A NEW CIROLANID ISOPOD (CRUSTACEA) FROM THE CRETACEOUS OF LEBANON: DERMOLITHS DOCUMENT THE PRE-MOLT CONDITION

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ABSTRACT

Discovery of a single specimen of cirolanid isopod from the Late Cretaceous of Lebanon permits definition of a new species, *Cirolana garassinoi*. Preservation with the ventral surface exposed is unique among isopod fossils. The evidence of a thin, apparently transparent cuticle and three pairs of dermoliths suggests that the specimen died while in the pre-molt condition. The ability to sequester calcium and possibly other mineral salts in a marine isopod may indicate a preadaptation to terrestrial lifestyles where the process is common in extant forms.

KEY WORDS: Cretaceous, Isopoda, Lebanon, dermoliths, pre-molt condition DOI: 10.1651/08-3096.1

INTRODUCTION

Cretaceous decapod crustaceans have been described from fine-grained limestones in Lebanon since Brocchi (1875) described the shrimp Penaeus libanensis. Since that time, numerous other decapods, including shrimp and erymid, nephropid, and palinurid lobsters have been described, which have recently been re-examined and the systematics modernized by Garassino (1994). He also provided a brief, useful history of the study of the area. The specimens are excellently preserved as compressed specimens so that morphology can be described in detail. Throughout the 135 years of study of these crustaceans, only a single fossil isopod has been collected. The purpose of this work is to describe that specimen and to comment on the remarkable nature of its preservation that permits interpreting it as representing a corpse in the pre-molt condition. This represents the first such occurrence known to the author of a fossil isopod in pre-molt condition. Furthermore, the animal bears three pairs of dermoliths, which are evidence that Cretaceous marine isopods sequestered calcium and possibly other mineral salts for strengthening the newly formed exoskeleton.

The rocks that yield fossil crustaceans in Lebanon are exposed in quarries within about 30 km of Beirut (Fig. 1). Most come from Hakel and Hadjula (Garassino, 1994). The locality from which the isopod was collected is at Sahel Alma, the same site from which *Benthesicymus* (= *Penaeus*) *libanensis* was described by Brocchi. The quarry is now abandoned.

SYSTEMATICS

Class Malacostraca Latreille, 1802 Order Isopoda Latreille, 1817 Suborder Cymothoida Wägele, 1989 Cirolanidae Dana, 1852 *Cirolana* Leach, 1818

Type Species.—*Cirolana cranchii* Leach, 1818, by original designation.

Included Fossil Species.—*Cirolana enigma* Wieder and Feldmann, 1992, Early Cretaceous, South Dakota, USA; *C. fabiani* De Angeli and Rossi, 2006, early Oligocene, Vicenza, Italy; *C. harfordi japonica* Thielemann, 1910 (*fide* Hu and Tao, 1996), Pleistocene, Taiwan, Republic of China.

Diagnosis.—"Cephalon lacking projecting rostrum. Frontal lamina distinct, but not projecting prominently. Antenna longer than antennule. Pleon consisting of five free pleonites plus pleotelson (pleonite 1 often obscured by pereionite VII). Lateral margins of pleonite 5 overlapped by those of pleonite 4. Pleopods 1 and 2 similar, not operculiform. Inner apex of uropod peduncle produced." (Kensley, 1978, p. 61).

Remarks.—Systematic placement of fossil isopods is always challenging because the morphology of the exoskeleton can vary considerably within a single genus of extant isopods. Further, many of the essential characters for identification of extant forms are expressed on the ventral surface and are rarely, if ever, preserved. As a result, it is typically difficult to identify descriptors that are useful in distinguishing very ancient taxa from modern ones. Thus, the fossil record of isopods suggests that genera are particularly long-ranging. Such is the case in this study, where the morphology of the fossil fits well within the range of forms of the modern genus, *Cirolana*. This may either be an example of a long-ranging isopod genus, or a demonstration that no basis for excluding the fossil form from a modern genus is apparent.

It is tempting to consider placement of this specimen within *Excirolana* Richardson, 1912, because this is the only marine or marginal marine genus is which dermoliths have been identified. However, *Excirolana* is characterized by having pleonite 5 extending to the margin, whereas it is overlapped by pleonite 4 in *Cirolana* (Kensley, 1978). The Cretaceous specimen assigned herein to *Cirolana* clearly has pleonite 5 overlapped marginally by pleonite 4. It is also noteworthy that the dermoliths noted in *Excirolana* occur on pereionites IV and V; those on the new Cretaceous



Fig. 1. Map of Lebanon showing the Sahel Alma quarry site from which *Cirolana garassinoi* n. sp. was collected in relation to the other Cretaceous localities at Hakel and Hadjula, where the majority of decapods have been found.

species are situated on pereionites II, III, and IV. In all other regards as well, the fossil closely resembles extant representatives of *Cirolana* as will be discussed below.

Distinguishing genera within the fossil record of the isopods formerly placed within the Flabellifera Sars, 1882, is difficult, particularly when ventral features are not preserved. That suborder has recently been subdivided into the Cymothoida, containing the single family Cirolanidae, and the Cymnothooidea Leach, 1814 (Brandt and Poore, 2003). In the present case, many features distinctive of Cirolana are evident. The cephalon shows no indication of bearing an anterior projection. Antennae and fragments of the antennules are present, and the former are distinctly larger than the latter. The specimen exhibits five free pleonites and a pleotelson, and the pleon is only slightly narrower than the pereion and is of a general form well within the range of variation of those of extant species. The inner apex of the peduncle of the uropod is produced into an elongate spinelike structure extending along the margin of the pleotelson. The most important morphological point that is not known is whether all the pereiopods are ambulatory, as they should be in the Cirolanidae (Kensley, 1978, p. 55). The anteriormost pereiopods, which are prehensile in the morphologically similar family, the Aegidae White, 1850, are not preserved. Despite the inability to distinguish the two families on the basis of the nature of the anterior pereiopods, the other characters strongly suggest placement within the Cirolanidae and genus Cirolana.

Cirolana garassinoi n. sp. Fig. 2

Diagnosis.—Maximum width at pereion 6; head prominent, smoothly rounded anteriorly; eyes with few large facets; ratio of pereion/pleon length 1.3; pleotelson broadly rounded; endopod of uropod extends approximately length of pleotelson; exopod somewhat shorter.

Description.—Moderate sized cirolanid, 17.4 mm long, 10.9 mm wide, widening uniformly from smoothly rounded head to pereion 7, attaining greatest width at pereion VII; pleon width 8.7 mm, equally wide throughout; pleotelson tapers posteriorly to smoothly rounded termination; uropods prominent, broad, as long as pleotelson.

Cephalon ca. 1.7 mm long, 4.6 mm wide, widest posteriorly. Eyes sessile, moderately large with large facets set in rows parallel to lateral margin of cephalon; 7 facets in most complete row. Antennules not preserved. Antenna with peduncle slightly wider than flagellum which tapers slightly distally; termination missing. Mandibles and maxillipeds crushed, indistinguishable.

Pereionite I narrowest, anterior margin curves slightly anteriorly around posterior margin of cephalon but does not embrace lateral margin of cephalon; lateral margins lacking coxal plates. Pereiomeres II-VII similar in form, widening posteriorly; coxal plates increase in size posteriorly, not markedly distinguished from tergum when viewed ventrally. Pereiomeres II-IV with prominent, transversely ovoid, domal excrescences, each ca. 2 mm wide, extending axially from near origin of coxal plates. Each excrescence is opaque, nearly black on upper surface, becoming translucent and amber marginally. Anterior pereiopods not preserved. Ambulatory pereiopods on pereiomeres V-VII long, appear to be dorso-ventrally flattened.

Four pleonites similar in length and width; pleurae about as long as wide, curved distally to blunt point.

Pleotelson about as wide as long, tapering distally; posterior margin smoothly rounded, lacking obvious spines.

Uropods broad; peduncle extends posteriorly as narrow spine lying along margin of pleotelson; exopods extend to end of pleotelson; endopods slightly shorter. Exopod ovoid in outline. Endopod triangular, attains greatest length along axial margin.

Dorsal surface not exposed.

Etymology.—The trivial name honors Dr. Alessandro Garassino, Museo di Storia Naturale di Milano, Italy, a specialist in the paleontology of decapod crustaceans, who acquired the specimen and made it available for study by the author.

Type.—The holotype, and sole specimen (part and counterpart), MSNM i27211, is deposited in the Museo di Storia Naturale di Milano, Milan, Italy.

Occurrence.—The specimen was collected from the *Globotruncana concavata* zone (Ejel and Dubertret, 1966), Late Cretaceous (Santonian) lithographic limestones from the Sahel Alma quarry, Lebanon (A. Garassino, personal communication). Associated arthropods include the penaeidean shrimp, *Benthesicymus libanensis* (Brocchi,

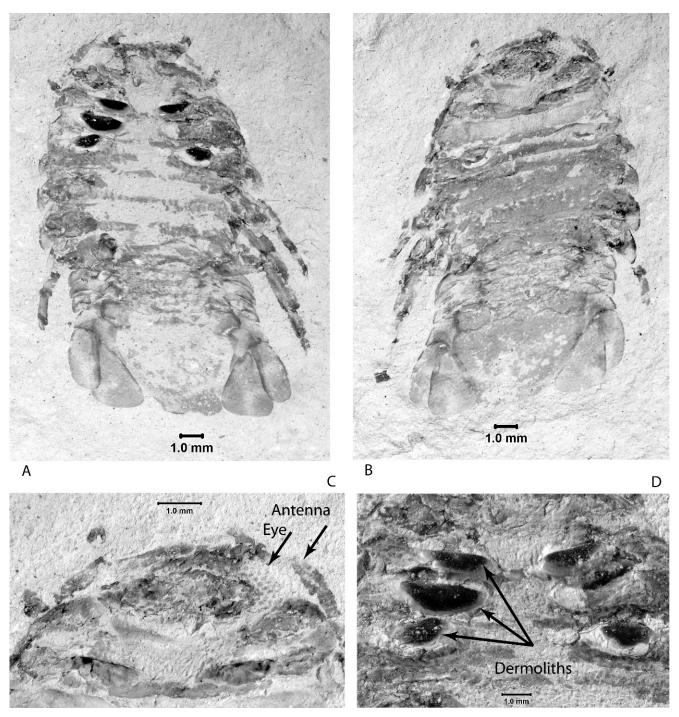


Fig. 2. *Cirolana garassinoi* n. sp., MSNM i27211. A, part, and B, counterpart, of entire specimen exposing the ventral surface; C, enlargement of the head region showing the position of the large compound eye and the peduncle and part of the flagellum of one of the antennae; D, enlargement of pereiomeres II-IV showing the paired dermoliths.

1875) (Garassino, 1994) and thylacocephalan crustaceans (Garassino, personal communication).

DISCUSSION

Cirolana garassinoi n. sp. can be distinguished readily from other species known from the fossil record. *Cirolana enigma*, the only other species within the genus known

from the Cretaceous, exhibits a more reniform head, has more prominent pleurae on the pereiomeres, is more cylindrical overall, and has a pleon and pereion that are nearly the same width. The uropods are not known. *Cirolana fabiani* has a much larger pereion than pleon, has a cylindrical cross section, attains its greatest width at pereion 4 or 5, and bears uropods that are longer than the pleotelson. *Cirolana harfordi japonica* is much more elongate than any of the other fossil species, bears a pereion that is proportionately much longer than the pleon, is cylindrical in cross section, and has a triangular pleotelson. Thus, there is no difficulty in distinguishing the fossil species from one another.

In terms of comparison with extant forms, *Cirolana* garassinoi bears close resemblance to *C. parva* Hansen, 1890, from the tropical Atlantic and Pacific (Brusca et al., 1995). *Cirolana parva* exhibits moderately large eyes with large individual facets, has antennal peduncles that extend approximately to the base of the eyes, shows similar proportions of the pereion length to pleon length, has a rounded pleotelson, and bears uropodal endopods that extend approximately to the tip of the pleotelson. The width/length proportions are quite different. *Cirolana garassinoi* is much broader than *C. parva*, but that may be exaggerated in the former because it is a soft, premolt individual that has been flattened out on the bedding plane.

To my knowledge, no fossil isopods have been preserved with the ventral side exposed. The evidence for the ventral orientation is based upon two primary areas. The pereiopods on the last pereiomeres can be traced over the exposed carapace remains. This could only be possible if the ventral surface was exposed. In addition, the placement of the uropods relative to the pleotelson strongly suggest a ventral view. Normally, when viewed from the dorsal side, the exopods of the uropods would lie beneath the endopod and both would lie beneath the pleotelson. That arrangement is reversed in this specimen, so that the pleotelson lies below the endopod which, in turn, lies below the exopod. This ventral orientation provides information about the organism that is not commonly available in fossils, but it also make comparison with other species difficult.

The specimen is further unusual in exhibiting evidence of being in the pre-molt condition which has also not been reported in the fossil record. One line of evidence for this stage in development is that the exoskeleton is apparently extremely thin and transparent. The transparency is indicated because the eyes, which are dorsal and sessile, are visible from the ventral surface. The cuticle appears to have been very thin because it has been pressed flat without fracturing or distortion, and some of the pleurae lie on top of one another and the lower pleuron is visible through the upper one. An extant specimen of Cirolana sp. from Panama is also transparent and the eyes and its facets are clearly visible when viewed from the ventral side. This animal, which is preserved in the spirit collection in the Department of Geology, Kent State University (KSU D1075), appears to be in the intermolt condition so that transparency is not the most important criterion for recognizing the pre-molt condition.

Cirolana garassinoi exhibits an additional feature that confirms the pre-molt condition. Paired, thick, opaque structures are positioned on pereiomeres II-IV. The structures are lenticular in plan view with a nearly straight anterior margin and a convex posterior margin. They are transversely flat and slightly arched longitudinally. The anteriormost pair are about 1.7 mm wide and about 0.75 mm long; those on pereionite III are about 2.0 mm wide and 0.8 mm long; those on pereionite IV are about 1.3 mm wide

and 0.5 mm long. As they are positioned on the specimen, they appear to be imbricated with the structures of pereionite II overlapping those on pereionite III and those on pereionite III overlapping those on pereionite IV. This imbricate positioning may be the result of preservational flattening and distortion. The pair on pereionite II are situated in a more axial position than those on the other pereiomeres and they become progressively more lateral in position posteriorly. Most of the surface of the structures is smooth, vitreous, and amber or black and opaque, but the rims are either chalky or very light tan and translucent.

In an attempt to investigate the structures in more detail, the part and counterpart specimens were examined using an Inov-X System Model a4000 SL x-ray fluorescence unit. The diameter of the detector, ca 14 mm, is large enough that the elemental composition was integrated over nearly the entire specimen and some of the surrounding matrix. The elements that were most abundant in the samples of part and counterpart were phosphorous, ranging between 79,710 and 238,439 ppm, and calcium, ranging between 531,318 and 579,185 ppm. There was no systematic difference between the values determined on the part and counterpart. It is tempting to suggest that the phosphorous, at least, may be concentrated in the dermolith structures; however, the size of the detector is large enough that this conclusion cannot be drawn with certainty. The high calcium value is likely attributable to the isopod being preserved in limestone.

Structures very similar to those described above were first noted by Klapow (1972) in Excirolana chiltoni collected from Scripps Beach, La Jolla, California. Klapow termed the structures dermoliths and interpreted them as sites of calcium and phosphorus mineral storage during the pre-molt condition. The structures he described were situated on pereiomeres IV and V and were different in outline. They were more complexly sculpted, had a stalk that extends dorsally to contact the dorsal integument, and exhibited a crispate margin. Klapow (1972, p. 572) also noted that the dermoliths increased in size throughout the pre-molt phase and concluded that they functioned for storage of calcium and phosphorus salts. He associated the structures with the dorsal integument and indicated that they arose from the mineralized layer of the dorsal integument. extended downward into the body cavity, and were visible through the dorsal integument (Klapow, personal communication 2008). To my knowledge, this is the only time that storage sites for mineral salts have been associated with the dorsal surface.

There is a robust literature on calcium storage during the molt cycle of isopods, but it seems to be confined almost exclusively to terrestrial forms. Greenaway (1985) summarized what was then known about the process and related calcium storage to the biphasic molting cycle characteristic of isopods (Tait, 1917). Calcium sequestering during the pre-molt phase occurs as development of deposits on the sternal elements of pereiomeres I-IV resulting from dissolution of calcium from the posterior part of the exoskeleton (Greenaway, 1985, p. 437). Upon casting off the posterior part of the exoskeleton, the calcium is mobilized and serves to harden the newly formed posterior

exoskeleton. The details of this process have been studied from morphological, chemical, and physiological standpoints in a series of papers subsequently (Ziegler, 1997; Ziegler and Miller, 1997; Zidar et al., 1998; Ziegler and Merz, 1999; Glötzner and Ziegler, 2000; Moreau and Rigaud, 2002; Fabritius and Ziegler, 2003; Ziegler et al., 2005). Notably, the ultrastructure of the deposits has been recognized to be up to three discrete layers of amorphous calcium carbonate deposited as minute spherules (Ziegler and Miller, 1997), presumably functioning for rapid dissolution and mobilization.

This work has recently led to the recognition of a scenario involving progressive adaptation of isopods to a terrestrial lifestyle (Fabritious et al., 2005). Recognizing that marine isopods have little need to sequester calcium because the element is abundant in seawater, these animals do not typically form mineral storage structures during the pre-molt phase. Likewise, aquatic isopods are able to extract calcium from their environment and, although some aquatic forms do store calcium, the need to do so is less than for terrestrial isopods who have their food resources as their only source of the element. As a result of these observations, Ziegler and Miller (1997) and Fabricius et al. (2005) have suggested evolutionary sequences in which the storage of calcium salts becomes progressively more sophisticated as animals radiated from semi-aquatic to moist terrestrial and finally to dry terrestrial environments. Certainly, the observation that a progression from single layered to 3-layered calcium deposits is well documented.

The discovery of Cirolana garassinoi in which well developed dermoliths occur in a Cretaceous, marine isopod introduces the possibility that the sequence and the requirements for calcium sequestering may not follow that precise pathway. It is possible that geologically older marine isopods had mechanisms for storing and remobilizing mineral salts, including calcium and phosphorus, and that this mechanism may have pre-adapted marine isopods for a subsequent terrestrial lifestyle. Klapow documented both calcium and phosphorus in the dermoliths of Excirolana chiltoni. Because phosphorus is not abundant in seawater, it may be possible that the development of dermoliths in a Cretaceous marine species may have served primarily as a storage site for phosphorus and only secondarily for the more readily available calcium (Klapow, personal communication, 2008) It is also possible that modern marine isopods have evolved more efficient means of extraction of calcium from seawater that obviates the need to store calcium salts during molting.

Certainly, calcium storage by marine crustaceans is well known. Herrick (1911) described the formation of paired gastroliths in the American lobster, *Homarus americanus*, during the molt cycle, but he questioned the significance of the structures as sources of calcium for hardening of the new cuticle. Without doubt, development of gastroliths is better known in non-marine decapods (Glaessner, 1969; Greenaway, 1985), but the midgut gland within the marine decapods is also a site for storage of calcium (Greenaway, 1985). Thus, the process of calcium sequestration occurs in marine as well as non-marine crustaceans and interpreting the precise pathway by which it permitted isopods or decapods to adapt to terrestrial environments must involve an historical perspective.

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