, 2007). Speculations about invertebrates are still in need of experimental investigation. Nevertheless, with the available data, a sea-bottom water of abnormal salinity also cannot be considered disproven generally or automatically for all depositional sites of such plattenkalks. However, the hypothesis for increased salinity cannot be ruled out. The taphonomical experiments of Barthel (1970), who provided the evidence (opposing, for example, Young and Hagadorn 2010) that cnidarians are capable not only of sinking to the bottom in water of high salinity, but also of leaving highly detailed

imprints in the carbonate ooze, demonstrate that different environments can produce a likewise fossil record.

#### *Sedimentation rates*

A high degree of articulation of a multiple-component skeleton is considered in sedimentology and palaeontology as a sure indication of a rapid embedding or burial (e.g. Brett and Seilacher 1991; Etter 2002; Wetzel and Reisdorf 2007). If rapid sinking into a conserving medium (e.g. Hess and Etter 2011; Martill 1993; Munnecke et al. 2008; vs. Milsom and Sharpe 1995) or obrution (e.g. due to submarine slumping, turbidity current deposits or tempestites: Keupp et al. 2007; Link and Fürsich 2001; Mäuser 1984; Schweigert 2009; Viohl 1990) can be ruled out, then it can be concluded that a sufficiently high sedimentation rate can lead to a burial at the site. The determination of an adequate sedimentation rate encounters difficulties, especially in such marine lagerstätten whose formation was in a low-energy, hostile environment in the water layers close to the seafloor and in the sediment (= “*Konservat-Lagerstätte*” sensu Seilacher 1970). The Late Jurassic plattenkalks of the Southern Franconian Alb and their conservation lagerstätten are for many reasons exemplary of this problematic issue. We present here some of the reasons for which we can generally only estimate the embedding time frame of vertebrates, and thus as a rule speak only of a relatively quick or slow burial (= sedimentation rates).

- (1) The biostratigraphical resolution accuracy discussed today for the plattenkalk sequences (e.g. 250,000–500,000 years for the plattenkalks of the Solnhofen Basin; e.g. Bausch et al. 2008; Keupp et al. 2007; Viohl in Etter 2002) are far below the range of time that is commonly seen as needed for allowing fossils with a high degree of articulation to be formed (cf. Keupp et al. 2007; Viohl 1998).
- (2) The first and later approximations of sedimentation rates come from Rothpletz (1909: >5 cm/a) and de Buissonjé (1985: 0.057–0.228 mm/a), among others. Because of the depositional models they are based on, these are now considered obsolete. At present, stratigraphic high-resolution calculations based on the current state of knowledge of the sedimentation rates have been made only for compacted, laminated plattenkalks of the Solnhofen Formation. For such plattenkalks of the Solnhofen and Eichstätt basins, Bausch et al. (2008) calculated an average sedimentation rate of 0.18–0.36 mm/a (based on a formation time of 250,000–500,000 for a thickness of approx. 90 m). The published sedimentation rates by Park and Fürsich (2003), based on cyclostratigraphic calculations, are on average 0.0482 and 0.1387 mm per year. According to Park and Fürsich (2003), each lamina represents a

multi-year interval (from 1.42 to 3.13; an average of 2.3 years per lamina; see also Schwark et al. 1998). Viohl (1998, 2000) and Keupp et al. (2007), in contrast, hold the view that the totality of the laminae making up a single limestone bed (“Flinz”) as a rule represents a storm event and is therefore of a significantly shorter time frame.

- (3) The model put forth by Röper et al. (1999, 2000), in which particular plattenkalks and lagerstätten could be formed also in tide-influenced depositional environments, offers theoretically relatively fast embedding mechanisms, yet these are not applicable to all—that is, to bathymetrically deeper—deposits. Advocates of the hypothesis that the plattenkalk basins could be in general ranked bathymetrically at approximately 60 m fundamentally contradict the scenario of a tidal lagerstätten formation (e.g. Viohl 2000).
- (4) The taphonomic scenario of fossil lagerstätten apparently allows a carcass to persist longer in toto on the seafloor than is usually the case for marine environments (cf. Keupp et al. 2007; Viohl 1998). Potential disarticulation phenomena therefore need to be interpreted differently in their temporal progression than in the case of a life-conducive and/or oxygenated and well-circulated environment. In addition, there is a lack of autochthonous sessile benthos on skeletal elements that could be used as potential biogenetic evidence for the minimal duration of the subaquatic exposition (cf. Arnaud et al. 1980; Kauffman 1982; Martill 1993; Sorg et al. 1997; Haglund and Sorg 2002; Muñiz et al. 2010; Kiel et al. 2011; Rouse et al. 2011).

Accordingly, the degree of articulation of fossils and especially the integrity of vertebrates are used as an indicator of sedimentation rates (e.g. Janicke 1969; Keupp et al. 2007), but this is currently still mostly a speculative endeavour. Nonetheless, for the time being this taphonomic indicator serves as the only way to test the plausibility of other calculations of the sedimentation rates of the plattenkalks. By way of such a plausibility test, sedimentation rates such as those calculated by Park and Fürsich (2003) and Bausch et al. (2008) are all seen as problematic (cf. Park and Fürsich 2001; Keupp et al. 2007; Bausch et al. 2008).

In this regard, an isolated 18-cm-long scale armour of the fish *Aspidorhynchus* has often been referenced (e.g. Janicke and Schairer 1970; Keupp et al. 2007; Mayr 1966, 1967; Viohl 1994, 1998; ESM Fig. 2). Five beds are in this specimen, all of which show an internal lamination (total thickness: 23 mm). We ourselves have identified in this specimen approximately 29 laminae (= 14.5 lamina couplets; ESM Fig. 2). As a unit, the specimen and sediment fill did not experience any significant compaction or deformation. In the literature

there is a general consensus that the individual beds filled up the scale armour in a short period of time (Bausch et al. 2008; Keupp et al. 2007; Park and Fürsich 2001; Viohl 1994, 1998). Keupp et al. (2007) estimate about 2 years for this. We are of the opinion, however, that this process could have taken a longer time. We base our view on forensic data that document a high degree of articulation for human cadavers that remained for decades in a subaquatic setting (e.g. Berg et al. 1969; König 1892; Rabl et al. 1991; Wasmund 1935). The oldest corpse of that kind known to us from a fully aquatic depositional environment comes from an alpine lake, where it was submerged for 50 years (Rabl et al. 1991). Our assumption perhaps receives a greater support in König (1892), who published the obduction findings of bodies that remained in the saline waters of mines for 3 and 41 years, respectively. Aside from perimortem and postmortem injuries, these bodies were not only fully articulated but they also preserved fine details of the soft tissue anatomy (see also Krause 2004). In view of such a great preservation potential of such environments, we turn to the results of the cyclostratigraphic study of Park and Fürsich (2001, 2003). These authors conclude that each lamina represents between 1.42 and 3.13 years (on average 2.3 years). The simple multiplication of the minimum time for forming a lamina (=1.42 years) with 29, the number of laminae whose existence we have determined, results in a time of 41.18 years. With the average value of 2.3 years, this would be 66.7 years, and the maximum time of 3.13 years would result in 90.77 years. In the light of the forensic data, the magnitude of these values, especially the minimum and middle ones, appear to us not to be unrealistically high.

- (5) Different types of laminated plattenkalks are subject to different interpretations. According to Viohl (1998, 2000) and Keupp et al. (2007), the fine lamination of typical Solnhofen Plattenkalks is not the result of bacterial mats. If this interpretation is accepted, then at the very least the formation mechanism these authors suggest for the individual lamina (= sedimentation rate: repeated delivery of suspended sediments by a storm event) should not be transferred to silicified plattenkalks. These plattenkalks, those from Schamhaupten in any case—the origin and embedding medium of *Juravenator starki*—are interpreted as bindstones: the dark filaments in silicified plattenkalks visible under light microscopy are considered to be trichomes of cyanobacteria (Viohl and Zapp 2006, 2007; Fig. 7).

#### Subaquatic decomposition and adipocere

The model proposed by us mainly deals with the palaeoenvironment of the place of deposition, yet not necessarily

with an individual's dying place. These basic conditions therefore essentially differ from the taphonomic scenario of Faux and Padian (2007).

Faux and Padian (2007) essentially demand three factors as basic preconditions for the post-mortem persistence of an opisthotonic posture from the moment of death until the burial: (1) buried soon after death, (2) no substantial transport and (3) no extensive deterioration from currents or scavengers.

We agree with Faux and Padian's (2007) view that hydrodynamic currents and scavengers can prevent or break an opisthotonic posture. Contrary to the basic conditions formulated by Faux and Padian (2007), however, our model pre-supposes no rapid embedding, but quite the opposite: for obvious reasons, this would even be detrimental to an opisthotonic posture (and against all expectations at the obrution of fresh dead bodies). Moreover, theoretically, even changes of place of a dead body in the process of maceration (but still articulated) could be imagined.

If a rapid burial is demanded for skeletons of vertebrates conveyed articulate in the case of the lagerstätten of the South Franconian plattenkalks, this precondition implies a period of time open to multiple interpretations in the presently discussed models (cf. [Sedimentation rates](#)). According to the models, it is possible to consider periods of time which range from a short duration (e.g. turbidites, tidal sediments; Keupp et al. 2007; Röper et al. 2000; Viohl 1998, 2000) to several years (successive deposition of laminated plattenkalks; Faux and Padian 2007). The overgrowing of a vertebrate's carcass by mats of microbes belongs to the category of short periods of time of a burial (cf. definition "burial" of Bates and Jackson 1980). However, it is possible with all of these periods of time to establish the MLPP typical of submerged bodies.

Also, according to the principle of uniformitarianism, the phenomena of putrefaction regularly occurring today in the subaquatically bedded vertebrate carcasses can also be expected at the Solnhofen archipelago. This explicitly includes the formation of adipocere, which can extend over longer periods of time.

The idea that adipocere represents a form of arrested decay of postmortem tissue (Fründ and Schoenen 2009; Ubelaker and Zarenko 2011) was a view favoured by many of the earlier palaeontologists, and around the beginning of the last century, adipocere was considered to be a precursor of the subsequent fossilisation process (reviewed in Wasmund 1935). The formation of adipocere is promoted by bacteria, especially the anaerobic *Clostridium*, and by an anaerobic environment, warm temperatures and a mildly alkaline pH (Forbes et al. 2005; Mellen et al. 1993; Vass 2001). The main components involved in adipocere formation are fats that may become hydrolysed and hydrogenated, even though adipocere is mostly a mixture of insoluble fatty

acids and hydroxy stearic acids [Mant and Furbank 1957; Ruttan and Marshall 1917; reviewed by Takatori (2001) and Ubelaker and Zarenko (2011)].

de Buissonjé (1985) discussed adipocere forming as an agent for the 3D preservation of fishes out of the Late Jurassic Plattenkalks of the Eichstätt basin, after they were "sealed off by a swiftly settling and compacting micritic suspension", creating an anaerobic environment within the pore space (see also Viohl 1994; Wasmund 1935; Wiman 1942). The material inside the 3D fishes was not analysed chemically by de Buissonjé (1985). In his opinion "macrofossils such as fish ... had passed through an intermediate stage of adipocere-pseudomorphose before they finally collapsed." The hypothesis of de Buissonjé (1985) is supported by a model of Berner (1968) that adipocere is a prerequisite for carbonate concretions being formed [inside the "Solnhofen fishes"], by calcium concentrating in a decomposing carcass and a following precipitation of "calcium ions concentrated by as a mixture of calcium fatty acid salts or soaps". Raiswell (1976) proposed an alternative bacterial driven model for nodule-forming processes by analysing stable isotopes of concretions from the Lower Jurassic of Yorkshire, UK. According to this model, bacterial sulphate reduction and methanogenesis produces bicarbonate ions as a prerequisite of the nodules. Allison (1988) described decomposition experiments in seawater which show that alkalinity produced by decomposing proteinaceous organisms "can promote the development of calcium-enriched pore-water micro-environments around decomposing carcasses". But a further replenishment of calcium ions from an open pore space is necessary to "form carbonate species within the decay aureole of decomposing carcasses".

An open question is whether *Compsognathus* and *Juravenator* pass through an adipocere-forming process. It is the probable content of their subcutaneous and mesenteric fat deposits that is crucial to answering this question. In poikilotherms (amphibians and reptiles) subcutaneous fat is usually very minimal (Smith and Wuttke 2012, this issue). Frey (1988) reported fat bodies in the neck and tail of *Alligator mississippiensis*. Mass deaths of crocodiles in South Africa by pansteatitis [inflammatory reaction that accompanies the generalised necrosis and hardening of fat], associated with the intake of rancid fish after a fish die-off (Ashton 2010; Oberholster et al. 2010) show that fat tissues are disseminated throughout the body of crocodiles. Therefore, it seems that there is enough fat inside a reptilian corpse which can be broken down to fatty acids. These might be distributed throughout the corpse by migrating decay fluids and then altered to adipocere.

The two specimens analysed by us indirectly hint more or less strongly at having passed through a stage of decomposition somewhat like the one just described. Several authors have already pointed out that the surface texture along the

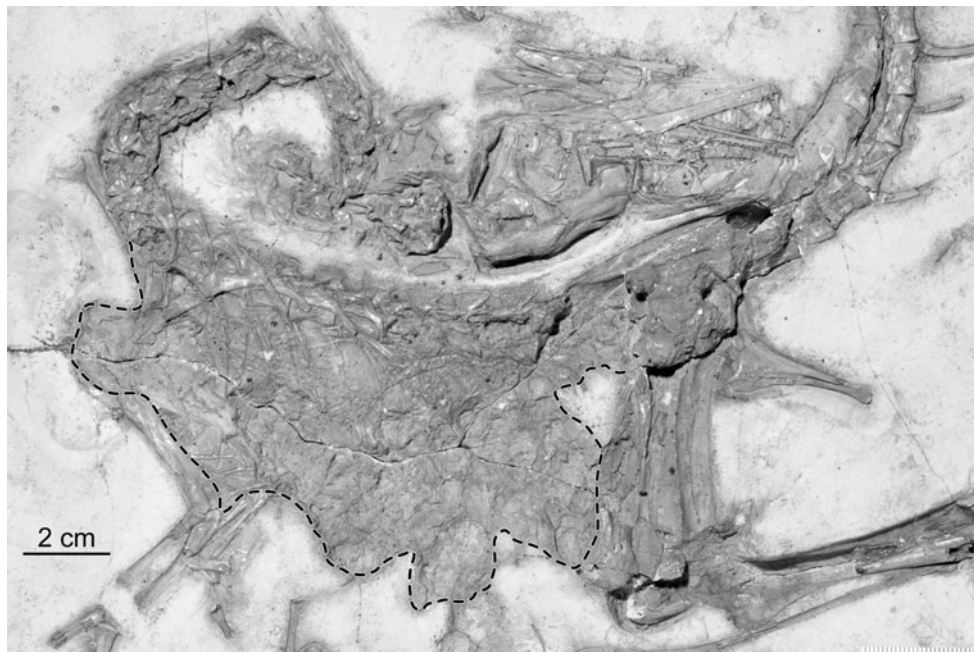
ventral regions of the trunk and the abdomen differs from the normal facies of the *Compsognathus* slab (e.g. Griffiths 1993; Huene 1901; Mäuser 1983; Nopcsa 1903). According to Ostrom (1978), the surface texture shows a granular texture and irregular “hummocky surfaces” inside prominent depressions. The appearance of these surfaces reminds us of the textures of adipocere of submerged bodies described in forensic literature (cf. Mueller 1953; O’Brien and Kuehner 2007; Prokop and Göhler 1976). Ostrom (1978), however, interprets the surface texture as a recent, subaerial phenomenon of weathering (“etched depressions”). In contrast to this, Nopcsa (1903) establishes an immediate connection between the process of putrefaction of the *Compsognathus* specimen and the embedding medium. “At this moment, the gradual passing into the normal rock is attracting attention and still argues against the skin nature of the granulated part; due to this, one almost feels bound to attribute the local granulation of the slab to an interaction between decomposing animal matter and inorganic mass of matrix.” [translation by the authors]. Even if we are of Nopcsa’s (1903) opinion, we would like to discuss whether the structures considered to be “skin-armour” by Huene (1901) embody pseudomorphoses of adipocere (Fig. 8). If this were the case, the “prominent depressions” might correspond with a pseudomorphosis of adipocere as well; a concretion developed on the counter slab not handed down.

That adipocere also developed in the *Juravenator* specimen may be hinted at by the isopods associated with it. These isopods are preserved as impressions or three-

dimensionally within the skeleton of the *Juravenator starki*, which, otherwise and as a whole, is heavily compacted (Fig. 3; Chiappe and Göhlich 2010; Göhlich et al. 2006). It is possible that the three dimensionality of the fossils of the isopods indicates an early diagenetic precipitation of carbonate, which assumed the place of the adipocere’s precursor.

Whichever is the case, we have little doubts as to there having been available a suitable medium for the generation of adipocere at the bottom of the basins of plattenkalk, as it is the rule in aquatic environments (e.g. Anderson and Hobischak 2004; Dumser and Türkay 2008; Haglund and Sorg 2002; Kahana et al. 1999). We are of this opinion, whether or not an intermediate stage of adipocere really served as a suitable micro-environment for the precipitation of minerals and, therefore, its former existence is testified in the sediment by pseudomorphoses. We also think that the existence, in the meantime, of adipocere can guarantee a high degree of articulation in carcasses for years even without a burial (cf. Sedimentation rates). This is true especially in aquatic environments which are characterised by a stagnant anoxic milieu. We further assume that the resistance of a carcass in adipocere preservation can be increased by overgrowing with mats of microbes (possibly also related to the long-term maintenance of an anoxic milieu).

If water of a moderate temperature fosters the formation of adipocere, the latter is also generated in aquatic environments of low temperature. Our only reservations as to the potential of the generation of adipocere concern hypersaline water postulated in the genesis model of plattenkalk by



**Fig. 8** *Compsognathus* specimen, irregular texture inside the abdominal area of the eventually pseudomorphoses of adipocere (photograph courtesy of G. Janßen, O. Rauhut; cf. Griffiths 1993; Mäuser 1983; Nopcsa 1903)

Seilacher et al. (1985), Barthel et al. (1990/1994), Viohl (1998, 2001) and Keupp et al. (2007). Diagnostic findings published by König (1892) of postmortem examination of persons having lain for more than 40 years in saline mine drainage water hint at the possibility that the bacteria responsible for the formation of adipocere cannot find suitable living conditions there. The diagnostic findings imply that no adipocere was formed in the conserved bodies. We also think that the observation of salt crystals “up to the size of a hemp seed” having formed inside their bodies (cf. also Krause 2004) is especially remarkable. This phenomenon may be regarded as evidence that, due to osmosis, the salt concentration inside the soft tissue corresponded with that of the mine drainage water. According to Krause (2004), the inner organs are first subjected to the processes of autolysis and decomposition, until the biotope becomes sterile due to dehydration and increases in the salt concentration. Due to changes in the ion milieu, the body’s own enzymes also can no longer transform their substrates. In how far this kind of process is relevant to the basins of the South Franconian plattenkalks can not be decided with absolute certainty, as, with today’s state of knowledge, the hypothesis of hypersaline water at the bottom of the sea can neither be refuted nor confirmed (cf. [Palaeobathymetry and salinity](#)). However, in this context, we would like to stress the point once again that the distortions of fossils of the plattenkalk, regularly cited and allegedly caused by osmosis, are no proof for hypersaline water at the sea bottom (see [Palaeobathymetry and salinity](#)). It is also worth noting that fermenting processes can also occur in hypersaline environments (e.g. Kobayashi et al. 2000; Zhilina and Zavarzina 1990).

Closely connected with the above explanations are further essential processes of subaquatic decomposition. If sterilising salt concentrations at the seafloor can be excluded, then a decomposition under anaerobic, possibly also dysaerobic conditions must be assumed (it is probable that the water temperatures at the sea bottom in the Solnhofen Archipelago were sufficiently high; cf. [Palaeobathymetry and palaeo-water temperatures](#)). Anaerobic or rather facultative anaerobic bacteria are involved in this decomposition caused by bacteria (cf. references in Reisdorf et al. 2012, this issue). These bacteria, on the one hand, are from the carcass of the vertebrate itself (= intrinsic bacteria). On the other hand, it is probable, due to drowning or the hydrostatic pressure at the sea bottom, that bacteria contained in the sea water gain access to the inside of the body—for example through the respiratory tract (= extrinsic bacteria; cf. Reisdorf et al. 2012, this issue). Such bacteria-controlled decomposition processes result in liquid and gaseous products of decomposition.

It is of immense importance to the fossilisation potential of multiple component skeletons whether or not gaseous decomposition products generate positive buoyancy in a

vertebrate carcass, which can then rise to the water’s surface. In addition to the temperature mentioned above and the chemical milieu prevailing in a depositional setting, the hydrostatic pressure is also of importance in this context as it determines whether the decomposition gas generated within a dead body dissolves immediately (Boyle’s law; calculations are given in Allison et al. 1991, and Smith and Wuttke 2012, this issue) or whether it can display its buoyancy-promoting characteristics (e.g. Reisdorf et al. 2012, this issue; Smith and Elder 1985; Tomita 1975, 1976; Wasmund 1935). Moreover, the dissolubility and the compressibility of the decomposition gas is highly dependent on its composition (e.g. Reisdorf et al. 2012, this issue).

To the best of our knowledge, no analysis values are as yet available on the composition of decomposition gases, which are generated by extrinsic (= marine) and intrinsic bacteria (i. e. inside a vertebrate’s dead body that had been subjected to subaquatic putrefaction in a marine environment). However, it is a fact that there are at least some significant differences in the composition of the decomposition gases in dead bodies from different terrestrial environments (subaerial and fluvial; e.g. Mallach and Schmidt 1980; further references in Reisdorf et al. 2012, this issue). Therefore, we have reasons to assume that the gaseous putrefaction products having formed themselves in a marine environment significantly differ from those generated under subaerial decomposition. Consequently, all conclusions based on a hypothetical gas compound are highly uncertain—such as those of authors who consider methane to be the main component of a decomposition gas (cf. Allison et al. 1991 and Reisdorf et al. 2012, this issue).

Another important factor is the dimensions of a carcass (e.g. Kemp 2001; Reisdorf et al. 2012, this issue; Smith and Wuttke 2012, this issue). With respect to the composition of the fauna of the South Franconian plattenkalks, Kemp (2001) has already expressed the essential points of these problems: “As gas diffusion and production is governed by the ratio of mass to surface area, small animals produce proportionally less gas. So, even if all animals sank and decayed at the same time, internal gas production would be more likely to refloat larger carcasses.”

#### Decay resistance of soft parts

As the uniformitarian experiments with the chicken necks and the analysis of the taphonomy of *Compsognathus* and *Juravenator* have shown, muscles and their tendons and the ligaments responsible for bone-to-bone connections have varied resistances to decay (e.g. Briggs 2003; Richter 1994; Sansom et al. 2011; Wuttke 1983a, 1983b; this paper). All of these proteins differ in their resistance to degradation by bacteria (e.g. Nimni 1983; Peterkowski 1982; Suzuki et al. 2006; Watanabe 2004). This is especially true for

structural proteins (collagen and elastin) from which ligaments are made. Structural collagens have a molecular weight of approximately 300,000, “their three helically  $\alpha$ -chains, causing the collagens’ stiff structure and insolubility, make degradation difficult.” (Suzuki et al. 2006). As Suzuki et al. (2006) report, only a small number of known microorganisms can decompose collagen.

In our experiments, the ligaments as well as the musculature (in part) resisted decay for more than 5 months. This observation is in agreement with the report of Lingham-Soliar and Glab (2010) that only microbial breakdown of the matrix between collagen fibrils occurs “rapidly” [without time specification] in decomposing soft tissue.

#### Consequences for the taphonomy of *Compsognathus* and *Juravenator*

In all vertebrates with a tail, the Ligamentum elasticum extends from the second cervical vertebra to the proximal part of the tail as, for example, in crocodiles (Frey 1988). This is likely true as well for the long-necked and long-tailed bipedal dinosaurs *Compsognathus* and *Juravenator*. Therefore, as was posited by Dean (1919) and as was proven by our experiments on *Gallus gallus*, the tensile forces of the preloaded and hard-to-degrade ligaments are gradually released when the antagonistically working muscle fibres become more and more decayed. This movement is limited only by the passive intramusculature restraints, as long as the ventral ligaments and the intervertebral discs have not yet decayed. Precisely the example in *Compsognathus* of the cervical vertebrae being curved beyond the bony restraints shows by way of the partially disarticulated vertebral connections that the recurvature process can persist even after the intervertebral discs have decayed. This possibility was foreseen by Dean (1919).

*Juravenator* does not display the “opisthotonic posture” in the area of the vertebral column. This is probably attributable to the ventral-up position of the animal on the bedding plane (see chapter [Orientation of the slab of \*Juravenator starki\*](#)), especially of the skull and tail, as well as to the not very strongly developed Lig. elasticum of the short neck with low dorsal spines of *Juravenator*, compared to that of *Compsognathus*. In this case, during the decay of the muscles the released forces were not sufficient to overcome the sticking friction of the sediment and/or the weight of the body to pull the neck or tail into a curved posture. Instead, the proximal part of the tail was pulled into a zigzag line.

#### Consequences for Moodie’s opisthotonic posture hypothesis

In their considerations of the formation of the opisthotonic posture in long-necked and long-tailed tetrapods, Moodie (1918, 1923) as well as Faux and Padian (2007) assume that

often the perimortem muscle spasm could be responsible for this phenomenon (see also Lingham-Soliar 2011). Their observations and experiments, and the conclusions drawn from them, for the most part involved vertebrate carcasses investigated under subaerial conditions. The only subaquatic decay experiment performed by Faux and Padian (2007), with specimens of the *Coturnix* quail, was discontinued early on because of “accumulated excessive bacterial overgrowth”. At that point in time, a backarching of the decaying neck of the *Coturnix* could not yet have occurred because of the early, or the much delayed, decay processes due to the high salinity of the water. The objections concerning anatomy and the necessary transport to the embedding site posited by Dean (1919) were neglected by these authors. In addition, the experiments by Heinroth (1923) and Davis (1996), with their significant results concerning ligaments, were also not considered by Faux and Padian (2007).

Even if Dean (1919) did not know of the pre-stress of the Lig. elasticum in tetrapods (Dean assumed there to be more of a bimetal effect—“the backbone eventually loosens up in the process of decomposition [and] the bodies of the vertebrae separate earlier than the arches, thus producing the inbent column.”), he still clearly had determined the direction in which a “physical phenomenon” solution was to be searched for.

#### Speculations on the cause and location of death

In this study, we are able to refute Faux and Padian’s (2007) hypothesis that the cause of death by cerebral disorder (e.g. poisoning) can frequently be deduced from the death posture (that is, the “opisthotonic posture”) of articulated skeletons. For example, the explanations above show that dead bodies in an aquatic environment will be skeletonised during shorter or longer periods of time. The decomposition of a vertebrate carcass (e.g. via autolysis and heterolysis), therefore, results in the irretrievable disappearance of the clues which might be in the soft tissue and could help settle the question of the cause of death. This is especially true for causes of death which terrestrial animals (with pulmonary respiration) may be subjected to: death by drowning or hypothermia (= the problematic issues of competing causes of death after Skrzeczka 1867; for humans, a long time in the water, there is even the danger of dying at water temperatures of 28°C and lower—Lunetta and Modell 2005; Newman 2001; Spitz 2006). As it now stands, causes of death based on skeletonised dead bodies can be determined only in exceptional cases, such as those with typical traumatic modifications of the bones; consequently, according to forensic criteria, there is frequently a great deal of uncertainty (e.g. Archer et al. 2005; Haglund and Sorg 2002; Sorg et al. 1997). This is also true for the diatom test in soft tissue or

bone marrow, which is frequently used by forensic scientists (Kan 1973; Koseki 1968; Lunetta and Modell 2005).

Statements on the reasons for how and why *Compsognathus* and *Juravenator* got into their respective aquatic depositional setting, and the state (dead or alive) in which they got into it, are mere speculations at our present level of knowledge. Deductions according to the principle of uniformitarianism as well as experimental data may lead to statements that will bear testing.

Göhlich et al. (2006) did not exclude the practising of locomotion by swimming for *Juravenator* because of this theropod species' tail, which probably was laterally flattened. Other authors (e.g. Coombs 1980; Ezquerro et al. 2007) also assume that non-avian theropods were able to practise locomotion by swimming.

Schoener and Schoener (1984) conducted experiments on the lizard's ability to swim. Some lizards show a great capacity for keeping their head above water by floating or paddling [supported by the Ligamentum elasticum, which is more effective under buoyancy]. However, the lizards keep up a surface drifting for hours only, before they drown.

In addition to the ability to swim or drift, the possibility of rafting on plant remains or flosses of plants that drifted far into the open sea by surface currents needs to be considered. This might be conceivable, for example, at Schamhaupten, where bigger tree trunks were handed down (Göhlich et al. 2006; Viohl and Zapp 2006). Rafting, favoured by storms and sea currents, has been proposed as a possible mechanism for transoceanic dispersal of amphibians, reptiles, birds, and mammals (Hart et al. 2012; Mayr et al. 2011 and references therein; Measey et al. 2007; Schiesari et al. 2003; Vences et al. 2003).

Tropical storms with accompanying flash floods might also have swept the animals into the sea (cf. Viohl 1999), from where surface currents might even have drifted them alive to the place of deposition. In such a scenario, drowning is the probable cause of death (accompanied by insufficient motivity due to hypothermia and exhaustion).

If little can be stated about the possible distances travelled before death, for the reasons explained above, it can be concluded, from a forensic–taphonomic point of view, that only a few hours can have passed between death and the sinking of the carcass to the sea bottom; otherwise, putrefactive bloating would have prevented the sinking process in toto. The distances the carcass might have travelled are probably in the range of one to tens of kilometres, rather than the distances Rieggraf (2007) discusses with a provenance from the Bohemian Massif (i.e. >100 km; see Meyer and Schmidt-Kaler 1990: fig. 4; cf. Schweigert 1998). However, it is a proven fact that currents can transport carcasses along considerable distances in short periods of time (e.g. Baduini et al. 2001; Blanco Pampin and Lopez-Abajo Rodriguez 2001; Bibby 1981; Carniel et al.

2002; Giertsen and Morild 1989; Haglund 1993; Hyrenbach et al. 2001; Wiese and Jones 2001).

In this context, an interpretation of the five isopods associated with the *Juravenator* skeleton (Fig. 4; Chiappe and Göhlich 2010; Göhlich et al. 2006) can also be nothing more but mere speculation. Based on the way of life of recent aquatic isopods, it can be concluded that these forms of life were parasites as well as scavengers (Bolin 1935; Krumbach 1915; Lester 2005; Polz 2004). Which one of these two ways of life of these isopods led to the association realised in the *Juravenator* must remain an open question due to the unexplained circumstances of its death.

The water column at the place and the time of deposition of the *Compsognathus* and *Juravenator* specimens was always large enough to prevent the carcasses from refloating to the surface of the water. Therefore, the decomposition processes released their products at the sea bottom. It seems that this led to the formation of spherical, vug-like structures on the slab which might be interpreted, as Barthel (1964) did, as former gas-containing sediment at the bottom of the sea (Fig. 4; see also Hecht 1933; Treude et al. 2009; cf. Griffiths 1993; Janicke 1969: p. 125; Joyce and Zelenitzky 2002; Mäuser 1983; Mayr 1966; Röper et al. 1999: fig. 10; Wellnhofer 2008: p. 46).

Statements of a speculative nature may be made regarding the real place of origin of the *Compsognathus* specimen. Bedding into an aquatic depositional setting situated beneath the wave base is very probable due to the high degree of articulation and the completeness of the specimen. Also, as we already explained, the *Compsognathus* specimen was exposed at the seafloor for a longer period of time. Adopting, for example, the views of Barthel (1964), Janicke (1969) and Röper (1997) on the depositional setting of the Painten basin (cf. Palaeoenvironment and taphonomic landscape of *Compsognathus* and *Juravenator*), the Kelheim basin would tend to be the more likely place of origin because the water in the Painten basin was, at least periodically (e.g., during Early Tithonian times), less deep, whereas in the Kelheim Basin, as far as we know, no indicators for shallow water have been found to date (cf. Palaeobathymetry and salinity; see also Mäuser 1984; Etter 2002; Schairer 1968). Therein, our speculation is supported by the greater potential of the Painten basin for allowing vertebrates to float to the surface due to decomposition. An *Archaeopteryx* from Jachenhausen, however, seems to contradict our statement (cf. Mäuser 1984; Wellnhofer 2008). Our conjectures, supported by taphonomic and palaeoenvironmental indications only, suppose that different sea levels established themselves in the Painten basin at different periods of times.

During the process of working with the *Juravenator* specimen, we noted small, spherical objects (diameter: 0.4–0.6 mm; Fig. 9) in the abdominal area that had not yet been described. Appearance-wise, they are very similar to ooids (which have thus far not been verified on isolated material).



**Fig. 9** Possible ooids: spherical objects (diameter: 0.4–0.6 mm) inside the abdominal area of the *Juravenator* specimen. The location of the spherical objects is shown in Fig. 4

These possible ooids (for the obsolete term “Pseudo-Ooid” see Bausch 1963; Flügel 2004; Flügel and Kirchmayer 1962; Streim 1961), as does the *Juravenator* itself, apparently come from a different facies area. There is a possible interesting causal connection between these associations of “foreign bodies”. An obvious explanation would be that *Juravenator* was the transportation medium not only for the isopods (discussed above) but also for the possible ooids. It also might be possible to derive some indication of the habitat of the *Juravenator* from this combination. Thus, as was the case for its phylogenetically close relative, the fish-eating *Scipionyx*, the *Juravenator*’s habitat might have extended into the marine environment (cf. Buffetaut 1994: p. 128; Dal Sasso and Maganuco 2011; Göhlich et al. 2006).

The alleged ooids could have reached the inside of the body either through the mouth or the respiratory system. With respect to the former possibility: if *Juravenator* hunted its prey in an intertidal area, ooids clinging to prey could have been ingested. In terms of the latter possibility: as is known from the etiology of drowning, along with water, foreign bodies could be aspirated, as it might have been the case if *Juravenator*—if it indeed did drown—was in water that was stirring the bottom (cf. Dunagan et al. 1997; Taylor 1994). Assuming the spherical shapes are at least allochthonic sediment particles, this would also be evidence of a postmortem transport of the *Juravenator*: to the best of our knowledge, ooids have yet to be found in the facies of the Schamhaupten silicified plattenkalks (Schamhaupten Member). The distribution of ooid deposits (facies) contemporary with the *Juravenator* is evidence that all of such facies are found east of the Schamhaupten Basin (see Fig. 1; Röper 2005a).

## Conclusions

As the above explanations concerning the palaeoenvironment of the basins of the Solnhofen Archipelago show, the conditions of deposition of the single basins can not be considered to be similar, even inside a time slice. Therefore, a generalised way of looking at the depositional setting must be excluded.

The traditional pro-arguments for hypersaline water at the sea bottom, such as the arched spines of different species of vertebrates or the distortions of cnidarians of the crinoid *Saccocoma*, can be regarded as refuted. This was demonstrated very early by Eberle’s (1929), Weiler’s (1929) and Hecht’s (1933) experiments with the decomposition of fishes, in which corresponding arching already occurred in water with normal salinity. This applies on all points to the experiments of Faux and Padian (2007) with extracted tendons under hypersaline conditions, but only with reservations to their completely submersed quails, since these experiments were not conducted up to a degree of advanced maceration [such that a potential influence of Ligamentum elasticum could not be checked].

In the course of our analysis, it has become obvious once more that an extensive and well-founded statement about the taphonomic history of single specimen is possible only if there is a good documentation of the find. In addition to the precise description of the place where the specimen was found, such documentation should especially include biostratigraphical and lithostratigraphical documentation, the recording of the sedimentologic and palaeontologic stock of a profile, as well as, last but not least, the original orientation of the slab.

In the preceding sections of this article we have listed arguments, facts and data extracted by experiments which, according to us, are clearly against the hypothesis of Moodie (1918, 1923) and Faux and Padian (2007). One of our fundamental counter-arguments is the essential demand of Faux and Padian (2007) that the carcasses of terrestrial vertebrates must not be subjected to any, or just a slight, postmortem transport. This continuation in a place is, in the case of terrestrial vertebrates, a general, inherent contradiction against an aquatic space of deposition.

Vertical transport, namely, the sinking through a water column, is inevitable for the deposition of that kind of vertebrate carcass. Judging by the opisthotonic posture hypothesis of Faux and Padian (2007), a change of place of that kind must be equated with a material transport. Under these circumstances, it is probable that a certain posture of an individual’s body, assumed while dying, is also subjected to modifications. However, in the aquatic environment, the postmortem persistence of an opisthotonus may also be doubted due to the MLPP, which regularly occurs in terrestrial tetrapods. In the case of the posture of the limbs, this MLPP is interpreted by Moodie (1918, 1923) as “rigid



limb” posture and by Faux and Padian (2007) as “decerebrate rigidity” or “decerebellate rigidity”.

The specimens treated in the available studies illustrate several inconsistencies in the hypothesis of Moodie (1918, 1923) and Faux and Padian (2007). The *Compsognathus* specimen in particular is suitable for refuting different views and conclusions uttered by Faux and Padian (2007) and generalise them as far as the terrestrial vertebrates discovered in the lagerstätten of the Southern Franconian Alb plattenkalks are concerned. According to today’s state of knowledge, the opisthotonic posture hypothesis is fundamentally contradicted by the fact that the Solnhofen Archipelago is palaeogeographically interpreted solely as a marine site of deposition. This paradox can only be resolved by a basic reinterpretation of the facies of the Southern Franconian Alb plattenkalks. A re-interpretation of that kind must aim at the central statement of the genesis model of the Solnhofen Archipelago and therefore lead to a paradigm shift. A conceivable scenario would be a recovery and adaptation of the so-called “*Trockenlegungs-Hypothese*” [“drying-out hypothesis”] (sensu Weigelt 1927; Mayr 1967; Schäfer 1941, 1962, 1972; cf. Barthel 1964). This obsolete hypothesis would hypothetically allow the depositing of terrestrial vertebrates without a place change. This would amount to the demand of an etiological opisthotonus fixing possibly occurring in these vertebrates after death (cf. Bickart 1984; Krauss et al. 2005). According to us, the present level of knowledge, however, does not in any way give grounds to questioning the basic palaeogeographic statement of the deposition theories concerning the Solnhofen Archipelago discussed today (e.g., Barthel et al. 1990/1994; Keupp et al. 2007; Röper et al. 2000).

From what has been presented above, it can be concluded that the formation of the “opisthotonic posture” in subaquatically deposited carcasses of long-necked and long-tailed reptiles is the result of a postmortem process. The fact that the gravitational influence was much reduced played a fundamental role, because even weak tensile and compressive forces inherent in the carcass were able to come into effect through the positional changes of body parts. These forces were released basically through the elastic, partially pre-stressed ligaments. The suggestions of Cutler et al. (2011) that the experimentally induced ongoing hyperflexion of the necks of the domestic fowls is “possibly due to further shortening of epaxial muscles”, which firstly were bent backwards by “natural muscle tone of the epaxial muscles” are to be rejected. In medical and anatomical literature (e.g. Leisman and Koch 2009; O’Sullivan 2006) the muscle tone is triggered by unconscious nerve impulses, which means that muscle tone acts pre- and postmortem, but not postmortem. As Lonergan and Lonergan (2008) demonstrated, the titin molecule is deactivated early during autolysis by endogenic proteases. Tenderisation and not “further

shortening” are the intrinsic factors of decomposition of muscles by autolysis [which starts immediately after death; e.g., Janssen 1984]. The duration of this process is dependent on temperature. At the beginning of this process, the extremities and the joints of the neck and tail became oriented into a MLP position. Through the continuous bacterial decay of the musculature (= heterolysis), the inherent, pre-stressed energies of the Lig. elasticum were increasingly released, which gradually pulled the vertebral column into an opisthotonic posture, which is as far as the Lig. elasticum ranged.

The interpretation of the “opisthotonic posture” as “various” perimortem “afflictions of the central nervous system” by Faux and Padian (2007), sensu Moodie (1918, 1923), is thus rejected by us. On the contrary, this posture must be seen as a normal phenomenon that occurs during subaquatic gradual embedding of these sorts of carcasses. What needs to be clarified in these cases is not the “opisthotonic posture” of the skeleton, but rather the possible deviations from this condition.

**Acknowledgements** The authors are grateful to Martina Kölbl-Ebert and Oliver Rauhut who provided access to the specimens under their care, for advice, permission to use photos and illustrations as well as fruitful discussions. At our stays in Eichstätt and Munich we enjoyed the support of their teams and colleagues. The same is true with Ursula Göhlich, Louis Chiappe and Helmut Tischlinger who kindly supplied advice, illustrations and photos. Winfried Werner (Zitteliana) kindly gave permission to use illustrations of Ostrom (1978). We wish to thank Pino Völkl and Klaus-Dieter Weiß for irreplaceable background information about *Juravenator* which otherwise would have been lost. We were given invaluable support in image processing from Thomas Bizer. Daniel Marty generously diagnosed and interpreted the dinosaur trackway and gave permission to publish it in this paper. Oliver Rauhut and an anonymous reviewer critically read the manuscript and made helpful suggestions. This paper greatly improved by generous support with the literature by Reinhold R. Leinfelder, Gerald Mayr, Holger Preuschoft, Oliver Rauhut, and Martin Sander. For fruitful discussions and advice we are grateful to Ulrich Betz, Justin K. Broadrick, Thomas Dumser, Martin Ebert, Franz Fürsich, Hans Hess, Dietmar Jung, Dean Lomax, Matthias Pfäffli, Holger Preuschoft, Günter Schweigert, Kris-ter Smith, Takanobu Tsuihiji, Günther Viohl, and Daniel Wyler. Special thanks to Elke Bitter, Iris Bitter, DeNae Flentje, Jeb Hogan and Andrea Voegelin who improved the English.

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