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VERTEBRATE COPROLITES FROM THE NUSPLINGEN LITHOGRAPHIC LIMESTONE (UPPER JURASSIC, SW GERMANY)

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Abstract—Various morphotypes of assumed vertebrate coprolites are reported from the Nusplingen Lithographic Limestone, a marine Upper Jurassic Konservatlagerstätte located in southwestern Germany. These coprolites are phosphatic and some contain undigested remains of prey, e.g. fish bones, fragments of crustaceans, and hooks of coleoid cephalopods. Most coprolites probably were produced by bony fish and sharks; others may derive from marine crocodiles. All these predators are well-represented by skeletons or isolated lost teeth. The remarkable diversity of coprolite morphotypes suggests a complicated food chain being developed in the Nusplingen lagoon despite the hostility of the sea floor itself.

INTRODUCTION

The Nusplingen Lithographic Limestone is an important Late Jurassic Fossillagerstätte similar to the Tithonian Solnhofen Limestones in Bavaria. It is situated in the western part of the Swabian Alb (Fig. 1), a classical area of Jurassic research since the 19th century (e.g., Quenstedt, 1843, 1857; Fraas, 1855). Today, the Nusplingen Lithographic Limestone covers an area of less than 1.5 square kilometers and reaches a thickness of 10-15 meters (Dietl et al., 1998). The local stratigraphy consists of alternating finely laminated limestones and turbidite layers; and several bioturbated beds in the lower part of the sequence.

Various commercial and scientific excavations of the Nusplingen Lithographic Limestone have taken place in the past, but the locality has been overshadowed in the past by the more famous Solnhofen Limestones. Today the Nusplingen Lithographic Limestone is exposed in few natural outcrops and in two small quarries, the Egesheim Quarry at the margin of the basin and the Nusplingen Quarry in the center of the basin. These quarries have been excavated by a team from the Stuttgart Natural History Museum since 1993 (Dietl et al., 1998). Numerous spectacular, well-preserved fossils have been recovered since the locality was first mentioned in the literature (Quenstedt 1843), among them marine crocodiles, sharks and many other fish, pterosaurs, various invertebrates such as cephalopods, bivalves, decapod crustaceans, land plants and insects (Dietl and Schweigert, 1999a, 2001, 2004). Most recently even a tiny fossil feather was recovered (Schweigert et al., 2010).

Besides ammonites (and their aptychi), which indicate a latest Kimmeridgian age for the locality (Schweigert, 2007), the most common fossils in the laminated beds of the Nusplingen Lithographic Limestone are coprolites. Surprisingly these coprolites have never been reported in the scientific literature on this locality, except for *Lumbricaria*-like calcitic or silicified coprolites (Fraas, 1855; Quenstedt, 1857). In older collections, only a single, but very large specimen, of a phosphatic coprolite was found (Fig. 2). It is obvious that prior sampling of the locality for commercial purposes totally ignored the coprolites. However, during recent excavations various fossils, sedimentary marks and other observations have been carefully recorded to provide a comprehensive understanding of the formation and evolution of this Fossillagerstätte.

The study of coprolites is crucial for the understanding of the interrelationships of predators and their prey (e.g., Häntzschel et al., 1968; Vialov, 1974; Boucot, 1990; Schmitz, 1991; Shimada, 1997; Hu et al., 2010; Eriksson et al., 2011). Direct evidence of such interaction via stomach or crop contents is rare. Several examples of such stomach or crop contents have been documented from invertebrates, such as ammonites, nautiloids and coleoids of the Nusplingen Lithographic Limestone (Schweigert and Dietl, 1999, 2010; Dietl and Schweigert, 1999b). Few vertebrate examples were recovered, among them several larger fish with remains of smaller fish in their mouths or digestive tracts, an unpublished specimen of the marine crocodile *Cricosaurus suevicus* with fish bones, belemnite, and ammonite remains in its stomach, and another specimen of *Cricosaurus* containing vertebrae of a shark. In addition to coprolites, regurgitalites with various fossil content are occasionally recovered from the Nusplingen Lithographic Limestones (see Vallon, this volume). Here, we focus on presumed vertebrate coprolites.

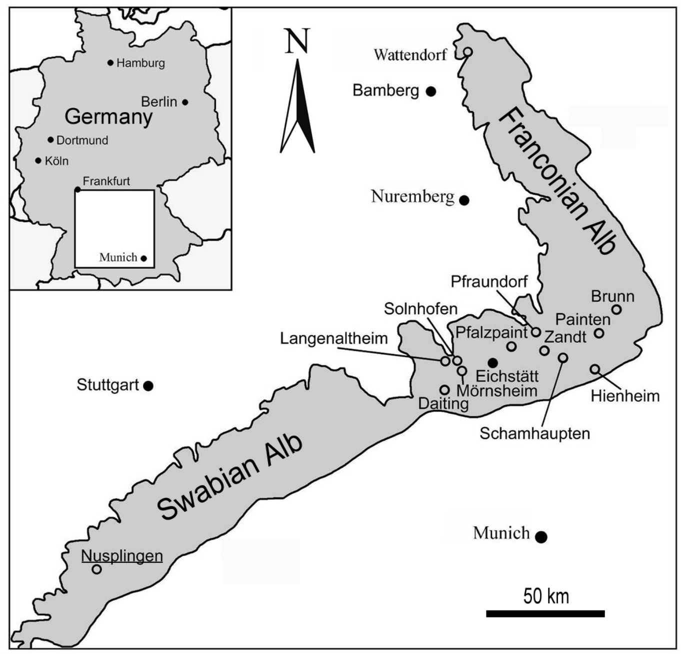

FIGURE 1. Location of the Upper Jurassic Fossillagerstätte Nusplingen in the southwest of Germany (modified from Fürsich et al., 2007).

PREVIOUS RECORDS OF COPROLITES IN UPPER JURASSIC LITHOGRAPHIC LIMESTONES

In the classic literature on the Upper Jurassic Solnhofen Limestones (Barthel, 1978; Barthel et al., 1990) the occurrence of coprolites is only briefly mentioned, based on a single example, and in the most recent comprehensive compilations of Solnhofen fossils, coprolites are practically missing (Frickhinger, 1994, 1999). As in Nusplingen, coprolites are the most common fossils in the Solnhofen Limestones (L.H. Vallon, personal commun., 2011). The coprolite string *Lumbricaria*, which consists almost exclusively of the skeletal elements of the planktonic crinoid

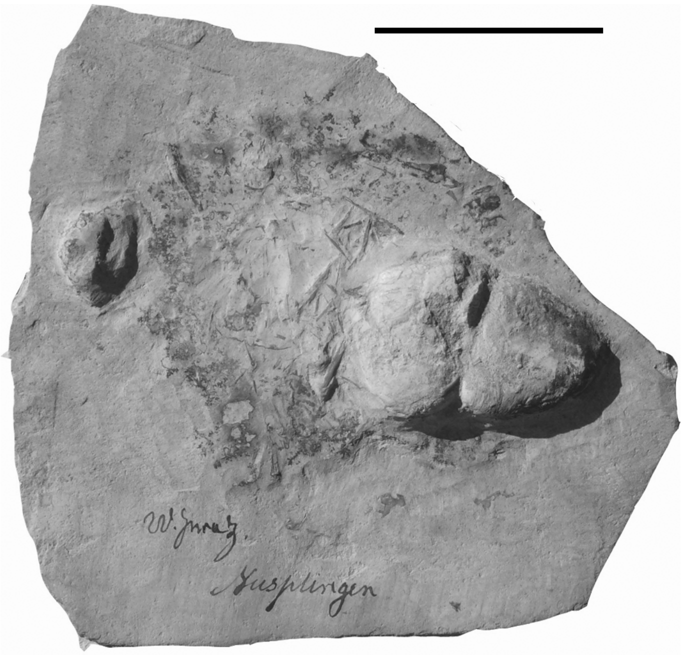

FIGURE 2. Large phosphatic coprolite from the collection of the University of Tübingen, GPIT/IC/145. Scale bar equals 5 cm.

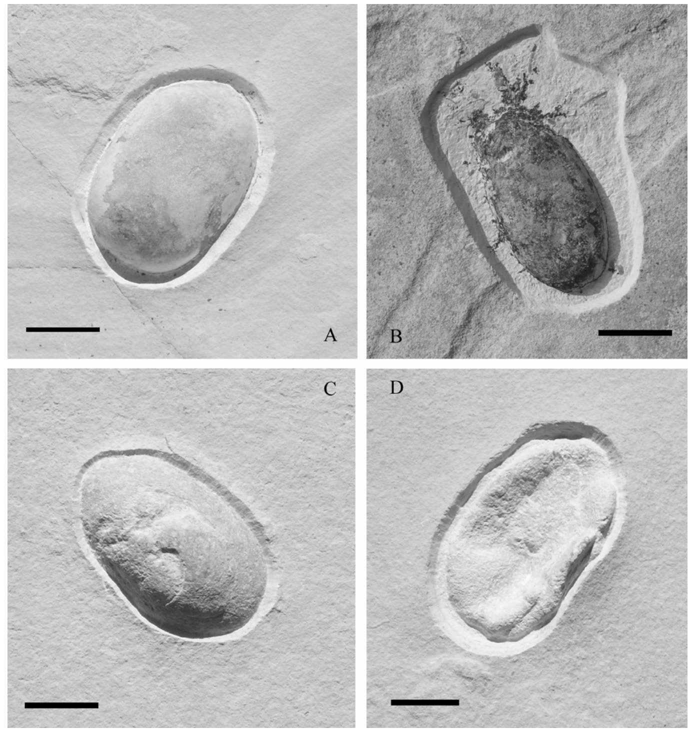

FIGURE 3. Egg-shaped coprolite, morphotype 1. **A**, Nusplingen Quarry, Bed G, SMNS no. 63221. **B**, Partly disaggregated specimen with fish bone inclusions, Nusplingen Quarry, Bed C, SMNS no.67868. **C**, Nusplingen Quarry, Bed C, SMNS no.67749. **D**, Specimen from Fig. 3C, view from lower side of the plate. Scale bars equal 2 cm.

Saccocoma tenella, has long been interpreted as a possible fish coprolite (Müller, 1969). However, ammonites have been demonstrated to be the producer of this coprolite, based on analyses of their crop content (Janicke, 1970; Lehmann, 1972; Schweigert and Dietl, 1999).

In contrast to the Solnhofen Limestones, the comparatively richer ichnofauna of the Nusplingen Lithographic Limestone has been well-documented (e.g., Schweigert, 1998, 2001), but coprolites were excluded from these studies, as coprolites are sometimes excluded from trace fossils (e.g., Seilacher, 2007, p. 93). Hitherto, only a short communication and a few examples in popular textbooks were dedicated to these common fossils (Dietl and Schweigert, 1999a, 2000, 2001).

DESCRIPTIVE EVALUATION OF VERTEBRATE COPROLITES FROM NUSPLINGEN

In the Nusplingen Lithographic Limestone phosphatic matter occurs both as replaced muscle material in fossil arthropods (Briggs et al., 2005) and in coprolites.

Vertebrate coprolites are variable in size – within some limits – and consistency even when the producer is a single taxon. Therefore we refrain from classifying the (presumed) vertebrate coprolites from the Nusplingen Lithographic Limestone as discrete ichnogenera and ichnospecies, but prefer using an informal, descriptive classification based on similar morphologies. Only one form can be tentatively related to a recently erected ichnotaxon.

Institutional abbreviations: GPIT, Palaeontological collection of the Institut für Geowissenschaften, Tübingen University (formerly: Geologisch-Paläontologisches Institut Universität Tübingen), Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

Morphotype 1

This rarely occurring type of coprolite is rather large in size (~ 4 to 5 cm long), oval in longitudinal outline and does not show any significant structures on its surface (Fig. 3). The phosphatic matrix may contain remains of undigested fish bones, which become visible either in broken specimens or in some cases when the coprolites started disintegrating. Some morphotype 1 coprolites are quite massive and three-dimensionally preserved, whereas other examples are compacted with a convex upper surface and a concave lower surface. The relatively large size of this morphotype points to rather large animals as their producers, possibly large fishes like *Caturus furcatus* Agassiz, which is known from Nusplingen based on specimens over one meter long. Much smaller, egg-shaped coprolites attributed to fish were reported from the Danian of Faxe, Denmark (Milàn, 2010).

Morphotype 2

This comparatively rare type of coprolite exhibits a clear spiral or helical internal coiling (Fig. 4). The outline of the resulting coprolite, however, is oval, not elongate, as in the presumed shark coprolite illustrated by Barthel (1978). The maximum diameter of this morphotype is approximately 40 mm. In apical view this morphotype resembles closely the ichnogenus *Heteropolacopros* Hunt et al., 1998. However, the latter is elongate, and asymmetrical in outline and significantly smaller than the examples from Nusplingen. In general shape the specimens from Nusplingen resemble the ‘morphotype 3’ of Eriksson et al. (2011), recently reported from the Upper Cretaceous of Sweden. However, the Swedish coprolites are much smaller in size. The helical arrangement of the Nusplingen coprolites may derive from special anatomical structures at the end of the gut. Some larger chondrichthyan fishes, like sharks or holocephaleans, could be the producers of such spiral coprolites (cf. e.g., Jain, 1983; McAllister, 1985; Hunt et al., 2005). In the Nusplingen lagoon fossil sharks are well represented, both by complete skeletons and by isolated teeth, suggesting their presence throughout the deposition of these limestones.

Morphotype 3

This type of coprolite is several times longer than wide (Fig. 5). Superficially it resembles the densely coiled calcitic coprolites known as *Lumbricaria gordialis* Münster. However, in contrast to the latter it is not a coiled string, but consists of transversely segmented units of dense and spirally packed phosphatic matter, sometimes with isolated fish

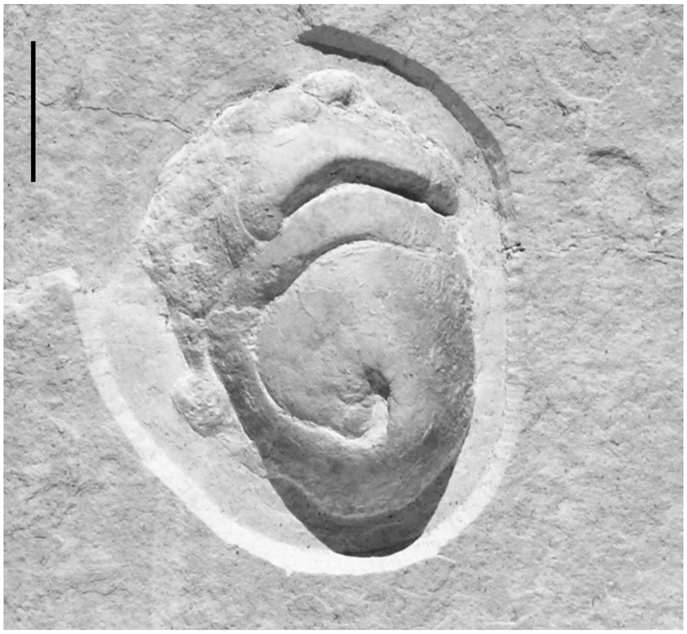

FIGURE 4. Spiral or helical phosphatic coprolite, morphotype 2. Nusplingen Quarry, Bed L, SMNS no. 64687. Scale bar equals 1 cm.

FIGURE 5. Densely packed phosphatic coprolite, morphotype 3. Nusplingen Quarry, Bed C, SMNS no. 67877. Scale bar equals 1 cm.

bones in-between. The small to medium size of this coprolite points to a medium-sized predator that mainly fed on small fish, possibly another larger fish.

Morphotype 4

This long, narrow coprolite morphotype (Fig. 6) is similar to *Lumbricaria intestinum* Münster, but appears straighter, with a significantly larger and more irregular diameter than the latter, and consists of phosphatic, not calcitic matter. In general it is close to morphotype 3, but lacks any transverse structures. Although somewhat compressed during lithification and compaction, a helical coiling is discernible, resembling the shell of vermetid gastropods. Smaller, approximately 1 mm-thick, phosphatic coprolites, which are much more common, should not be confused with this morphotype. These smaller coprolites are probably producd by perisphinctid ammonites and represent their phosphatic crop content (cf. Schweigert and Dietl, 1999).

Morphotype 5

Morphotype 5 includes large-sized coprolites (length ~ 4 to 6 cm) that consist of thick strings of phosphatic matter that are partly coiled, sometimes in a helical pattern (Fig. 7). In many cases these coprolites are partially disaggregated. This type of preservation allows examination of the content of the coprolite, which includes fish bones, fragments of crustaceans, and even hooks of belemnites and other coleoids. Like the coprolites assigned to morphotype 2, this morphotype's producer was probably a chondrichthyan fish, based on the spiral to helical arrangement of the coprolite formed by the intestinal valves.

Morphotype 6

This morphotype includes one of the most common, large phosphatic coprolites of the Nusplingen Lithographic Limestone. Most examples are 5 cm long, but the largest example extends over 10 cm (Figs. 2, 8). It is characterized by an asymmetric, generally cylindrical outline. Constrictions subdivide the specimens into two or more parts of different size. The surface is always smooth, and no remains of undigested components are visible from an external view, although in cross section or in disaggregated examples they always contain fish bones or crustacean fragments in a fine phosphatic matrix. The large size, the sometimes cylindrical shape, and the remarkable constrictions point to crocodylians as their producers. Recently, Hunt and Lucas (2010) provided a compilation of putative fossil crocodile coprolites. The small thalattosuchian *Cricosaurus suevicus* (E. Fraas) is known from the Nusplingen limestones based on four skeletons and several isolated teeth, and therefore may be the tracemaker.

Morphotype 7

This rare morphotype is made up of strings of small phosphatic pellets, each of which has the size and shape of coffee beans (Fig. 9). Based on this unique arrangement it is probably that the producer excreted these coprolites close to the sea floor.

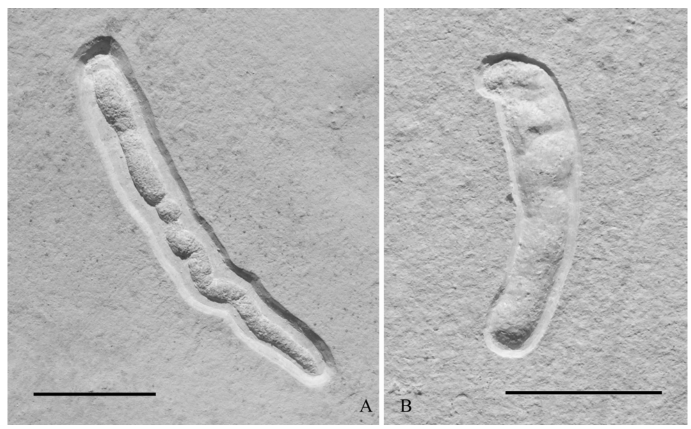

FIGURE 6. Long, narrow phosphatic coprolites, morphotype 4. **A**, Nusplingen Quarry, Bed C, SMNS no. 67873. **B**, Nusplingen Quarry, Bed C, SMNS no. 67875. Scale bars equal 2 cm.

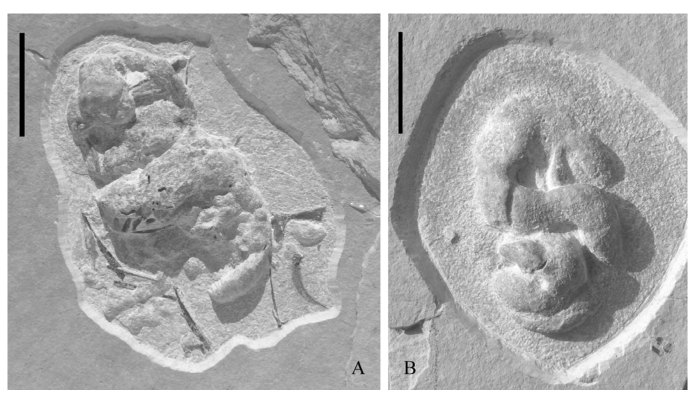

FIGURE 7. Helical phosphatic coprolites, morphotype 5. **A**, Partly disaggregated specimen with fish bones and a large belemnite hook (Onychites), Nusplingen Quarry, Bed C, SMNS no. 67878. **B**, Nusplingen Quarry, Bed C, SMNS no.67871. Scale bars equal 2 cm.

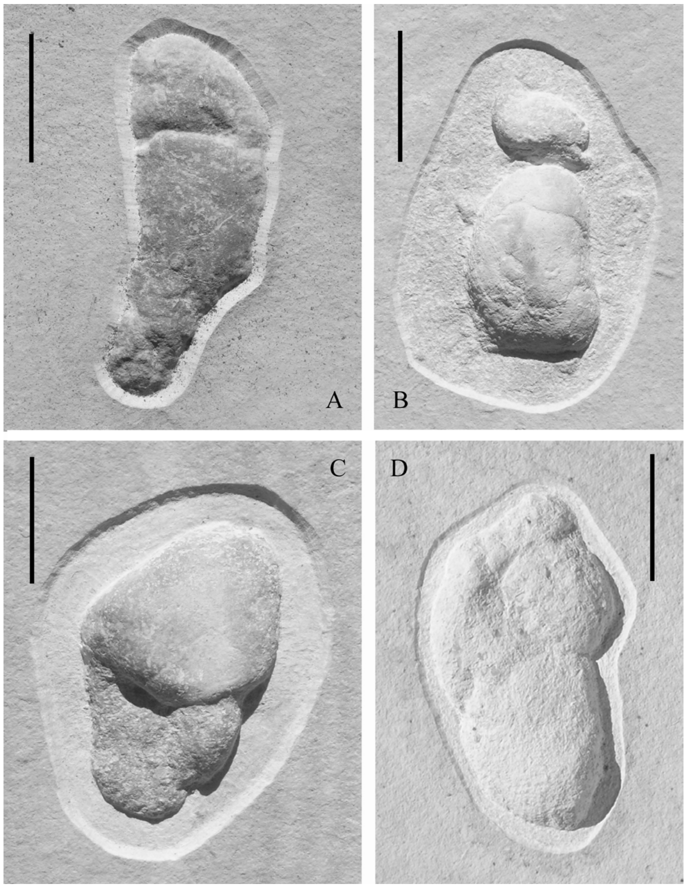

FIGURE 8. Asymmetric phosphatic coprolites, morphotype 6. **A**, Nusplingen Quarry, Bed G, SMNS no. 63989. **B**, Nusplingen Quarry, Bed L, SMNS no. 64634. **C**, Nusplingen Quarry, Bed L, SMNS no. 64553/1. **D**, Nusplingen Quarry, Bed L, SMNS no. 64638. Scale bars equal 2 cm.

Morphotype 8

Only a single specimen (Fig. 10) from the Egesheim Quarry differs from all other recorded phosphatic coprolites. It is unique based on its characteristic longitudinal internal structure, which are in the shape of fibrous strings. This internal morphology became apparent when the slab containing the coprolite split irregularly and small parts of the fossil remained on the counterpart.

Falcatocopros isp.

Only a single specimen (Fig. 11) of *Falcatocopros* (Hunt et al., 2007) was recovered during our excavations since 1993. The very long, spindle-like shape of this coprolite was not expected from the small cross section discernible before its extraction from the surrounding matrix. This type of coprolites could have been easily overlooked. In cross section, the specimen consists of very thin concentric layers. The phosphatic matter of these layers is very dense and fine, almost resembling the material of reptile teeth, but without any skeletal remains of the former prey.

Medusites isp.

Medusites capillaris Germar, a problematic fossil from the Solnhofen Limestones that consists of white or pinkish, coiled parallel strings of homogenous phosphatic matter was recently recognized as a coprolite (Schweigert, 2001a). As indicated by the genus name this fossil had been previously interpreted as the remains of jellyfish (Germar 1827). *Medusites capillaris* is extremely rare in the Upper Kimmeridgian

FIGURE 9. String of small phosphatic coprolites, morphotype 7. Nusplingen Quarry, Bed G, SMNS no.63999. Scale bar equals 1 cm.

FIGURE 10. Elongate phosphatic coprolite, morphotype 8. Egesheim Quarry, Bed Pk3, SMNS no. 63705. Scale bar equals 1 cm.

FIGURE 11. *Falcatocopros* ichnosp. Nusplingen Quarry, Bed C, SMNS no. 67874. Scale bar equals 1 cm.

Nusplingen Lithographic Limestone (Fig. 12), in contrast to the Tithonian Solnhofen Limestones in Bavaria. The producer of this coprolite could have well been either a smaller fish or a coleoid. Therefore the vertebrate origin of this coprolite is only speculative.

COPROLITE PRESERVATION

In many cases the phosphatic coprolites did not have a firm consistency to form a discrete coprolite nodule, but were rather liquid. They are that spread as flat clusters of phosphatic matter up to 20 centimeters or more in diameter, often with some remains of undigested skeletal material (Fig. 13). In most cases this preservation results from the primary consistency of the excrement, but it is possible that secondary diagenesis or even predation of the coprolite contents by nektonic animals living near the assumed hostile sea-bottom have led to the coprolites disaggregation.

The content of skeletal material within coprolites clearly correlates with the abundance of these groups in the original environment, as reflected by body fossils. Beds with a high abundance of decapod crustaceans also contain coprolites with a high amount of crustacean skeletal material, whereas in beds where crustaceans are rare or absent the coprolites predominantly contain fish bones and scales.

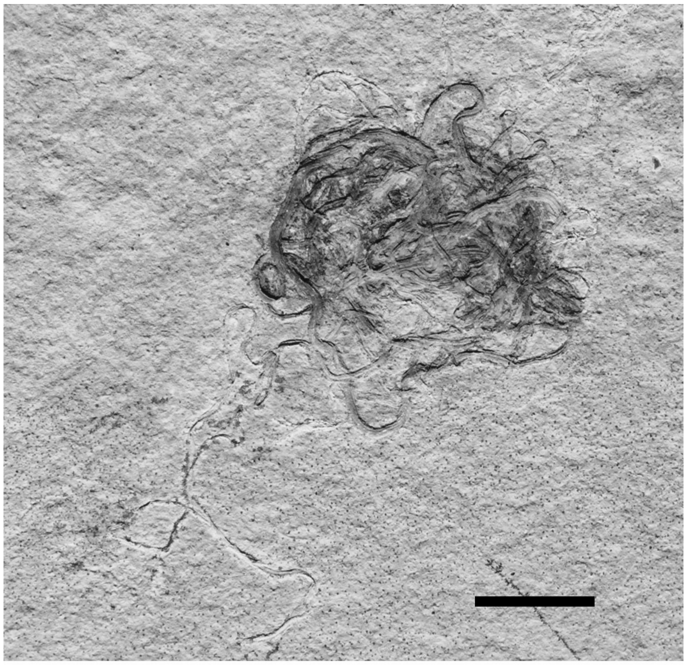

FIGURE 12. *Medusites capillaris* Germar. Phosphatic coprolite possibly produced by a fish. Nusplingen Quarry, Bed L, SMNS no.67872. Scale bar equals 1 cm.

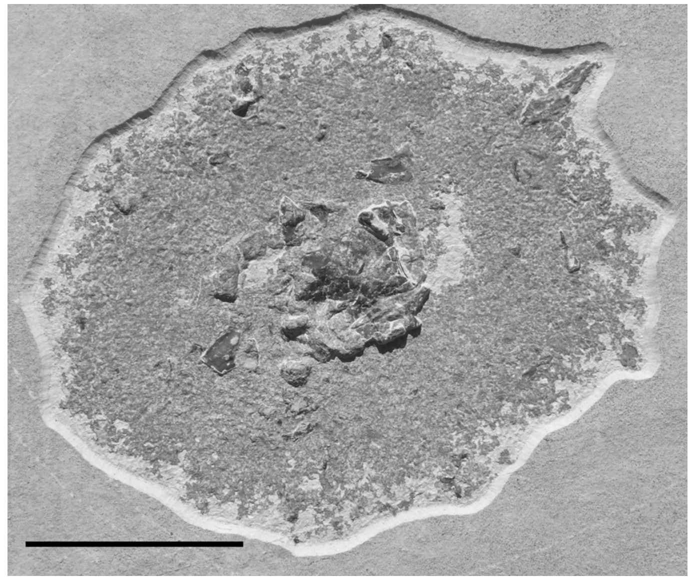

FIGURE 13. Phosphatic coprolite with a liquid consistency and crustacean remains as inclusions. Nusplingen Quarry, Bed G, SMNS no.64512. Scale bar equals 5 cm.

CONCLUSION

The high diversity of coprolite morphologies in the Nusplingen Lithographic Limestone – here only vertebrate coprolites are documented – together with bitten shells and carcasses illustrate the rich Jurassic sea life within the water column above the almost undisturbed and finely-laminated, and thus probably life-hostile, sea bottom.

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