Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda

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Abstract

We describe 54 fragmentary specimens from the Pliocene of North Carolina that represent isolated dactyli of mantis shrimps. These specimens are preserved uncompressed within three dimensions in calcium phosphate. The dactyli have an estimated maximum length of 15 millimeters and bear six spines. The specimens appear to be hollow and preserve fine details, especially a narrow crest on the dorsal side of the spines, a functional blade edge that has not been previously found on any fossil stomatopod. The specimens are provisionally attributed to the species *Squilla empusa*, found nowadays along the entire East coast of the United States of America. Fossil occurrences are known from the Pleistocene of Maryland and from the late Pleistocene or early Holocene of Connecticut. Though isolated dactyli are less informative on the taxonomic level, they can be important on the paleo-ecological level, positively demonstrating the presence of ambush predators in an investigated paleo-community. Given the scarce stomatopod fossil record and the exceptional three-dimensional preservation, the finding of these specimens, despite their fragmentary nature, is regarded as significant.

Keywords: *Squilla empusa*, three-dimensional preservation, imaging, phosphatized fossils, paleoecology, predators.

Resumen

Se describen 54 especímenes fragmentarios del Plioceno de Carolina del Norte, los cuales representan dactilos aislados de mantis marinas. Estos ejemplares se preservaron tridimensionalmenteen fosfato de calcio, sin compresión alguna. Los dactilos tienen una longitud máxima estimada de 15 milímetros y tienen seis espinas. Los especímenes parecen estar huecos y preservan detalles finos, especialmente una cresta estrecha en el lado dorsal de las espinas, que es una hoja afilada funcional no reportada previamente para ningún estomatópodo fósil. Los especímenes son provisionalmente asignados a la especie Squilla empusa, la cual se encuentra actualmente a lo largo de la costa Este de los Estados Unidos de América. Se conocen registros fósiles de esta especie del Pleistoceno de Maryland y del Pleistoceno u Holoceno temprano de Connecticut. Aunque los dáctilos aislados son poco significativos a nivel taxonómico, pueden ser importantes a nivel paleoecológico, puesto que demuestran la presencia de depredadores en una paleocomunidad en estudio. Dado el escaso registro fósil de estomatópodos y la excepcional preservación tridimensional, el hallazgo de estos especímenes, a pesar de su naturaleza fragmentaria, se considera significativo.

Palabras Clave: Squilla empusa, preservación tridimensional, manipulación de imágenes, fósiles fosfatizados, paleoecología, depredadores.

1. Introduction

Mantis shrimps, Stomatopoda (Latreille, 1816), are impressive representatives of the "higher crustaceans", Malacostraca (Latreille, 1802). Extant mantis shrimps are characterized by several morphological peculiarities that differentiate them from other malacostracans. Among these features are the highly specialized eyes (Kleinlogel and Marshall, 2006; Chiou *et al*., 2008) and, of course, the ferocious raptorial appendages (*e.g*., Patek *et al*., 2004). Other unique features are the possession of feathery gills on the pleopods (Boxshall and Jaume, 2009; Maas *et al*., 2009) and the structure of the tail fan (*e.g*., Schram, 1986).

While modern mantis shrimps are so different from other crustaceans, fossil representatives have provided insight into their evolutionary history, bridging these morphological differences (*e.g*., Schram, 2007; Haug J.T. *et al*., 2010). Fossil mantis shrimps are well known from the Carboniferous, Jurassic, Cretaceous, and Cenozoic (for a recent summary, see Schram, 2010). Most forms from pre-Cenozoic times represent offshoots of the evolutionary lineage towards the modern representatives of stomatopods, Verunipeltata Haug J.T., Haug, C., Maas, Kutschera, and Waloszek, 2010 (Haug J.T. *et al*., 2010). Very few representatives of Verunipeltata are present in the Cretaceous, yet all Cenozoic findings fall into this monophyletic group.

In general, the fossil record of stomatopods is considered to be scarce and fragmentary. Therefore, new findings provide additional information. We describe here isolated stomatopod dactyli from the Pliocene of North Carolina. We furthermore discuss how this finding will influence future search for fossil stomatopod material and which biological questions can be possibly addressed with the material presented here.

2. Material and Methods

2.1. Site location

The Upper Pliocene shell bed site that provided the background for this study is located at the Bladen County Landfill Annex site, Bladen County, south of Elizabethtown, North Carolina. The approximate coordinates for the site are 34° 36' 24.58" N, 78° 36' 35.56" W (Figure 1). The Pliocene layer at this locality overlies the Upper Cretaceous Bladen Formation (Campanian) pebble lag deposit (Figure 2). The Annex site has been claimed and is now closed until further notice.

2.2. Age of the shell beds at Elizabethtown, North Carolina

Carter *et al*. (1988) list three distinct Pliocene shell beds assigned to the Bear Bluff Formation overlying the
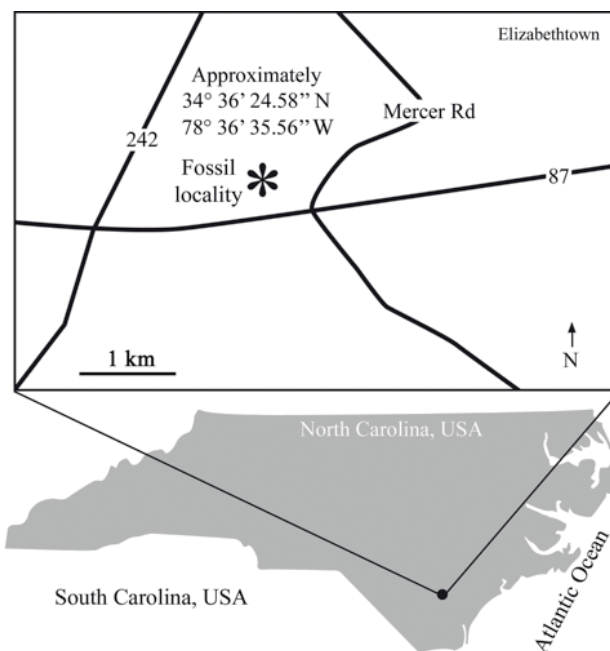

Figure 1. Generalized map of the fossil locality.

Campanian Black Creek (now Tar Heel) Formation at their Elizabethtown locality. Stratigraphic provenance of the stomatopod fossils is inferred to be from an aragonite leached section of Bed 1 of Carter *et al*. (1988) (lower unit in Figure 2). Ward and Gilinsky (1993) state that the well-preserved mollusk beds at Elizabethtown are the lateral shoreward equivalent of the leached calcarenites at Bear Bluff on the Waccamaw River near Conway South Carolina. Campbell and Campbell (1995) synonymize the Bear Bluff with the Upper Goose Creek Limestone. In that same publication, they place the age of the Elizabethtown mollusk beds as older than the Lower Waccamaw, but younger than the Duplin or between 2.7 and 2.9 Ma approximately. They also note the similarity of the fauna to the stratotype Chowan River Formation.

2.3. Collections and processing

Bulk sediment samples were collected from the Upper Pliocene Bear Bluff Formation (equivalent to Chowan River Formation) shell hash layer at the Elizabethtown Annex dumpsite. The majority of the samples were collected during the period of 1996-2001. The first stomatopod element, a raptorial dactylus, was recovered in 1996 with additional specimens recovered afterwards.

The sediments were first dried and gently fractionated through nested sieves of # 4 mesh (4.75 mm) down to # 35 mesh (0.500 mm) to remove smaller clay and sand particulates. The fractions were rinsed with copious amounts of water until the supernatant ran clear and the fractions were then dried. Further fractioning was not performed in order to reduce any undue breakage of the more delicate

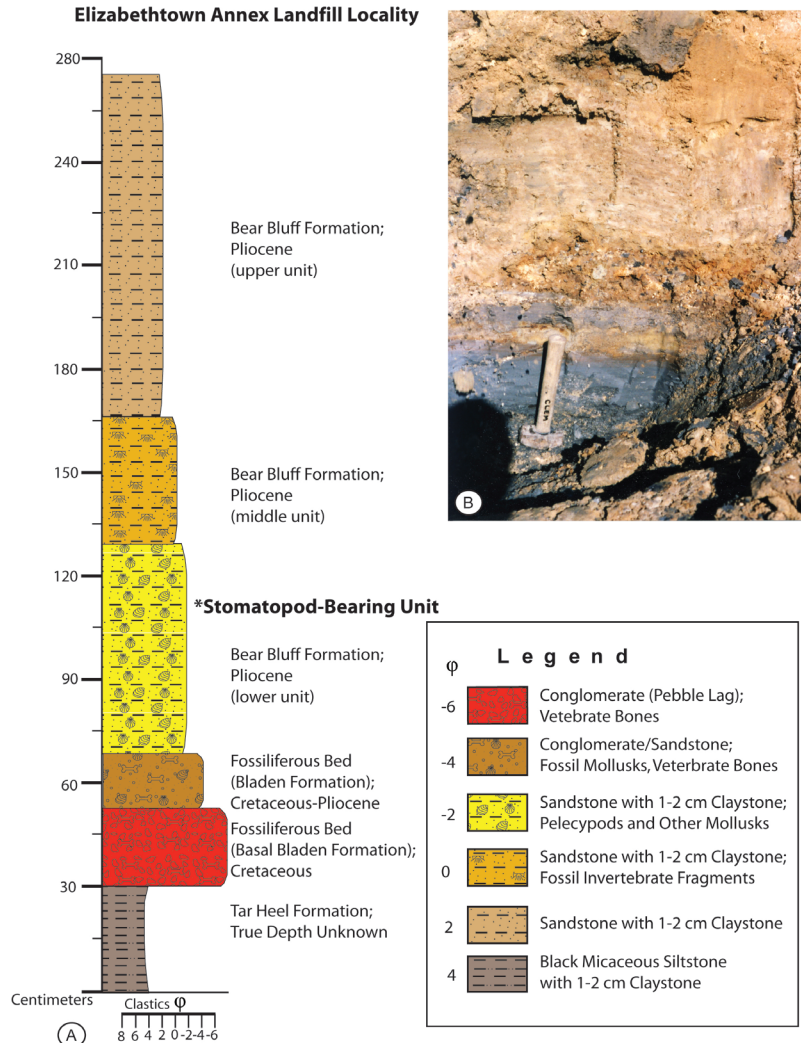**Elizabethtown Annex Landfill Locality**

Figure 2. The Elizabethtown (Bladen County) Annex Landfill Site Locality. A) Geologic profile. B) Excavation site.

fossils present.

Larger sediment fractions were scanned and specimens picked macroscopically. Sediment fractions of # 5 mesh (4.0 mm) and lower were scanned and picked with the aid of an American Optical Series Forty binocular microscope.

The stomatopod raptorial claws and fragments were found throughout all the Pliocene shell hash fractions. Since there is a definite bioturbated contact layer between the Pliocene shell hash bed and the underlying Cretaceous basal Bladen Formation (pebble lag) (Figure 2A), some of the claw fragments have the rust-colored, fine sand of the underlying Cretaceous layer embedded in the cavities of the dactyli fragments. Other dactyli fragments possess fine carbonate film and fine quartz sand matrix in some cavities as a result of deposition in the upper sections of the shell hash layer. Eventhough the fractioning process may have caused breakage of the stomatopod elements, there was no real evidence of fresh breakage during the scanning process.

Notation of the more numerous smaller mollusks found during the above mentioned fractionation process can

serve as a horizon marker. The more prominent gastropods found were a large number of *Prunum limatulum* (Conrad, 1834) and *Turbonilla* sp. (Risso, 1826). Bivalves include *Crassatella* sp. (Lamarck, 1799) and abundant fragments of *Raeta* sp. cf. *undulata* (Gould, 1851) throughout the entire shell hash layer (see Ward and Gilinsky, 1993).

Some of the more outstanding Pliocene fish elements found in the shell hash layer include a high number of well-preserved otoliths along with well-preserved tiny teeth. These otoliths exhibit characteristics associated with Scianenidae (*e.g.*, *Sciaenops* sp. Gill, 1863, *Cynoscion* sp. Gill, 1861, *Equetus* sp. Rafinesque, 1815, and/ or *Micropogonias* sp. Bonaparte, 1831; see Fitch and Lavenberg, 1983).

2.4. Documentation

All specimens were documented on a Leica DM 2500 P compound microscope, with a 2.5x pol objective and a Scopetek DCM 510 ocular camera, resulting in an effective

magnification of 25 times. Due to the limited depth of field, image stacks (50 micron z-distance) were recorded and later fused with the freely available program CombineZP. Due to the limited field of view and the larger size of some of the specimens, these were recorded with several stacks. The fused images were then stitched with the photomerge function of Adobe Photoshop CS3. The resulting image is a composite image *sensu* Haug C. *et al.* (2009a).

As the surface of the specimens is highly reflective, all images were recorded under crossed polarized light (Schaarschmidt, 1973; Bengtson S., 2000; Haug C. *et al.*, 2011; Haug J.T. *et al.*, 2011; Kerp and Bomfleur, 2011). The light was provided by four independent fiber light sources in an evenly arranged pattern.

Some specimens have a very wide range of brightness, from very dark brown to bright white areas. Although polarized light partly equalizes such differences, the brightness range of the camera could not document these specimens satisfactorily with a single exposure setting. Therefore, these specimens were documented in two steps. First, they were documented with a "normal" exposure time, which left the darker areas almost invisible, but provided structural details for the bright areas. In a second step, the same image detail was overexposed, which left the bright areas without information, but provided the details of the dark areas. The overexposed image was placed as a separate layer on top of the normally exposed image in Adobe Photoshop CS3. The white (uninformative) areas of the top layer were marked with the magic wand tool; the selection was assigned a feather and cut out. In this way, the brighter areas with structural details of the underlying layer became visible. The final image combines surface information for both very bright and very dark areas, resulting in a fully informative image. This procedure roughly equals an HDR-treatment.

Large specimens were documented from three directions, from both lateral sides and from the adorned side (Figures 3A-D, 4A-H, 4J-N). Smaller specimens were documented from two directions (Figures 4I, 5). Specimens representing broken off spines or smaller pieces of the dactylus were documented from the two lateral views. Broken pieces of the main dactylus body were documented from the outer and inner side. For better comparison, all specimens were depicted in the same scale (Figures 3-5). Additionally, details of the "cutting" edges of the spines and preservational peculiarities were documented as detailed views (Figure 6).

One specimen was analyzed with X-ray-fluorescence with a Bruker Tracer 3V+, which measures the elemental composition of a specimen. The same specimen was documented under optical macro-fluorescence settings, with a cyan filter in front of the light sources and a red filter in front of the camera (Canon Rebel T3i; for details see Haug J.T. and Haug C., 2011; Haug J.T. *et al.*, 2011). To restrict the information of the image to the light emitted due to autofluorescence of the specimen, the remaining green light that was not absorbed entirely by the filters

was artificially removed by reducing the green saturation in Adobe Photoshop CS3 (Figure 3E).

The four largest and most complete specimens were additionally documented as stereo images (Haug C. *et al.*, 2009a, 2011), also in three directions (Figure 7). As the natural color of the specimens interferes with the red channel, a disturbing flickering is perceived when observing red-cyan stereo images produced from the original color images, which dampens the depth effect of the images. Therefore, the images were reduced to gray scale before assembling the red-cyan stereo images.

3. Results

Fifty-four fragmentary specimens identified as parts of stomatopod dactyli have been investigated (Accession number NCSM 12837, specimens NCSM 11642 to 11675, 11677 to 11686 and 11689 to 11698). Specimens are deposited at the North Carolina Museum of Natural Sciences, Raleigh, NC. Due to the presence of spines, specimens are identified as dactyli parts of the large pair of raptorial appendages, as the three succeeding pairs of smaller raptorial appendages lack such spines in any stomatopod species. Four of the 54 specimens are rather complete (Figure 3). The dactyli have an estimated maximum length of up to 15 mm and carry six spines. Two of these specimens represent the dactylus of the right appendage and two represent the left appendage.

Fourteen specimens are identified as a central part of a dactylus, ranging from larger pieces to smaller fragments, in which only two insertions of the spines are recognizable (Figure 4). Of these specimens, five can be identified as parts of dactyli of the right appendage, three as parts of dactyli of the left appendage; six cannot be attributed to the left or the right appendage.

Thirty-six more specimens that are fragmentary represent isolated spines or cuticle parts of the main part of the dactylus (Figure 5). Due to the fragmentary nature of these specimens, they cannot be attributed to a particular body side.

An observed surface detail that represents the original morphology is a narrow crest on the functionally dorsal side of the spines of the dactyli (Figure 6A, B). This structure can be found on all four well-preserved specimens, but also on some of the isolated spines (*e.g.*, Figure 5B, D), which supports the hypothesis of the isolated spines and the better-preserved dactyli as being conspecific.

Another surface detail observable on many specimens is a pattern of grooves running in smooth spirals (Figure 6C, D). This pattern is present in many of the isolated spines (specimens in Figure 5H, I, M–P, R–U). Such pattern has no equivalent in any other stomatopod known, fossil or extant, and is here considered because of the quality of preservation found at the study site.

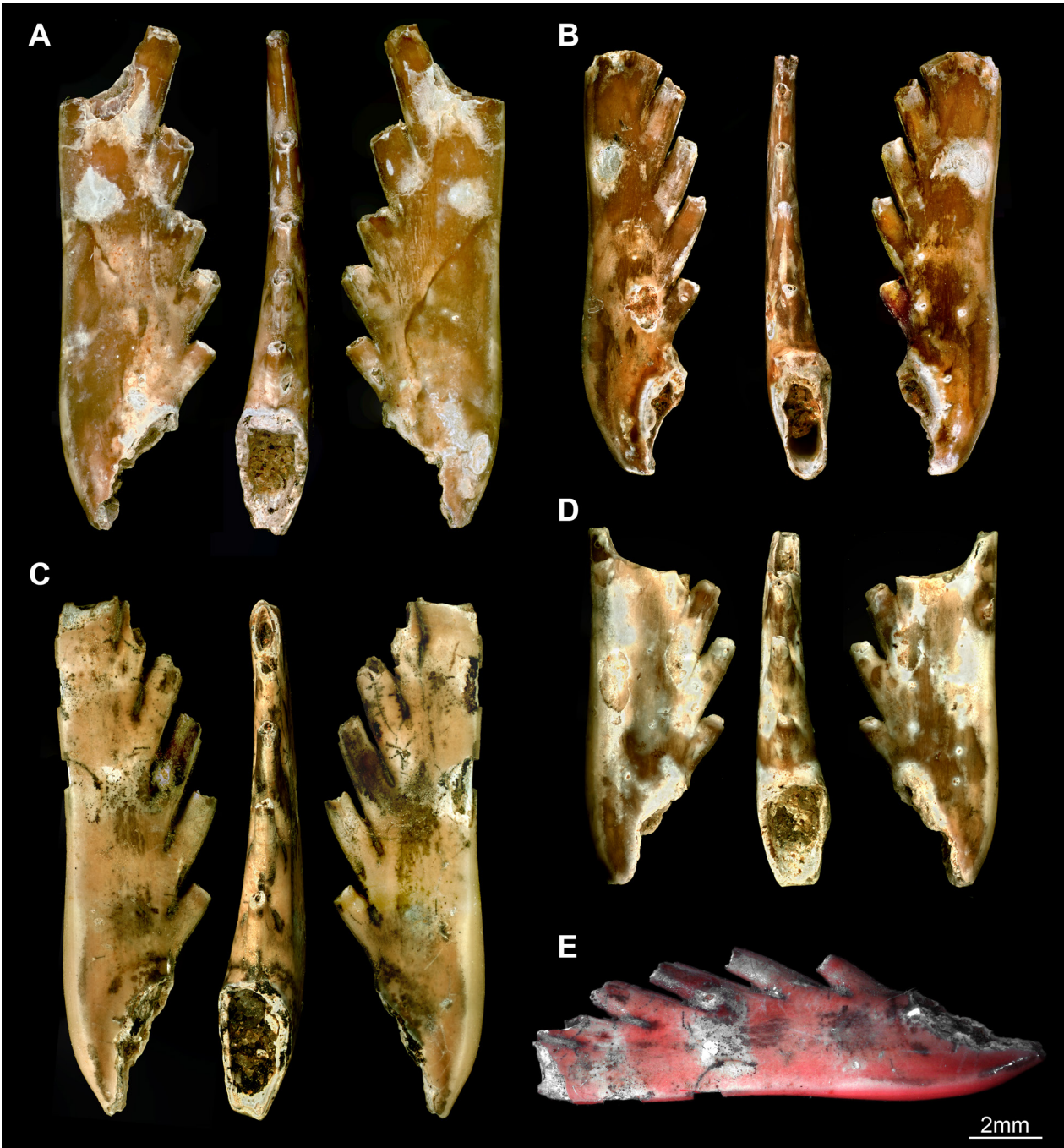With the length of the more complete dactyli as

Figure 3. Most complete dactyli of the material examined. A–D) Specimens under polarized light, documented from both lateral sides and the functionally dorsal, adorned side (NCSM 11642 – 11645). E) Same specimen as in C under macro-fluorescence settings; pink areas indicate the presence of calcium phosphate.

reference, the estimated body size of the entire animal is calculated to 100–120 mm roughly, based upon our own unpublished comparative measurements of complete extant squillids (see discussion below for supposed systematic affinities). The dactyli represent a certain size range, yet not a very pronounced one. Due to the small variation, we assume that the size of the dactyli represents the final adult size, given that the estimated body size corresponds to that of the adult stage.

The composition material measured on the largest dactylus (Figure 3C, E) seems to be calcium phosphate, according to the X-ray fluorescence analysis. The presence of relatively strong autofluorescence detected with optical macro-fluorescence settings supports the presence of calcium phosphate (Figure 3E) (Haug C. *et al.*, 2009a; Haug J.T. and Haug C., 2011; Haug J.T. *et al.*, 2011).
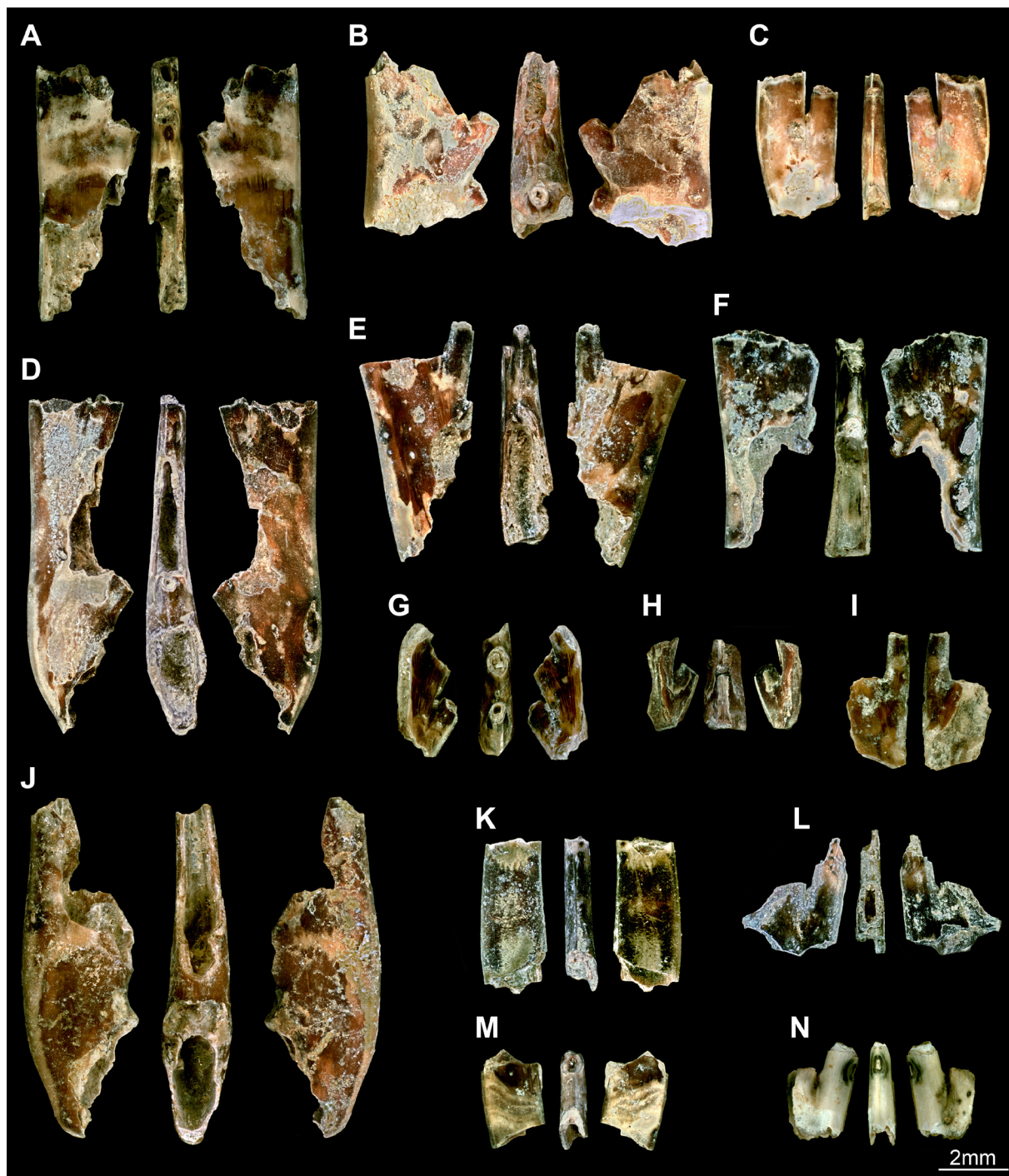
Figure 4. Central parts of dactyli. A–H, J–N) Specimens (NCSM 11646 – 11653, 11655 – 11659) documented from three sides as in Figure 3. I) Smaller specimen documented from two sides (NCSM 11654).

4. Discussion

4.1. Systematic affinities

Due to the fragmentary nature of the specimens, it is difficult to attribute the described dactyli to a particular species. We therefore compare the dactyli to those of stomatopods that live on the coast of North Carolina today.

Neogonodactylus bredini (Manning, 1969), *N. oerstedii* (Hansen, 1895), and *N. torus* (Manning, 1969) are boxer-type stomatopods, thus they do not possess spine-bearing dactyli and cannot be the species represented in the here-described material (Schwartz and Porter, 1977; Morgan and Goy, 1987; Müller, 1994). *Coronis scolopendra*
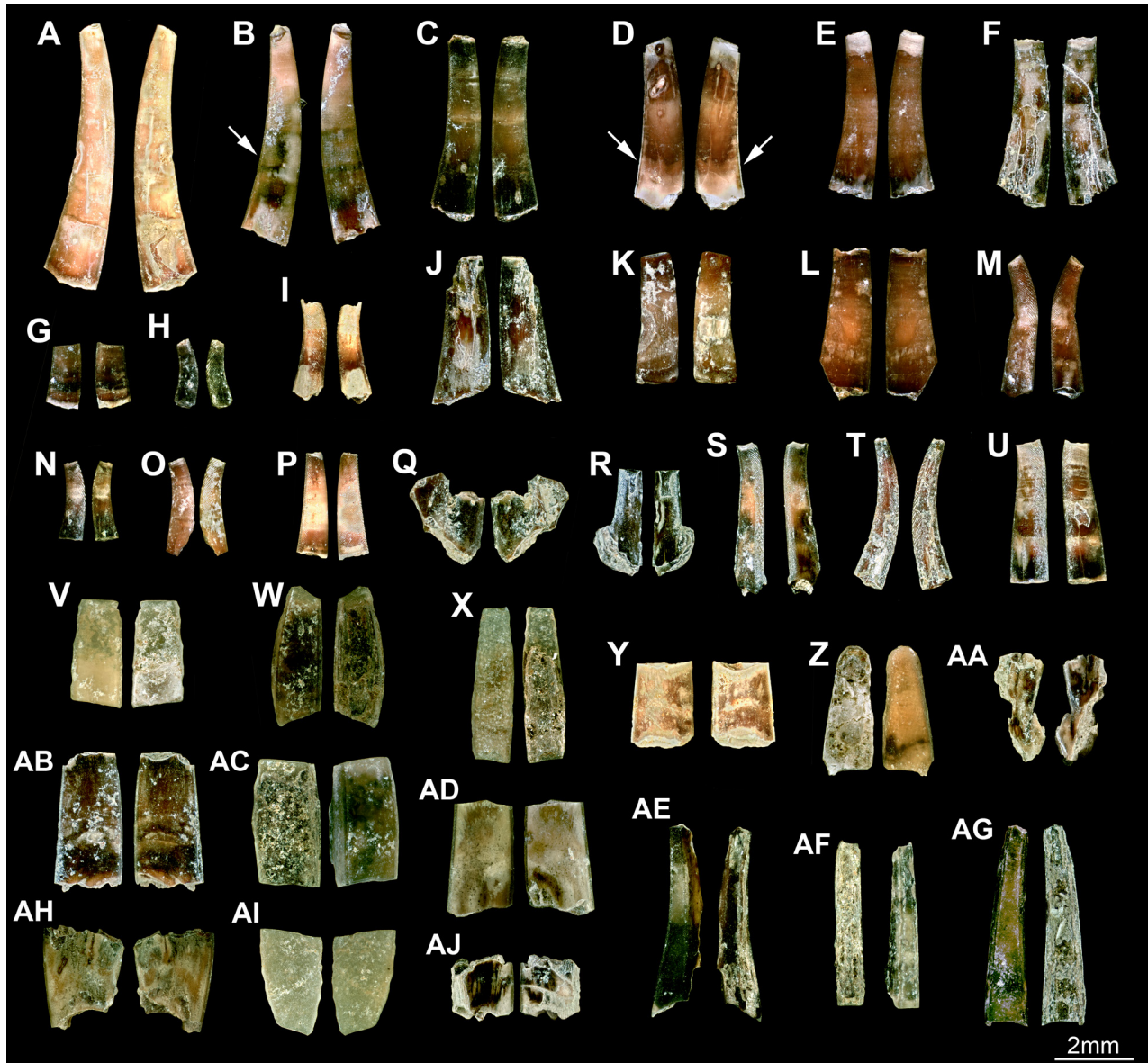
Figure 5. Isolated spines or cuticle parts of the main part of the dactyli (NCSM 11660 – 11675, 11677 – 11686, NCSM 11689 – 11698). Note the narrow crest on the functional dorsal side in some of the specimens, *e.g.*, in B and D (arrows) and the pattern of grooves running in smooth spirals in H, I, M–P, R–U; compare with Figure 6.
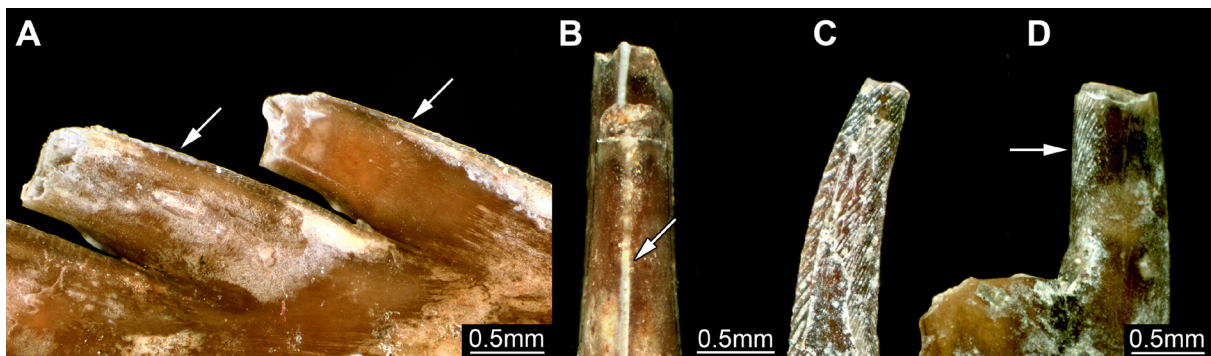

Figure 6. Details of the most complete dactyli. A–B). Narrow crest on the functionally dorsal side of the spines of the dactyli (arrows). A) Lateral view, same specimen as in Figure 3B (NCSM 11643). B) Functional dorsal view, same specimen as in Figure 4C (NCSM 11648). C–D) Pattern of grooves on the sides of the dactyli, probably of preservational origin. C) Pattern on complete specimen, same as in Figure 5T (NCSM 11680). D) Pattern near arrow, same specimen as in Figure 4I (NCSM 11654).
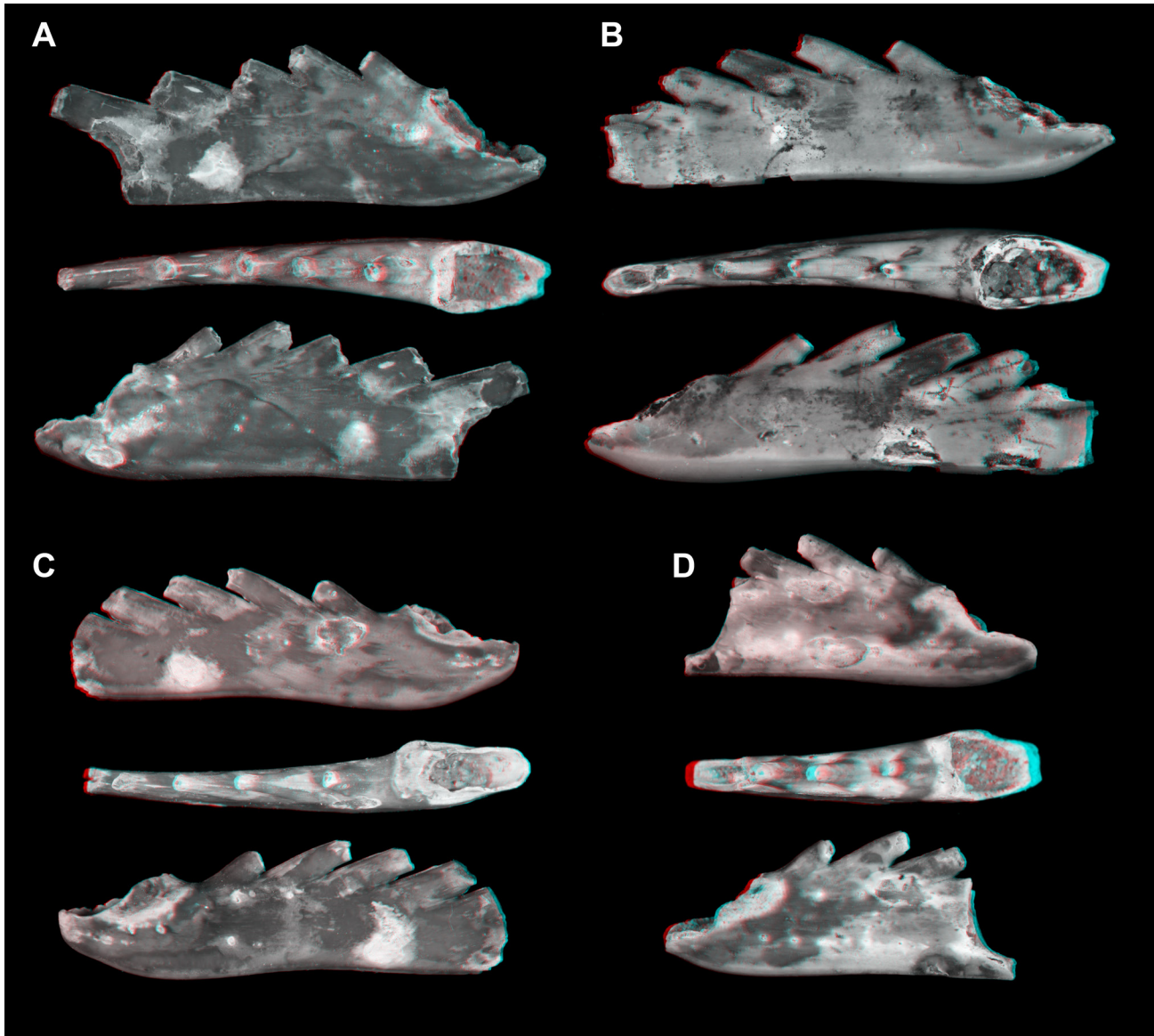
Figure 7. Stereo images of the most complete dactyli in three directions (like in Figure 3, same specimens); use red-cyan stereo glasses to view.

Latreille, 1828, *Nannosquilla carolinensis* (Manning, 1970), *Platysquilloides enodis* (Manning, 1962), and *Squilla deceptrix* (Manning, 1969) all do not exceed 70 mm in total length (Manning, 1970; Schram, 2010). The herein described dactyli are therefore too large to belong to representatives of these species.

Gibbesia neglecta (Gibbes, 1850) and *Meiosquilla quadridens* (Bigelow, 1893) both reach a size between 100-110 mm, thus correspond in size to the estimated body size for the animals bearing the dactyli described herein. Yet, in these species the dactyli bear five and four spines respectively (Werding and Müller, 1990; Foster *et al*., 2004), whereas the dactyli described herein always possess six spines.

Squilla empusa (Say, 1818) reaches larger body size up to 185 mm (Schram, 2010). Additionally, *S. empusa* is

known not only from extant forms, but the record reaches back into the Pleistocene of Maryland (Blake, 1953; trace fossils) and the late Pleistocene or early Holocene of Connecticut (Waage *et al*., 2001). The specimens described herein are relatively small, but still fit into the size range of *S. empusa* and closely resemble a fairly completely preserved dactylus in the material of Waage *et al*. (2001, their fig. 4C). An affinity based on the available characters cannot directly be shown. Yet, there is no character excluding an assumed affinity of the specimens described herein to *S. empusa*, which is also true for the size, and the Pleistocene–Holocene occurrences also bridge the time gap between the Pliocene material and the extant fauna. Until further evidence, the specimens should therefore be assigned to *Squilla*? *empusa*? (following the open nomenclature of Bengtson, 1988).

4.2. Scarcity of stomatopod fossil record

The fossil record of Stomatopoda begins in the Carboniferous (Schram, 2007 and references therein). A single fragmentary specimen from the Silurian was interpreted by Wetzel (1973) as a possible part of a stomatopod telson. Attempts at locating the specimen have not yet been successful; however, based upon the image published it is doubtful that the specimen has a stomatopod affinity. In the Carboniferous numerous sites have yielded stomatopod fossils, *e.g.*, the deposits of Mazon Creek and Bear Gulch, both North America, Hagen-Vorhalle in Germany, East Kilbride in Scotland, and Argenteau in Belgium. Fourteen species are currently recognized from this period, representing various evolutionary levels (*e.g.*, Peach, 1908; van Straelen, 1922; Schöllmann, 2004; Schram, 2007, 2010; Haug J.T. *et al.*, 2010).

There is no report of stomatopod fossils in the Permian and Triassic to date. Stomatopods have been found in the Lower Jurassic fossil in Osteno, Italy (Hof, 1998a) and they are currently under study by Italian and Australian researchers (Ahyong, pers. comm.). From the Upper Jurassic, four species have been described from lithographic limestones of southern Germany and a new species is yet to be named (summaries in Haug J.T. *et al.*, 2008, 2010; Haug C. *et al.*, 2009b). However, the taxonomic status of some of the species is currently under debate and it is most likely that some of these species will be synonymized (Haug J.T. *et al.*, 2010).

In the Cretaceous, fossil stomatopods have been found in Lebanon (three species; Dames, 1886; Ahyong *et al.*, 2007; Haug J.T. *et al.*, 2010), USA (one species; Franţescu, 2012), Mexico (one possible, but not yet named species; Vega *et al.*, 2007) and Colombia (one possible, but still to be named species; Feldmann *et al.*, 1999). Furthermore, two verunipeltatan species are known from the Cretaceous of Colombia (Schram, 1968) and Nigeria (Förster, 1982). Five fossil specimens representing stomatopod tail ends from Israel and Jordan have been attributed to another ingroup species of Verunipelta, *Ursquilla yehoachi* (Remy and Avnimelech, 1955) (Hof, 1998b; Haug C. *et al.*, 2013). *Squilla cretacea* (Schlüter, 1868) could not be successfully tracked yet, and its stratigraphic attribution has been considered as doubtful (Schram, 2010).

All Cenozoic occurrences appear to represent verunipeltatan species as well. No stomatopods have been found from the Palaeocene. From the Eocene to the Pleistocene, 30 species are known (five of them not yet formally described), with peaks in the Eocene and Miocene (although marine strata from the Oligocene are generally rare). Three of these species have survived until today (Schram, 2010). Deposits in northern Italy, mainly the famous lagerstätte Monte Bolca and the nearby Monte Postale, have yielded several stomatopod species (Secretan, 1975; Angeli and Beschin, 2006; Angeli and Garassino, 2008).

Given the relative incompleteness of the stomatopod fossil record, the finding of the here described isolated dactyli not only marks an additional occurrence, but it also gives the perspective that many stomatopod fossils could be represented by fragments, especially dactyli including by other parts, *e.g.*, the telson (cf. *Ursquilla yehoachi*). Many fragments like the dactyli described will most likely not be identified to genus or even species level, yet they can still provide a source of data for answering different scientific questions.

4.3. Impact on reconstructing the paleoenvironment

Stomatopods represent important predators within their ecotope. Predators of this ecotype have been identified indirectly as trace fossils, back to Cambrian strata (Pratt, 1998). Yet, such an indirect finding often remains ambiguous. Finding isolated dactyli provides positive evidence that such predators were present in the paleoecosystem, *i.e.*, a representative of the guild "ambush predator" was present. Additionally, it is difficult to estimate the population size from trace fossils such as hitting marks. Although it is also challenging to make such estimations based on fragmentary material, the amount of fragments found in North Carolina indicates that there was possibly a large population of mantis shrimps back in the Pliocene. Nevertheless, it must be considered that part of the material might stem from molts, which would distort the estimation of the population size.

As explained above, the number of stomatopod species is rather low in the fossil record, and individual fossils are relatively rare. Certain Carboniferous, Jurassic or Eocene species are known from numerous specimens (*e.g.*, Secretan, 1975; Jenner *et al.*, 1998; Angeli and Garassino, 2008; Haug J.T. *et al.*, 2010), but other fossil stomatopods are only known from very few individuals (Hof, 1998b; Haug C. *et al.*, 2009b, 2013) or in some cases from a single one (Ahyong *et al.*, 2007; Schram, 2007).

Fragmentary specimens, which could have been overlooked, can add significantly more specimens and provide additional information for estimating population sizes. The potential for drawing scientific conclusions from isolated dactyli of decapod crustaceans has been proposed by Agnew (2008). Larger sample sizes could be used in a similar fashion with stomatopods. Despite of being important predators, stomatopods are also an attractive food source for larger predators (see Grimes, 1979 for an extant example). Regarding the Pliocene fish species found in the shell hash bed, evidenced by the presence of otoliths, the juveniles may well have been a food source for the larger spearer stomatopods at that time. In addition, the larger fishes could have used the juvenile stomatopods as a food source, thus contributing to the high degree of element fragmentation. As many paleo-food webs are not necessarily based on distinct species but more on ecotypes or guilds,

the simple presence of these predators as indicated by such fragmentary specimens represents an important data point for such a kind of analysis.

The scarcity of the stomatopod fossil record has hampered a paleo-biogeographical approach, *i.e.*, revealing possible connections between specific paleo-biotas. The presence of the dactyli described herein, that possibly belong to *Squilla empusa*, could imply that its modern distribution along the East coast of the United States of America was already established back in the Pliocene. Yet, the scarcity and fragmentary nature of both the fossils and the fossil record of mantis shrimps in general should lead to conclusions that are more cautious. The species affinity of the presented material to *S. empusa* is only likely, but not definitive. Even if this statement should be accepted, it could also be explained by a migration northwards from the Pliocene in North Carolina over the Pleistocene in Maryland on to the late Pleistocene or early Holocene in Connecticut, followed by a rather recent distribution along the entire coast. More material is needed before such conclusions can be drawn; yet, the presented material definitely yields potential for such approaches.

4.4. Preservation

Being preserved in calcium phosphate and representing a three-dimensional hollow replicate of the non-calcified cuticle, the here described specimens could be characterized as being preserved in an "Orsten"-*sensu-lato*-type preservation (Maas *et al.*, 2006), which especially favors cuticle-bearing, unmineralized animals, and is restricted to a maximum size of *ca*. 2 mm; however, the dacytli are significantly larger. Further insight is needed on whether other minerals besides calcium phosphate can be found in the specimens that facilitated the preservation in this size range. The usual question, regarding to calcium phosphatic preservation, is where the phosphate was originated. One possibility is that another decaying organism could have provided this material (Bate, 1972; Weitschat, 1983). In this case, perhaps the body of the stomatopod could have provided the phosphate to preserve just a tiny part of itself. More details on the paleoenvironment could provide further insight on this mode of preservation.

Other stomatopod fossils are also preserved in calcium phosphate, *e.g.*, the specimens from the Upper Jurassic lithographic limestones of southern Germany (Solnhofen, Nusplingen). These fossils can also preserve their three-dimensionality to a certain degree (Haug J.T. *et al.*, 2010), but are usually affected by compaction (one notable exception of a decapod in Haug *et al.*, 2009a, their figures 4.6–4.8).

The isolated dactyli therefore represent an exceptional example from a preservational point of view, being relatively large, but with high detail and three-dimensionally preserved in "Orsten"-*sensu-lato*- preservation. This special preservation may be partly coupled to the comparably young age of the dactyli. Other specimens in "Orsten"-*sensu-lato*-preservation found in the Cenozoic, have been described from Australia, with preserved insects, *i.e.*, terrestrial fauna (Duncan *et al.*, 1998).

The preservation of the specimens described herein may not appear extraordinarily spectacular due to the fragmentary nature of the specimens. Yet, this is the first example in which the narrow crest on the functionally dorsal side of the spines is preserved on a fossil stomatopod. This crest acts mechanically as a knife-edge. The finding of this structure on the specimens presented herein emphasizes the exceptional preservation of these specimens.

5. Conclusions and outlook

The exceptionally preserved specimens of isolated stomatopod dactyli indicate that the fragmentary fossil record of stomatopods could be significantly amended with the search and description of additional fossil dactyli. Although such specimens do not allow exact taxonomic treatments, this kind of findings could be an important and underestimated data source for paleoenvironmental and paleobiogeographical studies.

Acknowledgments

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