Possible shell disease in 100 million-year-old crabs

Adiël A. Klompmaker[1,2,3,*], Andrei Y. Chistoserdov[4], Darryl L. Felder[4]

[1]Florida Museum of Natural History, University of Florida, 1659 Museum Road, PO Box 117800, Gainesville, Florida 32611, USA

[2]Department of Geology, Kent State University, 221 McGilvrey Hall, Kent, Ohio 44242, USA

[3]Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, 1005 Valley Life Sciences Building #3140, Berkeley, California 94720, USA

[4]Department of Biology, University of Louisiana at Lafayette, PO Box 42451, Lafayette, Louisiana 70504, USA

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

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 de-velop 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 cu-ticular 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)
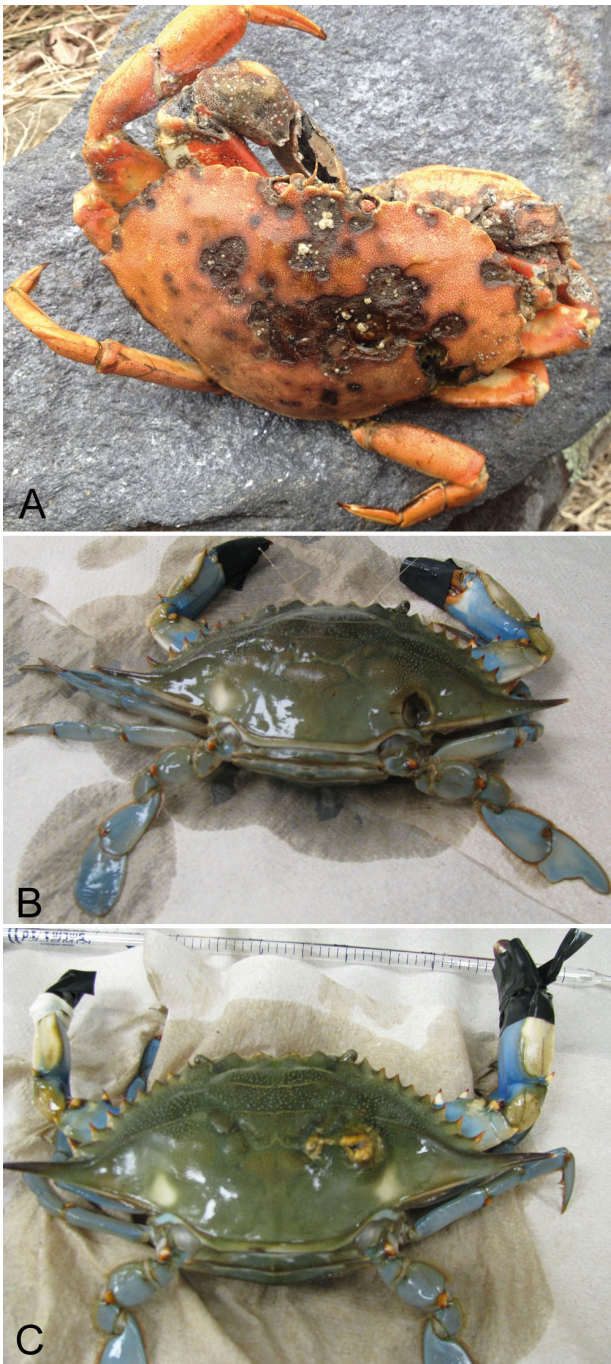
Fig. 2. Modern brachyuran crabs affected by black shell disease and trauma. (A) Example of black spot (= enzootic) shell disease in the Atlantic rock crab *Cancer irroratus* Say, 1817, collected from the Rhode Island Sound, Rhode Island (USA). Note that the lesion penetrates the shell in some areas. Exact specimen size not known. Photograph courtesy of Kathleen Castro (Rhode Island Sea Grant). (B) Blue crab *Callinectes sapidus* with bacterially induced shell disease (epizootic = black spot) and (C) another specimen of blue crab with trauma shell disease (note that melanization is minimal). The dactyli and fixed fingers of the blue crabs are held together by black tape. Both specimens were collected in the Gulf of Mexico near Grand Isle, Louisiana (USA) and measure ~90 mm × 130 mm carapace width and length

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.
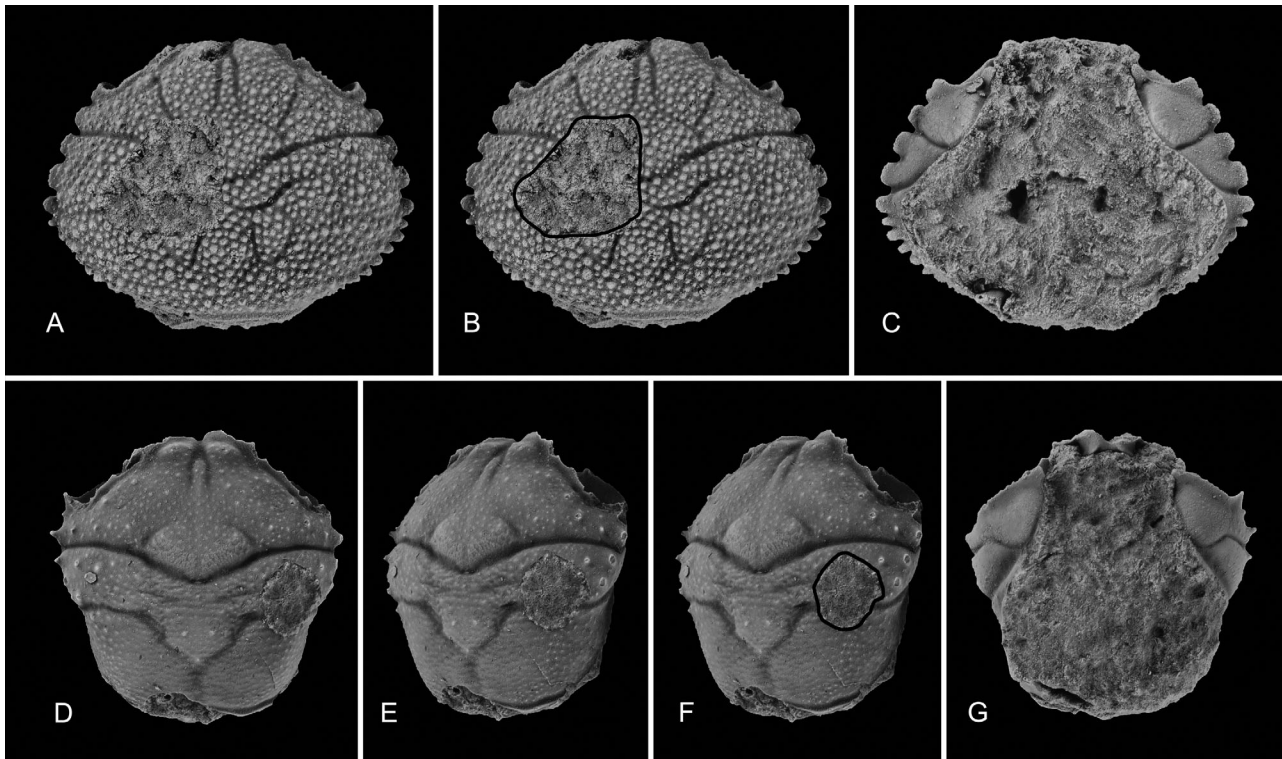
Fig. 3. (A–C) Internal molds of carapaces of the crabs *Distefania incerta*, archived at the Oertijdmuseum De Groene Poort, Boxtel, The Netherlands (reference no. MAB k2940), and (D–G) *Goniodromites laevis* (MAB k2499) from the Cretaceous (late Albian, ~100 Myr) of northern Spain with the damage shown from various angles. (A) Dorsal view, maximum carapace width (cw) excluding spines: 9.1 mm. (B) Dorsal view with damage outlined. (C) Ventral view showing that the specimen is a molt. (D) Dorsal view, maximum cw excluding spines: 6.5 mm. (E) Dorso-right-lateral view. (F) Dorso-right-lateral view with the damage outlined. (G) Ventral view showing that the specimen is a molt. Specimens were whitened prior to photography

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 mm^2. 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 mm^2. 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 (postmortem). 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, Bałuk & Randwański 1996, Fraaye 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, foraminiferans, 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 mm^2) is within the lower size range of modern shell disease lesions: Noga et al. (2000) reported affected areas from 1 to 200 mm^2 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.

LITERATURE CITED

Bałuk W, Radwański A (1996) Stomatopod predation upon gastropods from the Korytnica Basin, and from other classical Miocene localities in Europe. Acta Geol Pol 46: 279–304

Bell T (1863) A monograph of the fossil malacostracous Crustacea of Great Britain, Pt II. Crustacea of the Gault and Greensand. Palaeontographical Society Monograph, London

Bishop GA (1972) Crab bitten by a fish from the upper Cretaceous Pierre Shale of South Dakota. Geol Soc Am Bull 83:3823–3825

Bishop GA (1981) Occurrence and fossilization of the *Dakoticancer* Assemblage, Upper Cretaceous Pierre Shale, South Dakota. In: Gray J, Boucot AJ, Berry WBN (eds) Communities of the past. Hutchinson Ross Publishing Company, Stroudsburg, PA, p 383–413

Bishop GA (1986) Taphonomy of the North American decapods. J Crust Biol 6:326–355

Chistoserdov AY, Quinn RA, Gubbala SL, Smolowitz R (2012) Bacterial communities associated with lesions of shell disease in the American lobster, *Homarus americanus* Milne-Edwards. J Shellfish Res 31:449–462

Cobb JS, Castro KM (2006) Shell disease in lobsters: a synthesis. University of Rhode Island, Kingston, RI

Comeau M, Benhalima K (2009) Internal organ pathology of wild American lobster (*Homarus americanus*) from eastern Canada affected with shell disease. NZ J Mar Freshw Res 43:257–269

Costa-Ramos C, Rowley AF (2004) Effect of extracellular products of *Pseudoalteromonas atlantica* on the edible crab *Cancer pagurus.* Appl Environ Microbiol 70: 729–735

Felder DL, Thoma BP, Schmidt W, Sauvage T and others (2014) Monitored seaweeds and decapod crustaceans on northwestern Gulf deep banks following the Deepwater Horizon Oil Spill. Bioscience 64:808–819

Feldmann RM (2003) The Decapoda: new initiatives and novel approaches. J Paleontol 77:1021–1039

Feldmann RM, May W (1991) Remarkable crayfish remains (Decapoda: Cambaridae) from Oklahoma – evidence of predation. J Paleontol 65:884–886

Feldmann RM, Schweitzer CE, McLauchlan D (2006) Additions to the records for decapod Crustacea from Motunau and Glenafric beaches, North Canterbury, New Zealand. NZ J Geol Geophys 49:417–427

Fraaije RHB, Bakel BWM, Jagt JWM, Klompmaker AA, Artal P (2009) A new hermit crab (Crustacea, Anomura, Paguroidea) from the mid-Cretaceous of Navarra, Northern Spain. Bol Soc Geol Mex 61:13–16

Fraaije RHB, Klompmaker AA, Artal P (2012) New species, genera and a family of hermit crabs (Crustacea, Anomura, Paguroidea) from a mid-Cretaceous reef of Navarra, northern Spain. Neues Jahrb Geol Paläontol Abh 263:85–92

Fraaije RHB, Artal P, Van Bakel BWM, Jagt JWM, Klompmaker AA (2013) An array of sixth abdominal tergite types of paguroid anomurans (Crustacea) from the mid-Cretaceous of Navarra, northern Spain. Neth J Geosci 92:109–117

Fraaye RHB (1996) Late Cretaceous swimming crabs: radiation, migration, competition, and extinction. Acta Geol Pol 46:269–278

Geary DH, Allmon WD, Reaka-Kudla ML (1991) Stomatopod predation on fossil gastropods from the Plio-Pleistocene of Florida. J Paleontol 65:355–360

Getchell RG (1989) Bacterial shell disease in crustaceans: a review. J Shellfish Res 8:1–6

Glaessner MF (1969) Decapoda. In: Moore RC (ed) Treatise on invertebrate paleontology, Part R, Arthropoda 4,

Vol 2. Geological Society of America and University of Kansas Press, Boulder, CO and Lawrence, KS, p 400–533, 626–628

Gomez-Chiarri M, Cobb JS (2012) Shell disease in the American lobster, *Homarus americanus*: a synthesis of research from the New England Lobster Research Initiative: lobster shell disease. J Shellfish Res 31:583–590

Guinot D (1969) Recherches préliminaires sur les groupements naturels chez les Crustacés, Décapodes, Brachyoures. VII. Les Goneplacidae (suite et fin). Bull Mus Nat Hist Nat, 41(3):688–724

Hess E (1937) A shell disease in lobsters (*Homarus americanus*) caused by chitinovorous bacteria. J Biol Board Can 3:358–362

Huntley JW, Kowalewski M (2007) Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proc Natl Acad Sci USA 104:15006–15010

Hyžný M, Perrier V, Robin N, Martin JE, Sarr R (2016) *Costacopluma* (Decapoda: Brachyura: Retroplumidae) from the Maastrichtian and Paleocene of Senegal: a survivor of K/Pg events. Cretac Res 57:142–156

Jakobsen SL, Feldmann RM (2004) Epibionts on *Dromiopsis rugosa* (Decapoda: Brachyura) from the late Middle Danian limestones at Fakse Quarry, Denmark: novel preparation techniques yield amazing results. J Paleontol 78: 953–960

Kase T, Johnston PA, Seilacher PA, Boyce JB (1998) Alleged mosasaur bite marks on Late Cretaceous ammonites are limpet (patellogastropod) home scars. Geology 26: 947–950

Kauffman EG, Kesling RV (1960) An Upper Cretaceous ammonite bitten by a mosasaur. Univ Mich Contrib Mus Paleontol 15:193–248

Keupp H (2006) Sublethal punctures in body chambers of Mesozoic ammonites (forma *aegra fenestra* n.f.), a tool to interpret synecological relationships, particularly predator-prey interactions. Paläontol Z 80:112–123

Klompmaker AA (2013) Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. Cretac Res 41:150–185

Klompmaker AA, Boxshall GA (2015) Fossil crustaceans as parasites and hosts. Adv Parasitol 90:233–289

Klompmaker AA, Artal P, Gulisano G (2011a) The Cretaceous crab *Rathbunopon*: revision, a new species and new localities. Neues Jahrb Geol Paläontol Abh 260: 191–202

Klompmaker AA, Artal P, Fraaije RHB, Jagt JWM (2011b) Revision of the family Gastrodoridae (Crustacea, Decapoda), with description of the first species from the Cretaceous. J Paleontol 85:226–233

Klompmaker AA, Artal P, Van Bakel BWM, Fraaije RHB, Jagt JWM (2011c) Etyid crabs (Crustacea, Decapoda) from mid-Cretaceous reefal strata of Navarra, northern Spain. Palaeontology 54:1199–1212

Klompmaker AA, Feldmann RM, Schweitzer CE (2012a) A hotspot for Cretaceous goniodromitids (Decapoda, Brachyura) from reefal strata of Spain. J Crustac Biol 32: 780–801

Klompmaker AA, Feldmann RM, Robins CM, Schweitzer CE (2012b) Peak diversity of Cretaceous galatheoids (Crustacea, Decapoda) from northern Spain. Cretac Res 36: 125–145

Klompmaker AA, Ortiz JD, Wells NA (2013a) How to explain a decapod crustacean diversity hotspot in a mid-

Cretaceous coral reef. Palaeogeogr Palaeoclimatol Palaeoecol 374:256–273

Klompmaker AA, Karasawa H, Portell RW, Fraaije RHB, Ando Y (2013b) An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. Palaios 28:599–613

Klompmaker AA, Artal P, Van Bakel BWM, Fraaije RHB, Jagt JWM (2014) Parasites in the fossil record: a Cretaceous fauna with isopod-infested decapod crustaceans, infestation patterns through time, and a new ichnotaxon. PLoS One 9:e92551

Kowalewski M, Dulai A, Fürsich FT (1998) A fossil record full of holes: the Phanerozoic history of drilling predation. Geology 26:1091–1094

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius, Holmiae

Milne-Edwards A (1834–1840) Histoire naturelle des Crustaces, comprenant I'anatomie, la physiologie et, la classification de ces animaux, Vol 1–3. Roret, Paris

Milne-Edwards A (1873–1881) Études sur les xiphosures et les crustacés de la région mexicaine. Mission scientifique au Mexique et dans l'Amérique centrale, ouvrage publié par ordre du Ministre de l'Instruction publique. Recherches zoologiques pour servir à l'histoire de la faune de l'Amérique central et du Mexique, publiées sous la direction de M.H. Milne Edwards, membre de l'Institut. Cinquième partie, Tome premier. Imprimerie Nationale, Paris

Noga EJ, Sawyer TK, Rodon-Naveira M (1998) Disease processes and health assessment in blue crab fishery management. J Shellfish Res 17:567–577

Noga EJ, Smolowitz R, Khoo LH (2000) Pathology of shell disease in the blue crab, Callinectes sapidus Rathbun, (Decapoda: Portunidae). J Fish Dis 23:389–399

Ordway A (1863) Monograph of the genus Callinectes. J Boston Soc Nat Hist 7:567–583

Pasini G, Garassino A (2012) Naticid gastropod and octopodid cephalopod predatory traces: evidence of drill holes on the leucosid crab Ristoria pliocaenica (Ristori, 1891), from the Pliocene of the "La Serra" quarry (Tuscany, Italy). Atti Soc Ital Sci Nat Mus Civ Stor Nat Milano 153: 257–266

Pether J (1995) Belichnus new ichnogenus, a ballistic trace on mollusc shells from the Holocene of the Benguela region, South Africa. J Paleontol 69:171–181

Petit G, Charbonnier S (2012) Fossil sponge gemmules, epibionts of Carpopenaeus garassinoi n. sp. (Crustacea, Decapoda) from the Sahel Alma Lagerstätte (Late Cretaceous, Lebanon). Geodiversitas 34:359–372

Powell A, Rowley AF (2005) Unchanged prevalence of shell disease in the edible crab Cancer pagurus four years after decommissioning of a sewage outfall at Langland Bay, UK. Dis Aquat Org 68:83–87

Quinn RA, Smolowitz R, Chistoserdov A (2009) Eukaryotic communities in epizootic shell disease lesions of the American lobster (Homarus americanus H. Milne Edwards). J Shellfish Res 28:913–922

Quinn RA, Metzler A, Smolowitz RM, Tlusty M, Chistoserdov AY (2012a) Shell infections of Homarus americanus with three bacteria isolated from naturally occurring epizootic shell disease lesions. J Shellfish Res 31:485–494

Quinn RA, Metzler A, Tlusty M, Smolowitz RM, Leberg P,

Chistoserdov AY (2012b) Lesion bacterial communities in American lobsters with diet-induced shell disease. Dis Aquat Org 98:221–233

Quinn RA, Cawthorn RJ, Summerfield RL, Smolowitz R, Chistoserdov AY (2013) Bacterial communities associated with lesions of two forms of shell disease in the American lobster (Homarus americanus, Milne Edwards) from Atlantic Canada. Can J Microbiol 59:380–390

Radwański A (1996) The predation upon, and the extinction of, the latest Maastrichtian populations of the ammonite species Hoploscaphites constrictus (J. Sowerby, 1817) from the Middle Vistula Valley, Central Poland. Acta Geol Pol 46:117–135

Rathbun MJ (1896) The genus Callinectes. Proc US Natl Mus 18(1070):349–375

Robba E, Ostinelli F (1975) Studi paleoecologici sul Pliocene Ligure I. Testimonianze di predazione sui molluschi Pliocenici di Albenga. Riv Ital Paleontol Stratigr 81: 309–372

Robin N, Charbonnier S, Bartolini A, Petit G (2013) First occurrence of encrusting nubeculariids (Foraminifera) on a mobile host (Crustacea, Decapoda) from the Upper Jurassic Eichstätt Lagerstätte, Germany: a new possible relation of phoresy. Mar Micropaleontol 104:44–52

Robin N, Petit G, Charbonnier S (2015a) A newly recognized Mesozoic–Recent interspecific association: calcifying bacteria on decapod crustaceans. Lethaia 48:463–473

Robin N, Bernard S, Miot J, Blanc-Valleron MM, Charbonnier S, Petit G (2015b) Calcification and diagenesis of bacterial colonies. Minerals 5:488–506

Robin N, Van Bakel BWM, d'Hondt JL, Charbonnier S (2015c) A new early brachyuran (Crustacea, Decapoda) from the Middle Jurassic of northwest France, epibionts and ecological considerations. Contrib Zool 84:179–191

Robin N, Charbonnier S, Merle D, Simpson MI, Petit G, Fernandez S (2016) Bivalves on mecochirid lobsters from the Aptian of the Isle of Wight: snapshot on an Early Cretaceous palaeosymbiosis. Palaeogeogr Palaeoclimatol Palaeoecol 453:10–19

Say T (1817–1818) An account of the Crustacea of the United States. J Acad Nat Sci Philadelphia 1 (1–2):[1817] 57–63, 65–80, 97–101, 155–160; [1818] 235–253, 313–316, 317–319, 374–380, 381–401

Schäfer W (1951) Fossilisations-Bedingungen brachyurer Krebse. Abh Senckenb Naturforsch Ges 485:221–238

Shields JD, Overstreet RM (2007) Diseases, parasites and other symbionts. In: Kennedy VS, Cronin LE (eds) The biology and management of the blue crab. University of Maryland Sea Grant Press, College Park, MD, p 299–394

Sindermann CJ (1989) The shell disease syndrome in marine crustaceans. Tech Memo NMFS-F/NEC-64. NOAA, NMFS, Northeast Fisheries Center, Woods Hole, MA

Smith SI (1879) The stalk-eyed crustaceans of the Atlantic coast of North America north of Cape Cod. Trans Conn Acad Arts Sci 5:27–136

Smolowitz RM, Bullis RA, Abt DA (1992) Pathologic cuticular changes of winter impoundment shell disease preceding and during intermolt in the American lobster, Homarus americanus. Biol Bull (Woods Hole) 183:99–112

Stimpson W (1860) Notes on North American Crustacea, in the Museum of the Smithsonian Institution, No. II. Ann Lyceum Natl Hist NY 7:177–246

Stimpson W (1871) Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida by L.F. de Pourtales, Assist. U.S. Coast Survey, Part I.

Brachyura. Bull Mus Comp Zool Harv 2:109−160

➤ Tlusty MF, Metzler A (2012) Relationship between temperature and shell disease in laboratory populations of juvenile American lobsters (*Homarus americanus*). J Shellfish Res 31:533−541

➤ Tlusty MF, Myers A, Metzler A (2008) Short- and long-term dietary effects on disease and mortality in American lobster *Homarus americanus.* Dis Aquat Org 78:249−253

Tshudy DM, Feldmann RM (1988) Macruran decapods, and their epibionts, from the López de Bertodano Formation (Upper Cretaceous), Seymour Island, Antarctica. Geol Soc Am 169:291−302

Van Straelen V (1940) Crustacés Décapodes nouveaux du Crétacique de la Navarre. Bull Mus R Hist Nat Belg 16(4):1−5

➤ Vogan CL, Rowley AF (2002) Effects of shell disease syndrome on the haemocytes and humoral defences of the edible crab, *Cancer pagurus.* Aquaculture 205:237−252

➤ Vogan CL, Costa-Ramos C, Rowley AF (2001) A histological study of shell disease syndrome in the edible crab *Cancer pagurus.* Dis Aquat Org 47:209−217

➤ Vogan CL, Costa-Ramos C, Rowley AF (2002) Shell disease syndrome in the edible crab, *Cancer pagurus* — isolation, characterization and pathogenicity of chitinolytic bacteria. Microbiology 148:743−754

➤ Vogan CL, Powell A, Rowley AF (2008) Shell disease in crustaceans – just chitin recycling gone wrong? Environ Microbiol 10:826−835

➤ Waugh DA, Feldmann RM, Thomas KB, Crawford RS, Jakobsen SL (2004) Epibiont preservational and observational bias in fossil marine decapods. J Paleontol 78: 961−972

➤ Weinstein JE, West TL, Bray JT (1992) Shell disease and metal content of blue crabs, *Callinectes sapidus*, from the Albemarle-Pamlico estuarine system, North Carolina. Arch Environ Contam Toxicol 23:355−362

Wienberg Rasmussen H, Jakobsen SL, Collins JSH (2008) Raninidae infested by parasitic Isopoda (Epicaridea). Bull Mizunami Fossil Mus 34:31−49

Ziskowski J, Spallone R, Kapareiko D, Robohm R, Calabrese A, Pereira J (1996) Shell disease in American lobster in the offshore Northwest-Atlantic region around the 106-mile sewage-sludge disposal site. J Mar Environ Eng 3: 247−271