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Taphonomy of decapod crustacean cuticle and its effect on the appearance as exemplified by new and known taxa from the Cretaceous–Danian crab *Caloxanthus*

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ABSTRACT

Decapod crustaceans inhabited a variety of environments during the Cretacous. The crab *Caloxanthus* is an example of this environmental differentiation as the Cretaceous–Danian species lived in siliciclastic and carbonate habitats. Here, two new species of *Caloxanthus* are described from different sedimentary settings: 1) *Caloxanthus thompsonorum* sp. nov. from the Upper Cretaceous (Santonian) of Austria found in siliciclastic sediments, and 2) *Caloxanthus vignyensis* sp. nov. from the Paleocene (Danian) of France found in a limestone. After examination of the marly rock containing the holotype of *C. wrighti* (Santonian, France), another conspecific carapace specimen was discovered; both specimens are illustrated. *Caloxanthus* is a prime example of how the appearance of decapod carapaces can differ among conspecific specimens with the cuticle preserved and those lacking it (internal molds). This phenomenon is also found in other decapod taxa as illustrated herein (*Daira speciosa*, *Panopeus wronai* and *Chlorodiella mediterranea*) and affects carapaces and chelae. Importantly, although this is known among paleontologists, in only about half (50/108, 46%) of the in 2013 newly described fossil decapod species it could be deduced with certainty whether or not a cuticle was present. Even more surprising, in only 27% of the cases the presence or absence of the cuticle was specifically mentioned. It is recommended to state whether or not the cuticle is preserved in the species description to reduce the potential of misidentification of taxa and erecting erroneous taxa. We also show that whitening of specimens to increase contrast may also obscure features on the carapace of *C. wrighti*. This study highlights the effect that taphonomy can have on taxonomy.

1. Introduction

During the Mesozoic, decapod crustacean species and genus diversity increased markedly and a shift in dominance occurred with crabs (Brachyura) becoming the most diverse infraorder on both taxonomic levels. During this “Mesozoic decapod revolution” that also includes a variety of other changes (Klompmaker et al., 2013), crabs initially radiated and inhabited reefs primarily during the Late Jurassic (e.g., Förster, 1985; Müller et al., 2000; Krobicki and Zatoń, 2008), but they were living in a variety of environments in the Cretaceous (Klompmaker, 2013; Klompmaker et al., 2013, fig. 3). One of the crab genera that originated in the Cretaceous and serves as an example of environmental differentiation is *Caloxanthus* A. Milne Edwards, 1864. Members of this species-rich genus have been found in siliciclastics, reef limestones, and other carbonates during the Cretaceous and Paleocene, but their cuticle is not always preserved (Table 1). The goals of this paper are 1) to report on two new occurrences and species of *Caloxanthus* based on specimens found in the Bayerische Staatssammlung für Paläontologie und historische Geologie (Munich, Germany) plus a new specimen of *C. wrighti* Collins and Breton, 2011, and 2) to discuss effect that the presence, absence, or partial preservation of the cuticle has on the appearance of the carapace to show that, although this is a known phenomenon, it is often insufficiently reported.

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Table 1
Data about all known species of *Caloxanthus*.

Species	Country	Epoch and age	Stratigraphic unit or biozone	Sediment	Mold or cuticle	References with images other than first description
Caloxanthus americanus Rathbun, 1935	USA, England, France	Early and Late Cretaceous (Albian, Cenomanian: USA; Cenomanian: Eng. + Fr.)	Pawpaw, Weno, and Grayson Fms (USA), *Calycoceras naviculare* Zone + *Mantelliceras mantelli* Zone (Eng.), Craie glauconieuse Fm (Fr.)	Clays + shales (USA), limestone + sands (Eng.), sandstone (Fr.)	(Part) cuticle (USA), ? (Eng.), cuticle? (Fr.)	Wright and Collins, 1972; Breton and Collins, 2011; Schweitzer et al., 2012; Vega et al., 2014
C. formosus A. Milne Edwards, 1864	France	Late Cretaceous (Cenomanian)	Craie glauconieuse Fm, Sables du Perche Fm	Sandstone, sandstone	Cuticle?	Glaessner, 1969; Breton and Collins, 2011; Collins and Breton, 2011
C. kuypersi Fraaye, 1996	The Netherlands	Late Cretaceous (Maastrichtian)	Maastricht Fm (Meerssen Mbr)	Bryozoan-rich limestone	Cuticle (pers. comm. R. Fraaije 23 July 2014)	–
C. ornatus (von Fischer-Benzon, 1866)	Denmark	Paleocene (Danian)	Faxe Fm, Stevns Klint Fm (Korsnæb Mbr)	Coral-bryozoan limestone, bryozoan limestone	Both (cuticle, external mold, mostly internal mold)	Segerberg, 1900; Collins and Jakobsen, 1994; Jakobsen and Collins, 1997; Damholt et al., 2010; Rasmussen et al., 2011; Klompmaker et al., 2011; herein
C. paraornatus Klompmaker et al., 2011	Spain	Early Cretaceous (Albian)	Eguino Fm (Albinez Unit)	Coral limestone	Both (internal mold mostly)	–
C. purleyensis (Withers, 1928)	England	Late Cretaceous (Coniacian-Santonian)	*Micraster cortestudinarium* Zone	Chalk	?	Wright and Collins, 1972
C. simplex (Secrétan, 1964)	Madagascar	Late Cretaceous (Campanian)	*Pachydiscus grossouvrei* Zone	Sand and marl	Part cuticle	Charbonnier et al., 2012
C. wrighti Collins & Breton, 2011	France	Late Cretaceous (Santonian)	Marnes bleues de Sougraigne Fm	Marls	Cuticle (pers. obs. MH)	Wright and Collins, 1972; herein
Caloxanthus sp. (*sensu* Armstrong et al., 2009)	USA	Paleocene (Danian)	Wills Point Fm (Mexia Clay Mbr)	Clay	Cuticle?	–
C. thompsonorum sp. nov.	Austria	Late Cretaceous (Santonian)	?Hochmoos Fm	Fine-grained siliciclastics	Part cuticle	herein
C. vignyensis sp. nov.	France	Paleocene (Danian)	–	Calcirudites	Part cuticle	herein

2. Geologic setting

The oldest of the two new species described below originates from the vicinity of the village Gosau in Austria (Fig. 1A). The label associated with the specimens mentions "Finster Graben, Pass Gschütt hinter Rando-Graben". Some or all of the names are referred to in Wiedmann (1978, fig. 1), Summesberger (1979, fig. 1), Tröger and Summesberger (1994, fig. 1), and Wagreich et al. (2010, fig. 1). The specimens are very likely Santonian in age (pers. comm. H. Summesberger, July 2014), and possibly originate from the upper Santonian Hochmoos Formation as deduced from "Finster Graben" (pers. comm. M. Wagreich, July 2014). No decapods were known from this formation thus far. The sediments in which the specimens are embedded are fine-grained siliciclastics.

The second new species described is from the Paleocene (middle to upper Danian) rocks of Vigny in northern France, 35–40 km to the northwest of Paris (Montenat et al., 2002; Pacaud, 2004, fig. 1; Fig. 1B). The label associated with the sole specimen reads: "Paleozän (Mont), Calcaire pisolithique de Vigny, Vigny NW Paris". The Danian reef-associated and bioclastic limestones are surrounded by Upper Cretaceous (Campanian) chalks in the Vigny quarries (Montenat et al., 2002). These reefal and peri-reef environments were situated in open marine conditions with warm and well-oxygenated conditions inhabited by a diverse invertebrate fauna (Pacaud et al., 2000; Pacaud and Merle, 2002; Montenat et al., 2002). During the Danian, faulting took place resulting in topographic highs on which coralgal reefs developed, whereas depressions were filled with calcirudite channel deposits (Montenat et al., 2002, fig. 18). These calcirudites are also referred to as 'calcaire pisolithique' in which the specimen studied herein was found. These calcirudites consist primarily of well-rounded bioclastic gravels containing primarily red algae, but also green algae, sponges, corals, hydrozoans, brachiopods, bryozoans, echinoids, bivalves (Pacaud, 2001), gastropods (Pacaud, 2004, 2009), nautiloids (Bignot and Geyssant, 1998), and sepioids (Meyer, 1993) were present. To our knowledge, decapod crustaceans from Vigny have not been described scientifically, although a variety of species have been mentioned in the informal literature (Meyer, 1987; Conseil Général du Val d'Oise, 2003). These species include *Dromiopsis rugosa* (von Schlotheim, 1820), *D. minor* von Fischer-Benzon, 1866, *Titanocarcinus faxeensis* (von Fischer-Benzon, 1866), *Jakobsenius cretacea* (Segerberg, 1900), *Caloxanthus ornatus* (von Fischer-Benzon, 1866), *Munida primaeva* Segerberg, 1900, *Protomunida munidoides* (Segerberg, 1900), *Paguristes* sp., and *Dromilites* sp., but the presence of these species in Vigny needs to be verified. Taxa that can be confirmed here are *Dromiopsis* cf. *D. elegans* Reuss, 1858 (MGUH 30863) and *Jakobsenius cretacea* (MGUH 30864 and MGUH 30865) in addition to the new species of *Caloxanthus* described below.

Institutional abbreviations: To denote the repositories of specimens illustrated or referred to in the text, the following abbreviations are used: SNSB-BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, München (Munich), Germany; UF, Florida Museum of Natural History at the University of Florida, Gainesville, Florida, USA; GBA, Geologische Bundesanstalt, Vienna, Austria; MNHN, Muséum national d'Histoire naturelle, Paris, France; GM, MGUH, Natural History Museum of Denmark, Geological Museum, University of Copenhagen, Denmark; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NHML, The Natural History Museum, Department of Palaeontology, London, United Kingdom.

3. Systematic paleontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758