Late Cretaceous crest-bearing shrimps from the Sahel Alma Lagerstätte of Lebanon

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Decapod crustaceans are the most diverse group of fossil invertebrates from the Upper Cretaceous Sahel Alma Lagerstätte (Lebanon, Middle East). They are mainly represented by abundant crest-bearing shrimps which were first described as *Penaeus libanensis*. We review this species applying the new systematic nomenclature and we propose a more complete description based on 54 unpublished specimens. This review leads to the erection of *Palaeobenthesicymus* gen. nov. and to the new combination *Palaeobenthesicymus libanensis* that is the oldest record of the family Benthesicymidae. A neotype is herein designated. Detailed comparisons with extant analogues suggest that the crest bearing shrimps inhabited relatively deep water settings most probably exceeding 150 m, at the transition between the lower circalittoral and the upper bathyal zones, under dysphotic or aphotic conditions.

Key words: Arthropoda, Crustacea, Decapoda, Lagerstätte, Cretaceous, Santonian, Sahel Alma, Lebanon.

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Introduction

Interest in the Late Cretaceous Lebanese Lagerstätten dates back to the thirteenth century and the chronicle of Jean de Joinville. This French seneschal related in the *Histoire de saint Louis* that during his stay to Sayette (today Sidon, Lebanon), someone offered to the French king Louis IX a marvelous stone which once split in two parts revealed the shape of a marine fish (Petitot 1824). The three classical localities, Hakel, Hadjoula, and Sahel Alma (Fig. 1), contain a remarkably preserved marine fauna dominated by fishes (Actinopterygii, Chondrichthyes) and arthropods (Crustacea, Isopoda, Thylacocephala), with also numerous soft-bodied organisms (Coleoidea, Polychaeta). Hakel, known since the time of the crusades (Davis 1887), and Hadjoula, first recorded in the 1890s (Hay 1903; Woodward 1942), are both Cenomanian in age (Hückel 1970). Sahel Alma, known for at least 150 years (Davis 1887), is late Santonian in age (Roger 1946; Ejel and Dubertret 1966), and is now apparently worked out. By far, the most frequent animals of the Sahel Alma biota are the fishes with a prolific and varied assemblage of chondrichthyans and osteichthyans, both found in large numbers on bedding planes (Forey et al. 2003; Gayet et al. 2003). Arthropods are represented by decapods (Roger 1946; Garassino 1994, 2001), isopods (Feldmann 2009; Feldmann and Charbonnier 2011), and thylacocephalans (Schram et al. 1999; Lange et al. 2001) that are more frequently preserved as compressions on the surface of the chalky limestone beds. More enigmatic and also very abundant at Sahel Alma are the so-called thylacocephalans that were unusual "bivalved" arthropods armed with well-developed prehensile appendages (see Vannier et al. 2006 for complete references). The soft-bodied organisms are mainly represented by coleoid cephalopods (Roger 1946; Lukeneder and Harzhauser 2004; Fuchs et al. 2009). Marine worms also occur (Roger 1946) but the specimens are poorly preserved (Bracchi and Alessandrello 2005). Among decapod crustaceans, the crest-bearing shrimps are one of the most abundant fossil invertebrates. They were first described and illustrated by Brocchi (1875) as *Penaeus libanensis* (see Fig. 2A). Brocchi's description was based on a single specimen well preserved in lateral compression. This description of *P. libanensis* is one of the first scientific works on fossil crustaceans from the Lebanese Lagerstätten and has been discussed subsequently by numerous authors. Dames (1886) questioned the attribution of this species to *Penaeus* Fabricius, 1798. Later, Van Straelen (1930) redescribed succinctly the species and confirmed its attribution to this genus although his study was based on composite material. Glaessner (1945) provided the most important review, based on 26 specimens from the National History Museum of London. He assigned the crest-bearing shrimps to the extant *Benthesicymus* Bate, 1881. At the same time, Roger (1946)—who did not know

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Fig. 1. Map of Lebanon showing the main fossiliferous localities yielding exceptionally preserved Cenomanian faunas (Hadjoula, Hakel, En Nammoura, Maifouk, Lagerstätten) and Santonian faunas (Sahel Alma Lagerstätte).

Glaessner's (1945) work—proposed his own redescription of the species. Unfortunately, his review was also based on composite material that mixed several species and genera. Thus, since the work of Glaessner (1945), no review has been made so far by using modern techniques and detailed comparisons with recent analogues. In this paper, we review Brocchi's (1875) species and propose a more complete and modern description based on 54 unpublished specimens. We make detailed comparison between the crest-bearing shrimps from the Sahel Alma Lagerstätte and their Recent analogues of the family Benthesicymidae Wood-Mason in Wood-Mason and Alcock, 1891. These comparisons coupled with the geological data permit analysis of the palaeoecological significance of this species and refinement of the interpretation of the palaeoenvironment of the Sahel Alma Lagerstätte.

Institutional abbreviations.—MNHN.F, Collection de Paléontologie, Muséum national d'Histoire naturelle, Paris, France.

Other abbreviations.—CH, height of cephalothorax: linear distance measured perpendicular to the dorsal margin from its intersection with the branchiocardiac groove to the ventral margin; CL, length of cephalothorax, exclusive of rostrum: linear distance between the ocular incision and the dorsal posterior margin of the cephalothorax; TL, total length, linear distance measured dorsally between the ocular incision and the distal extremity of the telson; P1–5, pereiopods 1 to 5; s1–6, abdominal somites 1 to 6.

Geological setting

The fifty-four examined samples come from the chalky laminated limestone of Sahel Alma in northwest Lebanon, ca. 20 km northeast of Beirut. This locality is one of the most celebrated Upper Cretaceous fossil Konservat-Lagerstätten of Lebanon which include Hadjoula, Hakel, Maifouk and En Nammoura (Fig. 1). These localities are known for their sub-lithographic limestone 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 and Alessandrello 2005), and ammonoid and coleoid cephalopods (Wippich and Lehmann 2004; Fuchs 2006). Amongst the arthropods, crustaceans are the most common fossils. Over the past 150 years, they were reported and revised by various authors (Brocchi 1875; Fraas 1878; Dames 1886; Glaessner 1945; Roger 1946; Förster 1984; Garassino 1994, 2001; Larghi 2004; Garassino and Schweigert 2006; Feldmann 2009).

The "fish-beds" of the Sahel Alma Lagerstätte were described by Ejel and 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 and Dubertret (1966). All the authors agree that Sahel Alma is Senonian. The most precise study was performed by Ejel and Dubertret (1966) who analyzed the foraminiferan assemblage of the sediment and assigned a late Santonian age. Thus Sahel Alma is younger than the other Lebanese Lagerstätten such as Hadjoula and Hakel, which are of Cenomanian age (Wippich and 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: (i) Valanginian–late Aptian, (ii) late Albian–Turonian, and (iii) 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 in relative sea-level are responsible for a spectacular sandwich of shallow-water (often rudist-bearing) carbonate facies alternating with finely-bedded or even laminated mudstone of Mount Lebanon. The lithographic limestone from the Hadjoula, Hakel and En Nammoura Lagerstätten belongs to this second period and was probably deposited in small shallow basins corresponding to intra-shelf

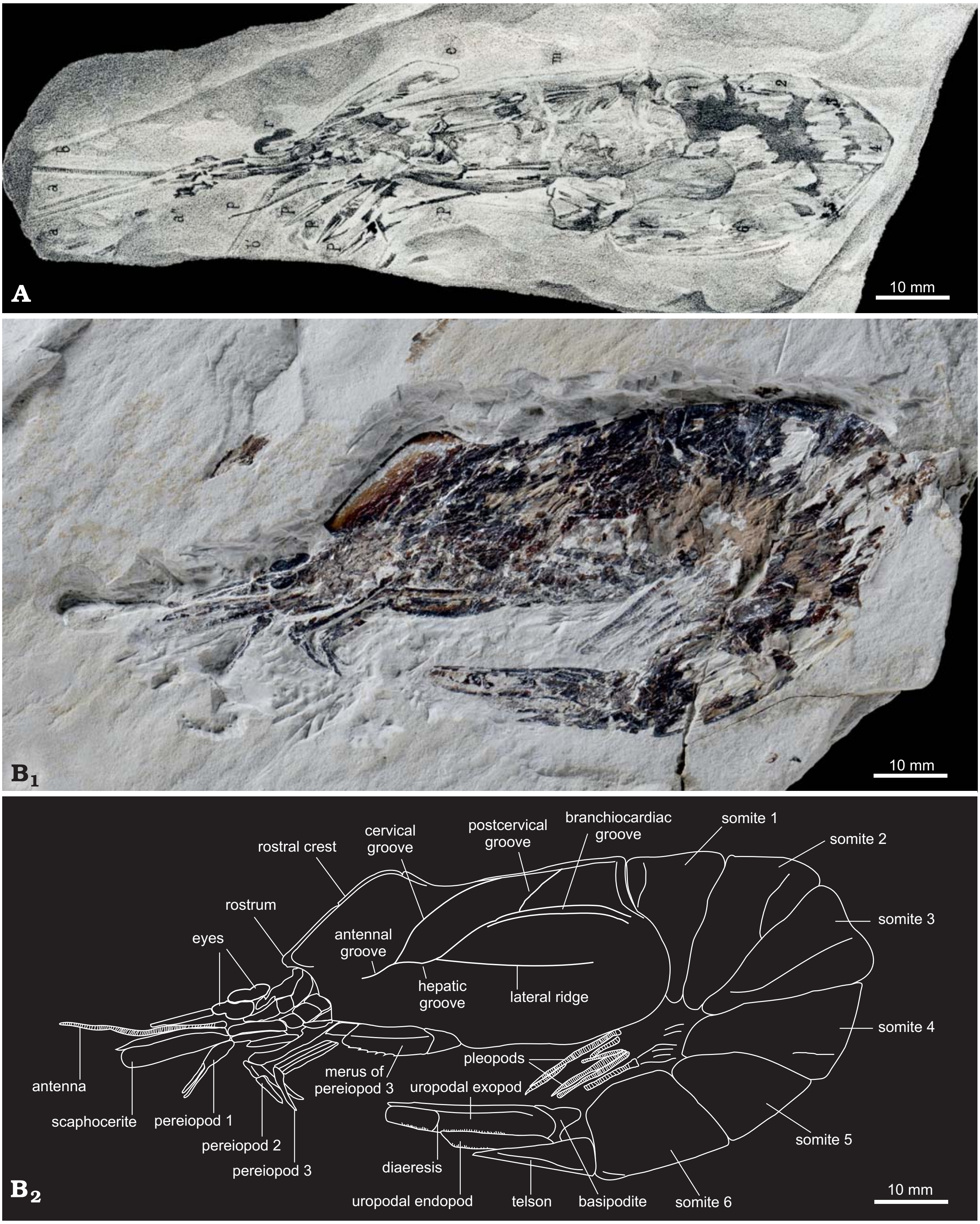

Fig. 2. Type material of crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875) from the Sahel Alma Lagerstätte (upper Santonian, Lebanon). **A**. Reproduction of Brocchi's (1875) lithography, left lateral view, specimen considered to be definitively lost. **B**. Complete specimen (MNHN.F.A30593, Arambourg collection), left lateral view, specimen chosen as neotype for *P. libanensis* (Brocchi, 1875). Photograph (B_1) and camera lucida line drawing (B_2), note the well-developed rostral crest and the bilobed eyes.

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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 and continues until the Eocene. The Santonian Sahel Alma Lagerstätte belongs to this third period and its chalky limestone was probably deposited in much deeper conditions than those recognized in Hadjoula or Hakel.

Material and methods

The studied specimens come from the Sahel Alma Lagerstätte (Lebanon). They were collected during the scientific mission of professor Camille Arambourg in Syria and Iran (1938–1939). They are housed in the palaeontological collections of the Muséum national d'Histoire naturelle, Paris. The fossils are compressed and laterally flattened on bedding planes. Only some specimens show dorso-ventral compression. Most of them are preserved in anatomical connection. The cuticle is relatively well preserved but shows numerous cracks due to the compaction. Some of the best-preserved specimens were partially prepared manually with a fine needle to make more detailed description. This preparation was made easy by the softness of the surrounding rock. Specimens were studied using a Wild Heerbrugg TYP 308700 binocular and a camera lucida. The line drawings were made by one of the authors (DA). The whole material consists of 54 specimens from the Fossil Invertebrate collections (MNHN.F.A30582–A30587, A30589–A30599, A30601, A30602, A305605–A305609, A30705–A30715, A30717–A30719, A30735, A30739–A30741, A30805–A30808, A32428, B18862) and from the Fossil Vertebrate collections (MNHN.F.SHA545, SHA1532, SHA1852dg, SHA2981). The type material of Brocchi (1875) was not found either in the old Collections de La Sorbonne now housed at the Université Pierre and Marie Curie (Paris 6) or in the collections of the Muséum national d'Histoire naturelle, Paris. Comparisons with extant shrimps (*Benthesicymus*, *Penaeus*) have been made with the specimens housed in the Collections de Zoologie from the Muséum national d'Histoire naturelle, Paris. The paleontological arrangement of this study follows the systematics proposed by De Grave et al. (2009) and Schweitzer et al. (2010).

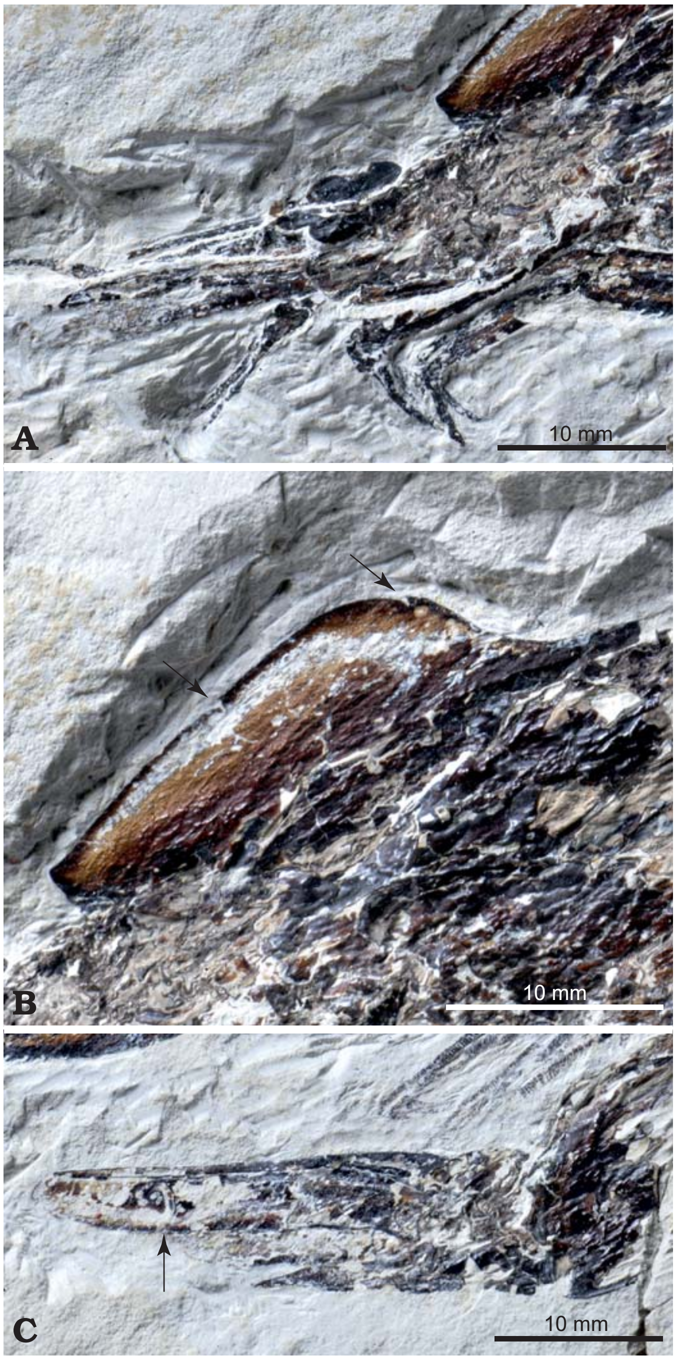

Fig. 3. Anatomical details of the neotype (MNHN.F.A30593, Arambourg collection) of crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875) from the Sahel Alma Lagerstätte (upper Santonian, Lebanon). **A**. Anterior part showing the pair of bilobed eyes and some fragmentary cephalic appendages, note the short rostrum with blunt anterior end. **B**. Rostral crest, very thin, with a thickened dorsal ridge, note two indentations (black arrows) probably corresponding to small healed wounds. **C**. Tail fan with well-developed uropods, note the very elongate uropodal exopod bearing a rounded diaeresis (black arrow).

Systematic palaeontology

Class Malacostraca Latreille, 1802

Order Decapoda Latreille, 1802

Suborder Dendrobranchiata Bate, 1888

Superfamily Penaeoidea Rafinesque, 1815

Family Benthesicymidae Wood-Mason in Wood-Mason and Alcock, 1891

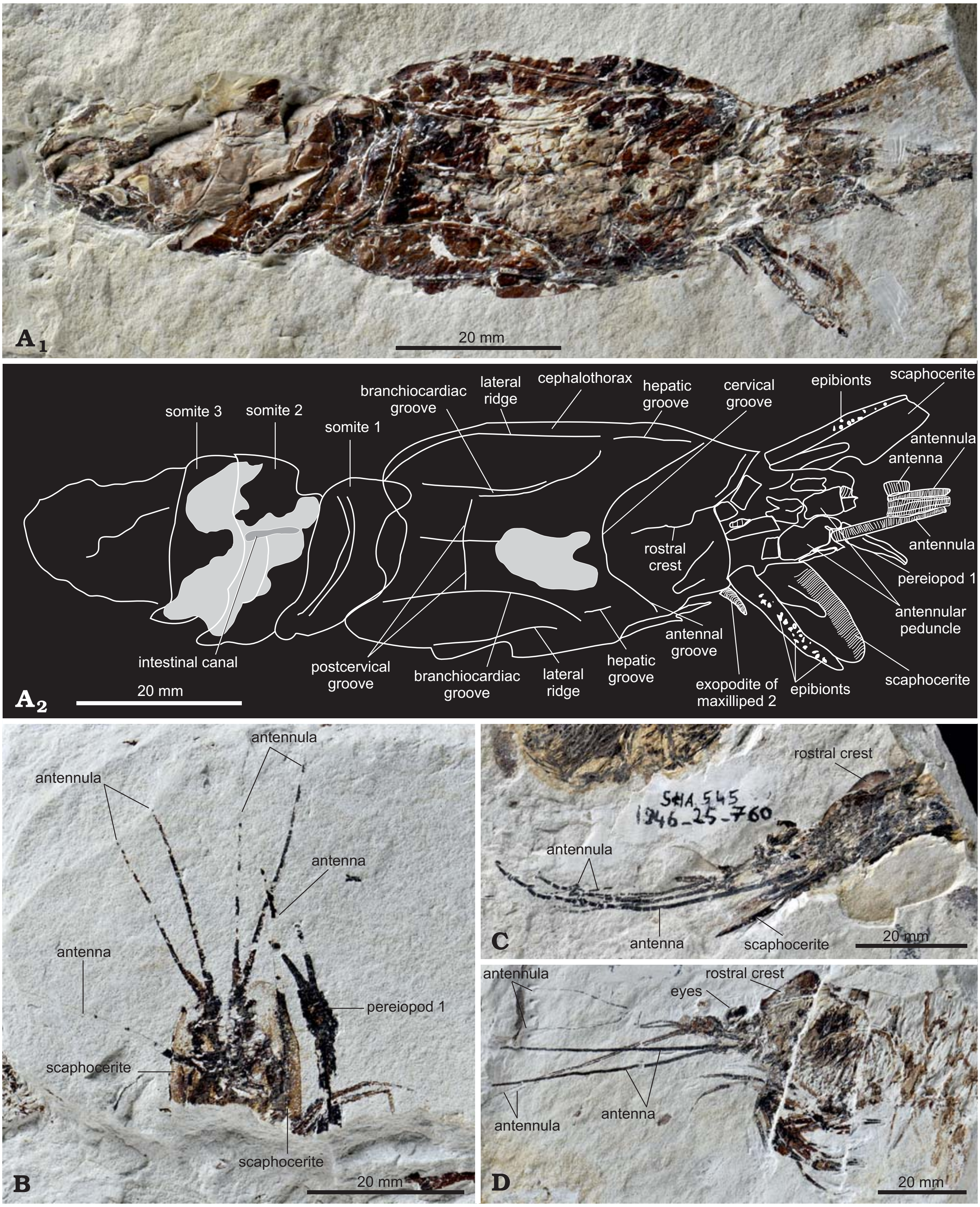

Fig. 4. The crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875) from the Sahel Alma Lagerstätte (late Santonian, Lebanon). **A**. Sub-complete specimen (MNHN.F.A30595), dorsal view (A_1) and camera lucida line drawing (A_2), note the cephalothoracic grooves, the scaphocerites with white small spheres on the outer margins (epibionts), and the fragment of intestinal canal; grey areas correspond to mineralized soft-tissues. **B**. Cephalic region of fragmentary specimen (MNHN.F.A30585), ventral view, note the two pairs of antennulae. **C**. Fragmentary specimen (MNHN.F.SHA.545), left lateral view, cephalic region showing well-preserved antennulae and antennae, note the very pointed distal extremity of the scaphocerite. **D**. Sub-complete specimen (MNHN.F.A30599), left lateral view, note the eyes and the multiarticulated antennae.

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Genus *Palaeobenthesicymus* nov.

Etymology: From Latin *palaeo*, ancient, and *benthesicymus*, modern genus that means "inhabitant of depth" after Bate (1888).

Type species: *Penaeus libanensis* Brocchi, 1875; Sahel Alma Lagerstätte, upper Santonian, Lebanon.

Diagnosis.—Subrectangular cephalothorax with very short rostrum; hypertrophied rostral crest, laterally compressed, obliquely triangular and very thin; bilobed eyes; very narrow cervical groove, intercepting dorsal margin posterior to the crest; short antennal groove; postcervical groove weakly marked, joined to branchiocardiac groove; well-marked branchiocardiac groove curved anteriorly, limited by two parallel ridges, joined to hepatic groove; short hepatic groove; well-marked longitudinal ridge, sub-parallel to the ventral margin, joined to branchiocardiac and hepatic grooves; s5 and s6 dorsally carinate; uropodal exopod with diaeresis.

Discussion.—*Palaeobenthesicymus* gen. nov. differs from the extant *Benthesicymus* Bate, 1881, as follows: the configuration of the cephalothoracic grooves, the subcomplete reduction of the rostrum, the absence of rostral teeth, the presence of bilobed eyes and, the diaeresis on the uropodal exopods. For the same reasons, the new genus differs also from the other genera of Benthesicymidae: *Gennadas* Bate, 1881, *Bentheogennema* Burkenroad, 1936, *Benthonectes* Smith, 1885, and *Altelatipes* Crosnier and Vereshchaka, 2008. However, *Palaeobenthesicymus* gen. nov. has different morphological characters such as the very thin, soft and flexible cuticle, the short rostrum, the rostral crest and, the configuration of the cephalothoracic grooves, which are typical of Benthesicymidae, justifying its ascription to this family.

Stratigraphic and geographic range.—Upper Santonian, Upper Cretaceous, (after Ejel and Dubertret 1966), Nannofossil Biozone UC13 Burnett, 1998—UC17 pro-parte Sissingh, 1977 (Silvia Gardin, personal communication 2010), Sahel Alma Lagerstätte (Lebanon, Middle East).

Palaeobenthesicymus libanensis (Brocchi, 1875) comb. nov.

Figs. 2–9.

1875 *Penaeus libanensis* sp. nov.; Brocchi 1875: 609, 610, pl. 21 (see Fig. 2A for original lithography).
1886 ?*Penaeus libanensis* Brocchi; Dames 1886: 554, 555.
1922 *Penaeus libanensis* Brocchi; Balss 1922: 131.
1929 ?*Penaeus libanensis* Brocchi; Glaessner 1929: 310.
1930 *Penaeus libanensis* Brocchi; Van Straelen 1930: 5.
1940 *Penaeus libanensis* Brocchi; Van Straelen 1940: 3.
1940 *Penaeus smyrnacus* sp. nov.; Van Straelen 1940: 4, 5; fig. 3.
1944 *Penaeus libanensis* Brocchi; Roger 1944: 848.
1945 *Benthesicymus libanensis* (Brocchi); Glaessner 1945: 645; fig. 4.
1946 *Penaeus libanensis* Brocchi: Roger 1946: 23–26 partim (not pl. 1, 3; figs. 15–17).
1965 *Benthesicymus libanensis* (Brocchi); Glaessner 1965: 117; fig. 6.
1967 *Benthesicymus libanensis* (Brocchi); Wolfart 1967: 98.
1969 *Benthesicymus libanensis* (Brocchi); Glaessner 1969: R447; fig. 253.2.
1975 *Benthesicymus libanensis* (Brocchi); Brugnoli Gioffredi et. al. 1975: 6, 7.
1994 *Benthesicymus libanensis* (Brocchi); Garassino 1994: 13, table 4.
1996 *Benthesicymus libanensis* (Brocchi); Briggs and Wilby 1996: 665.
2004 *Penaeus libanensis* Brocchi; Larghi 2004: 528.
2005 *Penaeus libanensis* Brocchi; Bracchi and Alessandrello 2005: 4.
2009 *Benthesicymus libanensis* (Brocchi); Feldmann 2009: 373.
2010 *Benthesicymus libanensis* (Brocchi); Schweitzer et al. 2010: 9.

Type material: Holotype of Brocchi (1875) presumably lost; neotype: MNHN.F.A30593 (Arambourg collection), herein designated.

Type locality: Sahel Alma Lagerstätte, Lebanon, Middle East.

Type horizon: Upper Cretaceous, upper Santonian (Nannofossil biozone UC13 Burnett, 1998—UC17 pro-parte Sissingh, 1977).

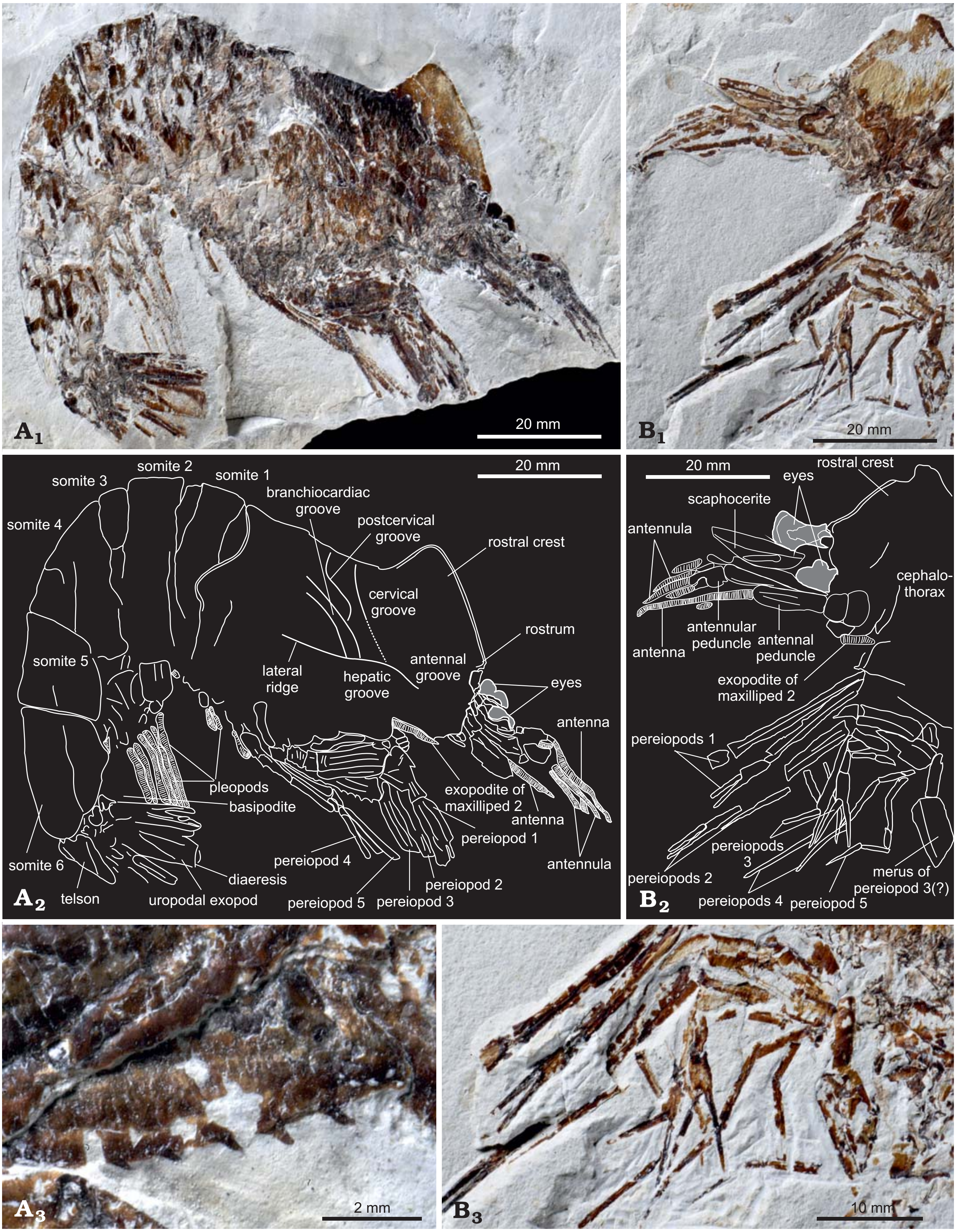
Material.—MNHN.F.A30582–A30587, A30589–A30599, A30601, A30602, A305605–A305609, A30705–A30715, A30717–A30719, A30735, A30739–A30741, A30805–A30808, A32428, B18862, SHA545, SHA1532, SHA 1852dg, SHA2981.

Diagnosis.—As for genus.

Synthetic description.—Large-sized shrimp with thin and slightly mineralized cuticle. Cephalothorax with obliquely triangular rostral crest, very thin, with a thickened dorsal ridge. Rostrum with blunt anterior end and without teeth. Cervical groove very narrow; branchiocardiac groove curved; postcervical groove weakly marked; inferior groove well developed sub-parallel to the ventral margin. Medio-dorsal ridge well-marked. Posterior margin with semi-circular curve in the inferior part. Pleon strong with short and high s1 to s5 all identical, s6 longer than the others. Compound eyes, ovoid, with median narrowing. Antennular peduncle with basal stylocerite; antennulae with two long flagella thick basally and tapering distally; antennal peduncle with well-developed scaphocerite (oval in outline and very thin) and long articulated flagellum. Third maxilliped short, with spines on the carpus. Pereiopods increasing in length posteriorly, P1 with short chelae, P2 and P3 with long and slender chelae; P4 and P5 very thin and achelate. Pleopods well developed, strong. Telson with pointed extremity and strong median ridge. Uropods with strong marginal ridge, uropodal exopod with semi-circular diaeresis, uropodal endopod longer than the telson. Intestine observable in the pleonal region. Description summarized after Brocchi (1875), Glaessner (1945), and Roger (1946) pro parte.

New observations.—Subrectangular cephalothorax (CH = 1/3CL; Fig. 2B). Rostrum very short with rounded distal extremity and smooth margins (Fig. 3A). Anterior margin with shallow ocular and antennal incisions. Anterior dorsal margin with hypertrophied rostral crest (Figs. 3B, 5A_1), very thin, compressed laterally, obliquely triangular, with thickened

Fig. 5. The crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875) from the Sahel Alma Lagerstätte (upper Santonian, Lebanon). → **A**. Sub-complete specimen (MNHN.F.A30582), right lateral view (A_1), note the well-developed rostral crest and the bilobed eyes; camera lucida line drawing (A_2); and detail of the merus of pereiopod 3 showing ventral spines (A_3). **B**. Well-preserved anterior part of a deformed specimen (MNHN.F.A30583), left lateral view (B_1); camera lucida line drawing (B_2); and detail of pereiopods (B_3).


A1
20 mm
B1
20 mm
20 mm
somite 1
somite 2
somite 3
somite 4
somite 5
somite 6
branchiocardiac
groove
postcervical
groove
rostral crest
cervical
groove
rostrum
lateral
ridge
hepatic
groove
antennal
groove
eyes
antenna
pleopods
basipodite
exopodite of
maxilliped 2
antenna
pereiopod 1
antennula
pereiopod 4
diaeresis
pereiopod 2
telson
uropodal exopod
pereiopod 5
pereiopod 3
A2
20 mm
rostral crest
eyes
scaphocerite
antennula
cephalo-
thorax
antennular
peduncle
antennal
peduncle
antenna
exopodite of
maxilliped 2
pereiopods 1
pereiopods
3
pereiopods 2
merus of
pereiopod 3(?)
pereiopods 4
pereiopod 5
B2
A3
2 mm
B3
10 mm

marginal ridge, triangular area with anterior angle narrower than posterior one, connection between crest and cephalothorax smooth, without ridge or carina (Fig. 3B). Posterior dorsal margin with small median ridge; posterior margin straight dorsally and semi-circular ventrally, bearing small ridge. Ventral margin poorly preserved, probably very thin. Cervical groove very narrow, slightly inclined, intercepting dorsal margin at an angle of ca. 35°, posterior to the rostral crest. Short antennal groove. Postcervical groove very weak, inclined, subparallel to cervical groove, joining the branchiocardiac groove at an angle of ca. 30°. Branchiocardiac groove well-developed, anteriorly curved and flanked by two parallel ridges, joining the hepatic groove anteriorly and the small ridge of the posterior margin. Hepatic groove short, slightly curved. Lateral ridge well-marked, longitudinally elongate in the middle height of the cephalothorax, slightly convex, subparallel to the ventral margin and joining the branchiocardiac and hepatic grooves (Figs. $2B_2$, $4A_2$, $5A_2$). Ornamentation of cephalothorax smooth, with very small, uniformly distributed pores.

Pleon with subrectangular somites; s1 slightly shorter than the others; s2–5 uniform in length; s6 subrectangular, longer than the other somites. Terga and pleurae of s1–6 smooth, with proximal margin reinforced by small ridge; terga with dorsal carina weak on s1–3 and well-marked on s5–6; pleurae with rounded ventral margin (Fig. $6A_1$, B, C). Intestinal canal parallel to the pleonal axis (Fig. $4A_2$), crossing s1–4 in the upper part of the pleon and s5 and s6 in lower part with a strong curvature from s5 (Fig. 6B). Telson triangular, with thick dorsal ridge and fringed lateral margins (Figs. $2B_2$, 6D).

Compound eye, elongated longitudinally, bilobed with anterior and posterior lobes separated by a dorsal narrowing (Figs. 3A, $5A_1$, $7A_4$); visual surface preserved as a quadrate ommatidia network (Fig. $8A_3$); ommatidia from the anterior lobe slightly smaller than those of the posterior lobe; ocular peduncle poorly preserved.

Cephalic appendages well preserved. Antennulae (a1) composed of antennular peduncle bearing two long multi-articulated flagella (length: ca. CL), very thick proximally and tapering distally (Fig. 4B–D); dorsal margin of antennular peduncle with small depression to accommodate the stalked eyes; triangular and pointed stylocerite attached to proximal margin of this depression. Antenna (a2) composed of antennal peduncle with three segments (distal segment is the shortest) and very long multi-articulated flagellum (length: ca. TL); lamellar and almost ovoid scaphocerite (Figs. $2B_2$, 4A, B), with fringed adaxial margin and opposite margin strengthened by a ridge separating from the lamellar part to form a pointed distal extremity (Fig. 4C); lamellar part rounded distally and reinforced along the two-thirds of its length by an oblique thickening. Scaphognathite with slender and crenulated posterior extension.

Thoracic appendages well preserved (Figs. $2B_2$, 5). First and second maxillipeds with multi-articulated exopodites composed of numerous short segments. Exopodite of maxilliped 2 well developed (Figs. $4A_2$, $5A_2$, E). Third maxilliped relatively long (ca. 40% CL), composed of slender segments decreasing in length distally, ending in a dactylus. Pereiopods 1–5 slightly increasing in length from first to fifth; P1–3 chelate, with outer surfaces reinforced by two longitudinal ridges (Figs. $2B_2$, 5B); P1, P2, and P3 chelae long and slender with occlusal opening narrow and occlusal margins of index and dactylus straight with a slight indentation; merus and carpus elongate (length: ca. 40% CL); P2 merus with distal spine above its articulation with carpus; P3 merus with denticulate ventral margin (Figs. $2B_2$, $5A_3$); P4 and P5 thin and elongate (length: ca. 1.4CL), both achelate, with outer surfaces reinforced by one longitudinal ridge; slender dactylus.

Abdominal appendages well preserved (Figs. 6, 7). Pleopods biramous, very long, equal in length, with two long multi-articulated flagella (length: ca. 33% CL) connected to well-developed protopodite; flattened and rounded protopodite, bearing transversally two opposite pairs of convex ridges (Fig. $7A_1$, A_2); petasma (modified endopodite of the first pleopod in copulatory appendage in a male decapod crustacean) with two distinct units (Fig. 6A): unit 1 composed of two thin elements joined on their distal extremity and unit 2 composed of one subtriangular scale with very rounded posterior margin and small parallel longitudinal furrows. Uropods with short coxopodite and large, stocky basipodite; very long uropodal endopod (ca. 45% CL) reinforced by longitudinal median ridge, rounded distal margin, inner lateral margin finely fringed; elongate uropodal exopod (ca. 60% CL) with well-marked semi-circular diaeresis, distal margin rounded, inner lateral margin finely fringed, outer margin thickened by a straight ridge (Figs. 3C, $5A_1$, A_2, $7A_3$, B).

Discussion.—After new observations of the Lebanese material from the MNHN, Paris, we do not agree with Brocchi (1875), Van Straelen (1930) and Roger (1946) who hypothesized that the rostral crest corresponded to the scaphocerite extended posteriorly. We agree with the observations of Glaessner (1945) and confirm that the rostral crest is clearly attached to the carapace. The descriptions proposed by Van Straelen (1930) and Roger (1946) are based on composite material that mixed different penaeid shrimps. Both authors described a well-developed rostrum bearing dorsal teeth. These characters are unknown in the crest-bearing shrimps and do not correspond to Brocchi's description. In fact, they probably correspond to another Cretaceous fossil shrimp from Sahel Alma: *Penaeus natator* Glaessner, 1945. Moreover, Roger (1946) confused the inferior groove with a well-marked lateral ridge, subparallel to the ventral margin.

After comparisons with the arguments and the line drawing proposed by Glaessner (1945: 696, fig. 1), we question his generic attribution to the extant *Benthesicymus* (see generic discussion above). According to the description of *Palaeobenthesicymus* gen. nov., we proposed the new combination *Palaeobenthesicymus libanensis* (Brocchi, 1875).

In addition, we question the validity of *Penaeus smyrnacus* Van Straelen, 1940 for several reasons: (i) the proposed description follows that of Brocchi's species, (ii) the illustration (Van Straelen 1940: pl. 1: 3) clearly shows a

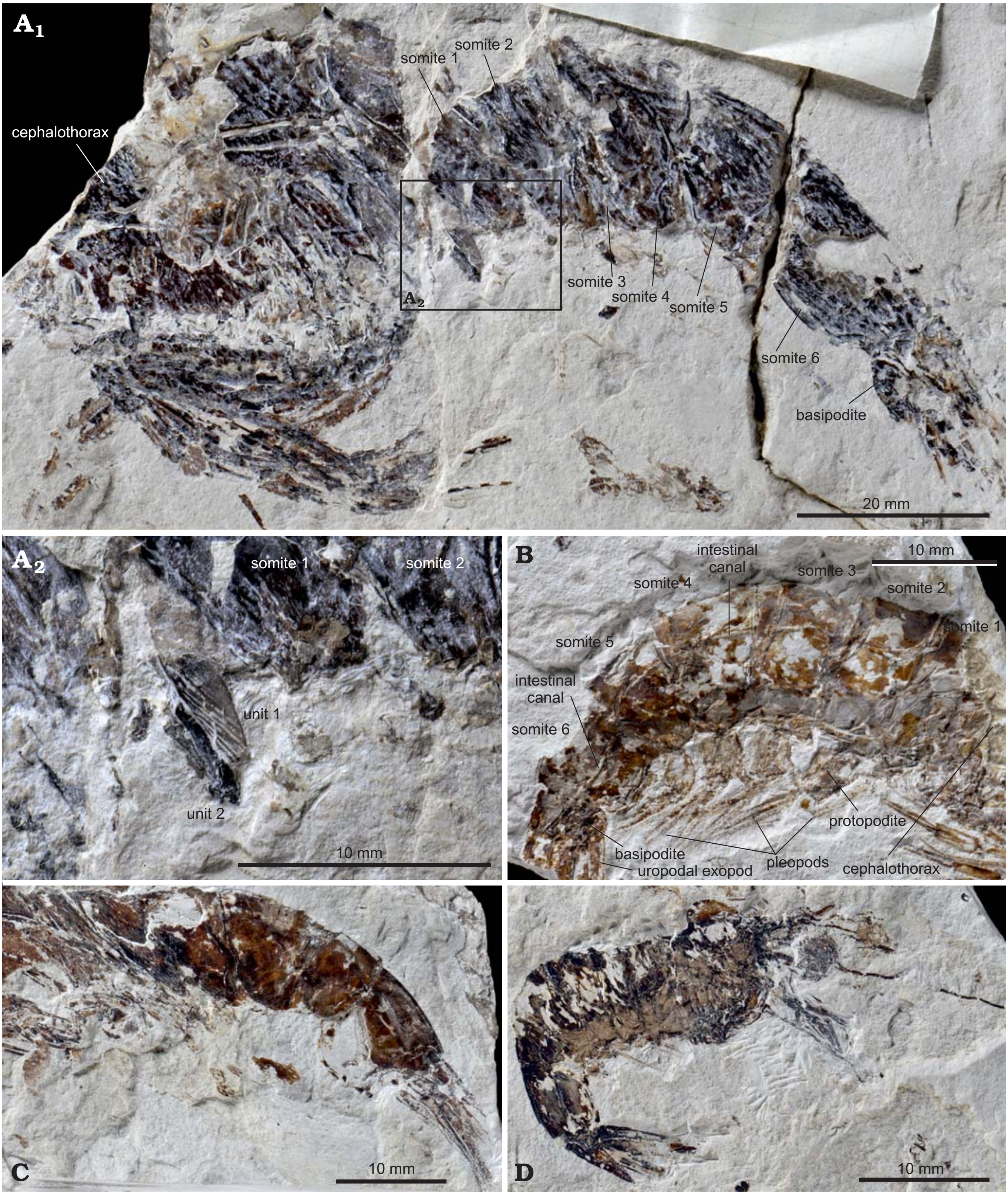


Fig. 6. The crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875) from the Sahel Alma Lagerstätte (late Santonian, Lebanon). **A**. Male specimen (MNHN.F.A30709), left lateral view (A_1), note the petasma, a modified endopodite of the first pleopod in copulatory appendage (black frame). Detailed view of the same petasma composed of unit 1 (two thin elements joined on their distal extremity) and unit 2 (subtriangular scale) (A_2). **B**. Pleon of fragmentary specimen (MNHN.F.A30708), right lateral view, note the well-developed pleopods connected to cylindrical protopodites and the long intestinal canal parallel to the pleonal axis. **C**. Pleon of sub-complete specimen (MNHN.F.A30602), left lateral view, note the rounded ventral margin of pleurae and the well-marked dorsal ridge on somites 5 and 6. **D**. Small specimen (MNHN.F.A30596), right lateral view, note the well-preserved tail fan.

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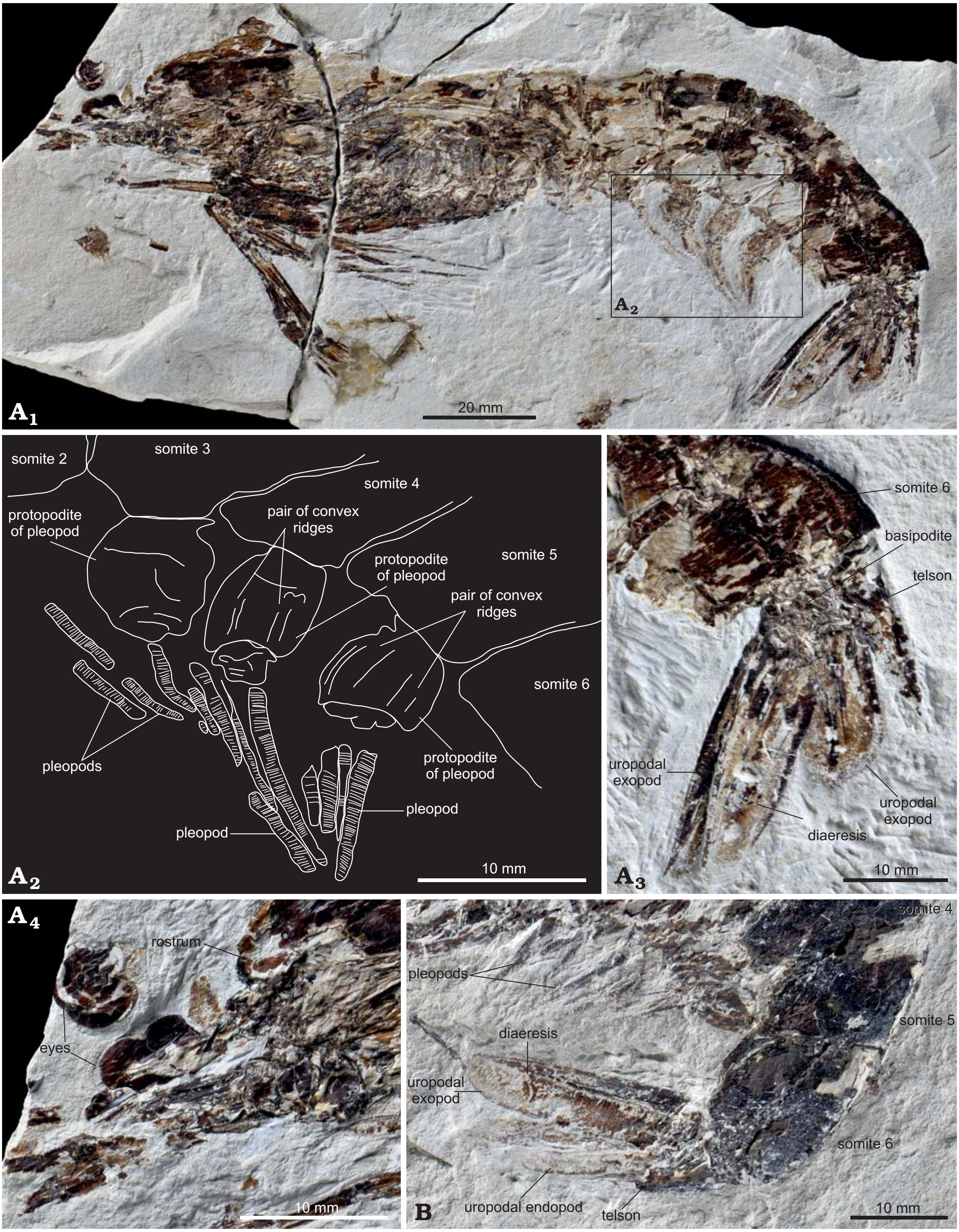
A1
A2
20 mm
somite 2
somite 3
somite 4
protopodite
of pleopod
pair of convex
ridges
protopodite
of pleopod
somite 5
pair of convex
ridges
somite 6
pleopods
protopodite
of pleopod
pleopod
pleopod
10 mm
somite 6
basipodite
telson
uropodal
exopod
uropodal
exopod
diaeresis
A3
10 mm
A4
rostrum
eyes
10 mm
somite 4
pleopods
diaeresis
somite 5
uropodal
exopod
somite 6
uropodal endopod
telson
B
10 mm

specimen with rostral crest, bilobed eyes and cephalothoracic grooves (e.g., curved branchiocardiac groove limited by two ridges) very similar to those of the Brocchi's species, and (iii) the specimen is preserved on a limestone slab very similar to those collected in the Sahel Alma Lagerstätte. Moreover, the holotype of *Penaeus smyrnacus* (specimen I.G. n°12747), originally housed in the collections of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium is not accessible (lost?); the type locality (Izmir, western Anatolia, Turkey) and the type age (Eocene) are very probably incorrect and linked to inversion of labels with another sample (Annelise Folie, personal communication 2010). For these reasons, we consider *Penaeus smyrnacus* to be a subjective junior synonym of *Palaeobenthesicymus libanensis* (Brocchi, 1875). In conclusion, based upon all the previous remarks, we consider it important to design a neotype for *Palaeobenthesicymus libanensis* because the holotype and sole specimen of Brocchi (1875) was not found either in the old Collections de La Sorbonne now housed at the Université Pierre & Marie Curie (Paris 6) or in the collections of the Muséum national d'Histoire naturelle, Paris. The neotype for *Penaeus libanensis* Brocchi, 1875 is the specimen MNHN.F. A30593 (Arambourg collection) that shows almost all the diagnostic characters of the species and also of the genus (Fig. $2B_1$). The type locality is the Late Cretaceous Sahel Alma Lagerstätte (Lebanon, Middle East).

Stratigraphic and geographic range.—As for genus.

Reconstruction.—Our new observations provide a more accurate description and allow a detailed iconographic reconstruction of *Palaeobenthesicymus libanensis* (Fig. 9). The general view is different from that proposed by Glaessner (1945). It is more precise and reveals new anatomical features that provide several lines of evidence to demonstrate the relationship of the fossil crest-bearing shrimps to the extant Benthesicymidae.

Taphonomy, paleobiology, and palaeoecology of crest-bearing shrimps

Taphonomy.—The exquisite preservation of the studied specimens allows detailed anatomical observations. Soft-tissues such as muscles and gills are preserved in grey-brown siliceous and probably phosphatized mineral displaying a weak fluorescence when exposed to ultraviolet light. Muscles are mainly located under desquamated cuticle in the pleonal region and in the pereiopods while remains of gills are located in the branchiostegal region (Fig. 4A). The intestine is also preserved and forms a small cylindrical canal in the pleonal region bearing numerous infra-millimetric fragments corresponding to unknown coprolithic material (Figs. $4A_2$, 6B). Some specimens (MNHN.F.A30584, A30587, A30599) show calcite spheres on the surface of their carapace (Fig. 8). Based on their morphology (spheres 1 to 1.5 mm in diameter) and position in the cephalothorax, Roger (1946) interpreted them as "eggs". Examination of similar structures in those specimens and other decapods from Lebanon (e.g., *Palinurus*, *Linuparus*, *Acanthochirana*, *Homarus*) revealed that they are calcite crystal bundles (Briggs and Wilby 1996). The bundles formed almost exclusively within the body of the crustaceans, suggesting that the cuticle envelope played a role in maintaining ion concentrations and pH levels generated by decay bacteria. The precipitation of these very early authigenic calcite bundles occurs in decaying carcasses and is influenced by microbial activity. Their presence in close association with phosphatized soft-tissues indicates that phosphate forms initially due to a decay induced drop in pH, calcite may precipitate subsequently once the pH has risen sufficiently (Briggs and Wilby 1996). The rarity of crystal bundles reveals very probable rapid burial and relatively closed conditions during the early stages of fossilization of the Sahel Alma fauna (Briggs and Wilby 1996).

Palaeopathology.—Epibionts have been recognized on several specimens of *Palaeobenthesicymus libanensis*. They are particularly visible after ultraviolet illumination. For instance, they occupy a large part of the scaphocerite of specimen MNHN.F.A30595 and form infra-millimetric isolated ovoid structures (Fig. $4A_1$). Similar subspheric structures have been recognized on the rostrum of other Sahel Alma crustaceans by Petit and Charbonnier (2012). They interpreted these epibionts to be marine sponge gemmules. Other specimens (MNHN.F.A30589, A30593, A30596) show indentations cutting the thick margin of the rostral crest (e.g., Fig. 3B). Their positions are not regular and probably correspond to small healed wounds.

Palaeobiology.—The exact mode of life of *Palaeobenthesicymus libanensis* remains an open question. Most of the authors (Brocchi 1875; Glaessner 1945; Roger 1946) did not discuss the palaeoecology of this species. Some important features of *P. libanensis* would suggest that crest-bearing shrimps were necto-benthic animals with well-developed capacities for swimming: (1) the whole exoskeleton is very thin and smooth, without ornamentation, as observed in numerous modern nektonic shrimps (Pérez Farfante and Kensley 1997); (2) the antennae are very long and therefore may act as a parachute in the water column (Bauer 2004); (3) the long and well-developed pleopods suggest active swimming; (4) the strong tail fan composed of uropods which exceed the length of the telson by three-quarters may indicate very active propulsion; and (5) the well-developed rostral crest may

← Fig. 7. The crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875) from the Sahel Alma Lagerstätte (late Santonian, Lebanon). A. Complete specimen (MNHN.F.A30607), left lateral view (A_1); camera lucida line drawing showing details of pleopods (A_2); detail of tail fan (A_3); and detail of bilobed eyes (A_4). **B**. Pleon and tail fan of specimen MNHN.F.A32428, note the uropodal exopod with rounded diaeresis.

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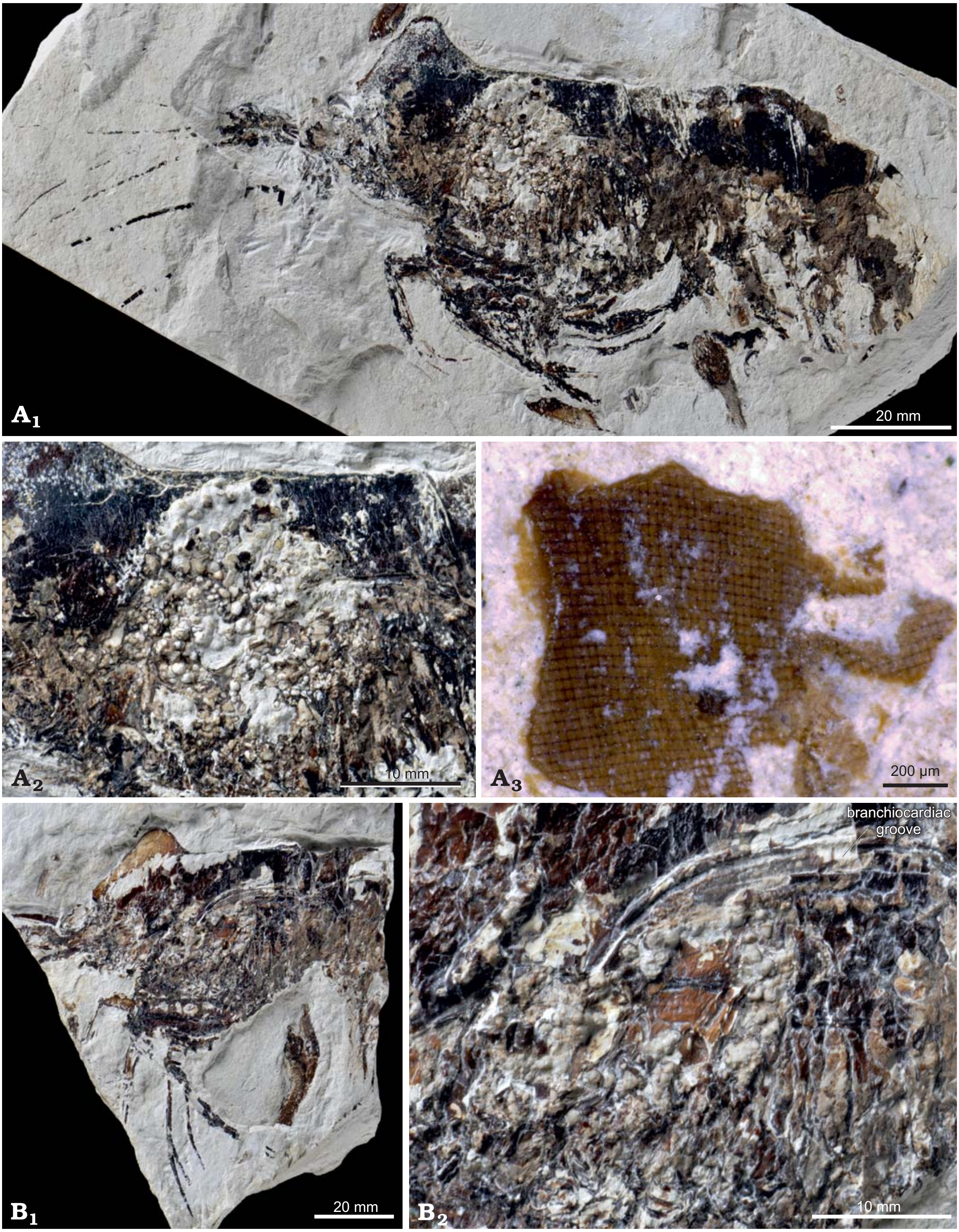
A1
20 mm
A2
10 mm
A3
200 μm
B1
20 mm
branchiocardiac
groove
B2
10 mm

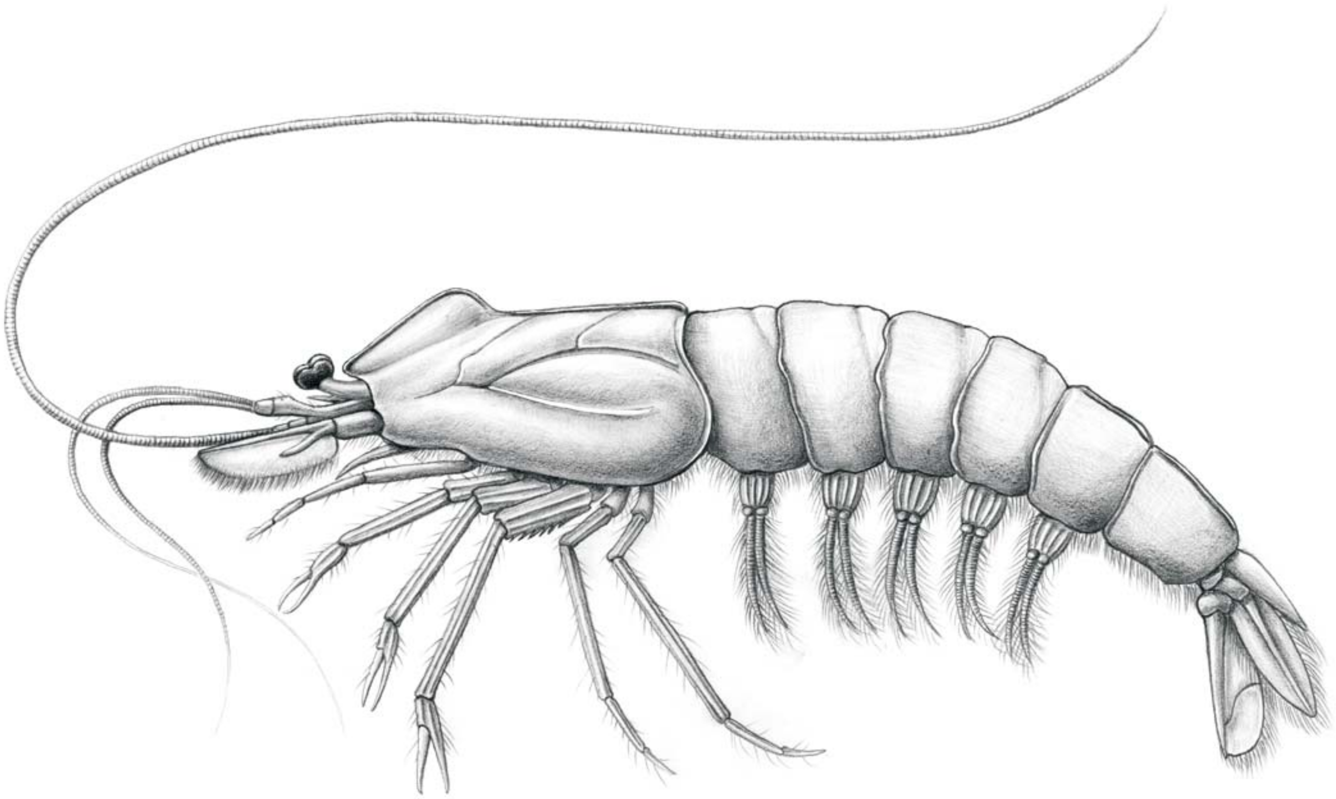

Fig. 9. Reconstruction of crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875). Drawing: Charlène Letenneur (MNHN, scientific draughtsman).

have played an important role in the stability and steering during the swimming. The relatively flattened pereiopods reinforced by longitudinal ridges also suggest good capacities for benthic locomotion. The very slender chelae of the first three pereiopods may indicate that *P. libanensis* was an active predator and principally fed on small organisms living in the soft muddy bottoms of the Sahel Alma Lagerstätte. The possible predatory habits of the crest-bearing shrimps are also confirmed by the presence of their bilobed eyes. Bilobed eyes are very rare among recent crustaceans. They are known in predator euphausiacids that live in very dim-light conditions, below the euphotic zone (Land 1980). Their eyes are characterized by two lobes: (1) the lower lobe with relatively large ommatidia to detect the bioluminescence emitted by potential preys and/or predators in the darkness of the water column and (2) the upper lobe with small ommatidia shows relatively limited capacities to detect faint lights but offers a higher image resolution to discern the outline of preys (often using counter-illumination or transparency) in the residual daylight coming from the water surface (Land 1980). Thus, bilobed eyes in *P. libanensis* may be interpreted as an adaptation to vision at low light intensities. They strongly suggest that these animals were visual predators and possibly were able to detect prey in dim light conditions (relatively deep environment and/or turbid waters).

Palaeoenvironmental significance.—*Palaeobenthesicymus libanensis* is relatively similar in size and general morphology to some extant Benthesicymidae such as *Benthesicymus crenatus* Bate, 1881. This species is a deep-water shrimp and only few biological and ecological data are available because it lives at depths where in situ observations are rare and dependent upon submersibles or camera sledges (Pérez Farfante and Kensley 1997). However, Jamieson et al. (2009) reported that *B. crenatus* lives at depths exceeding 7000 m and is an active predator that was observed preying upon smaller scavenging amphipods. There are also morphological resemblances (e.g., elongate chelipeds, small rostrum, long multiarticulated pleopods, body shape) between *P. libanensis* and some caridean shrimps of Pasipheidae that are known to make daily migrations moving to the water surface at night and returning to deep water during the day. These species are predator and principally feed on mysids, chaetognaths and small fishes (Cartes 1993). The comparisons with Recent Benthesicymidae and Pasipheidae seem to indicate that *P. libanensis* might

← Fig. 8. The crest-bearing shrimp *Palaeobenthesicymus libanensis* (Brocchi, 1875) from the Sahel Alma Lagerstätte (late Santonian, Lebanon). **A**. Complete specimen (MNHN.F.A30587), left lateral view, note cephalothorax with white traces of decay (A_1); detailed view of the cuticle with a concentration of calcite bundles probably influenced by microbial activity (A_2); detailed view of the eye showing a network of quadrate ommatidia (A_3). **B**. Sub-complete specimen (MNHN.F.A30584), right lateral (B_1) and detailed (B_2) views, calcite bundles are concentrated to the ventral margin of the cephalothorax and to the branchial region, note the branchiocardiac groove limited by two parallel ridges.

have been an active predatory and have played a key role between the benthic and pelagic palaeoecosytems. More precisely, *P. libanensis* was probably nectobenthic and might have preyed both on the small-sized crustaceans living in the muddy substrate typical of the chalky sediments of Sahel Alma and on those living in the water column. In summary, *P. libanensis* is an important component of the Sahel Alma Lagerstätte that has morphological and possible ecological analogues among the extant deep-water Benthesicymidae. That the crest-bearing shrimps lived in relatively deep water conditions is plausible and confirmed by other fossils such as coleoid cephalopods (Lukeneder and Harzhauser 2004), actinopterygians, chondrichtyians (Gayet et al. 2003) and crinoids (Roger 1946). All these organisms support the notion that the Sahel Alma area was situated in the lower circalittoral zone with a water depth most probably exceeding 150 m. This interpretation is compatible with the geological data suggesting that the chalky limestones from Sahel Alma were probably deposited in a small depression around the plateform-basin transition in the lower circalittoral zone or in the upper bathyal zone (depth ca. 150–200 m).

Conclusions

The study of the exceptionally preserved crustaceans from the Sahel Alma Lagerstätte shows that the crest bearing shrimps are major components of the fauna. The revision of these shrimps leads to the erection of *Palaeobenthesicymus* gen. nov. and to the new combination *Palaeobenthesicymus libanensis* (Brocchi, 1875) that is the oldest record of the family Benthesicymidae Wood-Mason in Wood-Mason and Alcock, 1891. Detailed comparisons with extant morphological and ecological analogues give new insights on the palaeoecology of the crest-bearing shrimps and provide new data to interpret the Sahel Alma marine palaeoenvironment. If our interpretations are correct, these shrimps belonged to a deep shelf assemblage characterized by chalky sediments under dysphotic or aphotic conditions. They inhabited relatively deep water settings most probably exceeding 150 m at the transition between the lower circalittoral and the upper bathyal zones. They provide key-information on the shrimps near the end of the Mesozoic and prefigure the development of the modern crustacean faunas.

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