



Taphonomy of fish concentrations from the Upper Jurassic Solnhofen Plattenkalk of Southern Germany

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With 11 figures and 1 table

Abstract: The density of vertebrate fossils on bedding planes is generally very low in the Upper Jurassic plattenkalks forming the Solnhofen fossil Lagerstätte. There are, however, a few bedding planes where large concentrations of the small fish *Leptolepides sprattiformis* (BLAINVILLE, 1818) occur. The aim of this paper is to analyse and interpret these fish concentrations from a taphonomic point of view. For this purpose, the taphonomic features of *L. sprattiformis* concentrations on three large slabs were semi-quantitatively analysed. The concentrations of individuals on bedding planes are explained as recording local mass mortality events caused by tropical storms that, for short intervals, disrupted the pycnocline which separated hypersaline, oxygen-poor to anoxic bottom waters from normal marine surface waters in the Plattenkalk basins. Mass mortality is supported by tetany features such as gaping jaws, hyperextended branchiostegal rays, and splayed fins, which occur in the majority of the specimens. The generally excellent preservation of the fish resulted from lack of post-mortem floatation, rapid burial and/or overgrowth by microbial films, and quick re-establishment of the pycnocline with inhospitable conditions on the basin floor. The post-mortem concave-arching of the backbones and various displacements of the vertebral column were most likely caused by varying decay resistance of soft tissues and the pressure of decay gases in the body cavities, respectively. The taphonomic analysis of fish concentrations can provide very detailed palaeoenvironmental information and serves as an independent line of evidence for palaeoenvironmental reconstructions that complements geochemical and sedimentary data.

Key words: *Leptolepides sprattiformis*, concave-arching backbones, taphonomy, palaeoenvironment, Plattenkalk, fossil Lagerstätte, Tithonian.

1. Introduction

The Solnhofen Plattenkalk, a finely laminated carbonate mudstone, is famous for its excellent preservation of fossils, providing a window into late Jurassic shallow-water carbonate ecosystems. Although the recorded species diversity is very high (SCHULTZE 2015 lists 861 species of metazoans, among them 223 species of vertebrates), the density is generally very low, except for the stemless pelagic crinoid *Saccocoma* that abounds on a number of bedding planes and rare small clumps of oysters and inoceramid bi-

valves. There are, however, a few bedding planes within the finely laminated succession of the Eichstätt – Solnhofen basins, where large concentrations of the small teleostean fish *Leptolepides sprattiformis* (BLAINVILLE, 1818) occur, with more than a hundred individuals per square metre. These occurrences clearly differ from the highly scattered occurrences of most other fossils in the Solnhofen Plattenkalk, in particular of vertebrates. Concentrations of fossils may be the result of a number of processes (e.g., BRONGERSMA-SANDERS 1957; KIDWELL 1986; KIDWELL et al. 1986; BELL et al. 1989; FÜRSICH & OSCHMANN 1993;



Fig. 1. Sketch map of Germany showing the location of the study area (box): Enlargement of the study area showing in more detail of the fossil localities (red points) mentioned in the text. The green coloured area denotes the outcrop belt of Jurassic rocks of the Franconian and Swabian Alb.

FÜRSICH 1995; TOMAŠOVÝCH et al. 2006; QI et al. 2007; MARTILL et al. 2008; VEZULLI et al. 2010; PAN et al. 2012). They can be physical in nature (concentrations by waves or currents), biological (e.g., mass mortality, gregarious behaviour), or involve extended periods of time (e.g., prolonged phases of low rates of sedimentation resulting in faunal condensation). The aim of this paper is to analyse and interpret the taphonomic history of these fish concentrations and to develop a better understanding of the environmental conditions that led to their formation as well as of the environmental fluctuations within the small basins represented by the Solnhofen Plattenkalk.

2. Geological background

The Lower Tithonian Solnhofen Plattenkalk of the Franconian Alb of southern Germany (Fig. 1) is one of the most famous fossil lagerstätten worldwide, renowned for its excellent preservation of fossils (articulated skeletons and soft parts of both marine and terrestrial invertebrates, vertebrates and plants) (e.g., BARTHEL 1978; BARTHEL et al. 1990; FRICKHINGER 1994; FRICKHINGER 1999; ARRATIA et al. 2015; EBERT et al. 2015). Lithostratigraphically, the finely laminated carbonates of the Solnhofen Plattenkalk belong to the Altmühltal Formation, which

biostratigraphically is part of the Hybonotum Zone (Riedense and Rueppelianus subzone) (SCHWEIGERT 2007; NIEBUHR & PÜRNER 2014; SCHWEIGERT 2015). The Solnhofen Plattenkalk was deposited in shallow basins within an archipelago at the northern margin of the Neotethys, bordering the Rhenish Landmass (e.g., MEYER & SCHMIDT-KALER 1989; VIOHL 2015a). The submarine topography was created by microbial-sponge reefs and peloid-lithoclastoid sandbars (KOCH et al. 1994) that covered large areas of the northern Neotethys carbonate shelf during the early Late Jurassic. These reefs had died off towards the end of the Kimmeridgian time interval in connection with a relative rise in sea-level (see VIOHL 2015a for a detailed review of the geological history). In some areas, however, carbonate production outpaced the relative sea-level rise and locally coral reefs became established on top of the microbial-sponge reefs (e.g., MEYER & SCHMIDT-KALER 1989). The pronounced sea floor topography produced a system of several small basins, in which thinly laminated, fine-grained carbonate ooze accumulated (VIOHL 2015b). A fairly equitable and hot climate (e.g., LEINFELDER 1994) led to stratification of the water masses of the Plattenkalk basins and the formation of a pycnocline/halocline, with hypersaline and oxygen-poor conditions in the lower water column (e.g., BARTHEL 1964; BARTHEL 1970; SCHWARK et al. 1998; Viohl 2015c). KEMP & TRUEMAN (2003), based on geochemical data, argued against a complete lack of oxygen on the sea floor. Locally, the floor of the basins was apparently covered with microbial mats or films (KEUPP 1977; SEILACHER et al. 1985; VIOHL 2015c). Tropical storms suspended large amounts of fine-grained carbonate mud on neighbouring shallow areas and transported it into the basins where, after waning of a storm, it settled forming a thin layer (“Flinz”). Rain storms brought fine-grained siliciclastic material from land areas into the basins where it formed mm-thick marly limestone laminae containing up to 20 % clay particles (“Fäule”) (e.g., BARTHEL 1978). Thus, sediment accumulated within the basins largely by episodic events (VIOHL 2015c). This scenario partly explains the excellent preservation of many fossils, which must have been covered by sediment relatively quickly and/or became overgrown by microbial films (KEUPP 1977; SEILACHER et al. 1985; INIESTO et al. 2013; INIESTO et al. 2015; VIOHL 2015c; see also BRIGGS et al. 2005 for the comparable Nusplingen fossil Lagerstätte). The other decisive factor controlling fossil preservation was inhospitable

conditions above the sediment-water interface that excluded scavengers and slowed down decomposition of soft parts (e.g., BRIGGS 2003). VIOHL’s (2015c) depositional model of the Solnhofen Plattenkalk is a modified version of two previous models, one emphasizing the role of microbial mats (KEUPP 1977), the other advocating monsoonal storms that brought suspended material into the basins and caused short-term disruption of the pycnocline and ensuing mixing of the water masses before increasing evaporation re-established the salinity stratification (BARTHEL 1964; BARTHEL 1970).

Environmental conditions within the basins were by no means uniform but differed in the various sub-basins with respect to water depth, oxygen availability, development of a pycnocline and sedimentation mechanisms (see extensive review by REISDORF & WUTTKE 2012). As a result, different types of Plattenkalk can be differentiated such as lithographic, siliceous, marly and very finely laminated Plattenkalk (VIOHL 2015b). The fish concentrations discussed here from the Eichstätt – Solnhofen area formed in relatively deep sub-basins, below the storm wave-base. As the storm wave-base most likely was distinctly less than 20 m due to the limited fetch in the archipelago, only storm-induced currents affected the deeper parts of these sub-basins.

No comprehensive quantitative taphonomic analyses of the Solnhofen biota exist so far, but remarks on some taphonomic aspects of several taxa can be found in numerous papers (e.g., MAYR 1967; VIOHL 1994; WILBY & BRIGGS 1997; REISDORF & WUTTKE 2012; VIOHL 2015c, see also the studies of CHELLOUCHE et al. 2012, EBERT et al. 2015, and CHELLOUCHE 2016 on similar Plattenkalk occurrences). They usually deal with specific groups of fossils or else with particular preservational aspects.

3. Material and methods

Large slabs with *L. sprattiformis* concentrations on bedding planes are stored in the Jura-Museum Eichstätt and the Bürgermeister-Müller-Museum of Solnhofen, southern Germany. Almost all the fish preserved in the Solnhofen Plattenkalk are rare, found widely scattered on bedding planes, except for *L. sprattiformis*, which may form rare high-density concentrations. On the studied bedding planes it has an average total length of 4 cm (maximum length: 50 mm) and is, together with *Tharsis dubius*, the most common fish fossil in the Solnhofen Plattenkalk.

Two slabs with fish concentrations were quantitatively and semi-quantitatively analysed. Slab 1

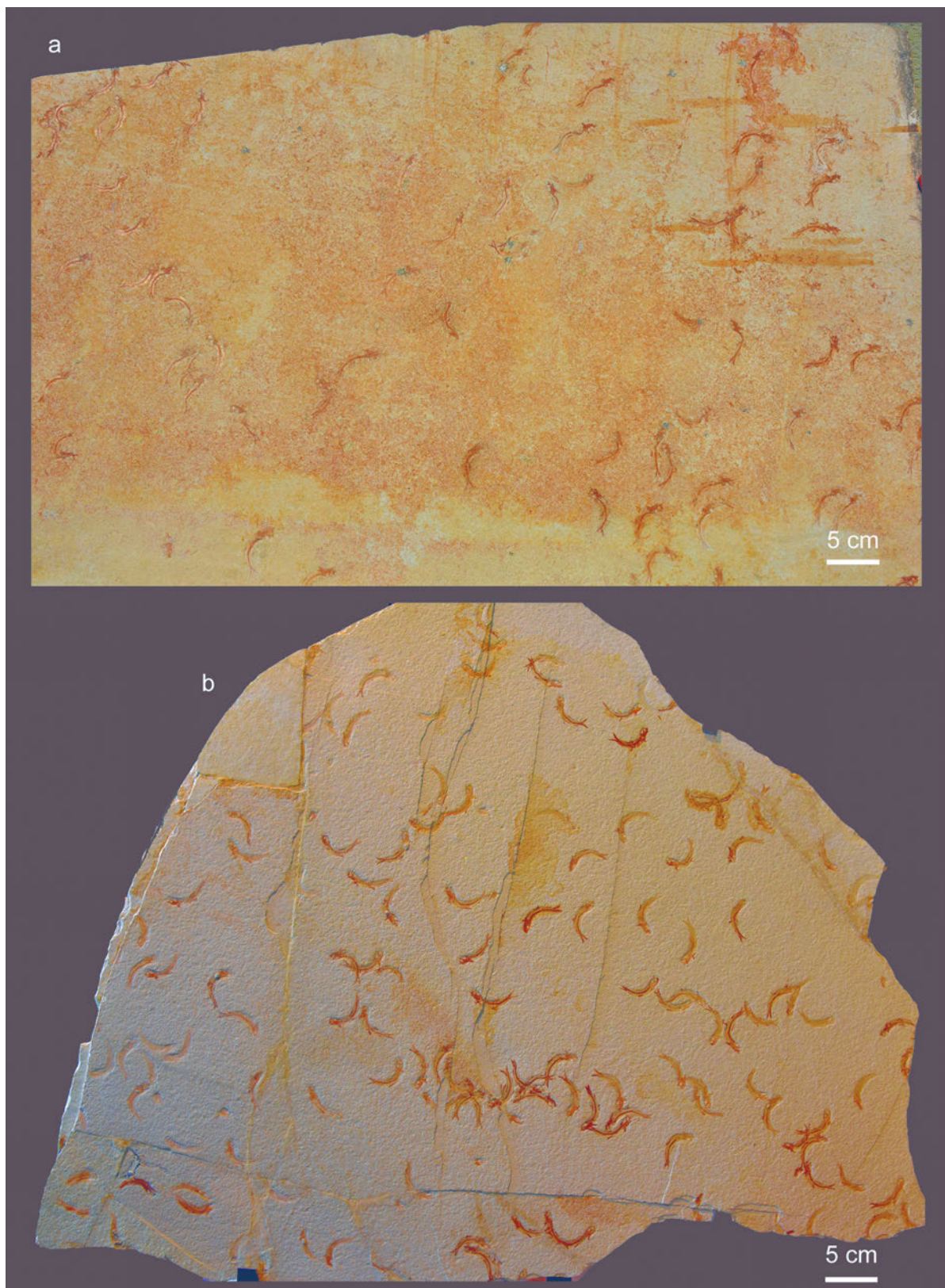


Fig. 2. Slabs with monospecific concentration of *Leptolepides sprattiformis* (BLAINVILLE, 1818) for quantitative analysis. **a** – Slab 1 (JME-SOS 2182) from Mörsheim. **b** – Slab 2 (JME-SOS8059) from Solnhofen.

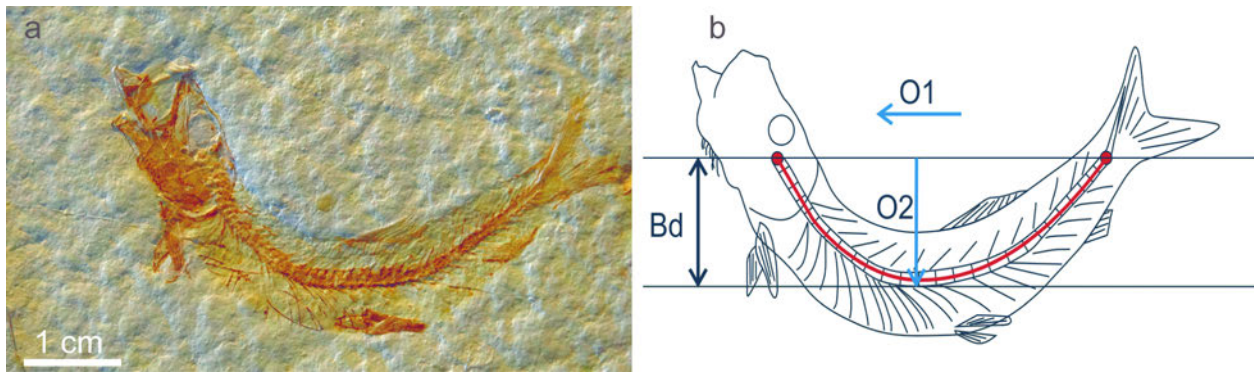


Fig. 3. a – Example of *Leptolepides sprattiformis*. **b** – Measurements used for orientations and size. O1, orientation of the long axis; O2, orientation of the curvature; Bd, degree of curvature expressed in mm; the length of the vertebral column (in red), up to the beginning of the hypurals was measured to determine size.

(~115 cm × ~62.5 cm with 83 specimens; collection number: JME-SOS2182) and slab 2 (~94 cm × ~56 cm with 134 specimens; collection number: JME-SOS8509) are in the collections and on display, respectively, in the Jura-Museum Eichstätt. Some information was also obtained from a large slab (slab 3; ~345 cm × ~150 cm) on display in the Bürgermeister-Müller-Museum, Solnhofen. Unfortunately, this slab was not available for a detailed study. Slab 1 was collected at Mörnsheim, while slab 2 and slab 3 were collected at Solnhofen (Fig. 1), slab 3 was collected from the quarry Alter Steinberg between Solnhofen and Langenaltheimer Haardt. Each slab contains a monospecific high-density assemblage of *L. sprattiformis* preserved on the bedding plane (Fig. 2). Slab 3 is the most densely packed with individual fish. The percentages of complete, articulated specimens on the slabs are high, and the body outline, highlighted by scales and partly stained in a brownish colour, can be clearly observed (Fig. 3a). Unfortunately, for none of the three slabs the counter slab exists, which would have allowed to clarify preservational ambiguities concerning the completeness of some specimens.

All examined specimens are preserved within the classical Solnhofen plattenkalks of Eichstätt and Solnhofen. No remains of benthic organisms co-occur with *L. sprattiformis* on the bedding planes. The planktonic crinoid *Saccocoma pectinata* and the coprolite *Lumbricaria* are common elements on both slab 1 and slab 2. In addition, a single ammonite was recorded on slab 2. No sign of bioturbation is observed.

In addition, four small slabs in the collection of the Bayerische Staatssammlung für Geologie und Paläontologie, Munich, ranging in size from 0.03 to 0.29 m² have been studied to obtain additional information. The number of *L. sprattiformis* is, however, too small (numbers of individual fish: 6–25) for a rigorous statistical analysis.

Articulated specimens often exhibit a continuous curvature along the length of the vertebral column. The linear measurements “Bd” represents the tightness of this cur-

vature. Bd is the orthogonal distance between two lines, the first joining the anteriormost (1st cervical) and posteriormost (last caudal) vertebra, and the second parallel to this drawn through the inflection point along the vertebral column (Fig. 3b). The features documented for the quantitative/semi-quantitative analysis are listed in Table 1.

The scales of *L. sprattiformis* are quite small and thin and thus very hard to detect on the fossils. As a result, detachment of scales is not considered in this study. Not all morphological and taphonomic features could be observed on each specimen; therefore, the numbers of specimens used for analysis of each feature differ.

The degree of taphonomic alteration to a fish carcass was quantified using the following methodology: pristine specimens = 0 (Fig. 5a), backbone distortion = 1 (irregular in Figs. 4a, 5e, with angle in Fig. 5f), vertebrae displacement = 2 (Fig. 5c), rib displacement = 2 (Figs. 4a, 5g), detachment of a fin = 1 (Fig. 4b, c) or fins = 2 (Fig. 5g). The values given to the various taphonomic features are supposed to reflect their importance. Subsequently, all alterations of each specimen are summed up to characterize its preservational state. The regular concave curvature of the backbone has not been included in the semi-quantitative analysis as it occurs in all specimens and did not alter the preservation quality.

4. Results

4.1. Orientation

All the specimens included in this study had the dorso-ventral axis of the body parallel to the bedding plane (lateral view; Figs. 4, 5). The plan-view orientation of the long axis of *L. sprattiformis* on the bedding plane was measured in order to detect any preferred orientation pattern. The chi square and Raleigh tests (to find

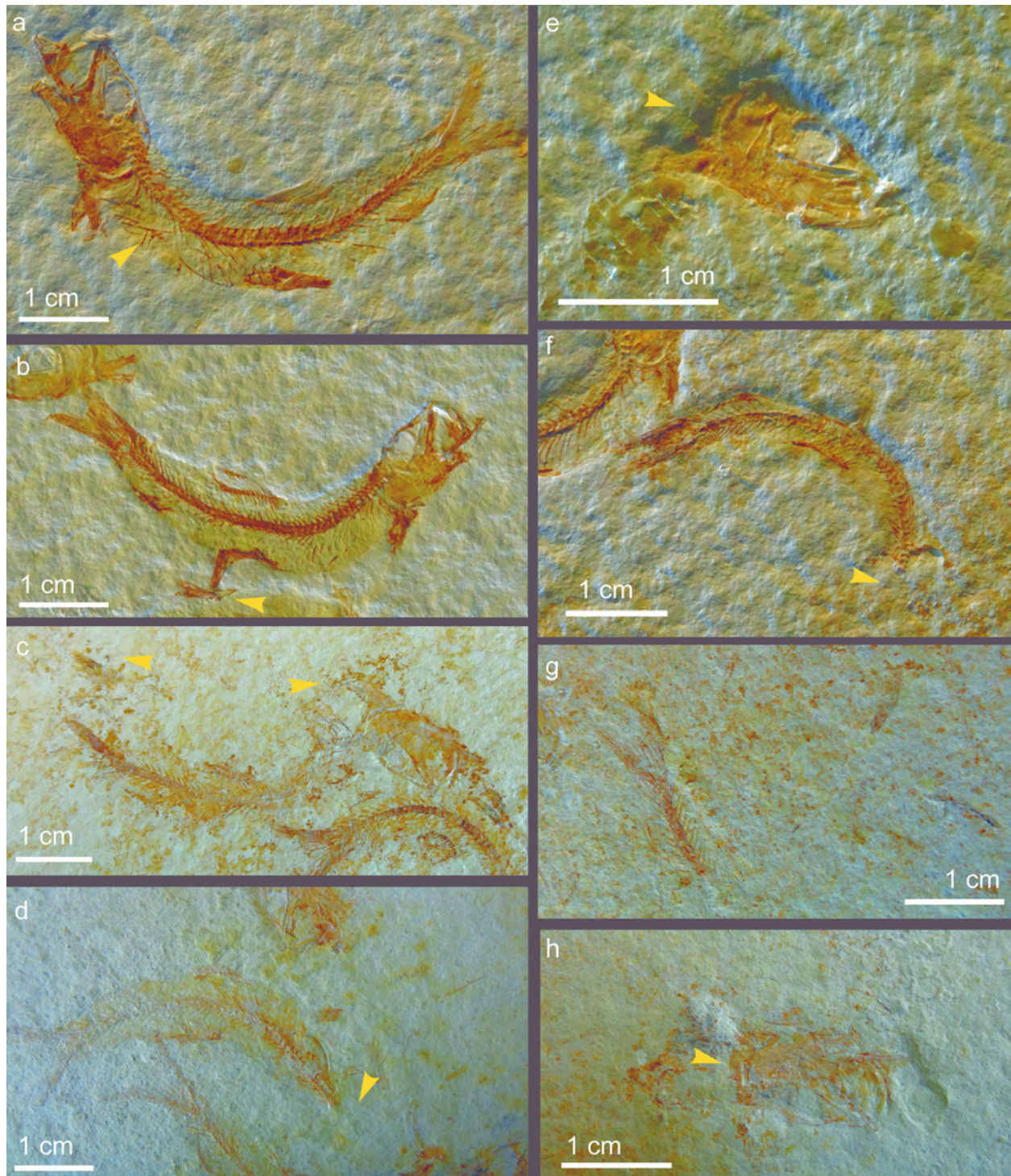


Fig. 4. Examples of various degrees of disarticulation observed on slabs 1 and 2. **a** – Complete specimen with the ribs slightly dislodged, arrow indicates. **b** – Complete specimen with one ventral fin detached, arrow indicates. **c** – Deformed specimen with partially detached caudal fin and scattered ribs, arrow indicates. **d, f** – Specimens with head missing, arrow indicates. **e, h** – Isolated head, arrow indicates in **e**. **g** – Incomplete specimen, with most of the body missing, but with articulated remnants.

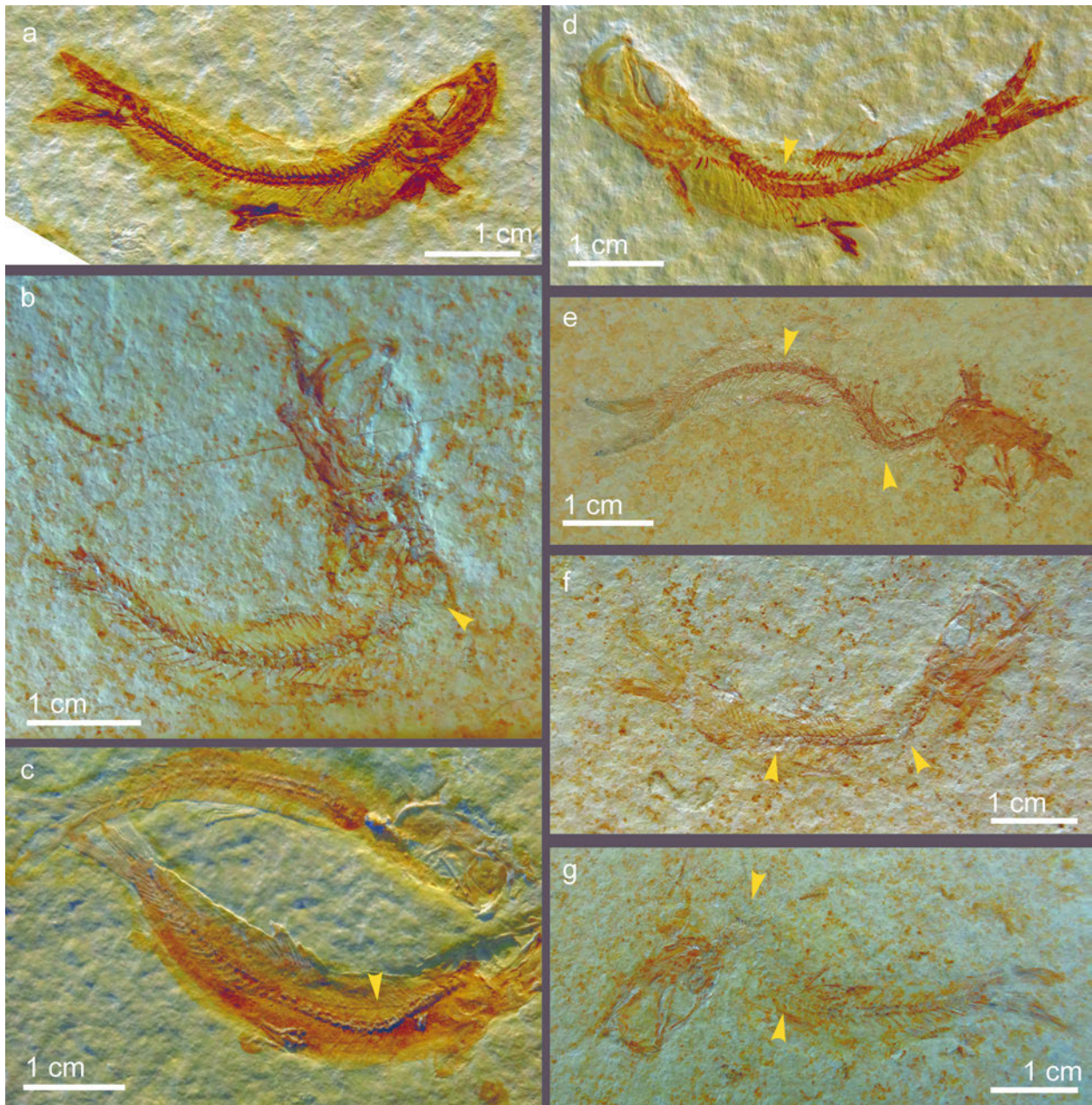


Fig. 5. Examples of deformation of the vertebral column observed on slabs 1 and 2. **a, d** – Complete specimen with concave-arched backbone. **b** – Specimen with concave-arched backbone that displays proximal breakage, arrow indicates. **c** – Complete specimens with concave-arched and partially detached backbone, arrow indicates. **e, g** – Complete specimens with undulous backbones, arrows indicate. **f** – Specimen with concave arching of backbone and proximal and terminal breakage, arrows indicate.

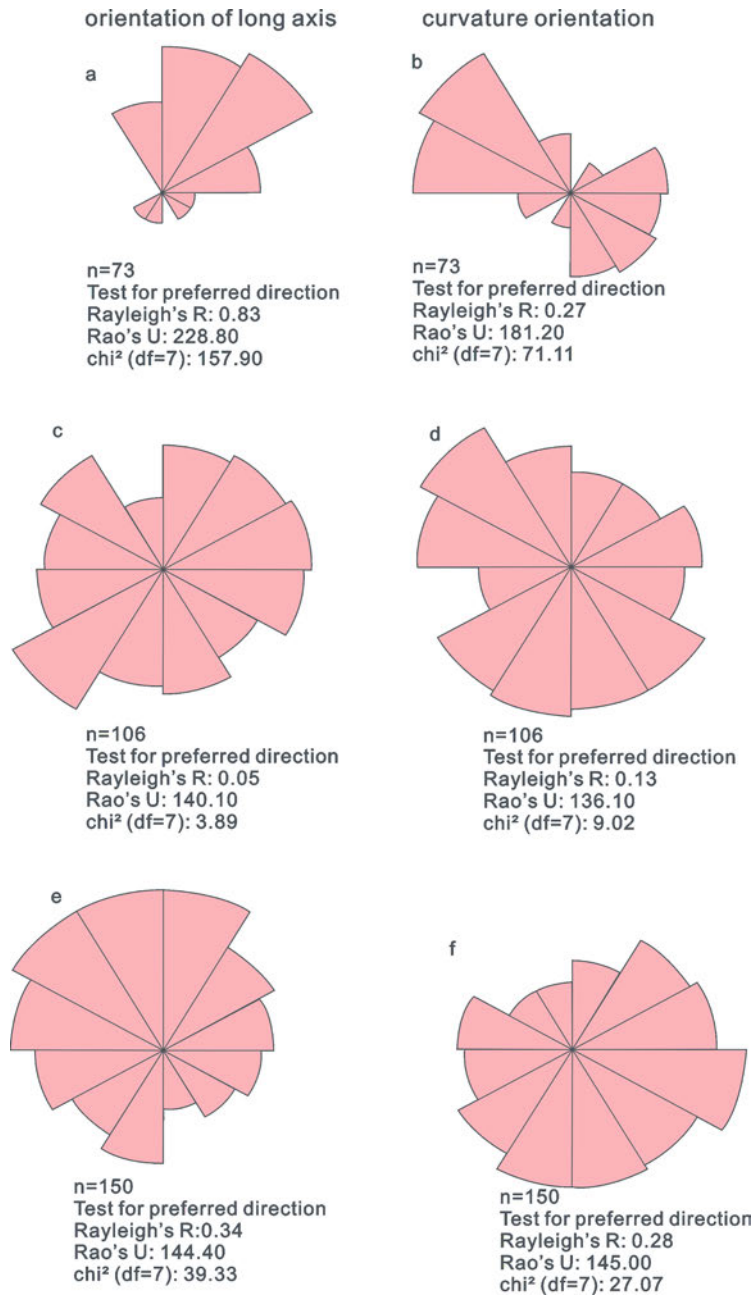


Fig. 6. Plan-view orientation of the long axis (a, c, e) and curvature orientation (b, d, f) of *Leptolepides sprattiformis*. a, b – Slab 1. c, d – Slab 2. e, f – Slab 3.

Table 1. Features recorded for the quantitative analysis. Taphonomic information on slabs 1–7 from the Jura-Museum Eichstätt (JME; slabs 1 and 2), the Bürgermeister Müller Museum Solnhofen (slab 3) and the Bayerische Staatssammlung für Geologie und Paläontologie, Munich (BSPG; slabs 4 to 7).

Slab	Area [m ²]	N Lepto-lepides	Density [m ²]	Remarks	Locality	Collection number
1	0.72	83	115	see text	Mörnsheim	JME-SOS2182
2	0.52	134	258	see text	Solnhofen	JME-SOS8509
3	~4.14	?	?	detailed analysis not possible	Solnhofen (quarry Alter Steinberg)	–
4	0.03	25	735	densely packed, some crossing-over occurs; all strongly recurved; long axis with preferred orientation	?Langenthaltheimer Haardt. Most likely Sappenfeld	BSPG-AS I 819
5	0.06	9	141	preferred orientation of long axis	Solnhofen	BSPG 1986 I 32
6	0.07	6	65	all with gaping jaws and strongly recurved; bedding plane irregular, microbial?	Eichstätt	BSPG 1967 XVI 29
7	0.29	13	45	very loosely packed; nearly all with gaping jaws; not all specimens are recurved	Eichstätt	BSPG 1964 XXIII 588

out the significance of the mean direction in a cycle histogram) show a clear preferred orientation of specimens on slab 1 (Fig. 6a) and slab 4. In contrast, the chi square and Raleigh tests of the rose diagrams on slab 2 and slab 3 show a lack of preferred orientation (Fig. 6c, e).

The orientation of the curvature of the backbone on the bedding plane was also measured. On slab 1, the curvature displays two preferred directions (Fig. 6b). On slabs 2 and 3, the rose diagram (Fig. 6d, f) suggests a random orientation of the curvature, but the chi square and Raleigh tests show that the orientation is not completely random.

4.2. Size distribution

The size (expressed by the length of the vertebral column) of *Leptolepides sprattiformis* was measured to understand the population structure of the monospecific assemblages and to obtain additional information on the ecology and living conditions of the fish population. Individuals on slab 1 (79 measurements) display a slightly wider size range (28–50 mm) than those on slab 2 (33–47 mm; 114 measurements) and slab 4 (26–42 mm; 17 measurements) (Fig. 7). In slab 1, a distinct size peak occurs around 41 mm. In contrast, the histogram based on slab 2 shows a bimodal size distribution; the first peak occurs between 39–41 mm, the second between 43–45 mm. As the number of in-

dividuals on slab 4 is fairly small (17), the size distribution is not regarded as significant.

4.3. Degree of articulation

On the slabs, the degree of completeness of the fish skeletons is very high (Fig. 8). In addition, several isolated heads (4 specimens out of 83 on slab 1 (= 4.8 %) and 10 out of 134 on slab 2 (= 7.5 %; Fig. 4e, h) or bodies with the head missing (5 out of 83 specimens on slab 1 (= 6.0 %) and 2 out of 134 on slab 2 (= 1.5 %; Fig. 4d, f, g) were found on all slabs. These separated parts do not show any further sign of disintegration, but exhibit the same excellent preservation as the complete individuals. As these isolated parts are thought to be the result of predation (see below) and not of physical decay, they were not included in the degree of taphonomic alteration.

The semi-quantitative analysis (Fig. 8) shows that 53 % of the specimens on slab 1 and 76 % of the specimens on slab 2 are perfectly preserved. The values 1 to 5 (i.e., the sums of the taphonomic alterations) indicate increasing alteration of the individuals. Minor modifications (values 1–2) such as an undulating or angularly curved backbone account only for 30 % (slab 1) and 18 % (slab 2) and stronger alterations are quite rare. For example, among the examined specimens partly disintegrated fins were rare (Fig. 4b, c), while ribs and other skeletal elements were occasion-

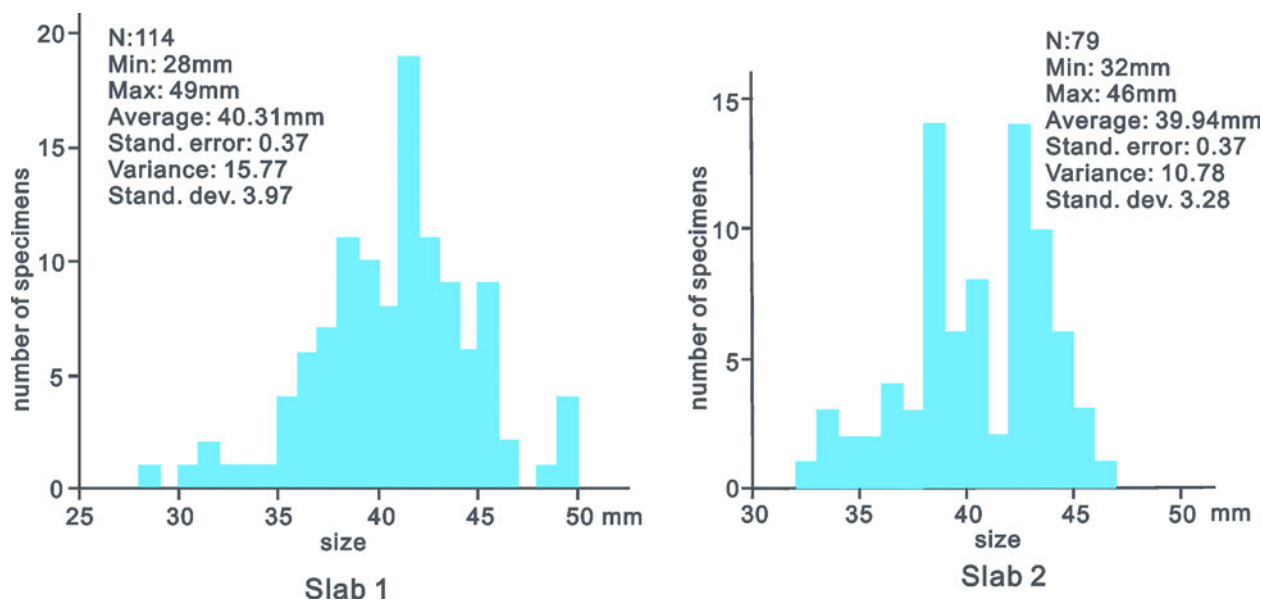


Fig. 7. Size-frequency histograms of *Leptolepides sprattiformis*.

ally dislodged from their original position within the fish, but usually only slightly so (15 out of 79 specimens (= 18.9%) on slab 1 and 13 out of 125 (= 10.4%) on slab 2). One should keep in mind that the single specimen with the highest alteration grade recorded (value 5) can still be regarded as comparatively well preserved.

4.4. Morphological deformation

All fossils suffered strong compactional compression normal to the dorso-ventral axis of the body. In nearly all specimens, bones are articulated or close to their proper anatomical position. Besides compactional deformation, there is another outstanding distortion that affected all fish bodies on the three slabs to a varying degree: a dorsally concave curvature (Fig. 2). Generally, the backbone is regularly curved, but in some cases, the backbone is slightly S-shaped (undulating, Fig. 5e, g), or forms an acute angle (angular curvature, Fig. 5b, f). On slab 1, undulating axial skeletons are more common than angular curvature (23 versus 8 specimens), while on slab 2, undulating axial skeletons were less common (8 versus 14 specimens). In specimens with a uniform body curvature, the ratio between the degree of the curvature of the backbone and its length was established (Fig. 9). The scatter dia-

grams show that the degree of the curvature increases with the size of the specimens.

4.5. Other taphonomic signatures

Features ascribed to tetany are common in well preserved fossil fish skeletons (e.g., PAUCA 1933; ELDER 1985; SMITH & ELDER 1985; FERBER & WELLS 1995; WHITMORE 2003; BARTON & WILSON 2005; BIENKOWSKA-WASILUK 2010). Apart from the “opisthotonic posture”, two tetany features were analysed in the material examined: gaping jaws and splayed/hyperextended pectoral and pelvic fins. Unfortunately, the lower jaw of *Leptolepides sprattiformis* is very delicate; this feature is therefore difficult to document in the examined slabs. The available data set (Fig. 10) shows that in a clear majority of the specimens the mouth is gaping and thus points to medium tetany (ELDER 1985; WHITMORE 2003). Pectoral fins, in contrast, are nearly all closed; only 16.7% (slab 1) and 9.0% (slab 2) are splayed/hyperextended. In pelvic fins, the splayed/hyperextended position is even scarcer (1.4% in slab 1, 4.6% in slab 2). Slab 4 from the Bavarian State Collections shows a similar picture: In 10 out of 17 specimens (59%) the mouth is gaping, but only 20% of the specimens have splayed/hyperextended pectoral fins.

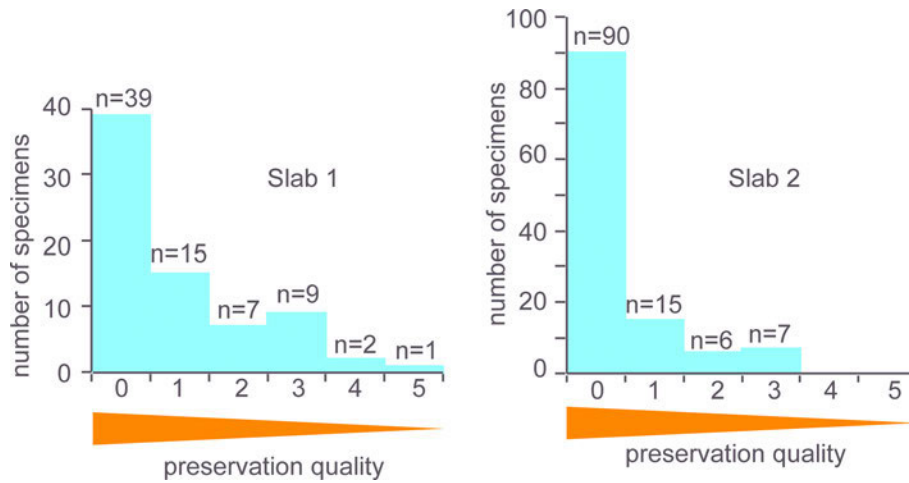


Fig. 8. The semi-quantitative analysis of taphonomic alterations documents excellent preservation (values 0 and 1) of more than half (slab 1) and more than two-thirds (slab 2) of the specimens. Note that even in the single specimen with the preservation value 5 the preservation is still far from poor.

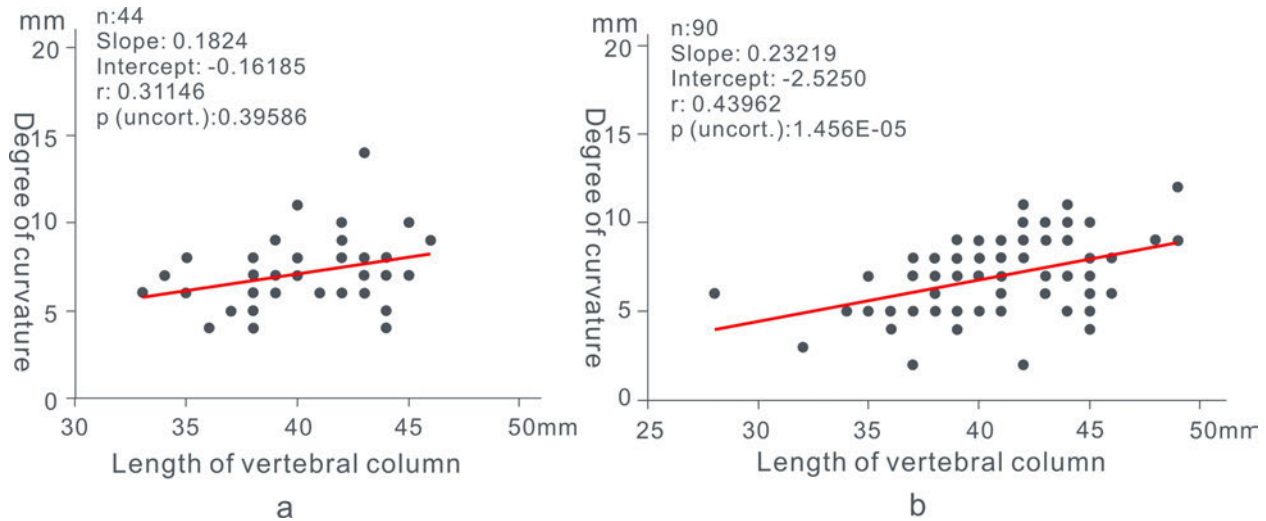


Fig. 9. Scatter diagrams with regression lines showing the relationship between the size of *Leptolepides sprattiformis* (expressed by the length of the vertebral column) and the degree of curvature of the backbone. **A** – Slab 1. **B**– Slab 2.

5. Discussion

5.1. Decay processes

The large percentage of well-preserved, complete specimens (Fig. 8) indicates that specimens came to rest in their final position before decay was far advanced. The very rare, partially disarticulated specimens with skeletal elements scattered around the carcasses suggest that any decay processes took place on the sea floor. Thus the death assemblages were not subject to floatation (e.g., [WEILER 1929](#);

[SCHÄFER 1972](#): 58; [ELDER 1985](#); [ELDER & SMITH 1988](#); [WILSON 1988](#); [FERBER & WELLS 1995](#); [WILSON & BARTON 1996](#); [BARTON & WILSON 2005](#); [BIEKOWSKA-WASILUK 2010](#); [PAN et al. 2015](#)) before reaching their final destination on the sea floor. All complete and partially complete specimens were lying on their side; none display subsequent re-orientation of the symmetry plane resulting in dorso-ventral compaction. Thus, the scenario that during decay considerable amounts of gases produced by bacteria expanded the abdominal cavity and caused re-orientation of the fishes with their bellies directed upwards can be ex-

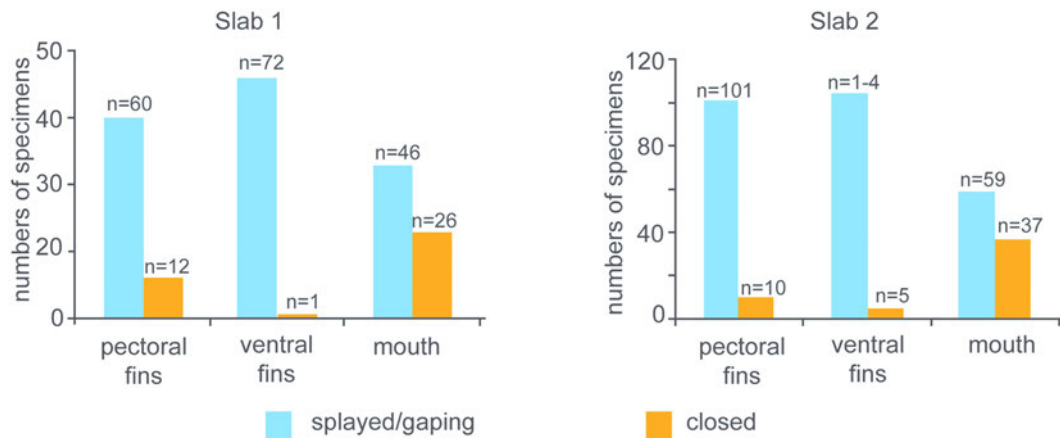


Fig. 10. The dominance of specimens of *Leptolepides sprattiformis* with gaping mouth as opposed to closed mouth on slabs 1 and 2 indicates tetany. In contrast, pectoral fins and in particular ventral fins only rarely show tetany (by being splayed).

cluded (PAN et al. 2015). This does not mean, however, that no decomposition gas was produced, but the oxygen-poor, hypersaline bottom waters most likely slowed down the decay process (see also SCHÄFER 1972: 58).

A few skeletal elements such as fins and ribs are displaced, but these scattered elements are still close to their original position, indicating that disturbance was not caused by bottom currents. Instead, it may point to the presence of a sticky microbial film that fixed parts such as fins on the substrate which then became dislodged from the main body when the backbones concavely arched (e.g., SEILACHER et al. 1985; VIOHL 1994; BIENKOVSKA 2004; CHELLOUCHE et al. 2012; HELLAWELL & ORR 2012; ORR et al. 2016).

Concave arching of the backbone is commonly observed in many fish lagerstätten (e.g., the Kimmeridgian Nusplingen and Wattendorf plattenkalks of Southern Germany, DIETL & SCHWEIGERT 2011; CHELLOUCHE et al. 2012; CHELLOUCHE 2016; the Eocene Green River Formation of the Central USA, HELLAWELL & ORR 2012; the Eocene Monte Bolca Lagerstätte of Northern Italy, MARRAMÀ et al. 2016; the Oligocene ‘Septarien-Ton’ of Germany, WEILER 1929; the Oligocene Carpathian Flysch of Poland, JERZMANSKA 1960; BIENKOVSKA-WASILUK 2010; the Oligocene of Suslănești-Muscel, Romania, PAUĂ 1933) and has been interpreted by some authors as a tetany feature (e.g., ELDER 1985; FERBER & WELLS 1995; WHITMORE 2003; MARRAMÀ et al. 2016). This feature prevails in all slabs examined. Here it is explained as a post-mortem feature, observed in many

vertebrates, resulting from varying decay resistance of soft tissues (REISDORF & WUTTKE 2012). In slender fish this common post-mortem feature might also be caused by overstretching of the ventral side due to the gas accumulating in the abdominal cavity or by the tension of ligaments (WEIGELT 1927; CHELLOUCHE et al. 2012). Our study supports that the concave arching of the backbone is a post-mortem feature, since the head-less bodies (the left-overs of predation) also show strong concave arching of the backbone (Fig. 4d, f). Adult individuals are thought to bend less, because younger fish have less ossified backbones, which are thus more flexible (cf. WEILER 1929). Based on our data, however, the degree of curvature actually increases slightly with the length of the backbone (Fig. 9). VIOHL studied the extreme concave curvature of young individuals of the teleost *Tharsis* and interpreted it as a result of a shortening of ligaments, not due to muscle contraction (VIOHL 1983; VIOHL 1990). According to him, these ligaments tied the neural arches together, which in turn articulated with the vertebral centra through cartilage. A strong contraction of the ligament would cause the detachment of the arches from the centra. SEILACHER et al. (1985), in contrast, proposed that extreme contraction of the ligaments was caused by the dehydrating effect of hypersaline waters, the latter a characteristic feature of the bottom waters in the Solnhofen Plattenkalk basins (e.g., VIOHL 2015b). As REISDORF & WUTTKE (2012) argued, the experimental data of FAUX & PADIAN (2007) in support of SEILACHER’s hypothesis are inconclusive. Moreover, the arching of the backbone has

also been observed in fishes, which had died in normal marine seawater (e.g., WEILER 1929; HECHT 1933). WEILER (1929) experimentally recreated this bending of the spinal column in clupeids (*Clupea harengus*) from the North Sea by letting them lie for a few days in water of salinity typical for the southern North Sea. Unfortunately, he did not record any precise information of initial salinity or salinity changes in the course of his experimental setup, so that a triggering of the bending by increased salinity caused by evaporation cannot be excluded.

In all slabs, there are some specimens where the vertebral column exhibits an undulous pattern, dislodgement, or even has been broken. Autolysis, decay, and production of decay gases go on as long as any soft tissue is left (SCHÄFER 1972: 49–61). Although the decay gases in the body cavities were not sufficient to lead to flotation of the carcasses, which would fit well with a depositional environment not shallower than 10 metres (ELDER 1985), their pressure apparently was high enough to cause such post-mortem displacements of the vertebral column.

5.2. Biostratinomic processes

The density of fish skeletons on a single bedding plane from the slabs examined may reach hundreds per square metre. Eighty-three *L. sprattiformis* individuals were recorded on slab 1 (0.72 m²) and 134 on slab 2 (0.52 m²) amounting to 115 and 258 specimens/m², respectively. Slab 4 with 735 specimens/m² exhibits the highest density, but its significance is difficult to evaluate due to its small size. Despite the large number of individuals, their preservation quality varies very little (Fig. 8). The vast majority of skeletons on the three slabs is complete and articulated, suggesting that they experienced the same taphonomic history.

The size histograms in slabs 1 and 2 differ. The bimodal histogram of slab 2 can be interpreted to represent two recruitment phases. In contrast, the size distribution in slab 1 is more likely unimodal, but the size range is even wider than in slab 2 (Fig. 7). This excludes sorting as an explanation for the size distribution in slab 1.

The plan-view orientation pattern of the fishes on slab 1 (Fig. 6a) statistically implies a preferred direction of individuals, whereas on slabs 2 and 3 orientation is nearly random (Fig. 6c, e). The preferred unimodal orientation pattern on slab 1 suggests the influence of currents (see also DIETRICH 2009). Such

currents could have been short-lived backflows following storm events (e.g., AIGNER & REINECK 1982; HÉQUETTE & HILL 1993) that oriented the carcasses when they arrived on the sea floor, but it is unlikely that they concentrated them in the first place. In the case of the death assemblages of slabs 2 and 3, more or less random orientation of the carcasses argues against any current influence while or shortly after they settled on the sea floor. Considering the taphonomic features discussed above, concentration of *L. sprattiformis* by time-averaging and physical agents appears unlikely, leaving local mass mortality as the most likely process leading to the dense concentrations, as *L. sprattiformis* was a shoal fish (MARTILL et al. 2008). Considering the assumed hot climate during formation of the Plattenkalk deposit, the lack of signs of prolonged flotation by specimens on all slabs implies that the depositional environment exhibited a water depth of at least 10 m (ELDER 1985). In addition, lack of scavenging traces on discussed specimens implies inhospitable waters surrounding the carcasses while they lay on the sediment surface (ELDER 1985; FERBER & WELLS 1995).

5.3. Mass mortality

As outlined in the introduction, concentrations of organisms can be caused by a number of processes. The excellent preservation of *L. sprattiformis* argues against physical processes as causative factors of the concentrations. The preferred orientation of *Leptolepides* on slab 1 points to the influence of currents that oriented the carcasses but did not concentrate them in the first place. Instead, three features strongly point to mass mortality as the main factor causing the sudden death of the populations: (1) the high density of individuals; (2) the identical preservation quality of the fossils on a single bedding plane; and (3) lack of pronounced sorting of the individuals. In addition, experiments have shown that, at least in some freshwater teleosts (e.g. *Notropis*), death by increased salinity and alkalinity led to a negative buoyancy response in the carcasses right after death, preventing prolonged flotation and therefore increasing the preservation potential (ELDER 1985). Mass mortality could have been caused by intrinsic factors such as diseases (e.g., LESSIOS 1988; GREENSTEIN 1989; VEZZULLI et al. 2010) or by extrinsic factors, i.e. changes in environmental parameters such as fluctuations in salinity (e.g., BENNETT 1985; MARTILL 1988), degree of

oxygenation, temperature (e.g., in connection with the El Niño on the western shelf of South America; GLYNN 1984, ARNTZ et al. 1988; for the Mediterranean see COMA et al. 2009), change in sedimentation rate and obrution (e.g., GALE & VILLIER 2013) or poisonous micro-organisms (e.g., CONNELL & CROSS 1950; BRONGERSMA-SANDERS 1957; SUBRAMANIAN & PURUSHOTHAMAN 1985; PINHEIRO et al. 2010; PYENSON et al. 2014) or multi-factorial (e.g., CRAWFORD et al. 2008; MARTILL et al. 2008).

Mass mortality as causative factor of the fish concentrations is supported by evidence of tetany, in particular the considerable percentage of individuals with gaping jaws (Fig. 10). Interestingly, splayed/hyperextended pectoral and in particular pelvic fins, another characteristic feature of piscine tetany, are far less common (Fig. 10). As observed in modern experiments (ELDER 1985), such tetany-related features are not necessarily lost after death by relaxation of muscle tissues, but can be preserved for extended periods of time. As physical stress causes the onset of rigor mortis at least in modern teleosts (ROTH et al. 2006), preservation of a posture of fish carcasses showing signs of tetany even in the post-depositional state seems to be quite possible and even empirically observed, although the underlying physico-chemical mechanisms are still largely unknown.

5.4. Evidence of predation

Isolated heads (Fig. 4e, h) and bodies with the head missing (Fig. 4d, f) have been documented in the examined slabs. MAYR (1967) ascribed the occurrence of half-preserved fish in the Solnhofen Plattenkalk to the activity of swimming predators. EBERT & KÖLBL-EBERT (2012: 32) interpreted the occurrence of isolated fish heads in the Solnhofen Plattenkalk as signs of predation by Coleoidea, especially *Plesioteuthis* and *Trachyteuthis*. Our research supports these suggestions. Because no traces of scavenging were seen around either isolated heads or bodies with heads missing on any of the three slabs examined benthic scavengers can be excluded. One specimen of the vampyromorph teuthoid *Trachyteuthis hastiformis* on display in the Jura-Museum Eichstätt (JME-SOS8329) contains numerous individuals of *L. sprattiformis* lacking their heads and this arrangement has been interpreted as stomach contents on the museum label. Obviously, the several isolated heads on the three slabs escaped being swallowed or were pur-

posely left out by the predator. Such a behaviour has been documented from modern squids (e.g., BIDDER 1950; NIXON 1987; DAWE et al. 1997). Other nektonic predators living in the basins were sharks and turtles, which have a dentition suitable for cutting. They could have bitten off the heads of the *L. sprattiformis*, leaving the head-less bodies behind, although, at least in sharks, no such selective behaviour has been recognized (HOBSON 1963). The occurrence of the few isolated heads or headless bodies suggests that predation was more or less contemporaneous with the local mass mortality event. It seems that the predators might have played a role in the sudden killing of the fish swarms (see below).

WEILER (1929) carried out decay experiments on herrings to explain the occurrence of isolated heads of clupeid fishes from the Oligocene of the Mainz Basin. He could demonstrate that the separation of the head from the remaining body during the decay process was facilitated by the backward bending of the fishes coupled with occasional water movements. In the case of the present material it is unlikely that this process played a role because in no case an isolated complete head has been observed close to the respective body. Moreover, isolated heads also occur in slab 2, where the fish do not show signs of orientation and hence of water movements.

5.5. Environmental model based on the taphonomy of *L. sprattiformis* concentrations

There was little macrobiological activity on the sea floor, which is supported by the lack of extensive bioturbation. This is usually regarded as indicating anoxic conditions, possibly in conjunction with presence of toxic H₂S (e.g., HEMLEBEN 1977). However, rare earth elements (REE) data from biogenic phosphates of the Solnhofen Plattenkalk, particularly coprolites, suggests that the bottom waters were not anoxic (KEMP & TRUEMAN 2003) but probably only dysoxic (VIOHL 2015b). Alternatively, it has been suggested that the water column of the basins was stratified, with hypersaline bottom waters and a concomitant lack of oxygen at the sea floor (e.g., BARTHEL 1972; BARTHEL 1978; VIOHL 1985; BARTHEL et al. 1990; VIOHL 1998). In the depositional model proposed by VIOHL (2015b: 99), tropical storms led to episodic mixing of hypersaline, oxygen-poor bottom waters and oxygenated surface waters around the pycnocline. This effect apparently caused the death of many nektonic and planktonic organisms. Usually, death by anoxia results in tetany fea-

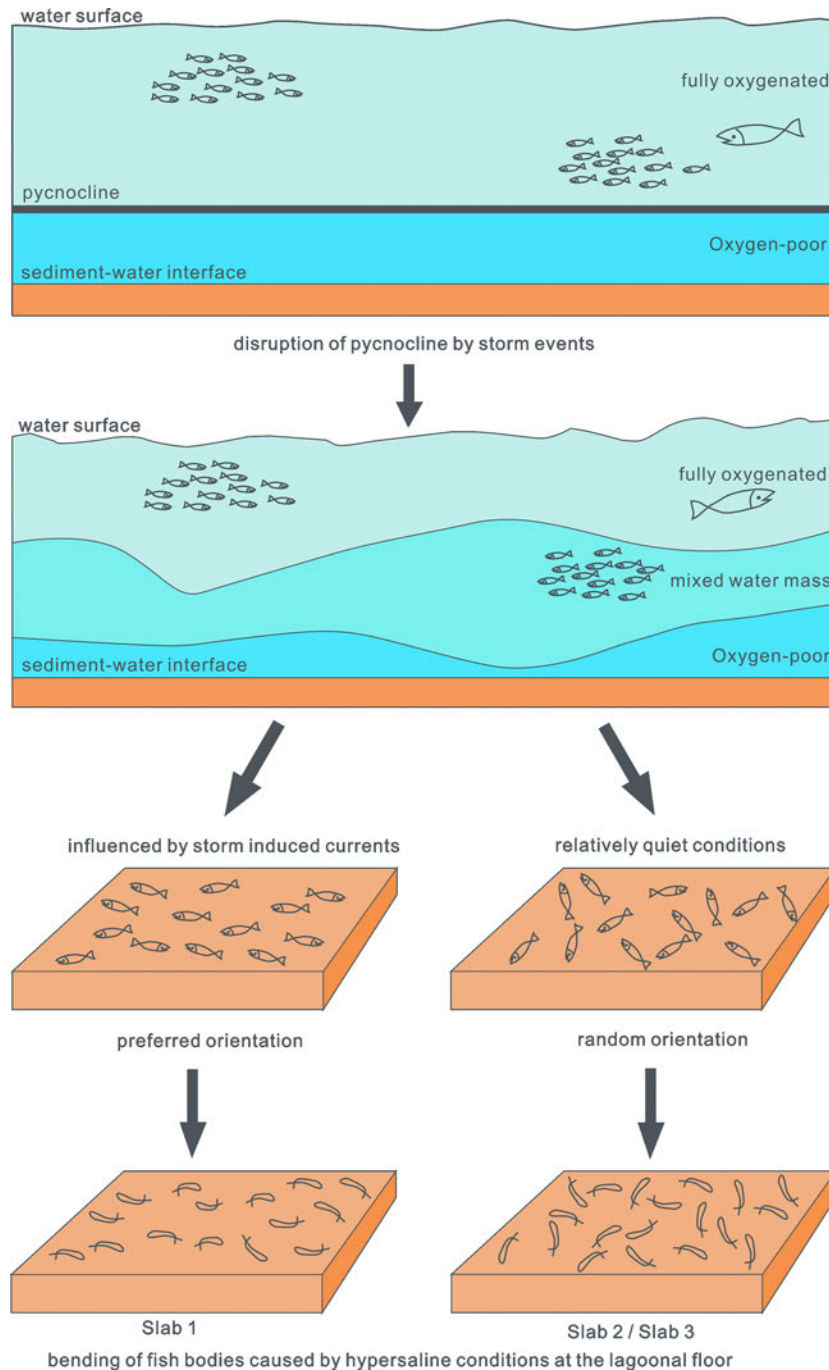


Fig. 11. Model explaining the *Leptolepides sprattiformis* concentrations in the Solnhofen Plattenkalk. The concentrations record mass mortality events of schools of fish caused by disruption of the pycnocline and the ensuing mixing of hypersaline, oxygen-poor bottom water-masses with shallower water masses in connection with stormy conditions. The preferred orientation of *L. sprattiformis* on the sea floor in the case of Slab 1 indicates the existence of short-lived storm-induced bottom currents. In contrast, no preferred orientation indicates the lack of such currents either due to a greater water depth or lower storm intensity. Although many individuals exhibit tetany features (gaping mouth), the arching of the fish bodies is not explained as a tetany feature but as a post-mortem feature caused by various decay resistance of soft tissues. Evidence of predation (e.g., isolated fish heads) might indicate that the fish schools were driven into the hypersaline/oxygen-poor clouds by predators.

tures (ELDER 1985; FERBER & WELLS 1995), which are also present in the majority of the *Leptolepides* individuals. Also, the events did not affect all nektonic and planktonic organisms. As discussed above, there are signs of predation by nektonic organisms, but no predators are preserved together with the fish concentrations, which indicates that the predators, probably due to their larger size and faster movements, could avoid the lethal anoxic cloud in time and thus were not affected by the mass-mortality event. This suggests that the mass mortality probably was a local event, occurring within a confined space.

Based on this discussion we propose a revised model for the *L. sprattiformis* concentrations in the Solnhofen Plattenkalk (Fig. 11). The concentrations are explained as recording mass mortality events of fish caused by disruption of the pycnocline during tropical storms (VIOHL 2015c). Schools of fish, which ventured to greater water depths in order to escape from the strongly turbulent surface waters or from predators, were caught in clouds of hypersaline, oxygen-poor waters and died. The preferred orientation of *L. sprattiformis* on slab 1 reflects the influence of short-lived bottom currents that originated after waning of the storms. The lack of preferred orientation of individuals on slabs 2 and 3 suggests the absence of any currents. The absence of currents aligning the carcasses in the latter case may be related to differences in storm intensity or to a more basal setting beyond the reach of such currents. The different orientation patterns thus document subtle environmental differences (differing levels of water energy and/or water depth). The post-mortem concave-arching of the backbones and various displacements of the vertebral column have most likely been caused by the dehydrating effect of hypersaline waters and the pressure of decay gases in the body cavities, when the fish had reached their final positions on the sea floor.

6. Conclusions

In the small basins, in which the sediments of the Solnhofen Plattenkalk accumulated, tropical storms caused mass mortality events due to the disruption of the pycnocline that separated hypersaline, oxygen-poor bottom waters from fully aerated, normal marine waters of the upper water column (e.g., VIOHL 2015c). During such storm events occasionally schools of the teleost fish *L. sprattiformis* were killed when they were caught in clouds of hypersaline and oxygen-poor

waters. Their excellent preservation suggests lack of post-mortem floatation, rapid burial and/or overgrowth by microbial films, and rapid re-establishment of the pycnocline. The preferred orientation of individuals in some of the mass concentrations indicates that they were aligned by probably short-lived currents in the aftermath of the storms. No preferred orientation of individuals on other bedding planes indicates lack of such currents. The differences in orientation may reflect differences in the strength of storms or differences in water depth at the sites the fish sank to the sea floor, i.e. stronger storms and shallower conditions in the case of aligned individuals. The concave-arching of the backbones of *L. sprattiformis* is a post-mortem feature, which occurs together with various displacements of the vertebral column, the former most likely caused by the varying decay resistance of soft tissues and the latter by the pressure of decay gases in the body cavities.

This study demonstrates that the taphonomic analysis of fish concentrations can provide us very detailed palaeoenvironmental information, which, besides geochemical and sedimentological approaches, is an independent line of evidence for palaeoenvironmental reconstructions. For taphonomic analysis of fish concentrations, we suggest the following steps: (1) Identification of the dominant species and co-occurring taxa on the bedding plane; (2) calculation of the density of the dominant species; (3) measuring the size of the dominant species; (4) measuring the plan-view orientation of the long-axis of the dominant species; (5) recording tetany features, such as open jaws, and splayed fins; (6) calculating the degree of articulation of the skeletons; and (7) recording deformation and displacement of the skeletons.

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