Bayerische Staatssammlung
für Paläontologie und Geologie

■ München, 2019

■ Manuscript received 17.09.2017; revision accepted 30.08.2018; available online: 12.03.2019

■ ISSN 0373-9627

■ ISBN 978-3-946705-05-5

Taphonomy of Tithonian Fishes from the Mörnsheim Formation of Southern Germany

Jack Thomas Rhodes Wilkin*

Camborne School of Mines, University of Exeter, Penryn, TR10 9FE, UK

**E-mail:* jack.wilkin@btinternet.com

Zitteliana 93, 83–87.

Abstract

The skeletons of teleost fishes dominate the Tithonian ichthyotaphocoenosis from the Mörnsheim Formation of Bavaria. Analysis of skeletal distribution, deformations of the vertebral column, and evidence of benthic currents originated from the long-term accumulation of carcasses in the plattenkalk under low sedimentation rates with evidence of prolonged exposure at the sediment-water interface. The spatial arrangement of disarticulated skeletal elements of fishes in the Mörnsheim resulted from the decay of soft tissues at the burial place in a calm environment. Disarticulation of some fishes as well as the convex-up arrangement of bivalve valves and ammonite aptychi may indicate weak current activity. Unlike other plattenkalk localities, there is no conclusive evidence of mass mortality. This suggests that the Mörnsheim Formation was subject to weak bottom currents indicating more open-marine circulation compared to the Solnhofen Formation.

Key words: Jurassic, Teleost, *Caturus*, Mörnsheim Formation, Taphonomy

1. Introduction

The Late Jurassic Mörnsheim Formation Southern Germany preserves a remarkable diversity of fishes. The study aims to determine the conditions under which fish carcasses were preserved. The Study of fish taphonomy has the palaeontological potential for determining depositional environment. Fish are taphonomically useful as they are comprised of many skeletal elements, making them sensitive to different depositional conditions (Tintori 1992). Schäfer (1972: 49) wrote: “fish carcasses are more vulnerable to decay than other vertebrates. This has one advantage: once we are familiar with the restricted conditions that permit total preservation, our conclusions about the mode of death, living conditions, and fossil preservation of extinct species will be more precise.”

In the context of this study, the Mörnsheim Formation was part of a complex series of isolated basins in Southern Germany and surrounding areas in Central Europe. The Southern German Jurassic is an example of a Konservat Lagerstätte and is famous for its beautiful and highly diverse fossil biota.

Much has been written about fish taphonomy (Elder & Smith 1988; Martill 1988, 1997), with many studies conducted on the underlying Solnhofen Formation (Viohl 1994) and other South German localities (Chellouche et al. 2012) but the Mörnsheim Formation, although rich in ichthyofauna, has received little recognition.

2. Material and methods

2.1 Field methods

The area of study was the commercial fossil quarry Fossilienbesuchersteinbruch, near the village of Mühlheim in central Bavaria. The grid reference for the site is 48.854, 10.987. The Mörnsheim Formation is comprised of a series of laminated lithographic limestones. The beds are tabular and can be traced over long distances, several tens of metres or more, without any noticeable changes in appearance or lithology. It is underlined by the Solnhofen Formation (Selden & Nudds 2012) and overlain by the Usseltal Formation (Niebuhr 2015). For this study, only a small section of the Mörnsheim Formation was examined; the Ammoniten-Lagen, the Erste Rosa, and Zweite Rosa (Fig. 1).

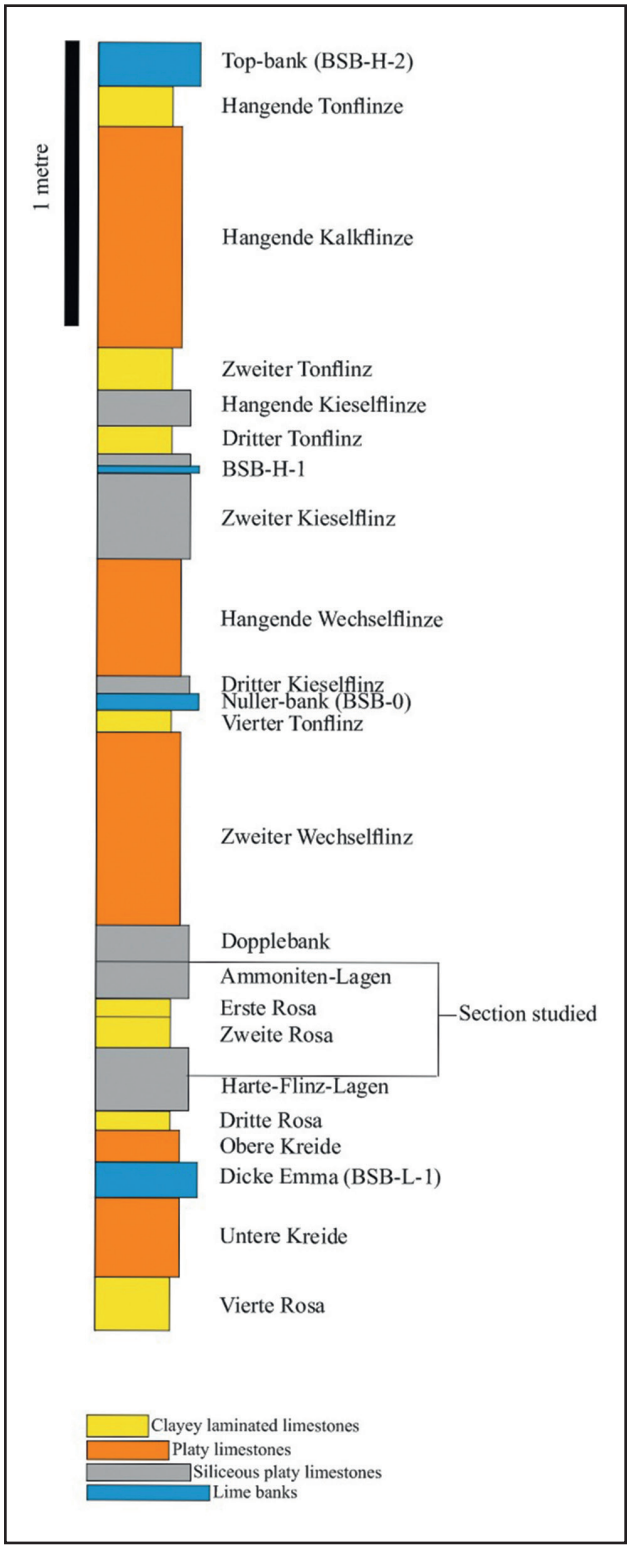

Figure 1: The Mörnsheim Formation at the quarry, showing the extent of the studied section.

2.3 Specimens

Numerous fishes were recovered during excavations. The most significate of which was nearly complete, though disintegrated, *Caturus furcatus* which demonstrates unmistakable evidence of unidirectional current activity as evidenced by scale distribution.

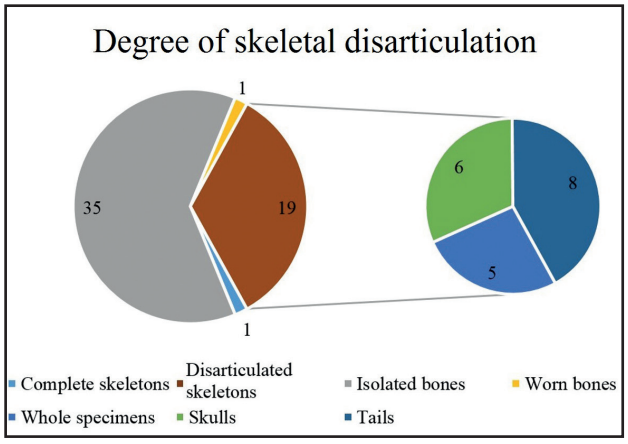

Figure 2: Results of disarticulation of fishes. Data clearly shows that complete specimens are much rarer than disarticulated ones. Demonstrating that carcasses were exposed at the surface long enough for soft tissues to disaggregate and taphonomic processes to manipulate skeletal elements.

3. Results

3.1 The degree of skeletal disarticulation

The skeletons were well preserved and retain their original shape. Most of the specimens, except for a few isolated vertebrae, are preserved two-dimensionally. Most of the fishes recovered from the section were isolated bones and scales followed by disarticulated skeletons (includes disarticulated complete skeletons, entire skulls and tails). This suggests exposure of the carcasses at the sediment for a length of time significant enough for soft tissue to disaggregate but not enough for the bone to become weathered. Most of the nearly complete specimens still show scales in life position, implying that some soft tissues remained at the time of burial.

The degree of skeletal disarticulation was estimated using the same methods as Bieńkowska-Wasiluk (2010) in her study of a fish taphocoenoses from the Oligocene of Poland. Each specimen recovered during excavations was given a code corresponding to one of five stages of disarticulation (Fig. 3): (1) Stage 5- the skeleton is very well preserved and completely articulated; (2) Stage 4: the specimen is well preserved with only slight disarticulation of scales and other small skeletal units; (3) Stage 3- the skeleton is moderately preserved with about half of the specimen articulated; (2) Stage 2- the specimen is poorly preserved with less than half of the skeleton being articulated; and (5) Stage 1- the specimen is poorly preserved with only a few bones, if any at all, still articulated (Fig. 2). None of the specimens recovered from the studied section represented stage 5 preservation with the number of specimens increasing with higher stages of disarticulation.

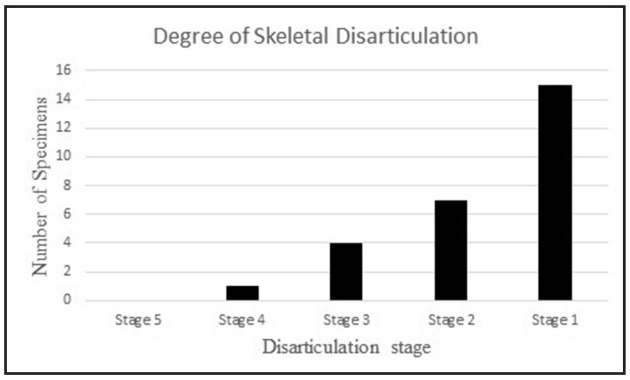

Figure 3: Results of disarticulation of fishes. Data shows that articulated skeletons are much rarer than disarticulated ones.

3.2 Current activity

Current activity is observed in some fishes from the recovered section including a specimen of *Furo* and the *Caturus* both show displacement of in a way consistent with bottom current activity (Fig. 4). Additionally, current activity is also demonstrated in the associated fauna, notably bivalves and ammonites. 51 out of 54, an over whelming majority. of the bivalve valves were found convex-up, a feature associated with bottom water currents (Gilinsky & Bennington 1994) (Fig. 5).

4. Discussion

4.1 Necrolysis

4.1.1 Causes of death

None of the fishes examined had agape jaws or erect fins which would indicate the cause of death was suffocation or poisoning (Bieńkowska-Wasiluk 2010). Instead, their deaths are attributed to several factors (e.g. disease, old age etc.) over a period.

4.1.2 Transportation in the basin

Despite the rich diversity of fauna, the Mörnsheim Formation does not represent a complete ecosystem. Instead, the biota is allochthonous. The organisms found within the plattenkalk inhabited the reefs that surrounded the basin. They were likely brought in by subtropical storms. The most common fossils are those of weak swimmers such as ammonites and small fishes, with stronger swimmers, such as vampyromorphs, and benthonic organisms (bivalves, brachiopods, and crustaceans), being proportionately rarer. Such as scenario as a clear example of a taphonomic bias. As a result, the plattenkalks are unrepresentative of the broader ecology. The high number of coprolites (*Lumbricara recta*) in the stu-

Figure 4: Partially disintegrated *Caturus* showing current activity. Scale bar = 5cm.

died section implies that organisms did survive, at least for a while, in the basins.

4.1.3 Post-mortem until burial

Some organisms may have floated to the surface waters due to an increase in buoyancy after death. In vertebrates, this is caused by bloating because gas builds up within the gut region during putrefaction. If disintegration occurs while the carcass is floating within the water column, various body parts can become dispersed, explaining the high amount of isolated skeletal elements. If the body loses buoyancy while entire, the body is deposited as a complete skeleton (Brenchley & Harper 1998).

4.2 Biostratinomy

4.2.1 Evidence of currents

In rare cases, the state of preservation of a specimen can provide unequivocal evidence of the action of bottom currents. The convex-up bivalve valves and ammonite aptychi are associated with bottom water currents (Gilinsky & Bennington 1994). In the case of the *Caturus* skeletal elements, notably scales, are arranged in a unimodal direction. Wind-driven waves were likely the cause such features. Another specimen from the section that demonstrates current activity is an isolated teleost tale that closely mirrors an actuopalaeontological experiment by Wilhelm Schäfer. In the experiment, a plaice (*Pleuronectes platessa*) was left exposed and subjected to minor bottom currents over a period of three months. This is not to say that the Mörnsheim fish where exposed for a similar amount of time as any number of factors (e.g. salinity, oxygen levels, temperature etc.) can affect the speed of the decay process, but it does suggest exposure at the sediment-water interface.

4.2.2 Decay stages

The time and distance of transportation are speculative because the spatial relationships between skeletal elements provide no evidence as to whether the *Caturus* was swept into the basin while alive or dead. The length of time from death to deposition of the fish varied considerably. But, this can be worked out based on the relative displacement of bones. Almost no displacement indicates a period of a few hours up to a few days and no more than 27 days for the less complete, disarticulated specimens (Wellnhofer 2013). Based on the complicated nature of the remains, a multiple-stage decomposition model can be created.

Decay Stage 1: The *Caturus* reached the basin floor, either ante-mortem, shortly after death, or in the initial stages of decay. During this time, bacteria built up within the gut though its effects, as seen by the relative completeness of the skeleton, was minimal. There is no evidence of scavenging on the skeleton.

Decay Stage 2: The degradation of muscles along the spine would have led to curvature of the spine. However, due to the heavily disarticulated nature of the fossil, it is not possible to draw any meaningful conclusions.

Decay Stage 3: The main muscles supporting the shape of the fish have degraded. During this time, weak underwater currents moved some of the smaller elements such as the scales.

Bed	Convex-up	Convex-down	Both valves
Ammoniten-Lagen	12	0	3
Erste Rosa	16	0	0
Zweite Rosa	5	0	0
Harte-Flinze-Lagen	18	0	0
Total	51	0	3

Figure 5: Table showing the positions of bivalve valves in each stratigraphic layer studied. The most common position was convex-up, this is conclusive evidence that the studied section was subject to weak current activity.

4.2.3 Discussion of spine curvature

Many of the fossil specimens show opisthotonic-posture. This occurs when the body arches over giving the fossil a characteristic ‘death-pose’. Several theories have been proposed for why this happens. (1) Perimortem death throes resulting from the affliction of the central nervous system resulting from brain damage and asphyxiation (Faux & Padian 2007). Such a scenario may have arisen in the plattenkalk basin if the waters were anoxic which is certainly seems to be the case at least at times (Barthel et al. 1990). (2) elastic pull of ligaments because of muscles relaxing after death; (3) rigor mortis combined with the contraction of various muscles; (4) contraction of ligaments; (5) head and tail dangling down whilst the carcass was floating in the water column; (6) anchoring of the skull in the sediment and the alteration of the post-cranial skeleton by water currents; (7) osmatic desiccation in a hypersaline environment (Faux & Padian 2007).

5. Conclusion

The Mörnsheim Formation represents a restricted basin on the northern margin of the Tethys Ocean. The taphocoenonoses originated from the long-term accumulation of carcasses in the plattenkalk under low sedimentation rates. The spatial arrangement of disarticulated skeletal elements of fishes in the studied section of the Mörnsheim Formation resulted from the decay of soft tissues at the burial place in a calm environment. Disarticulation of some fishes as well as the convex-up arrangement of bivalve valves and ammonite aptychi may indicate weak current activity. Unlike some other plattenkalk localities

there is no conclusive evidence of mass mortality, however, this is maybe due to the stratigraphic and physical size of the area being limited.

Acknowledgements

Thanks go to Dr David Martill (University of Portsmouth) for being my project supervisor while at the University of Portsmouth; Roland Pöschl (Fossilien Besuchersteinbruch, Mühlheim) for allowing me to use his quarry; Richard Hing (University of Portsmouth) for helping with UV photography; Günter Viohl (Eichstätt) for providing valuable comments and suggestions; and Michael Krings (Munich) for helping me publish my first scientific paper.

6. References

Barthel KW, Swinburne NHM, Conway Morris S. 1990. Solnhofen: A study in Mesozoic Palaeontology. Cambridge, University of Cambridge Press.

Bieńkowska-Wasiluk M. 2010. Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland. Acta Geologica Polonica 60, 479–533.

Brenchley PJ, Harper DAT. 1998. Palaeoecology: Ecosystems, environments and evolution. London, Chapman and Hall.

Chellouche P, Fürsich FT, Mäuser M. 2012. Taphonomy of neopterygian fishes from the Upper Kimmeridgian Wattendorf plattenkalk of Southern Germany. Palaeobiology Palaeoenvrionments 92, 99–117.

Elder RL, Smith GR. 1988. Fish taphonomy and environmental inference in paleolimnology. Palaeogeography, Palaeoclimatology, Palaeoecology 62, 577–592.

Faux CM, Padian K. 2007. The opisthotonic posture of vertebrate skeletons: post-mortem contractions or death throes? Paleobiology 33, 201–226.

Martill DM. 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. Palaeontology 31, 1–18.

Martill DM. 1997. Fish oblique to bedding in early diagenetic concretions from the Cretaceous Santana Formation of Brazil: implications for substrate consistency. Palaeontology 40, 1011–1026.

Schäfer W. 1972. Ecology and Palaeoecology of Marine Environments. Chicago, IL, University of Chicago Press.

Selden P, Nudds J. 2012. Evolution of fossil ecosystems (2nd ed). London, Academic Press.

Tintori A. 1992. Fish taphonomy and Triassic anoxic basins from the Alps: a case history. Rivista Italiana di paleontogia e stratigrafia 97, 393–408.

Viohl G. 1994. Fish taphonomy of the Solnhofen plattenkalk- an approach to the reconstruction of the palaeoenvironment. Geobios 16, 81–90.

Wellnhofer P. 2009. *Archaeopteryx*: The Icon of Evolution. Munich, Verlag Dr. Friedrich Pfeil.