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Another piece in the puzzle of mantis shrimp evolution – fossils from the Early Jurassic Osteno Lagerstätte of Northern Italy

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Another piece in the puzzle of mantis shrimp evolution – fossils from the Early Jurassic Osteno Lagerstätte of Northern Italy

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ABSTRACT

Mantis shrimps (Stomatopoda Latreille, 1817) are marine predatory crustaceans of the group Hoplocarida Calman, 1904 with an interesting, though incompletely known, evolutionary history. Here we introduce a new species of fossil mantis shrimps, *Ostenosculda teruzzii* n. gen., n. sp.

from the Early Jurassic (Sinemurian) limestone formation of Osteno (Northern Italy). We present distinctive features that characterize the specimens as a new species, such as a unique arrangement of maxillipeds 2-5 (maxilliped 2 is the major raptorial appendage). We also present a phylogenetic systematic interpretation of the species based on the available features of morphology and body organisation. The unusual arrangement of the maxillipeds appears to represent a plesiomorphic condition relative to extant mantis shrimps: the maxillipeds are arranged in an almost straight anterior-posterior line, with rather large distances between them. This contrasts with extant forms and slightly younger fossils of about 150 million years old lithographic limestones (Late Jurassic) where further anterior maxillipeds are inserting far laterally and further posterior ones more medially, with very small distances between the next posterior ones. The herein studied specimens are the first of their kind to be confirmed for this period and geographical region and further close gaps in our understanding of the evolution of mantis shrimps.

KEY WORDS
Body organisation,
Early Jurassic,
Hoplocarida,
raptorial appendages,
Sinemurian,
Stomatopoda,
new genus,
new species.

RÉSUMÉ

Une autre pièce du puzzle de l'évolution de la crevette-mante – fossiles du Lagerstätte d'Osteno du Jurassique précoce en Italie du Nord.

Les crevettes-mantes (Stomatopoda Latreille, 1817) sont des crustacés prédateurs marins du groupe Hoplocarida Calman, 1904 dont l'histoire évolutive est intéressante, bien qu'incomplètement connue. Nous présentons ici une nouvelle espèce de crevettes-mantes fossiles, *Ostenosculda teruzzii* n. gen., n. sp. provenant de la formation calcaire du Jurassique précoce (Sinémurien) d'Osteno (Italie du Nord). Nous présentons des traits distinctifs qui caractérisent les spécimens comme une nouvelle espèce, tels qu'une disposition unique des maxillipèdes 2-5 (le maxillipède 2 est le principal appendice raptoral). Nous présentons également une interprétation phylogénétique systématique de l'espèce basée sur les caractéristiques disponibles de la morphologie et de l'organisation du corps. La disposition inhabituelle des maxillipèdes semble représenter une condition plésiomorphe par rapport aux crevettes-mantes modernes : les maxillipèdes sont disposés en une ligne antéro-postérieure presque droite, avec des distances assez grandes entre eux. Ceci contraste avec les formes actuelles et les fossiles légèrement plus jeunes des calcaires lithographiques d'environ 150 millions d'années (Jurassique supérieur) où les maxillipèdes antérieurs s'insèrent loin latéralement et les postérieurs plus médialement, avec de très petites distances entre les postérieurs suivants. Les spécimens étudiés ici sont les premiers de leur genre à être confirmés pour cette période et cette région géographique et comblent les lacunes dans notre compréhension de l'évolution des crevettes-mantes.

MOTS CLÉS
Organisation du corps,
Jurassique inférieur,
Hoplocarida,
appendices raptoriales,
Sinémurien,
Stomatopoda,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Stomatopoda Latreille, 1817 is a group of predatory malacostracan crustaceans commonly known as mantis shrimps. They have a distinct body organisation with a number of striking features that differentiate them from other crustaceans, such as their huge and highly specialised compound eyes (Kleinlogel & Marshall 2006; Chiou *et al.* 2008) and hardened tail fans (Taylor & Patek 2010). Their most recognizable (and eponymous) body features, however, are their raptorial appendages, which can strike with impressive force and speed (Patek & Caldwell 2005). Based on the morphology of these raptorial appendages, adults are generally distinguished roughly into two categories: "spearers", impaling their prey with spines on the distal elements of their raptorial appendages, and "smashers" punching their prey with a massive club on the distal element on their raptorial appendages.

Worldwide, there are about 500 modern species of mantis shrimps, all exclusively marine (Ahyong *et al.* 2014). Mantis shrimps occur primarily at low latitudes with the highest species diversity and abundance in the tropical Indo-West Pacific, especially in the western Pacific between the South China Sea and Australia (Ahyong 2001; Schram *et al.* 2013). Mantis shrimp species diversity attenuates with increasing latitude with a few species in sub-antarctic waters but none at the poles (Reaka & Manning 1987; Ahyong 2004, 2012). Today, the Mediterranean Sea, with an intermediate latitudinal position, has only moderate mantis shrimp diversity of extant species (Lewinsohn & Manning 1980; Manning 1991; Ahyong & Galil 2006). However, owing to the very different latitudinal and ecological position of the region during the Palaeozoic and Mesozoic, the Mediterranean region has yielded a rich fossil record of mantis shrimps (Ahyong *et al.* 2007). These fossils are particularly important for informing knowledge of the palaeo-history of Stomatopoda, including younger fossils from the Palaeocene, Eocene, and Oligocene. Especially rich and important are fossils from the Mesozoic (Schram 2010). This diversity may not be surprising as the region was formerly part of the Tethys Sea, a Mesozoic shelf ocean with presumably tropical conditions (Biju-Duval *et al.* 1977). The earliest mantis shrimps fossils date back to the Carboniferous

Fig. 1. — **A**-**B**, Comparison of part (**B**) and counterpart (**A**) of the fossil *Ostenosculda teruzzii* n. gen., n. sp., ventral view, MSNM i13561: **B** flipped vertically. Scale bars: 3 mm.

(about 300 million years ago; e.g. Hof 1998), while the oldest fossils of the Mediterranean region are "only" from the Mesozoic. Yet, some of these fossils are the first to show the distinct size-differentiated morphology of raptorial appendages of modern-day mantis shrimps, with one pair developing into major raptorial appendages and three pairs of small-sized sub-chelate appendages (Haug *et al.* 2010). Thus, it is among these fossils that we witness the emergence of "true" mantis shrimps. Interestingly, these co-occur with other forms retaining a raptorial apparatus as seen in Carboniferous species (Haug *et al.* 2010), with one pair of large, one pair of medium-sized and two pairs of small-sized sub-chelate appendages, hence a large-medium-small-small pattern. Therefore, the Mesozoic Mediterranean fossils offer a crucial insight into the evolutionary history of mantis shrimps. This enables a further understanding of how the highly specialised modern-day mantis shrimp morphology evolved stepwise over time.

Herein, we describe two fossil mantis shrimp specimens from the Osteno Lagerstätte in the Italian Alps, one accessible in ventral and one in lateral view. These are not only the oldest fossil mantis shrimps from the Mediterranean region, but present an as yet unknown detail of morphology not found in modern-day relatives. This adds a new piece to the puzzle of reconstructing the evolutionary history of mantis shrimps.

GEOLOGICAL SETTING

Both specimens described in this study were found near the village of Osteno (Como, Lombardy, Italy) at disused quarries at the shore of Lake Lugano; see Pinna (2000) and Lamsdell *et al.* (2021) for detailed information and history of the field site.

The fossils were found in a grey micritic limestone with a high proportion of secondarily calcified sponge spiculae and radiolarians (Pinna 1985; Lamsdell *et al.* 2021). The ultra-fine lamination of the sediment is assumed to be caused by gradual precipitation of tiny calcareous sediment particles (Briggs & Kear 1993, 1994; Wilby *et al.* 1995; Garassino & Donovan 2000).

At the quarries near Osteno, the fossiliferous limestone (Osteno lens) has a total thickness of about ten meters (Lamsdell *et al.* 2021) and is part of the Moltrasio Limestone Formation (in Swiss literature: Lombardische Kieselkalk Formation; Garassino & Donovan 2000). The Osteno lens has been dated to the Early Jurassic *Arietites bucklandi* Zone by the occurrence of biostratigraphically relevant ammonites as well as by faunal similarities with the fossil site of Lyme Regis (Dorset, United Kingdom) (Pinna 1967, 1985). The *Arietites bucklandi* Zone is correlated to an age of about 197.8 to 199.3 million years (early Sinemurian; Ogg & Hinnov 2012).

Fossils recovered in the Osteno lens are heavily compressed, and from organisms with calcareous body parts only structures composed of calcite are preserved. However, the preservation of soft tissue by replacement with amorphous calcium phosphate down to a cellular level is exceptional (Pinna 1985; Wilby & Briggs 1997). Organisms found in the outcrop are mostly marine (Lamsdell *et al.* 2021). Along with crustaceans also fossil remains of xiphosuridans, nematodes, polychaetes, bivalves, cephalopods, ophiuroids, sharks, bony fishes and plants have been found in the limestone sediments (see Garassino & Teruzzi 2015 and Lamsdell *et al.* 2021 for complete references).

MATERIAL AND METHODS

Material

Two specimens were available for the study, each available as a part and a counterpart, preserved in limestone slabs. The abbreviations used for specimens are the serial numbers from the Museo di Storia Naturale di Milano (MSNM). To simplify descriptions in the following, the first fossil MSNM i13561 will be often referred to as “ventrally accessible specimen” and the second fossil MSNM i13562 will be referred to as “laterally accessible specimen”, based on their orientation.

Documentation methods

Part and counterpart of both specimens were documented using a Canon Eos Rebel T3i camera with a Canon MP-E 65 mm macro lens. Two Yongnuo Digital Speedlite YN560EX II flashes were used to illuminate the objects. In order to reduce flashlight induced image errors and to enhance the contrast, cross-polarised light was used (e.g. Haug *et al.* 2011a, b, 2013). For this purpose, polarizing filter foil was attached to the flashes and a perpendicular orientated polarizing filter was placed in front of the camera lens. With this set-up, multiple high-resolution images of each specimen were recorded. Morphological terminology of the major raptorial appendage follows Haug *et al.* (2016a) in which the second element (from the distal end) of the raptorial appendage is identified as the “carpopropodus”, rather than “propodus” of other authors (e.g. Schram *et al.* 2013).

Image processing

The resulting images were then stitched together, using the “photomerge” function of Adobe Photoshop CS3. Then, the images of parts and counterparts were virtually placed on top of each other, one image being mirrored and adjusted in size and orientation to fit together. Using the Z-project function of ImageJ (minimum intensity projection), these stacks were again combined, to fuse all information into a single image (e.g. Haug *et al.* 2009a). Finally, brightness, contrast, sharpness and saturation were optimised with Adobe Photoshop CS3. To highlight important morphological structures, body segments and appendages were colour-coded for an easier identification for the reader, using Adobe Photoshop CS2.

OVERALL DESCRIPTION OF THE SLABS

MSNM i13561

Consists of a large flat slab and its counterpart (Fig. 1), both with numerous cuticle remains. Preserved is the more or less complete body of a mantis shrimp in ventral view, lacking head structures and most of its appendages. Only the major raptorial appendages and parts of the uropods are easily recognizable, for the other appendages only the insertion areas (foramen) are recognizable. The segmentation of the body is clearly visible and the individual body segments can be identified by their tergites and sternites, which can both be distinguished by areas of hardened and darker cuticle. The sternites are dislocated relative to the tergites in that they seem to have slipped towards the anterior end of the body (Fig. 2).

MSNM i13562

Consists of a large flat slab and its counterpart (Fig. 3), both with numerous cuticle remains. Preserved is the more or less complete body of a mantis shrimp crustacean in lateral view. The most prominent feature of this specimen is the body segmentation: the shield (formed dorsally by the head segments), the posterior thoracomeres, the pleomeres and the telson are all clearly distinguishable. The body segments are parted into dorsal tergites and ventral sternites, which are recognizable as well. Furthermore, one large compound eye is apparent as well as the major raptorial claws (of maxillipeds 2) and potentially proximal elements of maxillipeds 2 or further posterior maxillipeds (Fig. 4).

SYSTEMATIC PALAEONTOLOGY

STOMATOPODA Latreille, 1817
UNIPELTATA *sensu lato* J.T. Haug,
C. Haug, Maas, Kutschera & Waloszek, 2010
Higher group (e.g. family) *incertae sedis*

Ostenosculda n. gen.

urn:lsid:zoobank.org:act:30E1D19D-C038-45DC-A85E-D971F27DB86D

Type species. — *Ostenosculda teruzzii* n. sp., by present designation.

Diagnosis. — As for the species.

Derivation of name. — Referring to the Lagerstätte from which the studied specimens originate and the superficial similarities to some specimens of *Sculda*. Gender: feminine.

Ostenosculda teruzzii n. gen., n. sp.
(Figs 1-7)

urn:lsid:zoobank.org:act:7C2C839B-81D7-4C97-9280-3DA3F62FB6BC

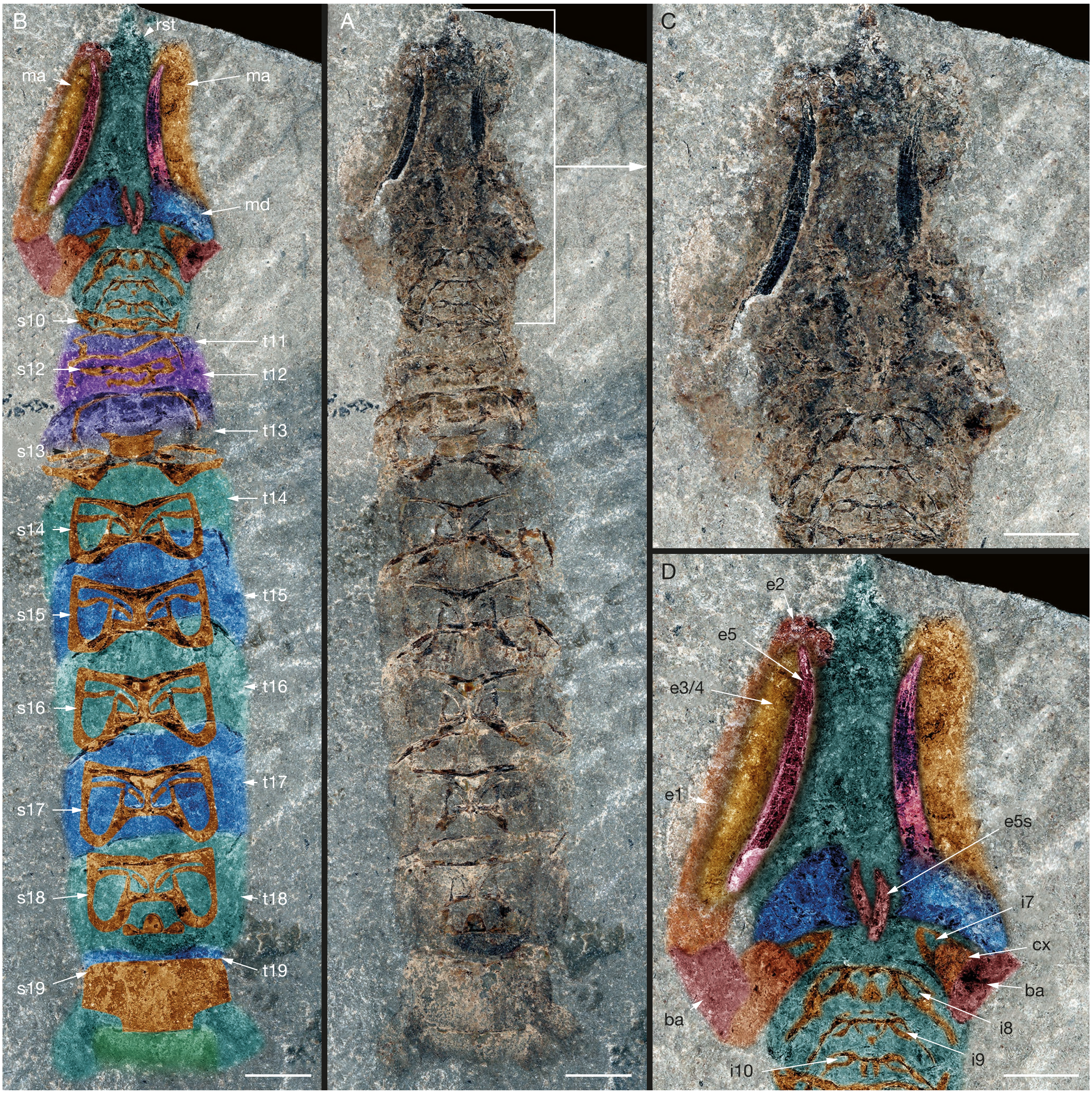

Fig. 2. — *Ostenosculda teruzzii* n. gen., n. sp., MSNM i13561, composite images of part and counterpart: **A**, overview; **B**, colour-coded version of **A**, with body segments in different colours for easier identification of segment borders; **C**, detailed image of **A**, focus on the head and thorax; **D**, colour-coded version of **C**, with the numerous appendage elements and details in different colours for an easier identification. Abbreviations: **ba**, basipod; **cx**, coxa; **e1-5**, elements of the appendage 1-5; **i7-10**, insertion areas of the appendages of post-ocular segments 7-10; **ma**, major raptorial appendage; **md**, mandible; **rst**, rostrum; **s10-19**, sternites of the post-ocular segments 10-19; **t11-19**, tergites of the post-ocular segments 11-19. Scale bars: A, B, 3 mm; C, D, 2 mm.

Type specimens and only material. — **Holotype**. MSNM i13561 (Figs 1; 2).
Paratype. MSNM i13562 (Figs 3; 4).

Diagnosis. — Compound eyes without apparent midband, on short peduncles. Short tapering rostrum. Shield rectangular in ventral and lateral view with postero-lateral corners elongated. Major raptorial appendages with thick ovate carpopropodi and spineless scythe-shaped dactyli. Eight circular insertion areas (foramina) of posterior four maxilliped pairs arranged evenly spaced in anterior-posterior axis. The first pair of insertion areas positioned further laterally, the following three pairs arranged successively medially in two anterior-posterior running, almost straight lines. Insertion area of each pleopod subdivided into three individual areas separated by bar-shaped sclerites.

Derivation of name. — Named after Giorgio Teruzzi, Milano, in honour of his scientific work including fossils from Osteno.

Type locality. — Early Jurassic (Sinemurian), limestone quarry, Osteno, Lombardy, Italy (Pinna 2000).

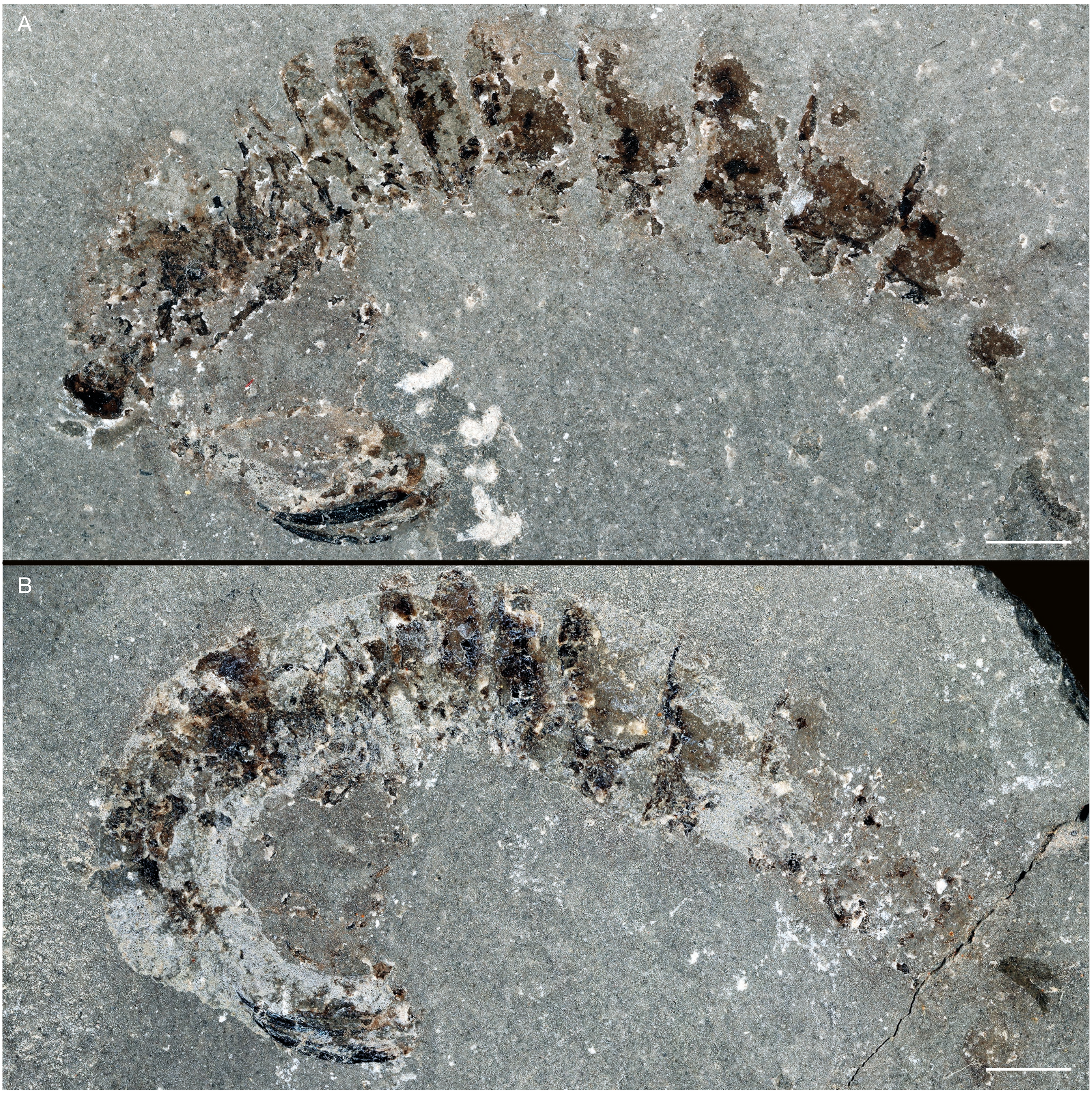

FIG. 3. — Comparison of part (**A**) and counterpart (**B**) of the lateral fossil of *Ostenosculda teruzzii* n. gen., n. sp., MSNM i13562: **B**, flipped horizontally. Scale bars: 3 mm.

DESCRIPTION

Body apparently organised into six functional units (Haug *et al.* 2012): 1) sensorial unit with ocular and post-ocular segments 1-2 (anterior head); 2) anterior food-processing unit with post-ocular segments 3-5 (posterior head); 3) posterior food-processing unit with post-ocular segments 6-10 (thoracic segments 1-5); 4) walking apparatus with post-ocular segments 11-13 (thoracic segments 6-8); 5) swimming and respiration unit with post-ocular segments 14-18 (anterior pleon); 6) tailfan with post-ocular segment 19 (pleomere 6) and telson (see Fig. 5 for comparison with extant mantis shrimp). The body length is 46.6 mm, from the tip of the rostrum to the end of the telson for the ventrally accessible specimen (Fig. 2); for the laterally accessible one this measurement is difficult due to the spaces between the body segments.

The only clearly visible structure of the sensorial unit is one (presumably the left) large compound eye on a short peduncle, protruding near the anterior end of the shield. The cornea is shorter but wider than the stalk; an ommatidial midband is not determinable. Antennula and antenna are not preserved (Fig. 4).

The only accessible feature of the food-processing unit (mandible, maxillula, maxilla) are the mandibles of the

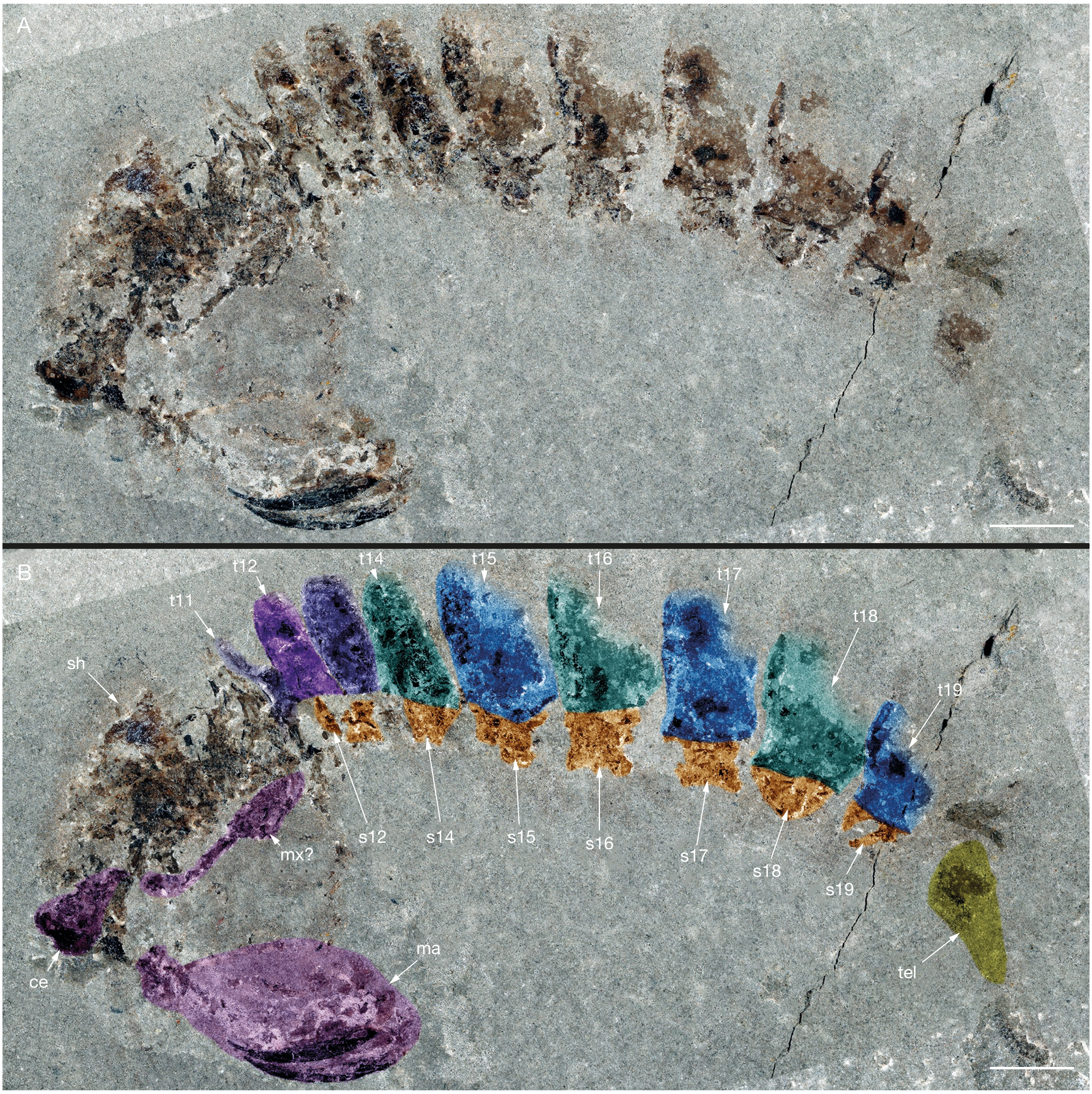

Fig. 4. — *Ostenosculda teruzzii* n. gen., n. sp., MSNM i13562, composite images of part and counterpart: **A**, overview; **B**, colour-coded version of **A**, with the numerous body segments in different colours for easier identification of segment borders. Abbreviations: **ce**, compound eye; **ma**, major raptorial appendage; **mx?**, possible maxillipeds (proximal parts either of maxillipeds 2 or of further posterior maxillipeds); **s12-19**, sternites of the post-ocular segments 12-19; **sh**, shield (carapace); **t11-19**, tergites of the post-ocular segments 11-19; **tel**, telson. Scale bars: 3 mm.

ventrally accessible specimen (Fig. 2). They insert anterior to the major raptorial appendages, but more laterally to them on both sides, on the lateral edges of the body. The mandibles appear to be roughly triangular in ventral view, though their proximal parts at the lateral sides of the body are very round and their distal parts at the median areas of the body are very rough and serrated, indicating grinding/cutting structures. They measure 2.7 and 3.1 mm in length, left and right mandible respectively. The segments to which the appendages of the food-processing unit belong are indirectly observable as they dorsally form the prominent shield. The shield is about two times as long as wide, about 12 mm long and 6 mm wide in the ventrally accessible specimen (Fig. 2), appearing subrectangular both in ventral and lateral view, covering the post-ocular segments 1-5 in ventral view and post-ocular segments 1-8 in lateral view. A short tapering rostrum bridging the gap between the eye peduncles is present at the anteromedial margin of the shield. The posterolateral corners of the shield are slightly produced posteriorly.

The posterior food-processing unit is mainly represented through the major raptorial appendage (maxilliped 2). The exact number of appendage elements of these is not observable. Only the two most distal elements are recognizable: the thick and bulky, in lateral view oval-shaped carpopropodus (propodus of other authors), and the long and spineless scythe-shaped dactylus (Fig. 4). The dactylus is arcuate, at least three-fourths as long as the carpopropodus, evenly tapering to a spiniform tip; the outer margin is smooth, lacking a proximal notch or swelling. The carpopropodus is twice as long as high, about 8.9 mm long in the ventrally accessible specimen and about 4.3 mm wide in the laterally accessible specimen, and is deepest at the midlength. Other appendages are not fully preserved, but two additional dactyli are visible between the posterior portion of the maxillipeds 2; these small dactyli are about one fourth of the length of the dactyli of maxilliped 2 (Fig. 2) and possibly belong to maxillipeds 3 or 4. In lateral view, darkened areas are visible ventral to the shield, which may represent proximal maxilliped elements stacked dorsoventrally on top of each other (Fig. 4: mx?). Furthermore, the insertions of the posterior four maxillipeds (appendages of post-ocular segments 7-10) are clearly recognizable. These are evenly arranged in anterior-posterior axis, slightly decreasing in size from anterior to posterior. The first pair of insertion areas is positioned further laterally, the following three pairs are arranged successively medially in an almost straight line. The most anterior pair of insertions belongs presumably to the major raptorial appendages (maxilliped 2) since the bulging cuticle rings surrounding the insertions are thicker than those of the more posterior maxillipeds and the diameter is significantly larger (Fig. 2). The next posterior insertion is smaller, but slightly larger in diameter and with a thicker bulging ring than the next two insertions. The last segment of this tagma has a distinct short dorsal sclerotisation (tergite) and a longer (anterior-posterior axis) ventral sclerotisation (sternite).

The thoracic segments 6-8, which form the walking apparatus, are clearly recognizable. Each segment seems to have an oval cross-section and is about four times as high as long (Fig. 4). Each segment has two cuticle plates, a dorsal tergite and a ventral sternite; in lateral view, the tergite occupies two-thirds of the segment height, the sternite only one-third, possibly as a result of compressional displacement (Fig. 4). While the tergites are continuous and broad rectangular-shaped cuticle plates, the sternites are interspersed with softer structures. Most anteriorly on each sternite, and probably marking its anterior edge, is a continuous crescent-like shaped sclerotised bar stretching over the full width of the segment and continuing in posterior direction (after a kink with roughly 90°) at both of its ends to the posterior end of the segment. Posterior to this bar, the seventh thoracic segment shows structures of hardened cuticle. These form two broadly connected ovate forms around the possible insertion areas of the walking appendages. Posterior to the sclerotised bar of the eighth thoracic segment is a broad rectangular cuticle plate with small anterior spines pointing laterally. Posterior to this is a structure mirrored on an anterior-posterior running middle line of the segment. The structure consists of a walking-stick-shaped cuticle bar (curved end pointing medially) above a rough triangle pointing posterior and has its anterior corners elongated laterally. These triangles reach into the gap between the eighth thoracic and the first pleon segment (Fig. 2).

The anterior pleon consists of a narrow anterior segment, followed by four broader segments, each two times higher than long (Fig. 4). Dorsally, the tergite of each of the five segments is a broad continuous plate covering the whole segment (Fig. 2). The sternites show multiple structures and soft spots that are best described by the letter "W", but with the three anterior tips being connected and by overall broader lines. This leads to two triangular gaps, which form the insertion areas (foramina) of the pleopods. Within these gaps, there are two cuticle bars, one running from the middle of the lateral side towards the midline and bending posterior after two thirds of the way, and one running from posterior towards the spot where the first line starts to bend. This pattern continues with slight variation for the other four sternites.

The tailfan is formed by the telson and the appendages (uropods) of pleomere 6, which is slightly narrower compared to the other pleon segments. Pleomere 6 again consists of a continuous broad cuticular plate that is the tergite, but in contrast to further anterior sternites, the sternite of pleomere 6 is broad and almost continuous, only with spaces postero-laterally for the uropods. The uropods (at least the parts that are preserved) are bent in ventral view and curved around the lateral edges of the telson (Fig. 2). The telson is flatter than the body segments and flattens out even further towards its posterior end (Fig. 4). It is about 6.9 mm wide in the ventrally accessible specimen and about 5.2 mm long in the laterally accessible specimen, yet it is neither in lateral nor in ventral view fully preserved, therefore we could draw no further information from it. Telson spines are not preserved.

DISCUSSION

Preservation

The two specimens described herein present a well-preserved body proper, yet most of the appendages are missing. Also, microstructures and especially details of the head are not preserved. The telson is only partly preserved. This hinders recognising details, such as spines along the margin.

In addition to the cuticle remains, some soft tissue seems to be preserved. Possibly, muscles are vaguely recognisable in the pleon, though this is not entirely clear. Yet, this would not be unusual for arthropods as these provide an internal source of phosphate, which enables the process of phosphatization (Wilby & Briggs 1997; Klompmaker *et al.* 2019).

The laterally accessible specimen shows slight segregation of body segments (compare Figures 3 and 4 with reconstructions in Figure 5). This is most likely an artefact of preservation (Hof & Briggs 1997) also known in other fossil mantis shrimps (e.g. Haug *et al.* 2015a: fig. 3). Overall, the preservation strongly resembles mantis shrimp specimens from the lithographic limestones of southern Germany (Haug *et al.*

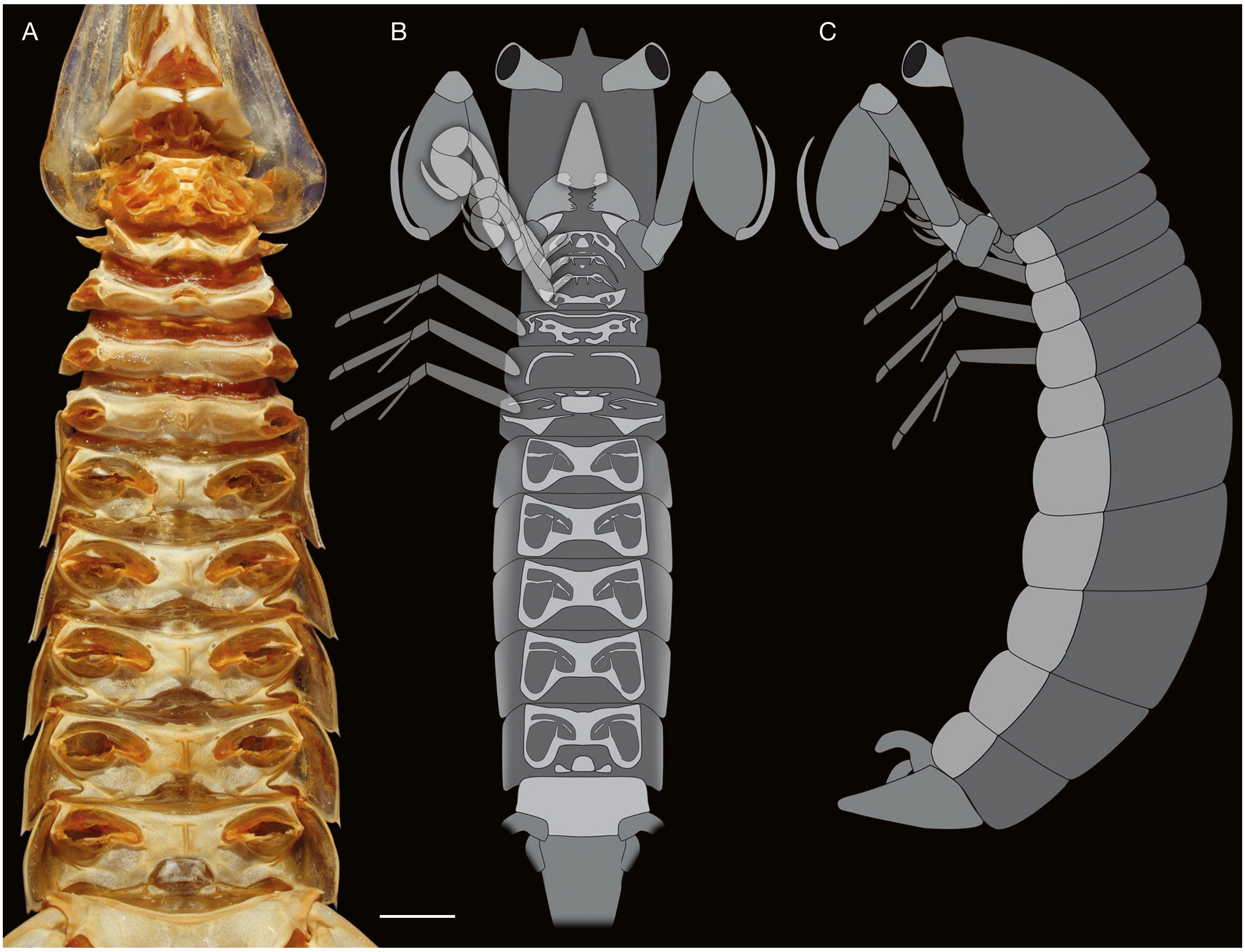

Fig. 5. — Comparison of ventral morphology of an extant mantis shrimp and *Ostenosculda teruzzii* n. gen., n. sp.: **A**, thorax and pleon of an extant "spearing" mantis shrimp (Squillidae); **B**, **C**, reconstruction of *O. teruzzii* n. gen., n. sp.: **B**, ventral view, third to fifth maxillipeds and walking appendages are blurred out, since they are not fully preserved and their morphology can only be estimated; **C**, lateral view. Scale bar: 8 mm.

2009b: fig. 3; Haug *et al.* 2010: fig. 2) and specimens from the lithographic limestones of Lebanon (Haug *et al.* 2009b: fig. 2). In particular, the comparison to the latter ones is important. Specimens of *Pseudosculda laevis* (Schlüter, 1872) from the Late Cretaceous limestones of Lebanon show different orientations in their embedding, sometimes more lateral, sometimes more dorsal, sometimes also slightly distorted.

Although the ventrally accessible specimen appears more contiguous, segregation of segments is apparent under close inspection here as well. Due to this effect, the sternites and tergites are not aligned perfectly, but are slightly offset against each other. This has complicated the identification of sclerotised borders, as, in some cases, the well-sclerotised rims of the tergites overlap with those of the sternites (e.g. pleon segment 2 left side, Fig. 2).

Preservation and orientation also explains the differences between the two herein described specimens: while the first specimen is accessible in ventral view and is more contiguous, the other specimen is accessible in lateral view and is more distorted due to further decay. The effect that the ventrally accessible specimen appears more coherent than the laterally accessible specimen is probably caused by the fact that the ventrally accessible specimen was not preserved horizontally, but rather was slightly inclined towards its anterior end, at least that is what we concluded from the shift of sternites and tergites. Still, we could not find any distinct differences that would justify considering the two specimens to represent separate species.

The lithographic limestones of southern Germany contain at least four species of mantis shrimps (but most likely more) (Haug *et al.* 2010, 2015b; Haug & Haug 2021), and three species have been reported from the Lebanon lithographic limestones (Charbonnier *et al.* 2017). It could therefore be argued that it is not unlikely that more than one species of mantis shrimps is present in the Osteno Lagerstätte. Yet, due to the lack of distinguishing characters for separating the two specimens we consider them conspecific.

Although the overall preservation appears less well than that of mantis shrimps from other Mesozoic limestone Lagerstätt*en*, the degree of detail still enables the conclusion of certain biological aspects.

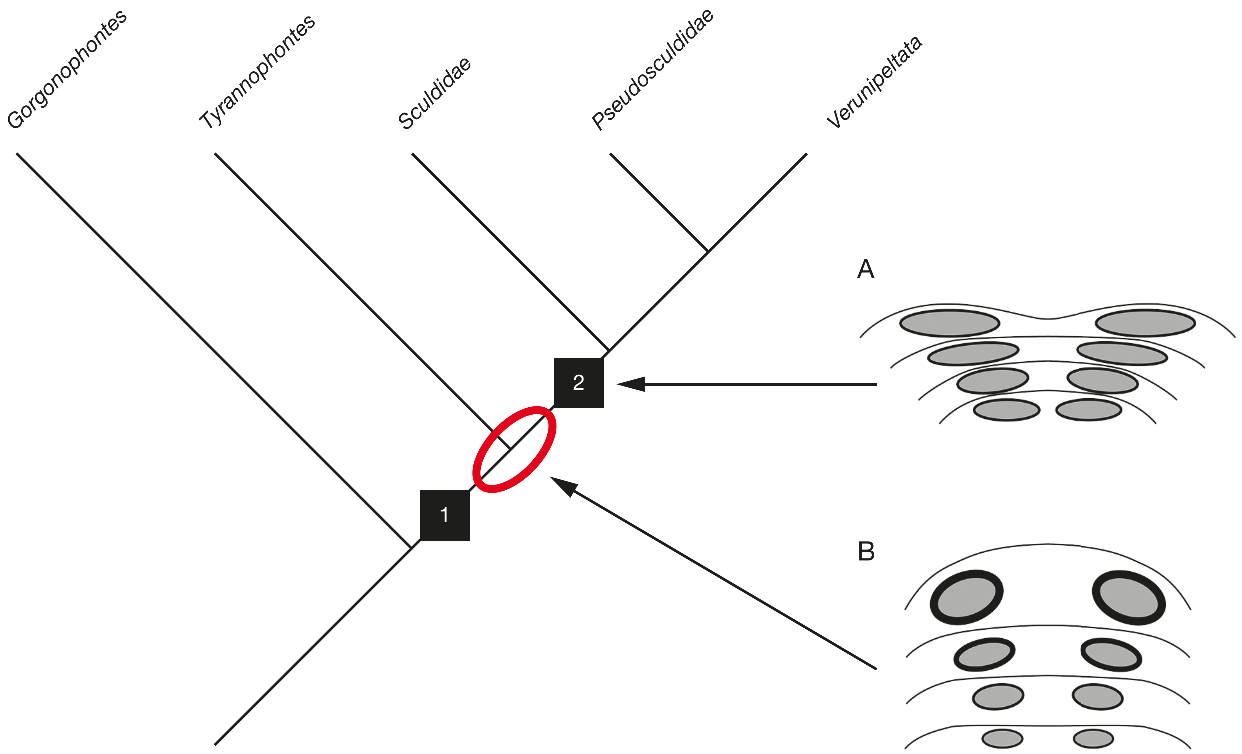

FIG. 6. — Simplified evolutionary reconstruction and possible phylogenetic affiliation of *Ostenosculda teruzzii* n. gen., n. sp. indicated by **red ellipse**; phylogeny based on Haug *et al.* (2010): evolutionary appearance of characters: **1**, further decrease in size of maxillipeds 4 and 5; **2**, distinct V-shaped arrangement of maxilliped insertion areas; **A**, **B**, schematic reconstruction of arrangement of insertion areas of maxillipeds 2–5 (post-ocular segments 7-10) in mantis shrimps; **A**, extant species; **B**, *O. teruzzii* n. gen., n. sp.

DEVELOPMENTAL STATUS OF THE SPECIMENS

Before discussing *Ostenosculda teruzzii* n. gen., n. sp. in an evolutionary context, we first have to consider the developmental status of the specimens given the large morphological differences between extant adult and larval mantis shrimps. Adult forms of extant mantis shrimps are almost exclusively benthic whereas their larval forms are pelagic and, in order to be so, possess adaptations that enhance buoyancy, such as an especially large shield with long, prominent spines (including long spine-like rostrum) comprising more than half the total body length, and widely separated eyes on the end of long peduncles (e.g. Feller *et al.* 2013; Ahyong *et al.* 2014; Haug *et al.* 2016b).

The studied specimens lack any such larval characters indicating their adult or at least subadult status. Yet, it should be pointed out that the simple dactylus of the major raptorial appendages superficially resembles that of some-modern-day larval or postlarval forms (e.g. Ahyong 2002: fig. 6B; Haug *et al.* 2016b), while modern-day adults usually have ornamented dactyli, either as “spearers” (with spines) or “smashers” (with a club). The only known extant exception is *Hemisquilla* Hansen, 1895, with simple dactyli lacking spines or a club, and which may represent the sister group to other modern stomatopods (Ahyong *et al.* 2007; Ahyong & Jarman 2009; Van Der Wal *et al.* 2017). However, a simple, unornamented dactylus is known for most adult Mesozoic mantis shrimps (Haug *et al.* 2010). In conclusion, the specimens most probably represent either adults or subadults that have already attained an adult morphology.

Comparison to other Mesozoic mantis shrimps

The material presented herein splits the 150 million year gap in the fossil record of the group Stomatopoda, by being roughly 100 million years younger than the material from the Carboniferous and about 50 million years older than the occurrences in the Late Jurassic limestones from southern Germany. While there are some other occurrences of Mesozoic mantis shrimps, the fossils from the lithographic limestones of southern Germany and Lebanon offer the most morphological details and hence represent the best comparison for the herein described specimens from Osteno.

The scythe-shaped dactylus of *Ostenosculda teruzzii* n. gen., n. sp. is similar to that of *Pseudosculda laevis* (e.g. Haug *et al.* 2010: fig. 5). It was probably this feature that led Hof (1998) to suggest that the specimens from Osteno are representatives of Pseudosculdidae Dames, 1886. Yet, a similar dactylus morphology is also known for specimens of *Tyrannosculda laurae* Haug & Haug, 2021 (Haug & Haug 2021; previously interpreted as representatives of *Sculda* Münster, 1840; see Haug *et al.* 2010). Also the carpopropodus shape is comparable to that of *P. laevis* and *T. laurae*, although the carpopropodus is more massive in *O. teruzzii* n. gen., n. sp.

The size differentiation of the maxillipeds is not directly observable in *O. teruzzii* n. gen., n. sp., as there are only the dactyli of the major raptorial appendages (maxilliped 2) and of one of the further posterior maxillipeds recognizable. Hence, we cannot easily identify whether there is a large-small-small-small type of maxilliped pattern (as in modern mantis shrimps and

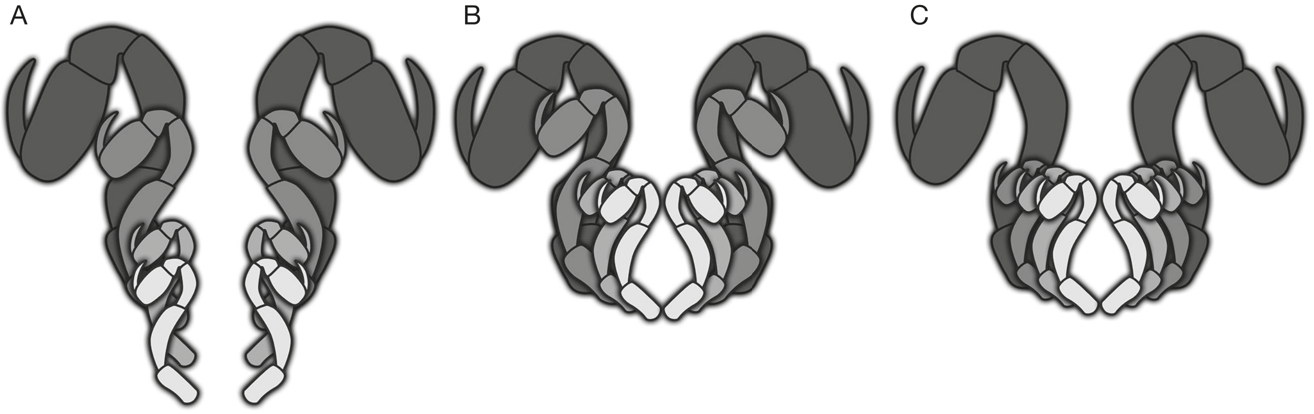

Fig. 7. — Reconstruction of the three different schemes of maxilliped arrangement in mantis shrimps: **A**, *Ostenosculda teruzzii* n. gen., n. sp., note that the exact size of maxillipeds 3-5 is mostly inferred; **B**, mantis shrimps from Solnhofen limestones; **C**, extant mantis shrimps.

P. laevis, presumably also in *Archaeosculda phoenicia* Ahyong, Garassino & Gironi, 2007) or a large-medium-small-small type as in *T. laurae* and *Sculda* (although slightly derived in some species) and the Carboniferous group *Tyrannophontes* Jenner, Hof & Schram, 1998. The sizes of the maxilliped insertions would indicate the second type. Yet, comparing the sizes based on insertions on the one hand and dactyli on the other is difficult as the exact correlation between these two structures is unclear.

Ostenosculda teruzzii n. gen., n. sp. uniquely combines the greatly enlarged second maxilliped and almost linear arrangement of maxilliped insertions. In modern mantis shrimps these insertions are appressed and tightly adjacent antero-posteriorly, and consecutively offset laterally. The insertions of the major raptorial appendage (maxilliped 2) are positioned far laterally, the further posterior ones are positioned consecutively further medially, with the last (maxilliped 5) having the insertion areas almost touching each other. This results in a tight V-shaped arrangement of the maxilliped insertions. This arrangement probably reflects the high degree of specialization in modern mantis shrimps with maximal division of labour between the maxillipeds within the posterior food-processing unit, enabling maxilliped 2 to form a massive raptorial appendage used for hunting and fighting, and the maxillipeds 3-5 to be specialised for food handling and processing. This compact antero-posterior compression of the maxilliped insertions probably also permits significantly greater flexibility between the anterior body region and the posterior thoracic segments of modern mantis shrimps, enabling them to easily move in the tight confined spaces of burrows or crevices, suggesting the potential influence of available habitat in the evolution of the modern mantis shrimp body organisation.

This specialization of the arrangement of the feeding apparatus can also be seen in representatives of *Sculda* (Haug *et al.* 2010: fig. 4) and *Spinosculda ehrlichi* Haug, Haug & Waloszek, 2009 (Haug *et al.* 2015b: fig. 4). Although yet to be directly observed for other species, such as *A. phoenicia*, *Gigantosculda ehrlichfeckei* Haug, Wiethase & Haug, 2015, or *P. laevis*, phylogenetic considerations (see also further below) suggest the V-shaped arrangement can be assumed for these species too.

Hence, the almost parallel and more widely spaced, almost linear arrangement of the posterior three maxillipeds in combination with the massive claw of the major raptorial appendage is indeed unique for *O. teruzzii* n. gen., n. sp. and emphasizes its identity as separate species. Whether the widely spaced arrangement of the maxillipeds is truly diagnostic in the strict sense needs to be discussed in a phylogenetic context (below).

Phylogenetic considerations

The evenly spaced and almost linear arrangement of the maxilliped insertions, as seen in *Ostenosculda teruzzii* n. gen., n. sp. is an unexpected find. Yet, in comparison to other malacostracan crustaceans, such an arrangement must be considered as plesiomorphic. Unfortunately, the arrangement of the insertions of the maxillipeds in the Carboniferous species of mantis shrimps has not yet been directly observed. However, a rather linear arrangement of the maxillipeds in specimens of *Daidal* Schram, 2007, *Gorgonophontes* Schram, 1984 and *Tyrannophontes* may be inferred from the conformation and consecutive positions of the proximal elements of the posterior maxillipeds in a number of more complete fossils preserved in lateral aspect (e.g. Jenner *et al.* 1998: pl. 1(4); Schram 2007: figs 2, 4(1-2), 7, 16). Dorsoventrally accessible fossils of these lineages showing details of the maxilliped insertions are yet to be discovered.

Still, an approximate position of *O. teruzzii* n. gen., n. sp. in the mantis shrimp phylogeny can be estimated (Fig. 6). Early branchings of the mantis shrimp lineage such as species of *Archaeocaris* Meek, 1872, *Bairdops* Schram, 1979, *Daidal* and *Perimecturus* Peach, 1908 are characterised by a lack of size-differentiation between the maxillipeds, i.e. there is a slight decrease in size of the appendages, but not a distinct one, especially not between the first and second pair of raptorial appendages (Haug *et al.* 2010).

In representatives of *Gorgonophontes* there is a recognizable size differentiation into one large and three pairs of medium-sized maxillipeds, hence a large-medium-medium-medium pattern. Representatives of *Tyrannophontes* are the first representatives of Stomatopoda possessing a size differentiation of the maxillipeds into large-medium-small-small (Schram 2007).

Ostenosculda teruzzii n. gen., n. sp. appears to be further specialised than *Gorgonophontes* concerning the size differentiation of the maxillipeds, as one of the posterior dactyli is only about 0.25 times as long as the one of the major raptorial appendages, classifying it as "small". Yet, as no more details of the sizes of the other maxillipeds of *O. teruzzii* n. gen., n. sp. are known, and there is also a lack of detail about the exact arrangement of the maxilliped insertions in the species of *Tyrannophontes*, the phylogenetic position relative to the new species cannot yet be fully resolved. The overall similarities of *O. teruzzii* n. gen., n. sp. to *T. laurae* and *Pseudosculda* could indicate that the new species is closer to these, hence branching off above the branch of *Tyrannophontes*. Yet, these similarities may account for more similar preservational aspects of the new species to the younger Mesozoic fossils. Therefore, an alternative situation cannot be excluded, with the new species branching off below the branch of *Tyrannophontes*, notwithstanding that this would result in a longer ghost lineage. Also a sister-group relationship between *O. teruzzii* n. gen., n. sp. and *Tyrannophontes* cannot be fully excluded. Yet, the differences between the new species and *Tyrannophontes*, for example spination of the carpopropodus, shape of telson and uropods (as far as observable) warrant the erection of a new species (and genus). The large geographic and chronological differences also support this view.

Evolutionary reconstruction

The newly observed details add a significant intermediate step to the reconstruction of the evolutionary history of mantis shrimps. The historical process can be further subdivided into the following steps (Fig. 6):

1. The first specialization, presumably the autapomorphy of Stomatopoda, is the transformation of post-ocular appendages 7-10 into sub-chelate appendages. The almost linear and not tightly spaced arrangement of the insertion areas of these appendages and their similar overall morphology, i.e. no (significant) size or functional differentiation of the maxillipeds, was retained as a plesiomorphy.
2. As a synapomorphy of *Gorgonophontes* + [*Tyrannophontes* + (Sculdidae + (Pseudosculdidae + Verunipeltata)], the maxillipeds 2-5 became size-differentiated to the large-medium-medium-medium pattern. The arrangement of the maxilliped insertions remained the same.
3. As a synapomorphy of *Tyrannophontes* + [Sculdidae + (Pseudosculdidae + Verunipeltata)] the maxillipeds 2-5 became size differentiated to the large-medium-small-small pattern. At this node, the maxilliped insertions remained plesiomorphically not tightly spaced and almost linear.
4. As a further specialization within *Tyrannophontes* + [Sculdidae + (Pseudosculdidae + Verunipeltata)], the arrangement of the maxilliped insertions became specialised to the tight and V-shaped arrangement as seen in *Sculda* and the modern forms (Fig. 7).

The present evolutionary scenario assumes that all mantis shrimps outside *Tyrannophontes* + [Sculdidae + (Pseudosculdidae + Verunipeltata)] did not yet possess the V-shaped arrangement and tight spacing of the maxillipeds as seen in modern mantis shrimps. This detail has so far not been addressed in the Palaeozoic representatives. Yet, reasonable inferences may be made based on the arrangement of the posterior maxillipeds in laterally preserved specimens of the groups *Daidal*, *Gorgonophontes* and *Tyrannophontes* which appear to insert in a rather linear fashion. However, these should be reassessed in the light of what we now know of the maxilliped insertions of *Ostenosculda teruzzii* n. gen., n. sp. If the Palaeozoic mantis shrimps already possessed the "condensed" condition of modern forms, this would indicate that *O. teruzzii* n. gen., n. sp. retains more plesiomorphies than one of the Carboniferous forms, and the derived condition would have evolved already in the Palaeozoic (because the convergently evolved condensed raptorial apparatus or reversal to the old arrangement in the new species are considered less parsimonious). If in *Tyrannophontes* the almost linear maxilliped condition is found, then *O. teruzzii* n. gen., n. sp. would be probably closer to the modern forms and the derived condensed condition would have not evolved prior to the Late Jurassic.

Ostenosculda teruzzii n. gen., n. sp. has drawn attention to a new character complex that has, until now, escaped attention, which should be further explored in future studies. It also demonstrates that rather fragmentarily preserved fossils can still offer crucial information that can lead to a more detailed view on a stepwise evolutionary character transformation.

Palaeo-Evo-Devo: integrating fossils and larvae into an evolutionary framework

As pointed out, *Ostenosculda teruzzii* n. gen., n. sp. supports a further elucidation of the evolution of mantis shrimps. Additionally, integrating developmental data to the fossil data, hence a palaeo-evo-devo view, could provide further details.

In this aspect, it is interesting to note that there is one early type of modern-day mantis shrimp larva that is similar to the here described fossils concerning the arrangement of the insertion areas of the maxillipeds. Antizoea larvae have their future raptorial appendages still developed as swimming appendages (e.g. Ahyong *et al.* 2014; Haug *et al.* 2016a: fig. 9). Only gradually over at least two moults (Haug *et al.* 2016a: fig. 4), these appendages are transformed into the raptorial structures seen in the adult forms; the larva is then in the erichthus phase. During the antizoea phase and also still in the transitional state the (future) maxillipeds are not condensed, concerning the anterior-posterior distance between their insertions, and there is no lateral shift of the insertions of anterior maxillipeds nor median shift of the posterior ones. Therefore, the larva apparently "recapitulates" the plesiomorphic / ancestral condition. Other early larval forms of mantis shrimps, the pseudozoea larvae, hatch with the anterior two pairs of maxillipeds already differentiated, but have the posterior three pairs of maxillipeds present only as limb buds, yet the insertion areas are also linearly arranged. By the time the developed posterior maxillipeds appear, however, they are positioned in a similarly condensed arrangement as in the adults.

This again indicates that the antizoea retains numerous ancestral features, for example the exopod on the maxillipeds (Haug *et al.* 2016a). Still, the situation is complicated by the fact that phylogenetic reconstructions have resolved the antizoea as a derived type of larva (Ahyong & Harling 2000) with the pseudozoea as the ancestral type of early larva. This conflict demonstrates that the knowledge on mantis shrimp larvae is still insufficient to develop a conflict-free evolutionary reconstruction. Yet, it also demonstrates that the integration of fossil and developmental data can reveal such conflicts that will have to be tackled in future research.

CONCLUSIONS

The newly described species of mantis shrimp, *Ostenosculda teruzzii* n. gen., n. sp., from the Lower Jurassic of Italy adds significant new details to the view of mantis shrimp evolution, their morphology and distribution:

1) Identifying the arrangement of the maxilliped insertions as a new suite of characters important in mantis shrimp evolution, prompting the reinterpretation of known Palaeozoic fossils.

2) Decreasing the gap in the mantis shrimp fossil record between the Carboniferous (300 million years) and the Late Jurassic (150 million years).

3) Identifying additional sub-steps in mantis shrimp evolution, implying that the arrangement of raptorial appendages followed their differentiation in size.

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REFERENCES

Ahyong S. T. 2001. — Revision of the Australian Stomatopod Crustacea. *Records of the Australian Museum* 26: 1-326. https://doi.org/10.3853/j.0812-7387.26.2001.1333

Ahyong S. T. 2002. — Stomatopod Crustacea from the Marquesas Islands: results of MUSORSTOM 9. *Zoosystema* 24 (2): 347-372.

Ahyong S. T. 2004. — Stomatopoda – Mantis shrimp, *in* Poore G. C. B. (ed.), *Marine Decapod Crustacea of Southern Australia: a guide to identification*. CSIRO Publishing, Collingwood: 517-549.

Ahyong S. T. 2012. — The marine fauna of New Zealand: mantis shrimps (Crustacea: Stomatopoda). *NIWA Biodiversity Memoir* 125: 1-111.

Ahyong S. T. & Harling C. 2000. — The phylogeny of the stomatopod Crustacea. *Australian Journal of Zoology* 48 (6): 607-642. https://doi.org/10.1071/ZO00042

Ahyong S. T. & Galil B. S. 2006. — First Mediterranean record of the Indo-West Pacific mantis shrimp, *Clorida albolitura* Ahyong & Naiyanetr, 2000 (Stomatopoda, Squillidae). *Aquatic Invasions* 1 (3): 191-193. https://doi.org/10.3391/ai.2006.1.3.16

Ahyong S. T. & Jarman S. N. 2009. — Stomatopod interrelationships: preliminary results based on analysis of three molecular loci. *Arthropod Systematics and Phylogeny* 67 (1): 91-98.

Ahyong S. T., Garassino A. & Gironi B. 2007. — *Archaeosculda phoenicia* n. gen., n. sp. (Crustacea, Stomatopoda, Pseudosculdidae) from the Upper Cretaceous (Cenomanian) of Lebanon. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 148 (1): 3-15.

Ahyong S. T., Haug J. T. & Haug C. 2014. — Stomatopoda, *in* Martin J. W., Olesen J. & Høeg J. T. (eds), *Atlas of Crustacean Larvae*. The Johns Hopkins University Press, Baltimore: 185-189.

Biju-Duval B., Dercourt J. & Le Pichon X. 1977. — From the Tethys ocean to the Mediterranean seas: A plate tectonic model of the evolution of the western alpine system, *in* Biju-Duval B. & Montadert L. (eds), *International symposium of the structural history of the mediterranean basins*. Éditions Technip, Paris: 143-164.

Briggs D. E. G. & Kear A. J. 1993. — Fossilization of soft-tissue in the laboratory. *Science* 259: 1439-1442. https://doi.org/10.1126/science.259.5100.1439

Briggs D. E. G. & Kear A. J. 1994. — Decay and mineralization of shrimps. *Palaios* 9 (5): 431-456. https://doi.org/10.2307/3515135

Charbonnier S., Audo D., Garassino A. & Hyžný M. 2017. — *Fossil Crustacea of Lebanon*. Muséum national d'Histoire naturelle (Mémoires du Muséum national d'Histoire naturelle; 210), 252 p.

Chiou T. H., Kleinlogel S., Cronin T., Caldwell R., Loeffler B., Siddiqi A., Goldizen A. & Marshall J. 2008. — Circular polarization vision in a stomatopod crustacean. *Current Biology* 18 (6): 429-434. https://doi.org/10.1016/j.cub.2008.02.066

Feller K. D., Cronin T. W., Ahyong S. T. & Porter M. L. 2013. — Morphological and molecular description of the late-stage larvae of *Alima* Leach, 1817 (Crustacea: Stomatopoda) from Lizard Island, Australia. *Zootaxa* 3722 (1): 22-32. https://doi.org/10.11646/zootaxa.3722.1.2

Garassino A. & Donovan D. T. 2000. — A new family of coleoids from the Lower Jurassic of Osteno, Northern Italy. *Palaeontology* 43 (6): 1019-1038. https://doi.org/10.1111/1475-4983.00160

Garassino A. & Teruzzi G. 2015. — Osteno, una finestra sul Giurassico. *Natura* 105 (1): 1-61. [Extended English abstract].

Hansen H. J. 1895. — Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung* 2: 1-105. https://doi.org/10.5962/bhl.title.10413

Haug C. & Haug J. T. 2021. — A new fossil mantis shrimp and the convergent evolution of a lobster-like morphotype. *PeerJ* 9: e11124. https://doi.org/10.7717/peerj.11124

Haug C., Haug J. T. & Waloszek D. 2009a. — Morphology and ontogeny of the Upper Jurassic mantis shrimp *Spinosculda ehrlichi* n. gen. n. sp. from southern Germany. *Palaeodiversity* 2: 111-118.

Haug C., Haug J. T., Waloszek D., Maas A., Frattigiani R. & Liebau S. 2009b. — New methods to document fossils from lithographic limestones of southern Germany and Lebanon. *Palaeontologia Electronica* 12 (3): 1-12.

Haug J. T., Haug C., Maas A., Kutschera V. & Waloszek D. 2010. — Evolution of mantis shrimps (Stomatopoda, Malacostraca) in the light of new Mesozoic fossils. *BMC Evolutionary Biology* 10 (290). https://doi.org/10.1186/1471-2148-10-290

Haug C., Mayer G., Kutschera V., Waloszek D., Maas A. & Haug J. T. 2011a. — Imaging and documenting gammarideans. *International Journal of Zoology* 380829, 9 p. https://doi.org/10.1155/2011/380829

Haug J. T., Haug C., Kutschera V., Mayer G., Maas A., Liebau S., Castellani C., Wolfram U., Clarkson E. N. K. & Waloszek D. 2011b. — Autofluorescence imaging, an excellent tool for comparative morphology. *Journal of Microscopy* 244 (3): 259-272. https://doi.org/10.1111/j.1365-2818.2011.03534.x

Haug C., Sallam W. S., Maas A., Waloszek D., Kutschera V. & Haug J. T. 2012. — Tagmatization in Stomatopoda – reconsidering functional units of modern-day mantis shrimps (Verunipeltata, Hoplocarida) and implications for the interpretation of fossils. *Frontiers in Zoology* 9 (31). https://doi.org/10.1186/1742-9994-9-31

Haug C., Shannon K. R., Nyborg T. & Vega F. J. 2013. — Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda. *Boletín de la Sociedad Geológica Mexicana* 65 (2): 273-284. https://doi.org/10.18268/BSGM2013v65n2a9

Haug C., Haug J. T., Nyborg T., Nyborg B. & Kovalchuk G. 2015a. — Pushing the limits to the north – a fossil mantis shrimp from Oregon, USA. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 278 (3): 281-290. https://doi.org/10.1127/njgpa/2015/0528

Haug C., Wiethase J. H. & Haug J. T. 2015b. — New records of Mesozoic mantis shrimp larvae and their implications on modern larval traits in stomatopods. *Palaeodiversity* 8: 121-133.

Haug C., Ahyong S. T., Wiethase J. H., Olesen J. & Haug J. T. 2016b. — Extreme morphologies of mantis shrimp larvae. *Nauplius* 24: e2016020. https://doi.org/10.1590/2358-2936e2016020

Hof C. H. J. 1998. — Fossil stomatopods (Crustacea: Malacostraca) and their phylogenetic impact. Journal of Natural History 32 (10-11): 1567-1576. https://doi.org/10.1080/00222939800771101

Haug J. T., Rudolf N. R., Wagner P., Gundi P. T., Fetzer L.-L. & Haug C. 2016a. — An intermetamorphic larval stage of a mantis shrimp and its contribution to the 'missing-element problem' of stomatopod raptorial appendages. *Annual Research & Review in Biology* 10 (3): 1-19. https://doi.org/10.9734/ARRB/2016/25938

Hof C. H. J. & Briggs D. E. G. 1997. — Decay and mineralization of mantis shrimps (Stomatopoda: Crustacea) – A key to their fossil record. *Palaios* 12 (5): 420-438. https://doi.org/10.2307/3515381

Jenner R. A., Hof C. H. J. & Schram F. R. 1998. — Palaeo- and archaeostomatopods (Hoplocarida: Crustacea) from the Bear Gulch Limestone, Mississippian (Namurian), of central Montana. *Contributions to Zoology* 67 (3): 155-186. https://doi.org/10.1163/18759866-06703001

Kleinlogel S. & Marshall N. J. 2006. — Electrophysiological evidence for linear polarization sensitivity in the compound eyes of the stomatopod crustacean *Gonodactylus chiragra*. *Journal of Experimental Biology* 209 (21): 4262-4272. https://doi.org/10.1242/jeb.02499

Klompmaker A. A., Hyžný M., Portell R. W., Jauvion C., Charbonnier S., Fussell S. S., Klier A. T., Tejera R. & Jakobsen S. L. 2019. — Muscles and muscle scars in fossil malacostracan crustaceans. *Earth-Science Reviews* 194: 306-326. https://doi.org/10.1016/j.earscirev.2019.04.012

Lamsdell J. C., Teruzzi G., Pasini G. & Garassino A. 2021. — A new limulid (Chelicerata, Xiphosurida) from the Lower Jurassic (Sinemurian) of Osteno, NW Italy. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 300 (1): 1-10. https://doi.org/10.1127/njgpa/2021/0974

Latreille P. A. 1817. — Les crustacés, les arachnides et les insectes, *in* Cuvier G. (ed.), *Le Règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Deterville, Paris, 653 p., i-xxix.

Lewinsohn C. & Manning R. B. 1980. — Stomatopod Crustacea from the eastern Mediterranean. *Smithsonian Contributions to Zoology* 305: 1-22. https://doi.org/10.5479/si.00810282.305

Manning R. B. 1991. — Stomatopod Crustacea collected by the Galathea expedition, 1950-1952, with a list of Stomatopoda known from depths below 400 meters. *Smithsonian Contributions to Zoology* 521: 1-18. https://doi.org/10.5479/si.00810282.521

Meek F. B. 1872. — Descriptions of new western Paleozoic fossils, mainly from the Cincinnati group of the Lower Silurian series of Ohio. *Proceedings of the Academy of the Natural Sciences of Philadelphia* 23 (3): 335-336. https://www.jstor.org/stable/4624198

Münster G. zu 1840. — Ueber einige Isopoden in den Kalkschiefern von Bayern. *Beiträge zur Petrefactenkunde* 3: 19-23.

Ogg J. G. & Hinnov L. A. 2012. — Jurassic, *in* Gradstein F. M., Ogg J. G., Schmitz M. & Ogg G. (eds), *The Geologic Time Scale*. Elsevier, Oxford: 766.

Patek S. N. & Caldwell R. L. 2005. — Extreme impact and cavitation forces of a biological hammer: strike forces of the peacock mantis shrimp *Odontodactylus scyllarus*. *The Journal of Experimental Biology* 208 (19): 3655-3664. https://doi.org/10.1242/jeb.01831

Peach B. N. 1908. — Monograph on the higher Crustacea of the Carboniferous rocks of Scotland. *Memoirs of the Geological Survey of Great Britain Palaeontology* 1908: 1-91.

Pinna G. 1967. — Découverte d'une nouvelle faune à crustacés du Sinémurien dans la region du Lac Ceresio (Lombardie, Italie). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 106: 183-185.

Pinna G. 1985. — Exceptional preservation in the Jurassic of Osteno. *Philosophical Transactions of the Royal Society of London* B 311 (1148): 171-180. https://doi.org/10.1098/rstb.1985.0149

Pinna G. 2000. — Die Fossillagerstätte im Sinemurium (Lias) von Osteno, Italien, *in* Pinna G. & Meischner D. (eds), *Europäische Fossillagerstätten*. Springer-Verlag, Berlin Heidelberg: 91-136.

Reaka M. L. & Manning R. B. 1987. — The significance of body size, dispersal potential, and habitat for rates of morphological evolution in stomatopod Crustacea. *Smithsonian Contributions to Zoology* 448: 1-46. https://doi.org/10.5479/si.00810282.448

Schlüter C. 1872. — Ueber einen fossilen Stomatopoden vom Libanon. *Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande und Westphalens* 29: 194-195.

Schram F. R. 1979. — British Carboniferous Malacostraca. *Fieldiana Geologica* 40: 1-129.

Schram F. R. 1984. — Upper Pennsylvanian arthropods from black shales of Iowa and Nebraska. *Journal of Paleontology* 58 (1): 197-209.

Schram F. R. 2007. — Paleozoic proto-mantis shrimp revisited. *Journal of Paleontology* 81 (5): 895-916. https://doi.org/10.1666/pleo05-075.1

Schram F. R. 2010. — *Catalog of the fossil and recent Stomatopoda*. Bay Ridge Press, Langley, 294 p.

Schram F. R., Ahyong S. T., Patek S. N., Green P. A., Rosario M. V., Bok M. J., Cronin T. W., Mead Vetter K. S., Caldwell R. L., Scholtz G., Feller K. D. & Abelló P. 2013. — Subclass Hoplocarida Calman, 1904: Order Stomatopoda Latreille, 1817, *in* Von Vaupel Klein J. C., Charmantier-Daures M. & Schram F. R. (eds), *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea*, 4 (A). Brill, Leiden: 179-355.

Taylor J. R. A. & Patek S. N. 2010. — Ritualized fighting and biological armor: the impact mechanics of the mantis shrimp's telson. *The Journal of Experimental Biology* 213 (20): 3496-3504. https://doi.org/10.1242/jeb.047233

Van Der Wal C., Ahyong S. T., Ho S. Y. W., Lo N. 2017. — The evolutionary history of Stomatopoda (Crustacea: Malacostraca) inferred from molecular data. *PeerJ* 5: e3844. https://doi.org/10.7717/peerj.3844

Wilby P. R. & Briggs D. E. G. 1997. — Taxonomic trends in the resolution of detail preserved in fossil phosphatized soft tissues. *Geobios* 30 (1): 493-502. https://doi.org/10.1016/S0016-6995(97)80056-3

WILBY P. R., BRIGGS D. E. G. & PINNA G. 1995. — *Soft tissue preservation in the Sinemurian of Osteno, Italy – comparisons with Solnhofen and with experimental results*. Second international symposium on Lithographic Limestones, extended abstracts, Universidad Autonoma de Madrid, Cuenca, Spain: 163-164.

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