Fossil sponge gemmules, epibionts of *Carpopenaeus garassinoi* n. sp. (Crustacea, Decapoda) from the Sahel Alma Lagerstätte (Late Cretaceous, Lebanon)

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ABSTRACT

The fossil crustaceans from the Sahel Alma Lagerstätte (Late Cretaceous, Lebanon), housed in the collection de Paléontologie of the Muséum national d'Histoire naturelle, Paris, were examined in order to highlight the presence of epibionts. Marine sponge gemmules were recognized and are described for the first time on the rostrum of a new shrimp *Carpopenaeus garassinoi* Charbonnier n. sp. The exceptional conditions of fossilization in the Sahel Alma Lagerstätte also permitted the preservation of the gemmule germination and the first development stage of the young sponge. If the shrimp does not appear to benefit from the association, it ensures the transport and the colonization of new territories for the sponge. This association sponge/shrimp is not known either in the recent or in the past. It represents one of the first observations of a fossil shrimp epibiont. *Carpopenaeus garassinoi* Charbonnier n. sp. is the youngest record for the genus *Carpopenaeus* Glaessner, 1945 which was previously known from the Tithonian of Zandt (Germany) and from the Cenomanian of Lebanon (Hakel, Hadjoula Lagerstätten).

KEY WORDS
Crustacea,
Decapoda,
Carpopenaeus,
gemmules,
sponges,
epibionts,
Sahel Alma,
Lagerstätte,
Santonian,
Lebanon,
Paleoparasitology,
new species.

RÉSUMÉ

Des gemmules d'éponges fossiles, épibiontes de Carpopenaeus garassinoi *Charbonnier n. sp. (Crustacea, Decapoda) dans le Lagerstätte de Sahel Alma (Crétacé supérieur, Liban).*

Les crustacés fossiles du Lagerstätte de Sahel Alma (Crétacé supérieur, Liban), conservés dans la collection de Paléontologie du Muséum national d'Histoire naturelle (Paris), ont été observés afin de mettre en évidence la présence d'épibiontes. Des gemmules d'éponges marines ont été reconnues et sont décrites pour la première fois sur le rostre d'une nouvelle crevette *Carpopenaeus garassinoi* Charbonnier n. sp. Les conditions exceptionnelles de fossilisation dans le Lagerstätte de Sahel Alma ont également permis la conservation de gemmules en sortie de dormance et des premiers stades de développement de la jeune éponge. Si la crevette ne paraît pas profiter de l'association, elle assure le transport et la colonisation de nouveaux milieux pour le spongiaire. Cette association éponge/crevette n'est pas mentionnée dans la nature actuelle ni dans le registre fossile. Elle représente l'un des premiers cas d'épibiontie connus pour une crevette fossile. *Carpopenaeus garassinoi* Charbonnier n. sp. est le plus récent représentant du genre *Carpopenaeus* Glaessner, 1945 connu jusqu'à présent dans le Tithonien de Zandt (Allemagne) et le Cénomanien du Liban (Lagerstätte de Hakel et de Hadjoula).

MOTS CLÉS
Crustacea,
Decapoda,
Carpopenaeus,
gemmules,
éponges,
épibiontes,
Sahel Alma,
Lagerstätte,
Santonien,
Liban,
Paléoparasitologie
espèce nouvelle.

INTRODUCTION

The study of interspecific relationships past and present is of great interest for the understanding of the environments and paleoenvironments. Competition, commensalism, mutualism, predation and parasitism relationships have had a great influence on the evolution and coevolution of species.The search for epibionts is a way of approaching these relationships particularly in the fossil record where these organisms may be fossilized at the same time as their basibiont. The term "epibiont" is used here to refer to a living organism attached on another living organism. There are variations of this definition and for some authors (e.g., Taylor & Wilson 2002), the basibiont may be an inert body. Since the discovery of the epibiontic relationship, many questions arise: 1) is the relation specific or accidental? 2) did the epibiont settle on after the death of the basibiont? 3) does the relationship have a cost or benefit for the epibiont or the basibiont? 4) is the relationship specific to a given environment or paleoenvironment? and 5) can the relationship be sustained during evolution?

We first looked for epibionts on fossil fishes from the Muséum national d'Histoire naturelle, Paris, particulary in places well-known for the quality of fossilization (Konservat-Lagerstätten). We did not find any epibionts but we did find perfectly preserved cutaneous tumours in the Monte Bolca Lagerstätte (Eocene, Italia), attesting to paleopathology (Petit 2010). Whilst pursuing this work with the Cretaceous fossils from the Lebanese Lagerstätten, we discovered by chance a new shrimp species with an unknown form of epibiontism: some marine gemmules attached to the rostrum of this crustacean.

GEOLOGICAL SETTING

The examined material comes from the chalky laminated limestones of Sahel Alma in northwestern Lebanon, *c.* 20 km northeast of Beirut. This locality is one of the most famous Late Cretaceous fossil Konservat-Lagerstätten of Lebanon which include Hadjoula, Hakel, Maifouk and En Nammoura. These localities are known for their sub-lithographic limestones yielding varied and exquisitely preserved fossils comprising fishes (Forey *et al.* 2003; Gayet *et al.* 2003), reptiles (Dalla Vecchia *et al.* 2001), arthropods (Garassino 1994), annelids (Bracchi & Alessandrello 2005), and ammonoid and coleoid cephalopods (Wippich & Lehmann 2004; Fuchs 2006). Amongst the arthropods, crustaceans are the most common fossils. Over the past 150 years, they have been reported and revised by various authors (Brocchi 1875; Fraas 1878; Dames 1886; Glaessner 1945; Roger 1946; Förster 1984; Garassino 1994, 2001; Larghi 2004; Garassino & Schweigert 2006; Feldmann 2009).

The "fish-beds" of the Sahel Alma Lagerstätte were described by Ejel & Dubertret (1966) as "a small patch of Senonian chalk, plotted on the surface of the Turonian" in reference to the very small size of the outcrop. The precise age of Sahel Alma was discussed by Zumoffen (1926), Roger (1946), and Ejel & Dubertret (1966). All the authors agree that Sahel Alma is Senonian in age. The most precise study was carried out by Ejel & Dubertret (1966) who analyzed the foraminiferan assemblage of the sediment and concluded that it is Late Santonian in age. Thus Sahel Alma is younger than the other Lebanese Lagerstätten such as Hadjoula and Hakel, which are of Cenomanian age (Wippich & Lehmann 2004).

During the Cretaceous, Lebanon and the whole Arabian Peninsula were part of the African platform in the northern part of the Gondwana continent (Philip *et al.* 1993). Ferry *et al.* (2007) proposed dividing the Cretaceous of Lebanon into three parts: 1) Valanginian-Late Aptian; 2) late Albian-Turonian; and 3) post-Turonian-Eocene. The first period is represented by several depositional sequences, each bounded by emersion surfaces. These sequences are tectonically-controlled and start with the deposition of volcaniclastics that may continue into the overlying, deepening-up, shallow-water marine deposits. The second period corresponds to the emplacement of a large system of carbonate platforms that covered much more of the Arabian craton. In this scenario, mild oscillations of relative sea-level are responsible for a spectacular sandwich of shallow-water (often rudist-bearing) carbonate facies alternating with finely-bedded or even laminated mudstones from Mount Lebanon. The lithographic limestones from the Hadjoula, Hakel and En Nammoura Lagerstätten belong to this second period and where probably deposited in small shallow basins corresponding to intra-shelf depressions. The Cenomanian-Turonian boundary corresponds to the beginning of a deepening trend that peaks in the Early Turonian age. The third period corresponds to an acceleration of the drowning of the Arabian craton, probably as a response to the beginning of the collisional trend responsible for the closing of the Tethys. On the Levant platform, deposition of micritic limestones and chalks begins after the Turonian age and continues until the Eocene. The Santonian Sahel Alma Lagerstätte belongs to this third period and its chalky limestones were probably deposited in much deeper conditions than those recognized in Hadjoula or Hakel.

MATERIAL AND METHODS

All the decapod crustaceans from the Sahel Alma Lagerstätte, housed in the collection de Paléontologie of the Muséum national d'Histoire naturelle, Paris, were observed in a search for epibionts (*c.* 60 specimens). The epibionts found on the rostrum of *Carpopenaeus garassinoi* Charbonnier n. sp. (specimen MNHN.F.A33532) were studied and photographed in place, either after ultra-violet illumination or else under white light. Some epibionts were extracted using tweezers to be studied and photographed in either white light or scanning electron microscopy (SEM). One epibiont was extracted to be studied in thin section. The shrimp was preserved anatomically complete as a compression in right lateral view. The specimen was exposed on the surface of a chalky laminated limestone slab. The epicuticle was relatively well-preserved but showed numerous cracks due to the compaction. For a more detailed description the sample was partially manually prepared with a fine needle. The paleontological description follows the systematics proposed by De Grave *et al.* (2009) and Schweitzer *et al.* (2010).

ABBREVIATIONS

CL	cephalothoracic length, excluding rostrum: linear distance between the ocular incision and the dorsal posterior margin of the cephalothorax;
CH	cephalothoracic height, linear distance perpendicularly measured in the branchiocardiac region from the dorsal margin to the ventral margin;
MNHN.F	Muséum national d'Histoire naturelle, Paris (France), paleontology collection.

SYSTEMATIC PALAEONTOLOGY

Classe MALACOSTRACA Latreille, 1802
Order DECAPODA Latreille, 1802
Suborder DENDROBRANCHIATA Bate, 1888
Infraorder PENAEIDEA de Haan, 1849
Superfamily PENAEOIDEA Rafinesque, 1815
Family CARPOPENAEIDAE Garassino, 1994

Genus *Carpopenaeus* Glaessner, 1945

TYPE SPECIES. — *Carpopenaeus callirostris* Glaessner, 1945 by original designation.

INCLUDED SPECIES. — *Carpopenaeus callirostris* Glaessner, 1945; *C. septemspinatus* (Dames, 1886); *Carpopenaeus peterbuergeri* Schweigert & Garassino, 2005.

Carpopenaeus garassinoi Charbonnier n. sp.
(Fig. 1)

TYPE MATERIAL. — Holotype (MNHN.F.A33532, collection Arambourg).

TYPE LOCALITY. — Sahel Alma Lagerstätte (*c.* 20 km northeast of Beirut), Lebanon.

TYPE HORIZON. — Late Cretaceous sublithographic limestones from the Sahel Alma quarry (Late Santonian after Ejel & Dubertret [1966]).

ETYMOLOGY. — In honor of Dr. Alessandro Garassino (Museo Civico di Storia Naturale di Milano, Italy), a specialist in the palaeontology of decapod crustaceans.

STUDIED MATERIAL. — Only the holotype is currently known.

OCCURENCES. — Known only from the type locality.

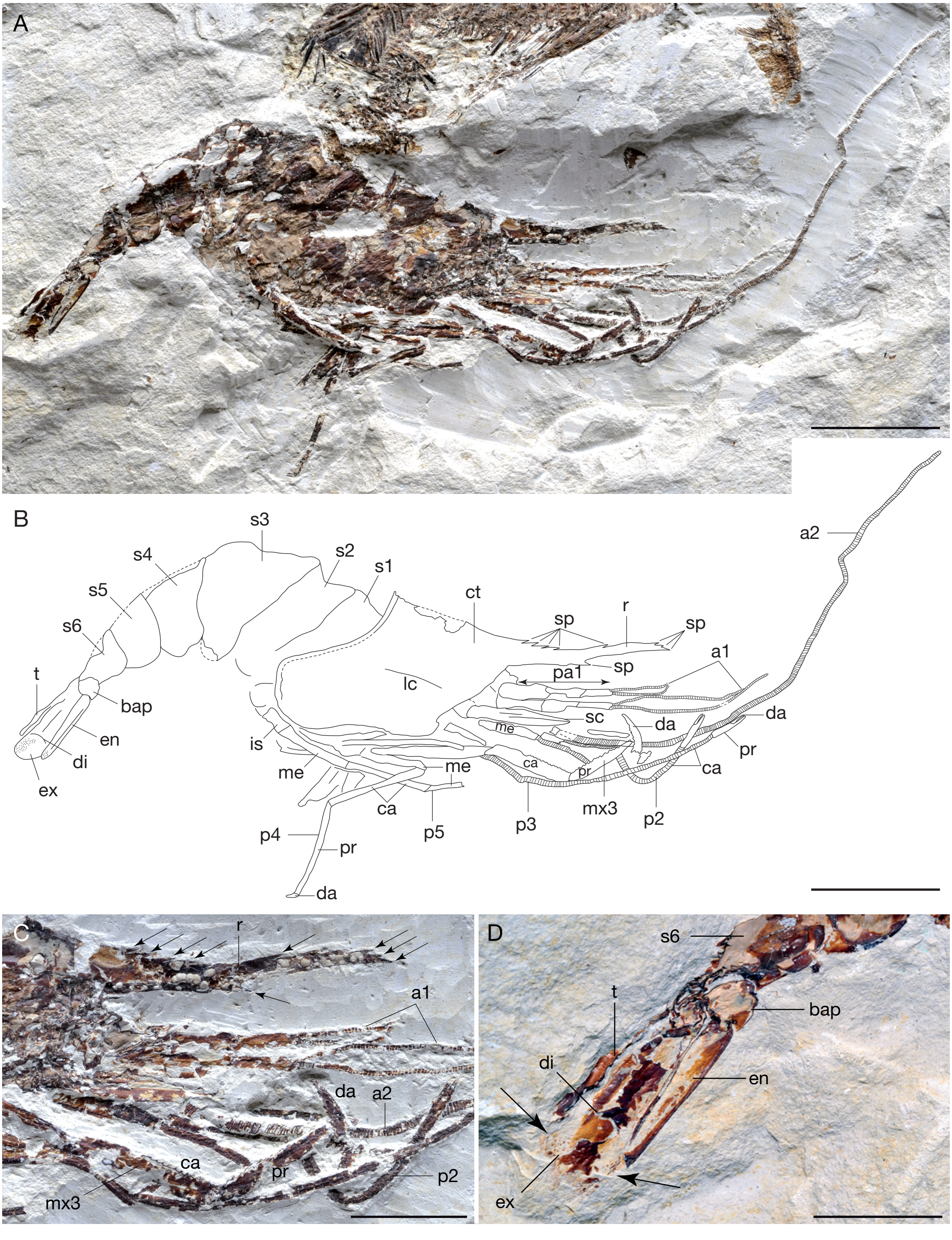
DIAGNOSIS. — Large species of *Carpopenaeus*; rostrum very elongated, curved upward distally, with four basal suprarostral spines, one median suprarostral spine, one median subrostral spine and three distal spines; third maxilliped well-developed, with serrated ventral margin; pereiopods 2 and 3 very elongated, with multiarticulate carpus; pereiopods 4 and 5 thin and achelate; basipodite well-developed; exopod with rounded diaresis and distal part bearing very small pits.

DESCRIPTION

Subrectangular cephalothorax, height nearly equal with length (holotype: CL = *c.* 22 mm, CH = *c.* 21 mm), with short longitudinal carina at mid-height (Fig. 1A, B); anterior margin fragmented; ventral margin not clearly visible; posterior margin slightly sinuous with a thin ridge; very elongated rostrum curved upward distally, with four basal suprarostral spines, one median suprarostral spine, one median subrostral spine and three distal spines (Fig. 1C); ornamentation smooth.

Cephalic appendages well-preserved (Fig. 1A, B): antennulae (a1) composed of long antennular peduncle with three segments diminishing in length distally and two long and thin multi-articulated flagellae (preserved length: *c.* 25 mm, Fig. 1B, C); antennae (a2) composed of antennal peduncle with a very long multi-articulated flagellum (preserved length: *c.* 90 mm); scaphocerite well-developed, oblong and pointed with a longitudinal lateral carina. – Third maxilliped relatively long ending in dactylus (Fig. 1B, C), ventral margin of carpus, propodus and dactylus bearing one row of small teeth (serrated pattern);

FIG. 1. — *Carpopenaeus garassinoi* Charbonnier n. sp. (holotype, MNHN.F.A33532, collection Arambourg) from the Sahel Alma Lagerstätte (Late Santonian, Lebanon): **A**, specimen flattened in right lateral view, note the exquisite preservation with cephalothorax, abdomen and appendages in connection; **B**, line drawing of the holotype; **C**, detail of the cephalic region showing the rostrum with its spines (black arrows), the antennulae, the base of one antenna, the 3rd maxilliped with serrated ventral margin and the 2nd pereiopod with multiarticulate carpus; **D**, detail of the tail fan, note the well-developed basipodite, the rounded uropods with diaresis on exopod and the distal part of each uropod uniformly covered by very small pits (black arrows). Abbreviations: **a1**, antennula; **a2**, antenna; **bap**, basipodite; **ca**, carpus; **ct**, cephalothorax; **da**, dactylus; **di**, diaresis; **en**, endopod; **ex**, exopod; **is**, ischium; **lc**, longitudinal carina;



me, merus; **mx3**, maxilliped 3; **p2-p5**, pereiopods 2 to 5; **pr**, propodus; **pa1**, antennular peduncle; **r**, rostrum; **sc**, scaphocerite; **s1-s6**, somites 1 to 6; **sp**, spine; **t**, telson. Scale bars: A, B, 2 cm; C, D, 1 cm.

Pereiopod 1 not preserved; pereiopods 2 and 3 very elongated, both displaying antennae-like multiarticulate carpus, ending in minute chela; pereiopods 4 and 5 almost equal in size, thin and smooth, achelate, ending in small dactyli.

Abdomen convergent distally with smooth ornamentation; somites 1 and 6 very reduced, somite 2 badly preserved, shorter than somite 3, somite 3 large and well-developed, somites 4 and 5 short; pleurae of somites ventrally smooth and rounded (Fig. 1B); pleopods not preserved; telson short (length: *c.* ⅔ length of uropods), pointed, only known in section; basipodite of the uropods well-developed, subcircular (Fig. 1D); uropodal exopod and endopod elongated, almost equal in length with lateral margins smooth and rounded inferior margins; exopod with median longitudinal carina and a well-developed diaresis with crescent-shaped suture delimiting a distal part uniformly covered with very small pits; endopod slender, with median longitudinal carina and distal part also bearing very small pits (Fig. 1D).

Discussion

We agree with the diagnosis of *Carpopenaeus* proposed by Glaessner (1945) and revised by Garassino (1994). The newly described form here is clearly a representative of this genus based upon the following main features: very long rostrum with one subrostral tooth; longitudinal carina on the carapace, pereiopods 2 and 3 with multiarticulated carpus, and exopod with a diaresis. *Carpopenaeus garassinoi* Charbonnier n. sp. differs from the Tithonian species *Carpopenaeus peterbuergeri* Schweigert & Garassino, 2005 in that it has: 1) much thinner pereiopods 4 and 5; 2) pereiopods 2 and 3 of equal length whereas in *C. peterbuergeri* pereiopods 2 longer than pereiopods 3; and 3) the absence of a branchiocardiac carina well-developed in *C. peterbuergeri*. *Carpopenaeus garassinoi* Charbonnier n. sp. differs from both Cenomanian species *C. callirostris* Glaessner, 1945 and *C. septemspinatus* (Dames, 1886) in that it has: 1) a rostrum with four basal suprarostral spines and only one median suprarostral spine whereas the rostrum of *C. Callirostris* shows six suprarostal spines uniformly distributed and that of *C. septemspinatus* is shorter with seven suprarostal spines and one distal subrostral spine; 2) the short longitudinal lateral carina on the carapace that is more elongated in *C. Callirostris* and duplicated in *C. septemspinatus*; 3) a third maxilliped with ventral margin serrated and composed of small rounded teeth whereas those of *C. callirostris* and *C. septemspinatus* display a row of small spines; 4) the well-developed basipodite; and 5) the distal part of each uropod is covered by small pits whereas the ornamentation is smooth on the uropods of *C. callirostris* and *C. septemspinatus*. Moreover, the uropodal exopod of *C. septemspinatus* does not show any diaresis.

In conclusion, *Carpopenaeus garassinoi* Charbonnier n. sp. from the Santonian Sahel Alma Lagerstätte is the youngest representative of the genus *Carpopenaeus* Glaessner, 1945 which was previously known from the Tithonian of the Lithographic Limestones of Zandt, Germany (Schweigert & Garassino 2005) and from the Cenomanian of Lebanon (Hakel, Hadjoula Lagerstätten).

DESCRIPTION OF THE EPIBIONTS

The epibionts of *C. garassinoi* Charbonnier n. sp. are particularly visible after UV illumination (Fig. 2). They occupy a large part of the rostrum, and are made up of white structures assuming four different forms.

Isolated ovoid elements

Isolated structures in the proximal part of the rostrum, with smooth wall (Figs 2; 3[a-f]). These ovoid elements are between 500 µm and 1 mm long and 400 µm to 500 µm wide. Elements a and b are broken and show a thick outer wall clearly visible in optical microscopy (Fig. 3A). Element b was extracted for observation under SEM, the external layer is of varying thickness, from 20 to 60 µm. Its appearance is also variable, being either amorphous or spongy (Fig. 3E), in both cases the limit between the external layer (coat) and the spongy interior is clear-cut. Element c (Fig. 3A-D) was also extracted. It is ovoid and shows a spherical bud visible in Figure 3B, but invisible in place as it is turned toward the cuticle (see arrow in Fig. 3A). The part opposite the bud is more visible on the photograph and forms a small circular protuberance (Fig. 3B). The SEM analysis (Fig. 3D) shows that the bud is an expand-

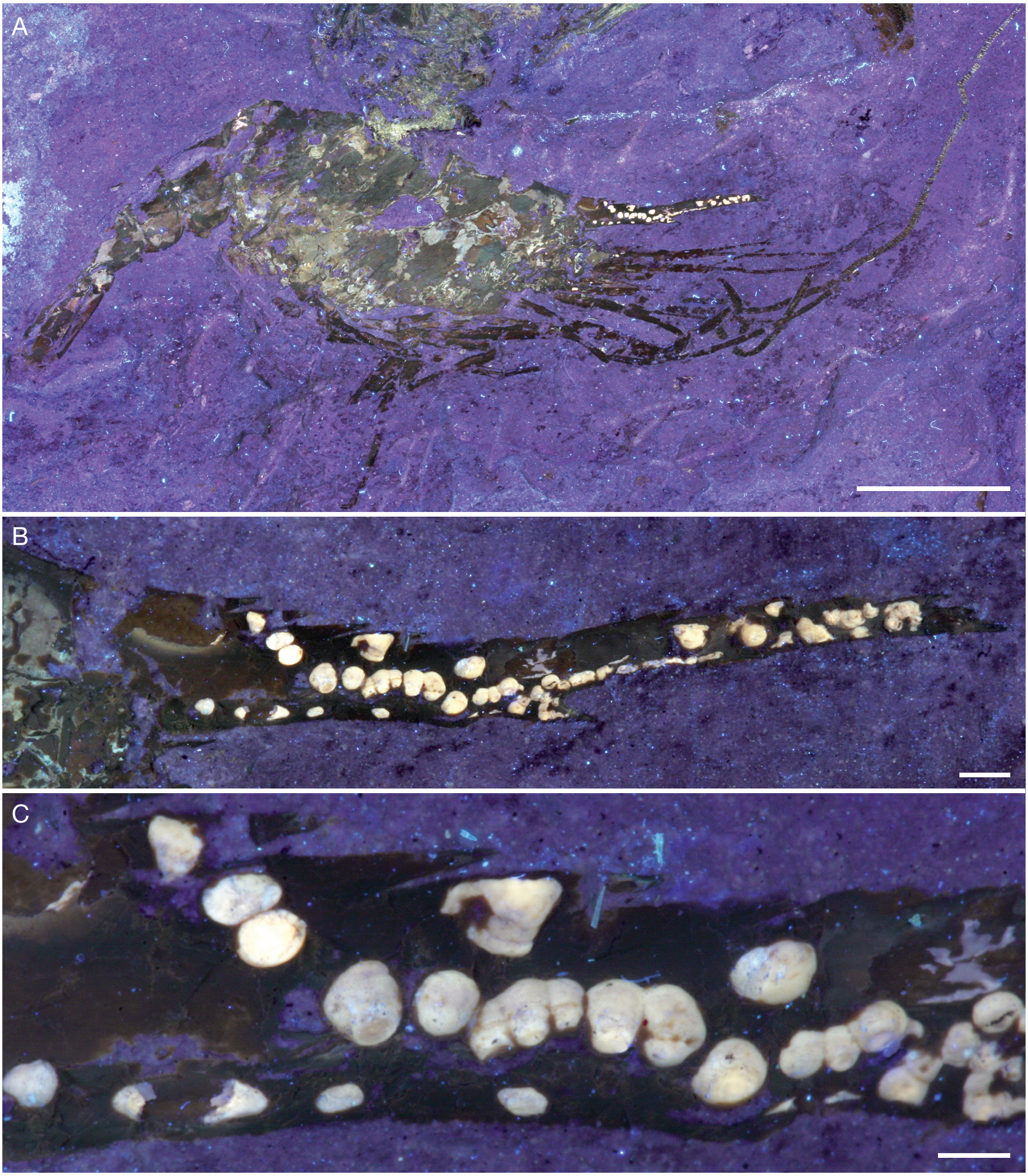


FIG. 2. — Sponge gemmules on the rostrum of the shrimp *Carpopenaeus garassinoi* Charbonnier n. sp. under UV light: **A**, general view of the shrimp, note the white color of the epibionts; **B**, general view of the rostrum; **C**, detail of the proximal part of the rostrum showing isolated gemmules or linked gemmules forming a network. Scale bars: A, 2 cm; B, C, 1 mm.

ing structure. A thin section (Fig. 3C) confirms the existence of this bud which presents a denser thick coat as does the element itself; in some places, the coat is no longer visible due to an artifact of cutting. The bud formation is connected to a radiant internal structure (see white star in Fig. 3C).

Interconnected ovoid elements

Smooth ovoid structures similar to the preceding ones but interconnected to form a network in the proximal part of the rostrum (Figs 3A[g-l]; 4A, B). After extraction, the element g shows the presence of an outer coat, which was partially torn, but quite visible on one part of the sample (Fig. 4A, B). It has an amorphous appearance; the maximum thickness is 50 µm.

Interconnected irregular elements

Structures also forming a network in the middle part of the rostrum, but of irregular size and shape (Figs 2; 3A[m-q and following ones]; 4C, D). Some elements, such as the element o, show a circular depression (Figs 3A; 4C[white star]). Element o (size: 600 × 650 µm) was extracted and its interfaces with the preceding element (Fig. 3A[n]) and the following one (Fig. 3A[p]) are flat and quite visible (Fig. 4C[white arrows]). Observation by SEM shows the spongy appearance and the absence of a coat at the junction between two elements (Fig. 4D).

Flattened irregular elements

Broad and flattened elements in the distal part of the rostrum, of irregular shape except for a globular element forming a kind of pore (Fig. 4E). The network structure is also seen; the elements becoming welded at the level of the narrowing of the rostrum (Figs 2B; 4E).

DISCUSSION

Epibionts are common in extant crustaceans but their presence in the fossil record is very rare and even unknown in fossil shrimps (Waugh *et al.* 2004; Fernandez-Leborans 2010). Fossil epizoans on the macruran decapods are reviewed and discussed by Simpson & Middleton (1985) and Feldmann (2003). Present-day shrimps show very diverse epibionts such as algae (Colorni 1989), cirripeds (Dawson 1957; Giri & Wicksten 2001), bryozoans (Giri & Wicksten 2001), hydrozoans (Widmer *et al.* 2010), bivalve molluscs and isopods (Itani *et al.* 2002), bacteria and diverse unicellular organisms (Fernandez-Leborans 2010), and also cysts of Trematoda Metacercariae (Jayasree *et al.* 2001).

Identification of epibionts

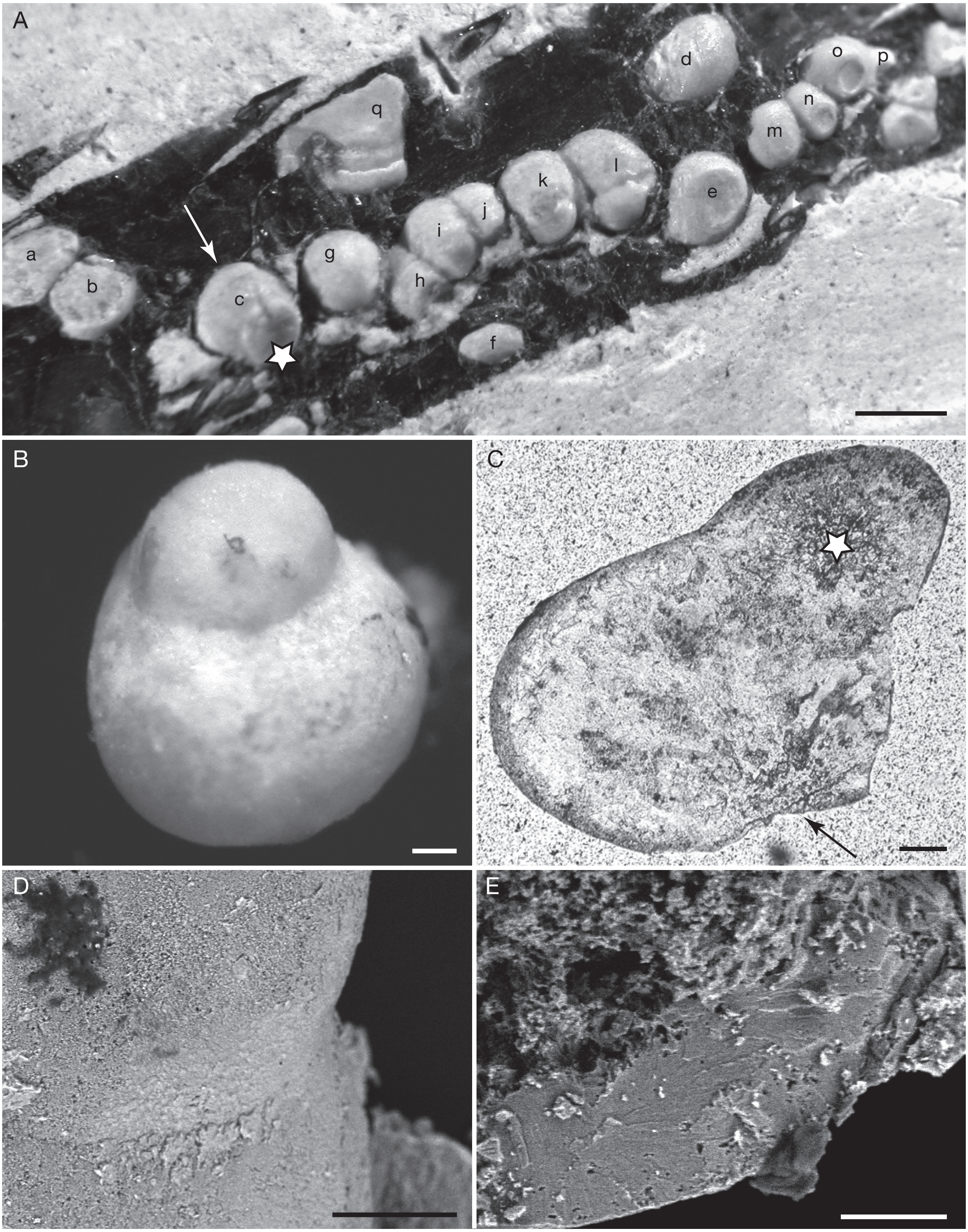
We consider that the fossilized organisms on the rostrum of *C. garassinoi* Charbonnier n. sp. are marine sponge gemmules. Several arguments support this interpretation:

1) the existence of isolated, thick-walled ovoid elements, whose size and structure are identical to those of recent sponge gemmules. Many Recent species of freshwater sponges and a few marine sponges are able to produce large number of gemmules when environmental conditions become unfavorable (Simpson & Fell 1974). As in *C. garassinoi* Charbonnier n. sp., they are made up of two parts: a protective outer acellular coat and an internal mass of cells containing reserve substances. Their size is altogether compatible with the one observed here;

2) the grouping of these ovoid structures into networks of varying size and shape as found in present day marine sponges. A very detailed study was conducted by Herlant-Meewis (1948). He studied the shape and distribution of the gemmules of the Recent marine sponge *Suberites ficus* (Johnston, 1842) that attaches to a snail shell. As on the rostrum of *C. garassinoi* Charbonnier n. sp., the gemmules are variable in size (250 µm to 1 mm), ovoid or more irregular in shape, either isolated or in networks, forming lines or clumps. Moreover, Simpson & Fell (1974) showed in another marine sponge, *Chalinula loosanoffi* (Hartman, 1958), several gemmules that may merge at the level of their coat during their development. These gemmules are genetically identical and are able to recognize each other during germination, when merging to form a new sponge (Pronzato & Manconi 1994);

3) the existence on the rostrum of *C. garassinoi* Charbonnier n. sp. of elements which represent

Fig. 3. — Sponge gemmules on the rostrum of *Carpopenaeus garassinoi* Charbonnier n. sp. from the Sahel Alma Lagerstätte: **A**, proximal part showing isolated ovoid elements (**a**-**f**) or grouped elements (**g**-**o**); **B**, detail of the surface of the ovoid element **c** after extraction and rollover, note the evidence of bud; **C**, detail of the ovoid element **c**, thin section through the bud (white star) and the circular



protuberance (black arrow); **D**, detail of the bud formation (element **c**) by SEM; **E**, detail of the isolated ovoid element **b** (SEM image), showing thick coat and intern spongy tissue. Scale bars: A, 1 mm; B-D, 100 µm; E, 50 µm.

the end of gemmular dormancy. In living marine sponges, gemmule hatching is caracterized by high metabolic activity and the breaking of the coat follows this phase (Jetton *et al.* 1987). We have no images of this phase in the marine environments, but it is possible to think that the budding observed for element c (Fig. 3B) precedes the breaking of the coat. Concerning the gemmules of recent freshwater sponges, the events are a bit different. There are very few metabolic events preceding hatching. The release of the material to the outside is done through a pore or micropyle which does not exist in marine gemmules (Jetton *et al.* 1987). This event has been photographed (see Hill & Hill 2002; Schill *et al.* 2006) and forms a similar bud to that observed in *C. garassinoi* Charbonnier n. sp. The end of dormancy is shown in the element o (Fig. 4C, D) which has lost its coat and which communicates with elements n and p through the spongy tissue. In the middle and distal parts of the rostrum, the phenomenon seems more advanced, the outer wall is no longer visible and the elements of the network have developed. The first initial elements of the new sponge seem to form themselves like this structure with a pore that can represent a young osculum (Fig. 4E);

and 4) the lack of spicules and of micropyle in the gemmule coat. In modern environments, the gemmule coat of freshwater sponges is armed with spicules, but these spicules are rare or absent in the gemmules from the marine environment (Simpson & Fell 1974). The palaeoenvironment of *C. garassinoi* Charbonnier n. sp. is clearly marine (see Roger 1946) and so the lack of spicules and micropyle in the structures attached to the rostrum is in accordance with the hypothesis of marine sponge gemmules.

SPONGE GEMMULES IN MODERN ENVIRONMENTS

Simpson & Fell (1974) identified numerous actual sponge species with gemmules. The freshwater sponges releasing gemmules are very common but those from the marine environment are much less abundant. The frequency of gemmules in freshwater seems related to the discontinuity of the environment and the stronger likehood of drying-up (Pronzato & Manconi 1994). These environmental constraints result in a thicker more complex coat (therefore more durable) and the presence of spicules in the coat, contributing to dispersal. This dispersal may be achieved by attachment to a moving support that may or not may be alive. The gemmules of 11 species of marine sponges have been described by Simpson & Fell (1974). They made a general and comparative morphological analysis of these gemmules: 1) micropyle is always absent; 2) there are no spicules in the coat of the five species of Suberitidae and two species of Clionidae; and 3) there are spicules in the coat of four species of Haploscleridae. Thus, the Cretaceous gemmules described in the present study are probably very close to the first two families.

FOSSIL GEMMULES

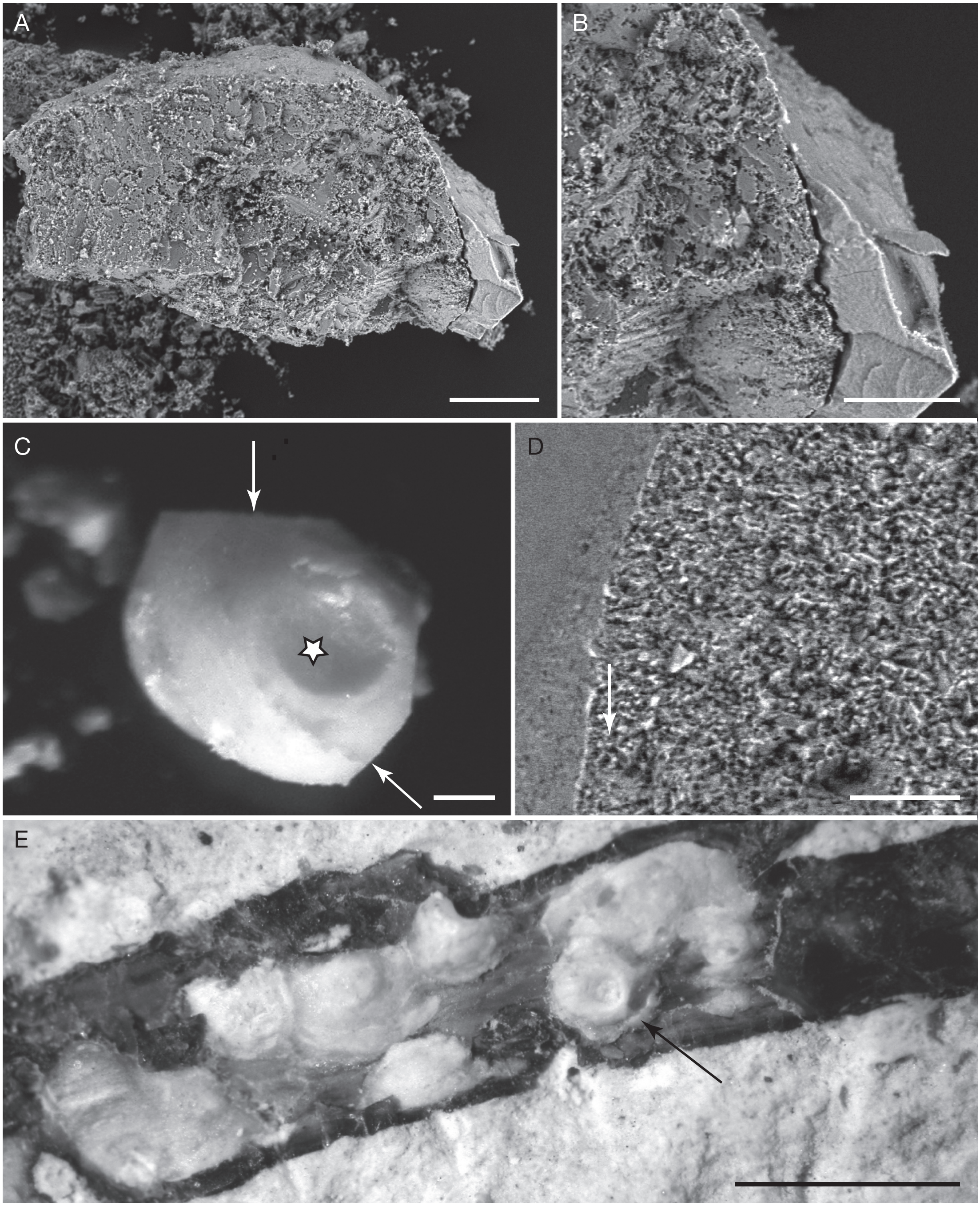
Previously, fossil sponge gemmules have been observed only in freshwater settings. The first ones along with their associated spicules were described by Ott & Wolkheimer (1972) in the Early Cretaceous of Patagonia. Subsequently, Harrison & Warner (1986) in the Holocene of Canada and Pisera & Saez (2003) in the Miocene of Chile have completed these observations.

The lack of fossil marine gemmules is linked to two main factors identifiable at present but certainly transposable in the past life: 1) the low number of marine sponge species with gemmules, a situation related to the stability of the marine environment; and 2) the lack of spicules in most marine gemmules which does not contribute to their fossilisation whereas the spicules are quite easily observable and identifiable in the sediments.

THE SPONGES IN THE LATE CRETACEOUS OF LEBANON

In his stratigraphic and micropaleontologic work, Saint-Marc (1974-1975) did not mention any

FIG. 4. — Sponge gemmules on the rostrum of *Carpopenaeus garassinoi* Charbonnier n. sp. from the Sahel Alma Lagerstätte: **A**, interconnected ovoid element *g* (see Fig. 3A) after extraction, showing the remain of the coat; **B**, detail of Fig. 4A showing the coat and the intern spongy tissue; **C**, upper surface of the interconnected irregular element **o** (see Fig. 3A), after extraction, showing the flat



interfaces (white arrows) at the junction between two neighbouring elements and a circular depression (white star); **D**, detail by SEM of the interconnected element **o**, showing a junction interface between two elements, the intern spongy tissue and the absence of coat; **E**, distal part of the rostrum showing the gemmule development (flattened irregular elements) and a globular structure forming a kind of pore (black arrow). Scale bars: A, C,100 µm; B, 50 µm; D, E, 1 mm.

sponges in the Senonian rocks of Lebanon. Only sponge spicules are reported at the base of the Cenomanian age. However, Flexer (1968) indicated that the Senonian sediments of Israel and adjacent areas such as Lebanon contain macro-organisms such as ammonites, bivalves, and sponges. Therefore, it seems likely that marine sponges were indeed present in the palaeoenvironment of the shrimp, *C. garassinoi* Charbonnier n. sp.

HYPOTHESIS ON THE PRESENCE OF GEMMULES ON THE ROSTRUM OF *C. GARASSINOI* CHARBONNIER N. SP.

It is likely that the holotype of *C. garassinoi* Charbonnier n. sp. was contaminated during feeding or breeding on sponge bioherms which may have been far from the basin of Sahel Alma. Indeed, shrimps sometimes make long migrations and the environment in which the epibiont attaches itself to the carapace can differ significantly from the site of fossilization. The fact that no sponge has been described in the Sahel Alma Lagersätte is consistent with the latter hypothesis. When sponges degenerate in adverse conditions, they constitute a carpet of gemmules which are forms of resistance, but also forms of dispersal and colonization of new environments (Pronzato & Manconi 1994). During the movement of the crustacean, the rostrum is certainly the first part to come into contact with the gemmules which attach themselves all the more easily since the rostrum has thorny structures. During migration, the shrimp may meet with new conditions inducing the gemmule hatching we have described above. The epibiont relationship here is probably not specific. It is an opportunistic association for the sponge which will find means of transport (phoresy) and dispersal. This relationship may have negative effects on the basibiont: if too many epibionts are attached to the carapace, the crustacean navigation may be hindered thereby contributing to predation. In this case, the death of the shrimp may well be related to the presence of the sponge gemmules.

The exceptional conditions of fossilization in the Sahel Alma Lagerstätte explain the exquisite preservation of the shrimp and the gemmules. The sediments from the Sahel Alma Lagerstätte were probably deposited in anoxic and anaerobic conditions, with a rapid burial of the organisms (Gayet *et al.* 2003). This last consideration excludes post-mortem colonization of the shrimp. The compaction of the sediments flattened and distorted the original appearance of the gemmules, particularly the developing forms.

CONCLUSION

The search for epibionts enables us to highlight here a special relationship between two fossil species: a sponge and a shrimp (*C. garassinoi* Charbonnier n. sp.). The shrimp does not appear to obtain any advantage, whereas the sponge (*via* gemmules) is transported (phoresy) which contributes to dispersal and the encounter of a more favorable marine setting. This observation is new in present-day and fossil environments. The conditions of fossilization have moreover permitted the preservation of a dynamic phenomenon: the hatching of sponge gemmules.

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