Shell disease in 100 million-year-old crabs

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ABSTRACT: Modern organisms exhibit evidence of many diseases, but recognizing such evidence in fossils remains difficult, thus hampering the study of the evolution of disease. We report on 2 molts of the goniodromitid crabs Distefania incerta and Goniodromites laevis from the mid-Cretaceous (late Albian) of Spain, with both species exhibiting damage to the dorsal carapace in otherwise well-preserved specimens. The subcircular to quadratical holes, found in <0.2% of the specimens, resemble damage caused by bacterial infections on the cuticle of modern decapods in terms of size and shape. Abiotic damage, predation, and encrustation followed by damage to the shell provide less satisfactory explanations, although these agents cannot be completely excluded from a role in shell disease etiology. We hypothesize that the observed fossil lesions are caused primarily by bacterial disease that started prior to molting, with or without other agents of initiation. If correct, this is the only known example of such bacterial infections in decapod crustaceans from the fossil record thus far, pushing back the evolutionary history of this type of shell disease by ~100 million years.

KEY WORDS: Bacteria · Cretaceous · Crustacea · Decapoda · Disease · Fossil · Infection · Lesion

INTRODUCTION

Shell disease in Crustacea is a complex syndrome, which includes several independent and apparently unrelated infections. It is characterized by various levels of damage to the crustacean integument from a singular pitting to an extensive loss of the integument (Smolowitz et al. 1992, Shields & Overstreet 2007), sometimes resulting in exposure of the underlying soft tissue (e.g. Comeau & Benhalima 2009). Shell disease has been studied extensively in economically important crustacean species such as the American lobster Homarus americanus H. Milne-Edwards, 1837 (reviewed by Cobb & Castro 2006 and Gomez-Chiarri & Cobb 2012) and the European edible crab Cancer pagurus Linnaeus, 1758 (Vogan et al. 2001, 2002, Vogan & Rowley 2002, Costa-Ramos & Rowley 2004), as well as, to a lesser extent, in the blue crab Callinectes sapidus Rathbun, 1896 (Noga et al. 1998, 2000). Microbial pathogens involved in shell disease are universally accepted to be chitinolytic bacteria (Shields & Overstreet 2007, Vogan et al. 2008, Gomez-Chiarri & Cobb 2012), although cases of fungally induced shell disease have been described for freshwater crustaceans, and true fungi and oomycetes are on occasion observed in lesions of marine crustaceans (e.g. Noga et al. 2000, Quinn et al. 2009).

At least 3 different forms of shell disease have been described in wild populations of the American lobster (epizootic, endemic, and ‘cigarette-burn’ shell disease; Cobb & Castro 2006). In addition, 2 forms of shell disease, impoundment (Hess 1937) and diet-induced shell disease (Tlusty et al. 2008), are known for the American lobster when kept in captivity. Unlike lobsters, crabs commonly develop shell disease on their ventral surfaces, and lesions appear to be shallow and

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diffuse (Shields & Overstreet 2007). Scraping of the sediment surface appears to be the most likely inoculating cause for this type of lesion. However, the manifestation of shell disease in crabs, when the lesions develop on the extremities or carapace, is sometimes very similar in appearance to endemic and/or ‘cigarette-burn’ disease in lobsters: lesions appear as scooped material in singular or multiple pits (Figs. 1 & 2).

Fig. 1. Modern brachyuran crabs from the Gulf of Mexico and Atlantic coast of Florida (USA) exhibiting varied examples of cuticular lesions and shell disease (black spots in A,B,D,E,F and white encircled area in C). (A) Paractaea nodosa (Stimpson, 1860), female, carapace width (cw) 11.4 mm, dorsal surface, archived in the University of Louisiana at Lafayette Zoological Collection (ULLZ 6760). (B) Chaceon quinquedens (Smith, 1879), female, cw 27.9 mm, ventral right surface (ULLZ 14055). (C) Callinectes ornatus Ordway, 1863, female, cw 31.0 mm, dorsal surface (ULLZ 9664). (D) Micropanope sculptipes Stimpson, 1871, male, cw 7.8 mm, dorsal surface (ULLZ 3655). (E) Euphrosynoplax clausa Guinot, 1969, female, cw 18.7 mm (ULLZ 14473). (F) Micropanope lobifrons A. Milne-Edwards, 1881, female, cw 6.9 mm (ULLZ 10935).
The environmental triggers of shell disease in crustaceans are not well known, but there may be multiple causes. In epizootic shell disease, 2 specific pathogens are suspected (Chistoserdov et al. 2012), and infection appears to be triggered by a higher than usual temperature (Quinn et al. 2012a, Tlusty & Metzler 2012). Similar pathogens are observed in lesions produced by impoundment and endemic shell disease, but not in cases of diet-induced shell disease (Chistoserdov et al. 2012, Quinn et al. 2012b). Remarkably, integument lesions of crabs only occasionally harbor the 2 lobster pathogens, but *Vibrio* and *Pseudoalteromonas* spp. appear to be ubiquitous (Getchell 1989, Vogan et al. 2002, Shields & Overstreet 2007). The role of metal contamination has been shown to usually be a minor factor for the development of shell disease in wild populations of crustaceans (Weinstein et al. 1992). The presence of environmental pollutants correlates with shell disease in some cases (Ziskowski et al. 1996, but see Powell & Rowley 2005). It is usually assumed, however, that a physical trauma may cause shell disease in crustaceans, although there is little field and experimental evidence for this assumption (Comeau & Benhalima 2009, Quinn et al. 2013). Apart from obvious teeth marks and scratches left by potential predators and those resulting from territorial/sexual behavior, breaking off of ectosymbionts, specifically barnacles, also cannot be ruled out. The latter particularly applies to singular, almost circular lesions sometimes found on crabs.

Bacteria and decapod crustaceans have co-existed in the biosphere for at least ~160 million years (Robin et al. 2015a,b). Despite extensive fossil collections of crustaceans, shell abnormalities with a biotic origin have not often been reported for fossil crabs, partly because they are not easily recognized in the fossil record and because they do not preserve well. The best known examples of shell abnormalities in fossil decapods in terms of stratigraphic coverage, numbers of specimens, and numbers of species infected are those evident as swellings caused by isopods in the metabranchial regions of fossil decapods, referred to as the trace fossil *Kanthyloma crusta* Klompmaker et al., 2014. They are known from the Jurassic onwards and are encountered in many different fossil decapod taxa (Wienberg Rasmussen et al. 2008, Klompmaker et al. 2014b, Klompmaker & Boxshall 2015). Here, we report on 2 mid-Cretaceous crabs from northern Spain with damage on the molted carapace that we hypothesize to be shell disease caused by bacterial lesions. To our knowledge, this is the first report of such disease in fossil decapods.
MATERIALS AND METHODS

The 2 fossil brachyuran crabs were found in the Koskobilo quarry, Spain (42.8823° N, 2.1990° W, WGS84) in the Albeniz Unit of the Eguino Formation, which is interpreted to be late Albian (~100 million years ago) in age (Klompmaker 2013). The carbonate rocks, in which numerous colonial and solitary corals and algae are the main reef builders, yielded a highly diverse decapod crustacean assemblage (Fraaije et al. 2009, 2012, 2013, Klompmaker et al. 2011a,b,c, 2012a,b, 2013a, Klompmaker 2013) consisting of 38 species based on ~1100 specimens. The 2 crab specimens were found in the southwestern corner of the Koskobilo quarry by breaking the limestones into approximately equal pieces. These specimens are deposited at Oertijdmuseum De Groene Poort, Boxtel, The Netherlands (specimen numbers preceded by the designation MAB k). Comparisons were made to external integuments of modern decapods photographed from the northern Gulf of Mexico and the Atlantic coast of Florida, USA, and archived in the University of Louisiana at Lafayette Zoological Collection (ULLZ). Comparison was also made to a photographed carcinid crab from Rhode Island Sound, RI, USA.

RESULTS

The 2 crab specimens are interpreted to represent nearly pristine molts of *Distefania incerta* (Bell, 1863) and *Goniodromites laevis* (Van Straelen, 1940) (Fig. 3), both from the Goniodromitidae family. Both carapace specimens are internal molds because no cuticle was observed. However, the general outline, groove pattern, tubercles, and lateral projections are remarkably well-preserved in general. Both specimens show a part where the cuticle was absent (i.e. the imprint of cuticle is missing and relatively structureless rocks remain). No evidence for regeneration is found around this damage. The damage in *D. incerta* is subcircular to subquadratical in outline without sharp edges located at the central-left por-
tion of the carapace (Fig. 3A–C). Its maximum width is 3.3 mm, the maximum length is 3.2 mm, and the area is ~8.0 mm². Although the very rim of the hole (~0.1 mm) was not fully prepared to avoid damage to the carapace, the damage in *G. laevis* is subcircular in outline and contains no sharp edges (Fig. 3D–G). It is located in the right branchial region of the carapace. Measurements include: maximum width = 1.7 mm, maximum length = 1.9 mm; area ~2.5 mm². Such damage was rare among complete and partially broken decapod carapaces from this locality (2 out of ~1100 specimens, or <0.2%).

**DISCUSSION**

**Molts or corpse remains?**

Crab molts are split along the pleural suture, whereas corpses are separated from the rest of the exoskeleton with the pleural suture intact (Schäfer 1951, Bishop 1972, 1986). When scavengers or predators consume a crab, the carapace may look different depending on the handling method of the scavenger or predator. Unequivocal evidence that a carapace is a molt is presented when the pterygostomial region is still attached to the rest of the exoskeleton and is associated with a carapace of the same specimen (Bishop 1972). Such evidence of molting caught in the act is very rare, however (e.g. Glaessner 1969, Bishop 1981). The present specimens are preserved without the pterygostomial regions resembling molts. Theoretically, it is possible that the 2 fossil specimens herein are corpses if 2 conditions are met: (1) the carapace needs to be disarticulated from the rest of the exoskeleton and transported away from the rest of the corpse, and (2) the pterygostomial region on both sides of the carapace needs to be split along the pleural sutures and transported away from the rest of the carapace. Also from a statistical standpoint, it may be more likely that the specimens represent molts rather than corpses because an individual produces multiple molts but only a single corpse. Thus, we render the hypothesis that the 2 specimens represent molts more likely.

**Shell damage**

The shell damage in the 2 crab fossil may have been caused by a variety of factors: (1) abiotic damage after molting, (2) predation, and (3) non-predatory biological damage, including shell disease.

**Abiotic damage**

Rolling along the sea bottom, abrasion, and reworking may cause damage to carapace molts (post-mortem). This is interpreted to be unlikely in the present case because the molts show nearly pristine dorsal ornamentation and lateral projections, both of which would be expected to be damaged substantially prior to erosion of isolated cavities in the carapace. This pristine preservation other than the holes also argues against damage as the molt ages and weakens. Breakage caused by sediment loading is unlikely because shell pieces have not been found in association with these molts.

**Predation**

Although predatory damage, for example by either crabs or stomatopods, may produce similar breakage, such damage usually is more angular, as shown in various fossil invertebrates (e.g. Robba & Ostinelli 1975, Feldmann & May 1991, Geary et al. 1991, Pether 1995, Baluk & Randwański 1996, Faye 1996, Randwański 1996, Keupp 2006). Unlike brachyurans, stomatopods are not known from Koskobilo thus far (i.e. absent in Klompmaker et al. 2013a). Predation by gastropods and octopods on decapods produces drill holes that are perfectly circular to oval and that do not resemble the damage shown here. Also, drill holes in decapods are thus far restricted to the Cenozoic (Pasini & Garassino 2012, Klompmaker et al. 2013b). Moreover, drilling predation in various invertebrate prey became numerically important only in the Late Cretaceous (Kowalewski et al. 1998, Huntley & Kowalewski 2007). Predation by fish or marine reptiles results in bite marks resembling multiple subcircular holes (e.g. Kauffman & Kesling 1960, Bishop 1972). Finally, predation is unlikely because the damaged specimens represent molts rather than corpses most likely, leaving no incentive to puncture or break the carapace for nutritional purposes.

**Non-predatory biological damage**

Encrusting organisms such as barnacles, foraminifers, and limpets may leave their traces behind on the carapace, resulting in weak spots that might collapse subsequently. Although epibionts are rare on fossil decapods compared to recent decapods, which may primarily be due to preservational biases (Waugh et al. 2004), various epibionts have been de-
scribed from fossil decapods (e.g. Tshudy & Feldmann 1988, Feldmann 2003, Jakobsen & Feldmann 2004, Waugh et al., 2004, Feldmann et al. 2006, Petit & Charbonnier 2012, Robin et al. 2013, 2015c, 2016, Hyžný et al. 2016). Limpets have been argued to cause perfectly circular holes, unlike the damage reported here, in the shells of Late Cretaceous ammonites (Kase et al. 1998), although others have suggested that these holes represent mosasaur bite marks (e.g. Kauffman & Kesling 1960). Barnacles usually leave at least some evidence of their basal plate behind on the crab shell upon death (Waugh et al. 2004, see their Fig. 2.2.), and thus would not likely cause the damage shown here. Some modern crabs use anemones and sponges for camouflage, but ‘these biotic relationships do not affect skeletal components’ (Waugh et al. 2004, p. 961). The nubeculariid foraminifera encrusted on Late Jurassic decapods have a diameter of only ≤300 µm (Robin et al. 2013). Although we cannot be certain, barnacles and limpets may also be ruled out because the shape of the damage is not symmetrical as may be expected for these encrusting organisms. Moreover, there is no trace of encrustation near the damage itself.

Rather, we hypothesize that the damage is primarily caused by shell disease, a common phenomenon affecting modern freshwater and marine crustaceans (Sindermann 1989). Morphologically similar damage caused by bacterial infection is known from the cuticle in modern decapod specimens (Fig. 1), including on shells of some decapod crustaceans following the massive BP ‘Deepwater Horizon’ oil spill in the northern Gulf of Mexico in 2010 (Felder et al. 2014). In some cases, the entire cuticle is affected (Smolowitz et al. 1992, Noga et al. 2000), which is consistent with our specimens, because the cuticle is lacking completely in the damaged areas. Molting can be effective in deterring the disease in the early stages of the bacterial infection for Homarus americanus (Smolowitz et al. 1992). The area of the observed fossil damage (2.5 and ~8.0 mm²) is within the lower size range of modern shell disease lesions: Noga et al. (2000) reported affected areas from 1 to 200 mm² for Callinectus sapidus. Moreover, they also reported that severe lesions accompanied by the loss of the epi-, exo-, and possibly even the endocuticle, may be as small as 3 mm in diameter, which is comparable to the diameter of the damage in Distefania incerta.

The shapes of these lesions vary. Noga et al. (2000) mentioned round, oblong, and irregular shapes for severe lesions in C. sapidus. The shapes usually do not have sharp angles (Fig. 1; see also Figs. 1–7 in Noga et al. 2000), which matches the damage in the fossil specimens reported here. The shape and singularity of the lesion is suggestive of bacterially induced enzootic shell disease. However, we cannot be sure, since the term enzootic implies something opposite of epidemic, and there is no way to establish whether shell disease was or was not widely spread in this crab population because the internal mold carapaces are often broken and shell disease does not always lead to complete loss of the cuticle. Bacterial infection initiated after molting rather than prior to molting seems unlikely in this case because the relatively pristine nature of the carapaces other than the holes suggests relatively rapid burial. This implies that bacterial infection is unlikely to have occurred between molting and burial, certainly not to the extent that it could have penetrated the shell.

We conclude that bacterial infection that started prior to molting is the most likely cause for the observed holes in the carapaces of D. incerta and Goniodromites laevis, although other agents may have initiated the damage. To date, this is the only known example of possible bacterial infections in decapod crustaceans from the fossil record. Thus, bacterial infection and subsequent shell loss in decapods may have been ongoing ~100 million years earlier than previously known.

Acknowledgements. Ninon Robin (Muséum national d’histoire naturelle, Paris) and the anonymous reviewers provided very useful comments that substantially improved this work. We further thank Rodney Feldmann (Kent State University, USA) for bringing the authors in contact with each other and for items of literature. The specimen of Distefania incerta was collected by A.A.K. in 2010 during a field trip supported by a Molengraaff Fonds, Amoco Alumni Scholarship, Graduate Student Senate (Kent State University) research grant, and Sigma Gamma Epsilon (Gamma Zeta Chapter) research grant to A.A.K. This work was further supported by the Jon L. and Beverly A. Thompson Endowment Fund to A.A.K. and a grant from the Gulf of Mexico Research Initiative (GoMRI) to D.L.F. The specimen of Goniodromites laevis was collected by René Fraaije (Oertijdmuseum De Groene Poort, The Netherlands) in 2008. We also thank Yvonne Coole, Barry van Bakel (Oertijdmuseum De Groene Poort & Naturalis Biodiversity Center, The Netherlands), Rodney Feldmann, Carrie Schweitzer (Kent State University), and Pedro Artal (Museo Geológico del Seminario de Barcelona) for their help in the field. Roxanna Smolowitz (Roger Williams University) kindly provided the image for Fig. 2. This is University of Florida Contribution to Paleobiology 769 and University of Louisiana at Lafayette Laboratory for Crustacean Research Contribution 181.

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*Editorial responsibility: Stephen Feist, Weymouth, UK*

Submitted: October 16, 2015; Accepted: February 25, 2016

Proofs received from author(s): April 18, 2016