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Mineralization of soft-part anatomy and invading microbes in the horseshoe crab *Mesolimulus* from the Upper Jurassic Lagerstätte of Nusplingen, Germany

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A remarkable specimen of *Mesolimulus* from the Upper Jurassic (Kimmeridgian) of Nusplingen, Germany, preserves the musculature of the prosoma and associated microbes in three dimensions in calcium phosphate (apatite). The musculature of *Mesolimulus* conforms closely to that of modern horseshoe crabs. Associated with the muscles are patches of mineralized biofilm with spiral and coccoid forms. This discovery emphasizes the potential of soft-bodied fossils as a source for increasing our knowledge of the diversity of fossil microbes in particular settings.

Keywords: horseshoe crab; Jurassic; *Mesolimulus*; Nusplingen; preservation; fossil microbe

1. INTRODUCTION

The Plattenkalk near Nusplingen, Baden-Württemberg, is Kimmeridgian in age. Discovered in 1839, it has yielded a range of remarkable discoveries: over 250 taxa including marine crocodiles, pterosaurs, fishes, ammonites and nautiloids with beaks and crop contents, crustaceans and other arthropods, and well-preserved land plants (Dietl & Schweigert 2001, 2004; older literature on the fossil Lagerstätte is summarized in Schweigert 1997).

A newly discovered specimen of the horseshoe crab *Mesolimulus walchi* preserves extensive details of *in situ* musculature replicated in calcium phosphate, enabling particular muscles to be identified. Comparable details are preserved in Tertiary insects from the Eocene lignite of Geiseltal, Germany (Voigt 1988), and in amber from the Dominican Republic (Henwood 1992). Mineralized muscles in other Mesozoic and older arthropods tend to be more fragmentary (Wilby & Martill 1992). Mineralized microbes occur in association with the muscles of *Mesolimulus*, including patches of three-dimensionally mineralized biofilm incorporating layers of spiral and coccoid structures, the first such example discovered in the fossil record.

2. SOFT-PART ANATOMY

Mesolimulus is one of the most well-known body fossils from the Solnhofen Limestone of Bavaria, particularly those examples at the end of the spiral death marches (Barthel *et al.* 1990, p. 78). Fragments of muscle tissue have been reported in specimens of *Mesolimulus* from the Solnhofen Limestone (Briggs & Wilby 1996; Wilby & Briggs 1997). The slightly older Nusplingen specimen, however, preserves much more extensive details. The specimen (Staatliches Museum für Naturkunde, Stuttgart, SMNS 65410) consists of the counterpart, with associated trace fossil (figure 1*a*), and partial part (figure 1*b*,*c*), which carries much of the preserved muscle tissue. Although swimming trails and tracks of horseshoe crabs are quite common, this is only the seventh body fossil of *Mesolimulus* to be discovered from Nusplingen and the first to represent a carcass as opposed to a moulted exoskeleton (Schweigert & Dietl 2002). It is one of the many important results of the excavation and research by the Staatliches Museum für Naturkunde, Stuttgart, since 1993. The maximum width of the prosoma is 10.4 cm. The impressions of the telson and the chelipeds on the sediment in the counterpart (figure 1*a*) indicate that the animal was dorsal side up on the sea floor. The part is exposed from the dorsal side (figure 2); two prosomal limbs are compressed against the carapace on the right side of the prosoma.

The exceptional preservation of the specimen allows the identification of individual muscles within particular groups: the circular muscles of the crop, extrinsic leg muscles and axial longitudinal muscles (figure 1*b*,*c*). The muscles apparently detached from the carapace and collapsed onto one another prior to mineralization. The muscles of the prosomal median axis or cardiac lobe region (dorsal longitudinal and gut muscles) retained approximate anatomical positions. Coupled with the low number of muscles in this region and dramatic differences in their fibre orientations, this allowed unambiguous homologization with those of extant *Limulus*. Comparison with extant horseshoe crabs indicates that the muscles lateral to the cardiac lobe represent numerous and tightly packed extrinsic appendicular muscles. Among these, only the extreme lateral components can be identified with any

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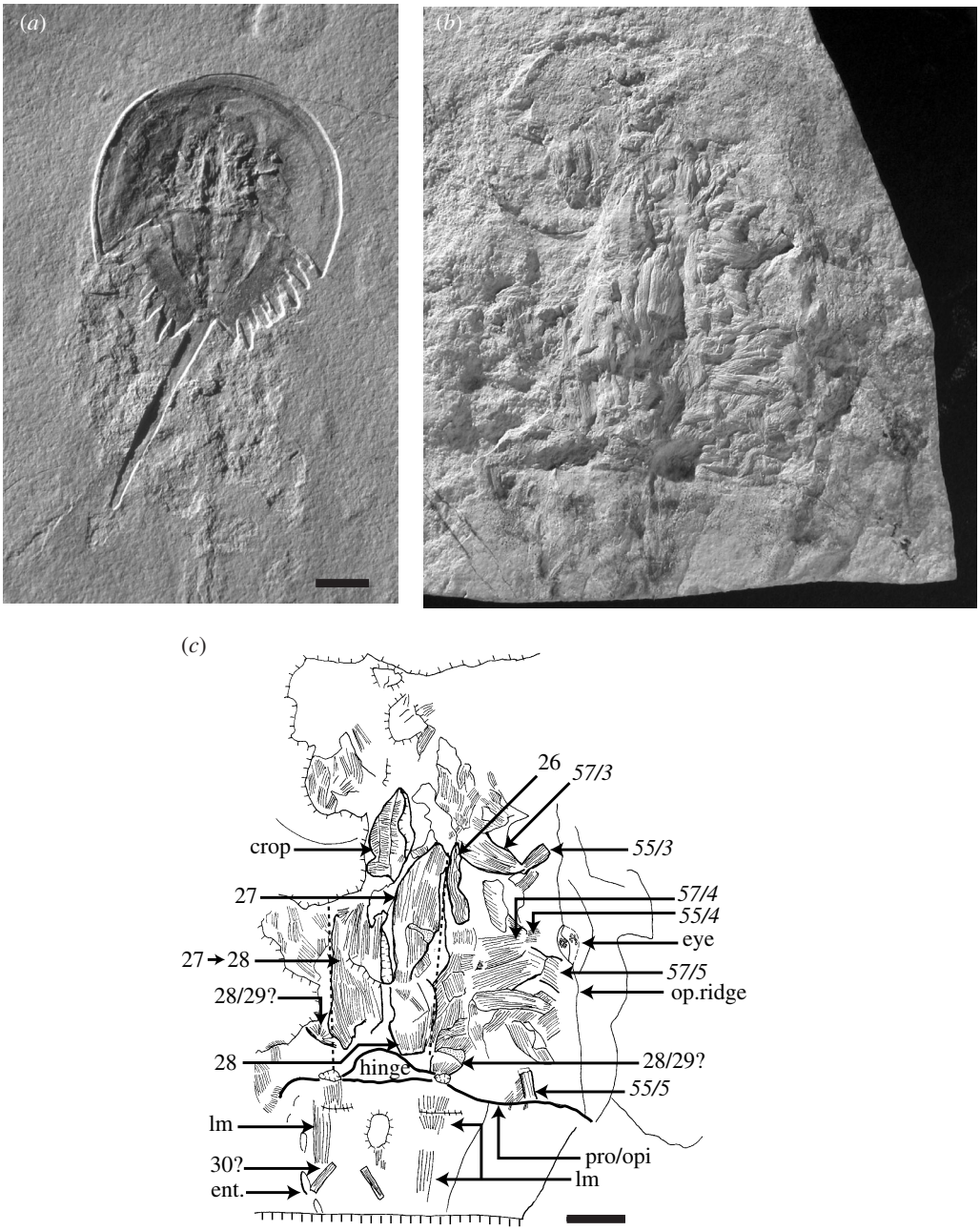


Figure 1. *Mesolimulus walchi* Desmarest, 1822, Kimmeridgian, Nusplingen Plattenkalk, Germany (SMNS 65410). (*a*) Entire specimen (counterpart) including some of the marks on the substrate left by the telson and chelipeds. (*b*,*c*) Photograph and camera lucida drawing of part. Individual muscle groups labelled according to Shultz (2001). Abbreviations: ent. entapophysis; lm, longitudinal muscles; op. ridge, ophthalmic ridge; pro/opi, prosomal/opisthosomal boundary; numbers in italics refer to appendage muscle groups followed by the appendage number. Scale bars, 20 mm (*a*) and 5 mm (*c* as for *b*).

certainty, based on approximate position, fibre orientation and segmental repetition.

The external surface of the muscle fibres preserves evidence of myofibrils and fibril banding, probably where the fibres ruptured along M lines during decay (figure 3*a*,*b*). The compound eye and patches of the cuticle have also survived as a thin mineral film as a result of partial replacement of the original organic material. Energy dispersive X-ray analysis (EDX) on the environmental scanning electron microscope (ESEM) revealed that the soft tissues are preserved in calcium phosphate (apatite). The apatite precipitated in very small crystallites directly onto the soft tissues to form a substrate microfabric preserving high fidelity detail. This implies minimal decay and high levels of available phosphate (Wilby & Briggs 1997). A decapod from the same locality (SMNS 65475) revealed similarly preserved muscles (figure 3*c*).

3. MICROBES

Microbes, which are also mineralized in apatite, are associated in places with the muscles of the *Mesolimulus* specimen (figure 4*a–f*). These microbes form biofilms that are preserved in patches a few millimetres in dimension within the mass of muscle. The biofilms consist of layers that are composed of one of three main types of microbes: spirals (figure 4*a*,*b*), small coccoids (figure 4*c*,*d*) or larger coccoids (figure 4*e*).

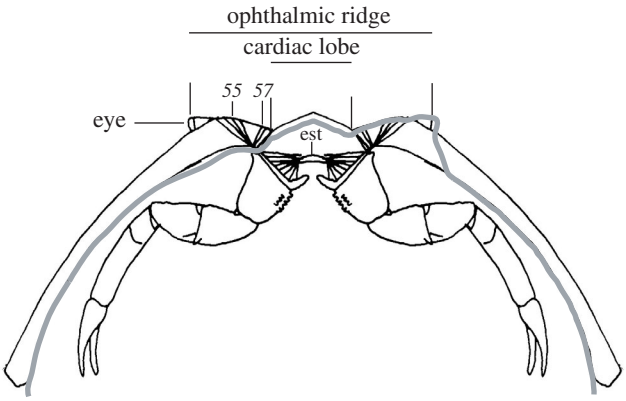


Figure 2. Diagrammatic transverse section showing the surface (thick grey line), along which the *Mesolimulus* specimen split to yield the part (below) and counterpart (above).

The spirals are arranged, for the most part, parallel to each other (figure 4*a*). They take the form of helically coiled ribbons approximately 2 μm wide and approximately 0.5 μm thick. The diameter of the helix is approximately 2.75 μm, and the wavelength of the spirals is 3–4 μm. The apatite precipitated in the space enclosed by the walls, and internal structures are rarely evident. Some examples show what appear to be divisions 3.5–5 μm long (figure 4*b*), but the boundaries between them may be fractures. The spirals reach lengths of over 20 μm, but their terminations are usually obscured, and they may be longer. One or two examples show evidence of tapering to a point. There is no evidence of a sheath.

The small coccoids (figure 4*c*,*d*) range from approximately 0.7 to approximately 3.0 μm in diameter. Some display a fuzzy texture on the surface of the spheres (figure 4*d*) which may represent the remains of the cell wall.

Larger coccoids (figure 4*e*) range from approximately 3.0 to approximately 7.0 μm in diameter. They are enclosed by a sheath of one or two layers with a total thickness of up to 1 μm; they are hollow inside.

Additional, rather structureless layers may represent mineralized extracellular polymeric substances (EPS). Associated with the bacteria are grains and patches of sediment. EDX analysis shows that these are composed primarily of calcium carbonate. The largest grains are coccolithophorids up to 14 μm in diameter (Bantel *et al.* 1999; Dietl & Schweigert 2004).

The closely packed spirals and small coccoids are often interlayered and are interpreted as elements of a biofilm. Neither microbes nor sediment are concentrated in a particular part of the muscle mass. After both musculature and microbes became mineralized, collapse in some areas of the carcass resulted in fragmentation of the mineralized remains (figure 4*f*), although elsewhere they remain intact. The muscle tissue preserved in the decapod crustacean (figure 3*c*) showed no evidence of associated microbes or sediment.

4. DISCUSSION

(a) *Preservation of Mesolimulus*

Muscle decays rapidly, so the soft tissue of the *Mesolimulus* specimen must have been replicated in calcium phosphate in a matter of days or at most weeks (Briggs & Kear 1993, 1994). In a depositional environment saturated in calcium carbonate pH must have been depressed in order to facilitate the precipitation of apatite (Briggs & Wilby 1996). This can be achieved by microbial mats where they grow on carcasses and generate a closed environment (Martill 1988; Wilby *et al.* 1996; Briggs 2003*a*,*b*). Here, however, the microbes grew within the carcass, and the enclosing agent may have been the carapace itself (Briggs & Kear 1994). Alternatively, pH may have been reduced within the sediment as indicated by the presence of a decalcified ammonite in the vicinity of the specimen. The amount of phosphorus required to facilitate replication of the muscle mass in apatite would have exceeded that available from the decay of other parts of the specimen, indicating an external source, presumably concentrations in the sediment (Wilby & Briggs 1997). The carapace itself was also replaced by apatite.

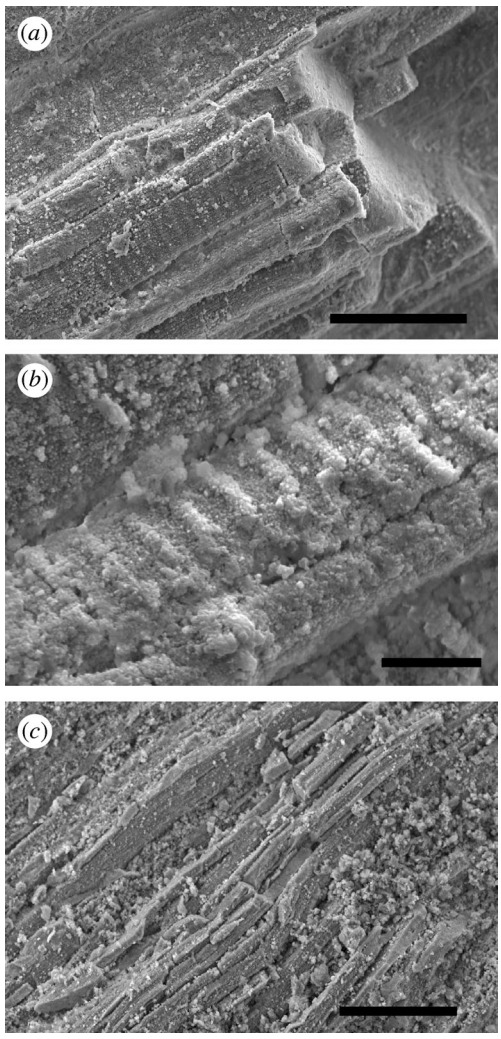


Figure 3. (*a*,*b*) *Mesolimulus walchi* Desmarest, 1822. Scanning electron microscope images of specimen SMNS 65410. (*a*) Muscle fibres. (*b*) Banding of fibres revealed by decay. (*c*) Muscle fibres from a decapod from the Nusplingen Plattenkalk (SMNS 65475). The granular material on the surface is apatite. Scale bars, 50 μm (*a*,*c*) and 10 μm (*b*).

The invasion of the soft tissues by sediment grains must have been the result of damage to the carapace in the axial

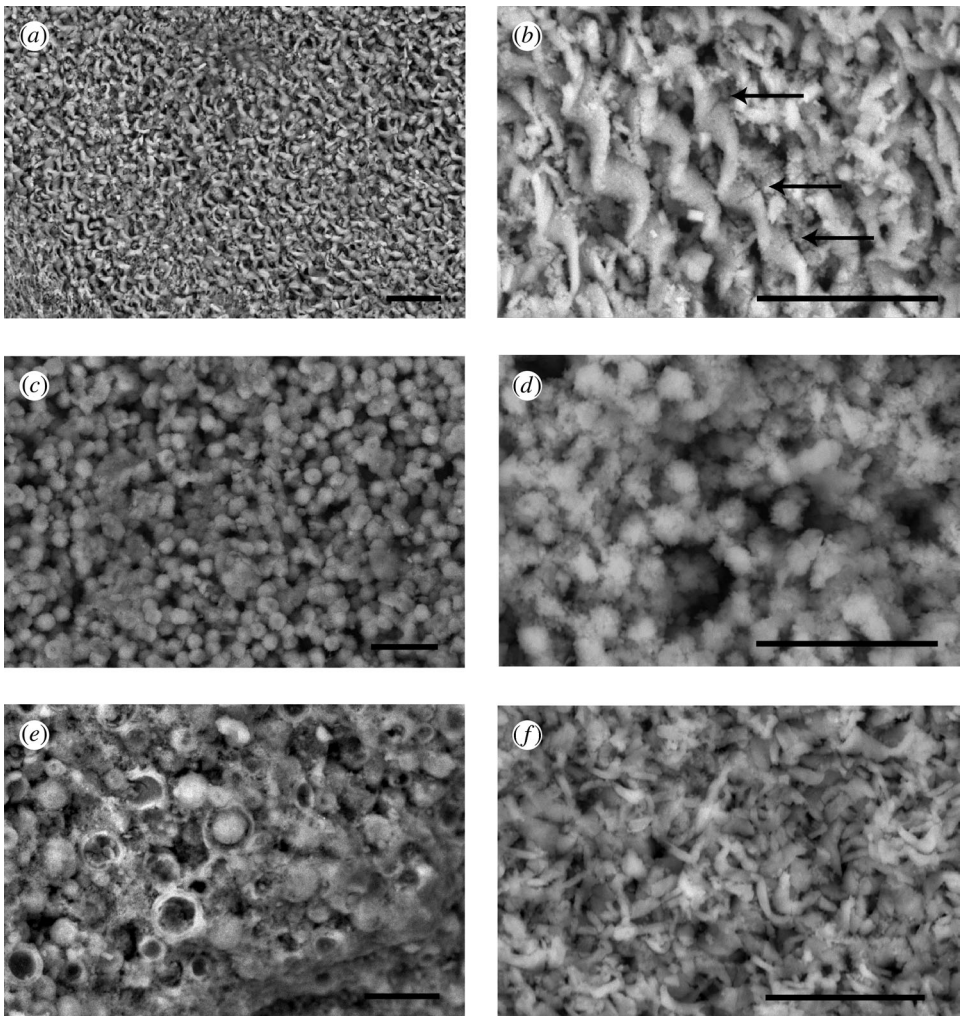


Figure 4. (*a*) Mat of phosphatized spiral microbes showing alignment of trichomes. (*b*) Trichomes showing possible cell boundaries (arrowed). (*c*) Small coccoid microbes. (*d*) Fuzzy texture on the surface of small coccoid microbes. (*e*) Larger coccoid microbes with associated glycocalyx. (*f*) Smaller spiral trichomes fragmented and disoriented as a result of collapse post-mineralization. Scale bars, 10 μm.

area, where it is concealed beneath mineralized soft tissue on the specimen. Sediment could not have penetrated the muscle as a result of decay of the carapace. Experimental evidence shows that the soft tissue of *Limulus* decays far more rapidly than the cuticle or arthrodial membranes (Babcock *et al.* 2000). There is no evidence that the sediment is concentrated in a particular area, such as along the junction between prosoma and opisthosoma. Decay of the cuticle and penetration of microbes and sediment, however, might have been hastened by disease; modern *Limulus* is subject to infection (Leibovitz & Lewbart 2003). Damage might have been inflicted by a predator. Although the periphery of the *Mesolimulus* carapace is intact (figure 1*a*), evidence of predation is common in the Nusplingen decapods (Schweigert 2001).

Myofibrils are evident in specimens of *Mesolimulus* from the younger Solnhofen Lagerstätte (Wilby & Briggs 1997; figure 3*a*,*b*). Fibril banding has not been reported previously from *Mesolimulus*, but is known in the ray *Squatina* from Solnhofen (Wilby & Briggs 1997; figure 3*e*), and a fish from the Lower Cretaceous Santana Formation (Martill 1990); it has also been replicated within a few weeks in laboratory experiments on shrimps (Briggs & Kear 1993, 1994). All these examples are preserved in calcium phosphate (apatite). Decapod crustaceans from Nusplingen, many of which were bitten by predators (Schweigert 2001), commonly preserve phosphatized soft tissue (figure 3*c*). Otherwise, phosphatization is restricted to a single specimen of the teuthoid *Leptotheuthis gigas* (see Dietl & Schweigert 2001) and, among vertebrates, to some specimens of the angel shark *Squatina acanthoderma* (R. Böttcher, personal communication). This level of detail may also be preserved elsewhere in clay minerals, as in the muscles of a conodont from the Upper Ordovician Soom Shale of South Africa (Gabbott *et al.* 1995).

(b) *Mineralization of microbes*

The presence of biofilms at Nusplingen has long been supposed (Temmler 1964, 1966; Seilacher *et al.* 1985; Westphal 1992; Bantel *et al.* 1999), but as microbial mats on the surface of sedimentary layers. Hollow spherical structures in the Solnhofen Limestone have been attributed to coccoid cyanobacteria that secreted crystallites of calcite in the cell wall (Keupp, 1977*a*,*b*) and similar structures have been recorded from the Nusplingen Limestone (Bantel *et al.* 1999). Identifying the constituents that make up fossil biofilms depends on the degree of

morphologic information available, and the requirement to distinguish between cyanobacteria, other prokaryotes and algae with similar morphology (Schopf 1993). For example, both spiral-shaped cyanobacteria, such as *Spirulina*, and large spirillum-shaped bacteria (e.g. Guerrero *et al.* 1999), occur in mats.

The dimensions of the coccoids (figure 4*c–e*) and spiral structures (figure 4*a*,*b*) associated with *Mesolimulus* and the apparent lack of flagella at the terminations of the helices are consistent with the interpretation of these organisms as cyanobacteria, and cyanobacteria infect the gills of extant *Limulus* (Leibovitz & Lewbart 2003). The coccoid structures could represent Chroococcales. Modern spirally coiled cyanobacteria fall within *Spirulina* or *Arthrospira* (Vonshak & Tomaselli 2000), genera that are distinguished on the basis of whether or not cellular divisions are evident externally. The type of preservation in the fossil (essentially as a mineralized internal mould) conceals this difference. It is impossible to confirm that the mineralized organisms are autotrophs based on the scanning electron microscope images (Krumbein *et al.* 2003). The occurrence of the biofilms *within* the muscle of *Mesolimulus* makes it more likely that they represent an assemblage of heterotrophic decay bacteria, including spirilla and cocci of different sizes. Biofilms including similar forms have been noted on the degrading carcasses of marine crustaceans (J. Reitner, personal communication).

Mineralization of microbes occurs most commonly where they form a biofilm covering a decaying carcass. The ornithomimosaur dinosaur *Pelecanimimus*, from the Lower Cretaceous lacustrine sequence of Las Hoyas, Spain (Pérez-Moreno *et al.* 1994), preserves the outline of the throat pouch and a possible occipital crest as thin layers of coccoids embedded in films mineralized in calcium phosphate (Briggs *et al.* 1997). The outline of the large tadpoles from the Oligocene of Enspel, Germany consists of biofilms, probably made up of heterotrophic bacteria, preserved in calcium phosphate and other minerals (Toporski *et al.* 2002). Phosphatized bacteria occur both within and independently of biofilms in the Eocene Messel Lake deposit (Liebig 1998) and a variety of microbes are phosphatized in association with soft tissue in the Cretaceous Santana Formation of Brazil (Martill & Wilby 1994).

5. CONCLUSIONS

The musculature of *Mesolimulus* conforms closely to that of modern taxa, such as *Limulus polyphemus* (Shultz 2001), in spite of the morphological and phylogenetic distance between the Mesozoic and living forms (Fisher 1984). The Nusplingen specimen provides the first direct evidence that the musculature of horseshoe crabs is a conservative feature, at least since the Mesozoic. It also shows that some phosphatized soft-bodied fossils can allow details of the muscle system to be described and homologized with modern forms (see also Kear *et al.* 1995).

Cellular preservation of most fossil microbes occurs in two taphonomic windows, cherts and phosphorites. Proterozoic cherts yield microbial mat communities (Horodyski *et al.* 1993) and examples have also been discovered in the Early Devonian Rhynie Chert (Kidston & Lang 1921), and as organic remains in Mesozoic cherts (Beraldi-Campesi *et al.* 2004). Proterozoic-Cambrian phosphorites preserve a wealth of microbes (Zhegallo *et al.* 2000; Doushantuo-type preservation of Butterfield 2003), and organically preserved and mineralized forms occur in other Cambrian settings, including the Burgess Shale (see review and listing in Peel 1988; Mankiewicz 1992). The discovery of biofilm of three-dimensionally mineralized spiral and coccoid forms inside the carcass of a Jurassic horseshoe crab highlights the potential of soft-bodied fossils, which provide a source of phosphorus and a locus of mineralization (Martill & Wilby 1994), for increasing the known diversity of fossil microbes.

The volunteer Rolf Hugger discovered the *Mesolimulus* from Nusplingen during the excavations by the Staatliches Museum für Naturkunde, Stuttgart. The specimen was skilfully prepared by Martin Kapitzke of the Museum. Stuart Kearns and Jon Wade (Bristol) provided assistance with the ESEM, Simon Powell took the photograph used for figure 1*b*. Stjepko Golubic, Wolfgang Krumbein, Greg Lewbart and Joachim Reitner kindly provided advice. R.A.M. was funded by a NERC studentship.

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