

Defensive enrolment in mantis shrimp larvae (Malacostraca: Stomatopoda)

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Abstract

We describe a possible new defensive behaviour of larval stages of mantis shrimps (Stomatopoda). Mantis shrimp larvae are rarely observed in nature, thus the study is based on postures of museum material and functional morphological aspects. Specimens described here are tightly enrolled, their pleon is bent forward, and the telson is locked into the frontal margin of the shield. This margin has two lobes into which the two postero-lateral spines of the telson fit. The shield shows further adaptations to enrolment; *e.g.*, the ventral gape of the shield perfectly matches the width of the pleon and leaves no major gaps when the pleon is bent forward. Based on these observations, we briefly discuss the possibilities to infer behavioural aspects from functional morphological aspects. Enrolment in modern day organisms is primarily known from terrestrial arthropods, *e.g.*, pill bugs and pill millipedes, but in the Palaeozoic it was mainly performed by marine organisms such as trilobites, agnostines and their relatives. Stomatopod larvae that appear to be able to perform enrolling in a marine environment are therefore a potential functional equivalent for better understanding the functional aspects of enrolment in extinct marine arthropods.

Contents

Introduction	185
Material and methods	187
<i>Material</i>	187
<i>Documentation methods</i>	187
<i>Conclusions on behaviour from museum material</i>	187
Results	188
<i>General observations</i>	188
Discussion	191
<i>Enrolment in stomatopod larvae</i>	191
<i>Indirect reconstruction of behavioural traits</i>	192
<i>Enrolment: a possible defensive behaviour</i>	192
Conclusions	193
Acknowledgements	193
References	193

Introduction

Arthropods display a large variety of defensive strategies against predators and other threats. For example,

numerous groups developed escape reactions. Well-known examples of groups with such a reaction are caridoid eucrustaceans, leaf hoppers, and orthopteran insects (*e.g.*, Carew, 2000; Burrows, 2007; Burrows and Picker, 2010). Other defensive strategies involve the development of defensive structures: the body of arthropods can be armed with strong spines, serrations or heavily sclerotised dorsal sclerites, or the entire body can be enclosed in large shields. In some arthropods, a combination of several of these defensive aspects can be found. For example, many orthopterans arm their jumping legs, which they use for their escape reaction, with stout spines (*e.g.*, Field and Glasgow, 2001). Daphniid crustaceans, with their bivalved shield enclosing their entire body, additionally employ strong spines for protection (*e.g.*, Swaffar and O'Brien, 1996).

Another such combined defensive strategy is enrolment, wherein both structural and behavioural aspects act in synergy. The entire body of the arthropod is strongly curved ventrally, forming more or less a ball, so that the anterior and the posterior end lie adjacent to each other. In such a position, the (often strongly sclerotised) dorsal surfaces of the segments face outside, while the more membranous ventral side including the appendages is protected in the inside of the ball. In the extant fauna, such a defensive behaviour is displayed, for example, by species of the myriapod groups Sphaerotheriida (*e.g.*, Golovatch, 2003) and Glomerida (pill millipedes; Fig. 1A-B), and by pill bugs, *i.e.*, species of the crustacean isopod group *Armadillidium* (Fig. 1C-D).

Trilobites are a diverse group of exclusively fossil euarthropods, of which most representatives also displayed enrolment. In some species, specialised structures (frequently referred to as 'coaptative structures') were developed on the ventral side of the head and tail shield (pygidium), which allowed a tight interlocking of these two structures (Feist *et al.*, 2010; Fig. 1E-F). This would additionally secure the enrolled position if a predator would try to 'open' the defending animal.

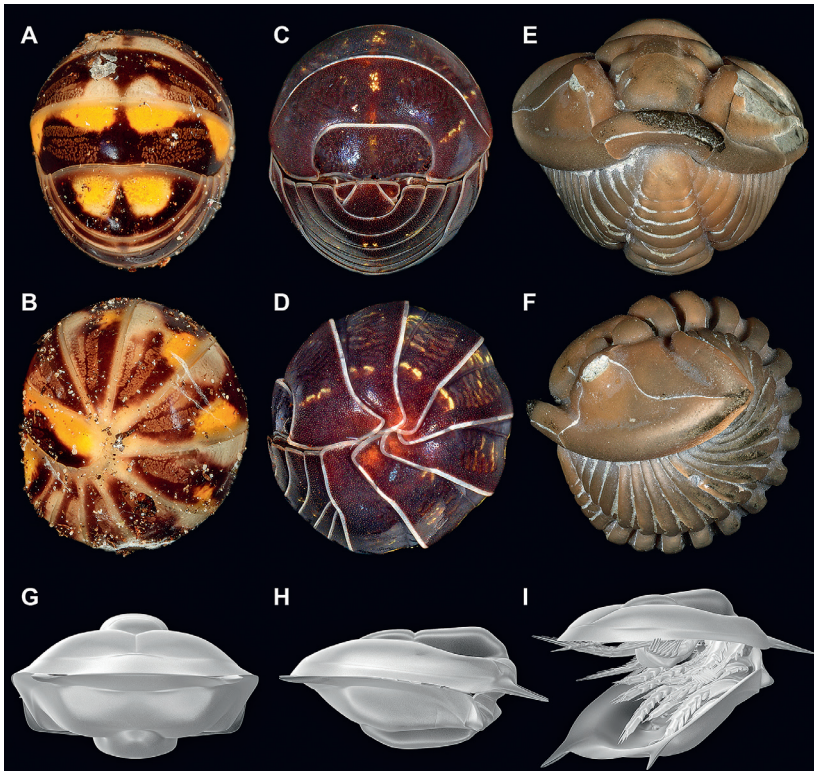


Fig. 1. Commonly known enrolling arthropods. A-B. Pill millipede, *Glomeris* sp. (Diplopoda). A. Frontal view. B. Lateral view. C-D. Pill bug (woodlouse), *Armadillidium* sp. (Isopoda). C. Frontal view. D. Lateral view. E-F. *Flexicalymene* sp. (Trilobita). E. Frontal view. F. Lateral view. G-I. *Agnostus pisiformis* (Wahlenberg, 1818) (Agnostina). G. Frontal view. H. Lateral view. I. Presumed life position. A-F are composite images under cross-polarised light; G-I are computer-generated 3D models based on Müller and Walossek (1987).

Other exclusively fossil euarthropods that were highly specialised for enrolment include the agnostines (often considered to be trilobites, but see, *e.g.*, Haug *et al.*, 2010; Stein and Selden, 2012) and certain nektaspidids, a group of superficially trilobite-like euarthropods (*e.g.*, Budd, 1999). Among agnostines, some spe-

cies such as *Agnostus pisiformis* (Wahlenberg, 1818) (Fig. 1G-I) even appear to have spent their entire life fully or partly enrolled, as they seem to have been unable to stretch their bodies straight (Müller and Walossek, 1987; Bruton and Nakrem, 2005).

Even among fossil chelicerates, some representa-

Table 1. Sampling information of the mantis shrimp larvae investigated in this study.

Repository number	Station	Latitude	Longitude	Date	Locality	Depth in m
ZMUC-CRU-20243	1192-7	17°43.4' N	64°54.3' W	15 Dec. 1921	W of St. Croix, Virgin Islands	410
ZMUC-CRU-20244	3809-3	6°22' S	105°12' E	4 Sep. 1929	W of Java, Indonesia	1050
ZMUC-CRU-20245	3949-2	11°33' S	41°44' E	6 Jan. 1930	N Mozambique	1890
ZMUC-CRU-20246	3958-1	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20247	3958-1	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20248	3958-2	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20249	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20250	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20251	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20252	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20253	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20254	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20255	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20256	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20257	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100
ZMUC-CRU-20258	3958-3	23°11' S	42°54' E	11 Jan. 1930	W of Tulear, Madagascar	3100

tives appear to have been able to perform enrolment. The 300 million year old xiphosuran *Alanops magnificus* possessed highly domed prosomal and opisthosomal shields, providing space for the sturdy appendages (Racheboeuf *et al.*, 2002). Other xiphosuran fossils that have been interpreted as representing enrolled specimens (Fisher, 1977; Anderson, 1994) have been questioned; for example, enrolled-appearing representatives of *Euproops* seem more likely to represent preservational positions of exuviae (Haug *et al.*, 2012a).

Given the broad taxonomic distribution of defensive enrolment, one could come to the conclusion that enrolling was a successful and widely distributed strategy for aquatic arthropods in the past, but today is only found in few specialised terrestrial forms. Here we report enrolling in extant marine arthropods, namely larval stages of mantis shrimps, based on museum material. We describe variations of this specific strategy and briefly discuss how museum material can be used to infer behavioural aspects of animals that cannot easily be observed directly.

Material and methods

Material

All investigated larval mantis shrimp (stomatopod) specimens come from the collection of the Zoological Museum of the University of Copenhagen (ZMUC). Specimens were collected during the famous Dana expeditions (1921-22 and 1928-30; Schmidt, 1926, 1931; Broch, 1936), and have come exclusively from plankton samples (for details on the sampling sites, see Table 1). All specimens are stored in 70% ethanol, but based on the appearance of the specimens, early storage, or at least fixation, seems to have been in formaldehyde.

Documentation methods

Specimens were documented directly within their storage liquid, *i.e.*, 70% ethanol. Specimens show a certain flexibility. For ventral and dorsal documentation, some specimens were carefully outstretched and fixed with a cover slip. For large specimens, posterior and anterior ends were fixed with a separate cover slip each. In other orientations, specimens were either leaned against glass or metal objects, or placed into depressions. Specimens in unusual positions were not

altered, but kept in this specific position.

Specimens were photographed with a Canon Rebel T3i digital camera with a MP-E 65mm macro lens. Light was provided by a Canon Macro Twin Flash MT 24 or a Meike FC 100 LED ring light. Light sources were equipped with polarisation filters. A cross-polarised filter was placed in front of the lens. Cross-polarised light reduces reflections and enhances the colour contrast (*e.g.*, Haug *et al.*, 2011 and references therein). To overcome limited depth of field in higher magnifications, stacks of images were recorded, each single frame in a different focal plane. Stacks were fused using CombineZM/ZP or Image Analyzer. To overcome limitations of field of view in higher magnifications, several adjacent image details were recorded, each one with a stack. Fused images for each image detail were stitched together using Microsoft Image Composite Editor or the photomerge function of Adobe Photoshop CS3 (for details see Haug *et al.*, 2009, 2011). Further processing such as optimisations of histograms, saturation, sharpness (mask unsharp filter) and manual cleaning of the background was performed in Adobe Photoshop CS3. Some specimens were additionally documented as stereo images. For this purpose, specimens were documented in different viewing angles (*e.g.*, Haug *et al.*, 2011). Red-cyan anaglyphs based on stereo pairs were produced in Adobe Photoshop CS3 or CS6.

Conclusions on behaviour from museum material

Direct observation of most larval stages of stomatopods is generally not possible in a laboratory setting, as it is very difficult to rear them. Nonetheless, fixed material from plankton samples of extant stomatopod larvae can provide valuable insights to their behaviour in a comparable way to how fossils allow the reconstruction of behavioural aspects of extinct organisms (*e.g.*, Haug *et al.*, 2012b, c, 2013). These indications comprise two aspects: 1) Functional morphology, *i.e.*, addressing questions such as which movements does the morphology allow the organism to perform or which functions could certain structures fulfil. 2) Positions in which specimens are preserved (see also Mayer *et al.*, 2013); here a careful consideration is necessary to differentiate possible true lifetime positions from 'dying poses', post-mortem poses, or simply storage deformations such as those resulting from a large specimen being stored in a small jar, or when numerous specimens have been stuffed together into a single jar.

Results

The following discussion is restricted to addressing certain morphotypes of mantis shrimp larvae, not species. Though currently almost 500 species of extant mantis shrimps are described, we know the larval sequences of only a handful of them (*e.g.*, Manning and Provenzano, 1963; Provenzano and Manning, 1978; Greenwood and Williams, 1984; Morgan and Goy, 1987; Diaz, 1998; Ahyong *et al.*, accepted). Although some work has been done on larval disparity of mantis shrimps (although the most important papers are mostly many decades old and did not utilize up-to-date imaging methods, *e.g.*, Giesbrecht, 1910; Shanbhogue, 1975) the exact assignment of larvae to specific species is still a very challenging task. Recent successes in culturing and DNA barcoding are promising (Tang *et al.*, 2010) and might allow future improvements in this respect. For the here presented observations, the ascription to specific species is not seen as an important aspect; therefore the restriction to morphotypes is, in our view, not necessarily problematic.

General observations

Numerous specimens in the extensive stomatopod larvae collection of the ZMUC show an unusual or at least unexpected position: their pleon is flexed far ventrally and anteriorly so that the telson comes close to the anterior part of the head. All specimens showing this posture are of an erichthus type of larva with a bulging shield. The ventral gape of the shield corresponds exactly to the width of the pleon and the telson.

Non-erichthus-type larvae also show a certain flexure of the pleon, but usually not that far anteriorly. A correlation between the ventral gape (in cases of alima-type larvae the shield is so flat that ‘gape’ is an inappropriate term) and the width of the often very narrow pleon and the often quite broad telson was not observed.

Specimen 1: In specimen ZMUC-CRU-20248 the pleon is flexed far anteriorly, and the telson comes to lie inside the shield, close to its anterior rim (Fig. 2). The pleon width fits perfectly into the ventral gape of the shield as does the telson. All appendages and the compound eyes are ‘inside’, protected by shield, pleon and telson. The entire specimen appears like a compact ball, armed with spines. This posture is referred to as fully enrolled; in the following listing of specimens, this morphology is referred to as morphotype 1.

The shield possesses two lobe-like elevations on its

anterior ventral rim, slightly laterally positioned. Under these lobes, the spines of the postero-lateral corners of the telson come to rest. These lobes appear to partly ‘lock’ the telson in this position.

Specimen 2: This specimen (ZMUC-CRU-20246) strongly resembles specimen 1 (ZMUC-CRU-20248) and is thus also considered morphotype 1, but is slightly larger, possibly representing a later instar of the same species, or corresponding to a later instar of another species. In this specimen a part of the large shield is broken off, allowing a view on arrangement of the appendages in the enrolled posture (Fig. 3A-C). ZMUC-CRU-20246 clearly demonstrates that none of the joints between the pleomeres is overflexed or overstretched in this position and that the appendages neatly fit into the space between the shield, pleon and telson.

Specimen 3: Specimen ZMUC-CRU-20244 appears to be of the same morphotype as the preceding two (morphotype 1), and about the same size class as specimen 1 (ZMUC-CRU-20248). It is only partly enrolled, allowing a partial view from the anterior into the enrolled arrangement of the appendages (Fig. 3D-F). It becomes obvious that in this slightly opened posture the eyes are among the first structures to become exposed.

Specimen 4: Specimen ZMUC-CRU-20243 resembles the preceding specimens in general morphology. However, the specimen was only slightly curled and could be easily outstretched (Fig. 4). This specimen shows that the morphology of this morphotype also allows a fully outstretched posture.

Specimen 5: Specimen ZMUC-CRU-20245 resembles ZMUC-CRU-20244 in the partly opened posture, but apparently represents another morphotype (morphotype 2) with longer shield spines and a shorter telson (Fig. 5A-D). Also the general shield morphology appears wider. The correlation between ventral gape and width of pleon and telson appears less strict in this morphotype, as some gaps remain when the pleon is flexed forward. Although the pleon is fully enrolled, the telson does not reach the anterior rim of the shield due to the shorter telson. Therefore, some structures remain unconcealed. Compound eyes, antennulae and antennae remain exposed, as do the distal three articles of the large raptorial appendages. The shield gape widens slightly in the middle region of the telson, apparently allowing the raptorial appendages also to be sticking out laterally from the telson.

Specimen 6: Specimen ZMUC-CRU-20247 appears to be of the same morphotype as specimen

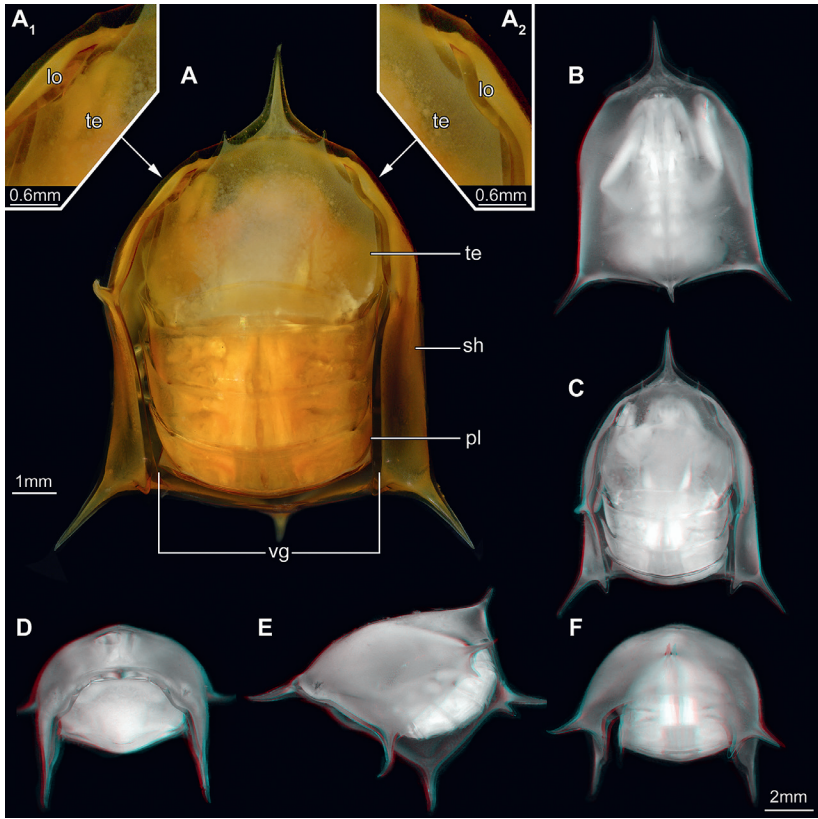


Fig. 2. Erichthus-type mantis shrimp larva of morphotype 1, fully enrolled, ZMUC-CRU-20248. A. Quasi-ventral view; note the ventral gape of the shield. A₁, A₂. Close-ups on the the region of the shield where the telson spines are locked below lobes of the shield. B-F. Red-cyan stereo-anaglyph images (please use red-cyan glasses to view, red left, cyan right); note that the enrolled specimen is a functional ball armed with spines. B. Dorsal view. C. Quasi-ventral view. D. Frontal view. E. Lateral view. F. Posterior view. Abbreviations: lo = lobe of shield; pl = pleon; sh = shield; te = telson; vg = ventral gape.

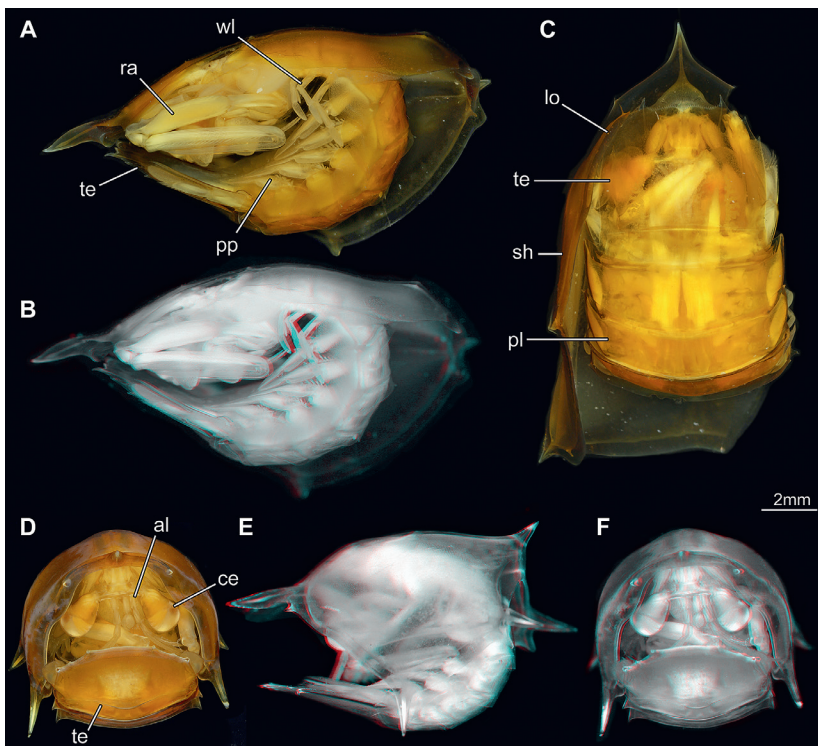


Fig. 3. Erichthus-type mantis shrimp larvae of morphotype 1. A-C. Fully enrolled specimen ZMUC-CRU-20246, parts of the shield broken off, facilitating a view onto the position of the appendages in enrolled posture. A-B. Lateral view. C. Quasi-ventral view. D-F. Partly enrolled specimen ZMUC-CRU-20244. D, F. Frontal view, E. Lateral view. B, E and F are red-cyan stereo-anaglyph images. Abbreviations: al = antennula; ce = compound eye; lo = lobe of shield; pl = pleon; pp = pleopod; ra = raptorial appendage; sh = shield; te = telson; wl = walking leg.

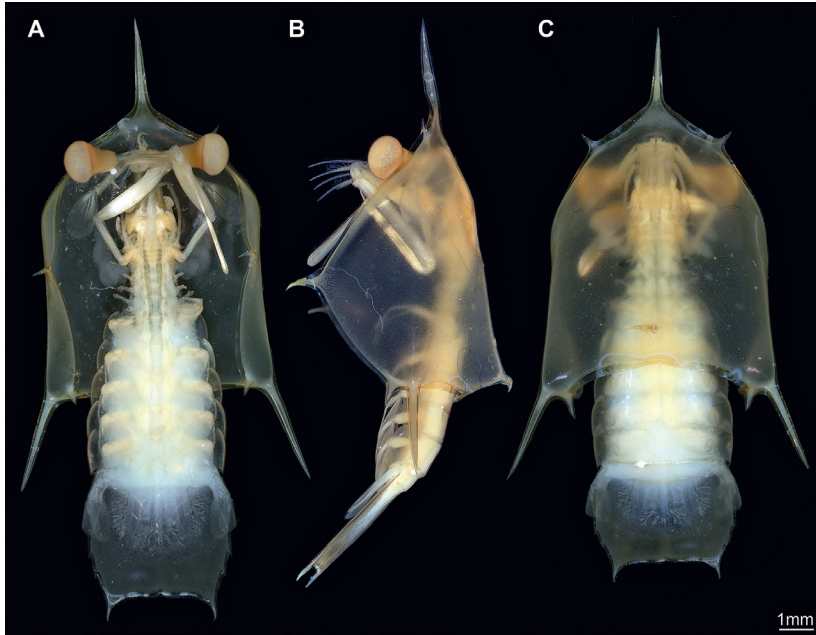


Fig. 4. Erichthus-type mantis shrimp larva of morphotype 1, fully outstretched, ZMUC-CRU-20243. A. Ventral view. B. Lateral view. C. Dorsal view.

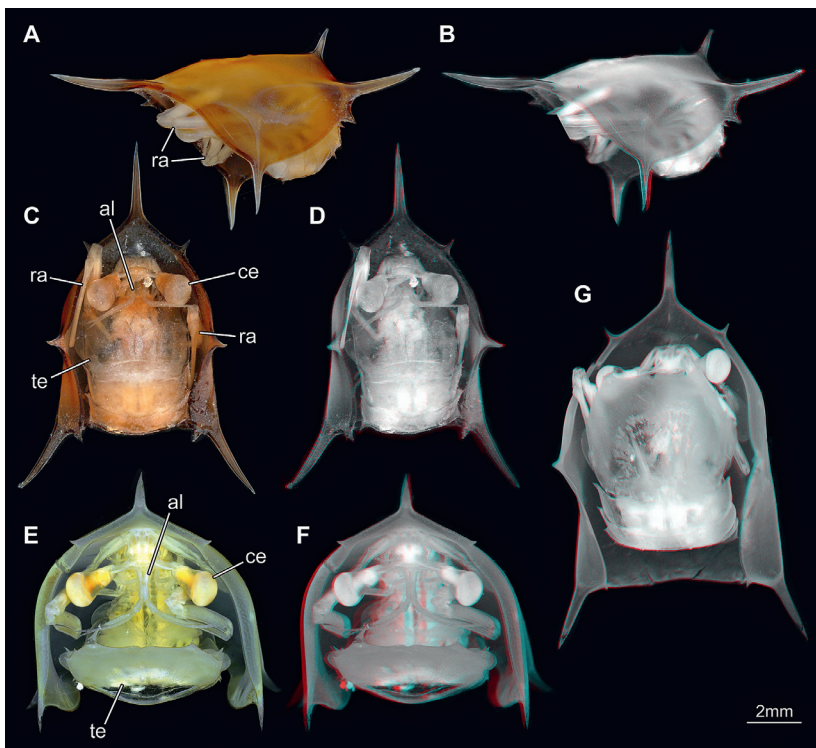


Fig. 5. Erichthus-type mantis shrimp larvae of morphotype 2. A-D. Fully enrolled specimen, ZMUC-CRU-20245. A-B. Lateral view. C-D. Quasi-ventral view. E-G. Partly enrolled specimen, ZMUC-CRU-20247. E-F. Frontal view. G. Ventral view. B, D, F-G are red-cyan stereo-anaglyph images. Abbreviations: al = antennula; ce = compound eye; ra = raptorial appendage; te = telson.

ZMUC-CRU-20245, yet of a slightly larger size class (Fig. 5E-G). The specimen is not as tightly closed as the previous specimen, and as in the latter, the eyes and anterior appendages are sticking out.

Specimens 7-16: Enrolled specimens are quite com-

mon within the samples. As an example, all enrolled specimens from a single sample are shown in Fig. 6 (ZMUC-CRU-20249 until 20258). The sample contains 99 specimens of stomatopod larvae of varying sizes, half of them being erichthus-type larvae (which

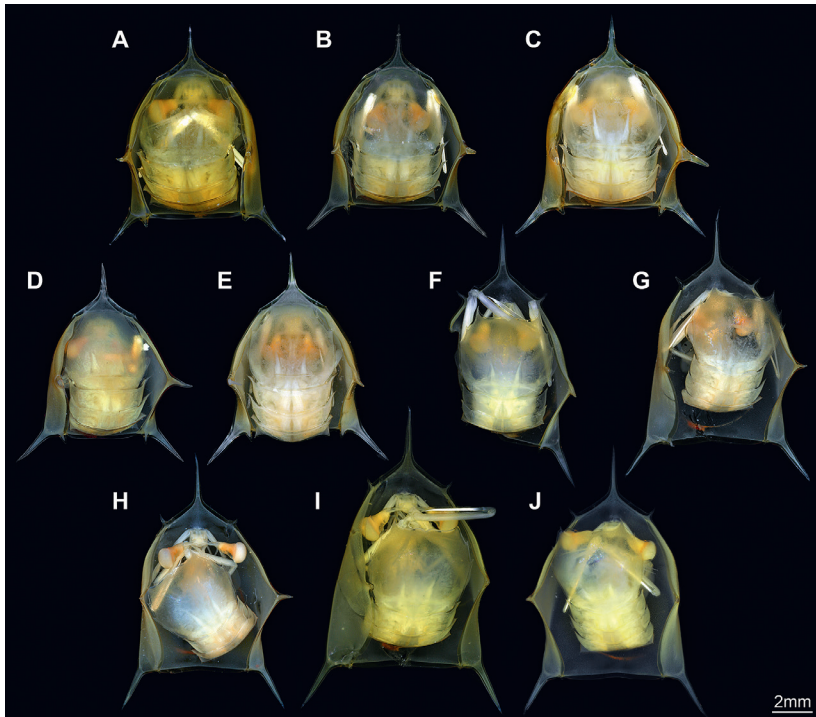


Fig. 6. Erichthus-type mantis shrimp larvae of morphotype 1 and 2. Ten specimens from a single sample in partly or fully enrolled posture, ZMUC-CRU-20249 until 20258.

is an unusually high value; normally, alima or smaller larvae dominate the samples). In total, ten of the erichthus-type larvae of this sample show a fully or partially enrolled posture. Although not a statistical measure, this number can give an indication that the partly or fully enrolled posture may be quite widespread.

Discussion

Enrolment in stomatopod larvae

As the specimens described here demonstrate, erichthus-type mantis shrimp larvae can flex their pleon far ventrally and anteriorly, so that the telson comes to be close to the anterior part of the head. The question then arises as to whether this posture represents a natural position, or simply a dying pose or a storage deformation? In fact, other types of stomatopod larvae also show a flexure of the pleon, so the position alone does not seem to be very telling. Yet, as discussed previously, posture is just one aspect that should be considered here, with another important aspect being functional morphology.

Considering the functional morphology, first of morphotype 1, the following points are important:

- 1) Unlike in other stomatopod larval forms, the shield is not very widely opened ventrally, but the left and right part come clearly closer together towards the ventral side of the body. This leads to a specific ventral gape of the shield.
- 2) The width of the pleon is closely correlated to the ventral gape, so that it 'just fits in', and that over the entire length of the pleon. In other larval forms, such as the alima, the pleon is very narrow and elongate.
- 3) The width of the telson is also closely correlated to the width of the ventral gape; it therefore has the same width as the pleon. In other larvae, the telson is slightly to drastically wider than the pleon.
- 4) The telson can interlock with the two lobes of the shield, leading to a very tight closure.
- 5) The segments of the pleon in the enrolled positions do not appear overstretched or overflexed.
- 6) All appendages fit well into the chamber formed by shield, pleon and telson.

From a functional morphological point, we can state that the erichthus-type larvae of morphotype 1 are in principle able to perform enrolling and appear to possess specialised coaptative structures to secure such a position. The body of these larvae appears to be

specifically adapted to perform such a movement. This observation, together with the fact that specimens in this posture are frequently encountered within the studied material, give an indication that this kind of enrolling represents a true aspect of the behavioural repertoire of the erichthus larvae of morphotype 1.

The case seems less strict for morphotype 2. Here the enrolling posture seems less fixed, and the pleon seems to have a certain flexibility in its position. Moreover, the correlation of width of the ventral gape and width of the pleon appears to be less strict. And finally, with the shorter telson and the lack of coaptative structures, there are clearly less specific adaptations for enrolling than in morphotype 1. Yet, as the case for morphotype 1 is based on numerous adaptations, there should be enrolment morphologies present with only part of these adaptations. Thus, we believe it is plausible that morphotype 2 also performed enrolling, but represents a form that is less specialised for this behaviour than morphotype 1.

Indirect reconstruction of behavioural traits

The argumentation presented here is best comparable to the reconstruction of behavioural or autecological aspects of extinct organisms. In extinct organisms, a direct observation of their behaviour is impossible, and only functional morphological aspects as well as positional information of numerous specimens can be used to infer possible aspects of the behavioural repertoire of the organisms (*e.g.*, Wedmann *et al.*, 2007; Benton, 2010; Poinar, 2010; Haug *et al.*, 2012b, c, 2013 and references therein).

For extant organisms, a direct observation of behavioural aspects is desirable. Yet, as in the case of stomatopod larvae, direct observation of many organisms is rather challenging. In general, the behaviour of stomatopod larvae is still a largely unstudied field. Therefore, an indirect consideration, as presented here, represents an important alternative to direct observation in the field. Especially functional morphological considerations can form an important basis for understanding how unobservable processes might take place. As with other scientific hypotheses in biological sciences, the case herein presented represents a plausible scenario that can only be corroborated by direct observation in the field (first hints noted by M. Erdmann, pers. com.).

Such an indirect reconstruction of behavioural aspects is especially valuable in groups of which we know only little about their actual behaviour. Stomato-

pod larvae are diverse, in fact comprising numerous morphotypes that must occupy also numerous different ecological niches and possess quite differentiated behaviour. The observations presented here provide merely a first glimpse into this diversity, but are therefore seen as especially important. This case furthermore stresses the potential of the use of museum collections for biological aspects beyond taxonomy and even biodiversity.

Enrolment: a possible defensive behaviour

In other arthropods that can perform enrolling, this strategy is employed as a defensive behaviour. This seems to be also a plausible explanation for the observed behaviour in stomatopod larvae. The shield of the erichthus-type larvae described here is armed with numerous strong spines. Moreover, the telson edge is equipped with spines and denticles, and the tergopleurae of the pleomeres are postero-distally drawn out into spine-like extensions. When enrolled, the entire animal appears like a spiky ball. Thus, the interpretation of the enrolment as a defensive posture is highly plausible. Especially for morphotype 1, in which the enrolling is additionally secured by coaptative structures, enrolling is best understood as a defensive reaction to a direct threat.

The type of enrolling seen in morphotype 1 is similar to that of many trilobites and pill bugs: the head shield forms a kind of ‘lid’ (not to be confused with the basket and lid enrolment of Bergström, 1973), with structures ‘gripping around’ the rim of the posterior end, in this case the telson. This posture is termed ‘sphaeroidal enrolment’ in trilobite terminology. Pill millipedes actually enrol in a different way; in those animals, the head is folded inside, more comparable to the ‘double enrolment’ in trilobite terminology.

For morphotype 2, several different interpretations are possible, although they must remain more speculative. The spines on the shield, besides being defensive structures, additionally should enhance buoyancy (*e.g.*, Gurney, 1942). Thus, when enrolled the animal would not immediately sink, but float for some time. As the eyes, antennulae, and the large first pair of raptorial appendages can stick out even if enrolled in morphotype 2, we can speculate that this posture was not only used under direct threat. The animal could float in this posture and still wait for possible prey passing by. As mantis shrimp larvae are ambush predators, this posture should not affect their general predation strategies, but would provide immediate protection if being

attacked by other predators. Additionally, the posture would alter the silhouette of the mantis shrimp larvae; specifically, it would make it smaller. Examples of arthropods feeding in an enrolled position are agnostinids, at least some representatives, such as *Agnostus pisiformis*. Yet, *A. pisiformis* was not a predator but swept in food particles (Müller and Walossek, 1987; Bruton and Nakrem, 2005).

Based on taxonomic examples of arthropods which can perform enrolment, it appears to be a strategy that was extremely successful in the past, especially in the Palaeozoic, in marine arthropods. The fact that dominant groups such as trilobites heavily relied on this strategy demonstrates the value of it. Enrolment was also not restricted to benthic animals, but, as in the case of agnostinids, was also performed by pelagic or better planktic forms. The list of modern animals that perform enrolment should now include stomatopod larvae. Particularly interesting is that these organisms are more similar in the use of enrolment to some of the Palaeozoic forms than other modern forms. While pill bugs and pill millipedes are exclusively terrestrial (and therefore more comparable to benthic organisms), stomatopod larvae as marine planktonic animals occupy a completely different ecological niche. Stomatopod larvae thus provide an interesting functional model for understanding enrolment in fossil organisms. In most cases, we only know the dorsal parts of fossil arthropods that performed enrolling, though a notable exception is *A. pisiformis*. Interestingly, the arrangement of the appendages in the fully enrolled position in *A. pisiformis* and in stomatopod larvae of morphotype 1 appears very similar. This arrangement might therefore well be a general solution for the space restriction inside the enrolled body and can serve for reconstructing appendage ‘storing’ in other organisms such as trilobites.

Conclusions

A general conclusion of our study is that our knowledge of stomatopod larvae seems still very limited. Larval biology of mantis shrimps would thus appear to be a promising field of research. Summarising the discussion, our observations indicate the following:

- Enrolment is very likely performed actively by stomatopod larvae.
- This behaviour is most likely employed as a defensive one under a direct threat, but other strategies could be coupled to it.

- Enrolment was not only successful in the sea in the Paleozoic and is today only found in few terrestrial groups, but is still also found in modern marine animals.
- Museum specimens can be used to infer behavioural and autecological aspects for animals which cannot be directly observed.

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