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crustacean faunas from the Jurassic of Germany
and Cretaceous of Lebanon

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ABSTRACT

Dendrobranchiate shrimps are abundant in Fossil-Lagerstätten (where fossils are exceptionally preserved). Despite their preservation, classifying them can be challenging as most diagnostic characters are based upon extant species. *Penaeus natator* Glaessner, 1945 (Late Cretaceous, Lebanon, Sahel Alma), is one of those cases in which the systematic assignment of the species can be difficult. It was assigned by “default” to *Penaeus* Fabricius, 1798, before being moved to *Metapenaepsis* Bouvier, 1905. The recent description of *Pseudodrobna kennigotti* Winkler, 2017 (Late Jurassic, Germany, Schernfeld, a Solnhofen-type Fossil-Lagerstätte) shows that *Penaeus natator* should be assigned to *Pseudodrobna* Winkler, 2017. This attests once again the similarity in composition of crustacean faunas between Late Jurassic Solnhofen-type Fossil-Lagerstätten and the Late Cretaceous Fossil-Lagerstätten of Lebanon. We also discuss the palaeoecological significance of bilobed eyes, which occur in three species from the Late Cretaceous of Sahel Alma: *Pseudodrobna natator* n. comb., *Palaeobenthonectes arambourgi* (Roger, 1946) and *Palaeobenthescymus libanensis* (Brocchi, 1875). These eyes seem to have evolved convergently due to the deep-water and dim-light palaeoenvironment of these three shrimp species.

KEY WORDS

Decapoda,
Dendrobranchiata,
Fossil-Lagerstätten,
Tithonian,
Santonian,
palaeobiology,
bilobed eyes,
new combination.

RÉSUMÉ

Pseudodrobna natator n. comb., un nouveau point commun entre les faunes de crustacés du Jurassique d'Allemagne et du Crétacé du Liban.

Les crevettes dendrobranchiates sont abondantes dans les gisements à conservation exceptionnelle. Malgré leur préservation, les classer reste difficile car la plupart des caractères diagnostiques de ce groupe ont été définis sur des espèces actuelles. *Penaeus natator* Glaessner, 1945 est l'un de ces cas difficiles. Cette espèce a été assignée « par défaut » à *Penaeus* Fabricius, 1798, avant d'être assignée à *Metapenaeopsis* Bouvier, 1905. La description de *Pseudodrobna kennigotti* Winkler, 2017 (Jurassique supérieur, Allemagne, Schernfeld, un gisement à conservation exceptionnelle de type Solnhofen) suggère que *Penaeus natator* pourrait être assignée à *Pseudodrobna* Winkler, 2017. C'est un point commun de plus entre les faunes de crustacés du Jurassique supérieur des gisements de type Solnhofen et ceux du Crétacé supérieur du Liban. Nous abordons ici également l'intérêt paléocologique de la découverte d'yeux bilobés, présents chez trois espèces du Crétacé supérieur de Sahel Alma : *Pseudodrobna natator* n. comb., *Palaeobenthonectes arambourgi* (Roger, 1946) et *Palaeobenthescymus libanensis* (Brocchi, 1875). Ces yeux semblent être le produit d'une convergence évolutive liée au milieu de vie profond et peu lumineux de ces trois espèces de crevettes.

MOTS CLÉS

Decapoda,
Dendrobranchiata,
Fossil-Lagerstätten,
Tithonien,
Santonien,
paléobiologie,
yeux bilobés,
combinaison nouvelle.

INTRODUCTION

Dendrobranchiate shrimps are a major group in modern marine and brackish-water environments, where they are often abundant and can be ecologically (Tavares & Martin 2010) and economically important (Pérez Farfante & Kensley 1997). In the fossil record, they are generally rare, except in outcrops with exceptional preservation (Fossil-Lagerstätten) where they can readily preserve. Such are the cases of the Late Jurassic Solnhofen-type outcrops of Germany (e.g., Solnhofen, Eichstätt, Zandt, Nusplingen, Wattendorf: Winkler 2012, Schweigert *et al.* 2016) and Late Cretaceous Fossil-Lagerstätten of Lebanon (Hadjoula, Hakel, En Nammoura, Sahel Alma: Garassino 1994, Charbonnier *et al.* 2017). Despite being separated by over 50 million years and being placed on either side of the Tethys Ocean, these Lagerstätten have some similarities in their crustacean faunas (Garassino 1994, Charbonnier *et al.* 2017).

The present research reinvestigates *Penaeus natator* Glaessner, 1945 (Figs 1A-H; 2A) from the Santonian of Sahel Alma (Lebanon), comparing it to *Pseudodrobna kennigotti* Winkler, 2017 (Fig. 1I-J) from the Tithonian of Schernfeld (Germany), and highlighting the phylogenetic affinities of both species and their implications.

MATERIAL AND METHODS

This study is based upon a total of 16 specimens: nine specimens of *Penaeus natator* Glaessner, 1945; four specimens of *Pseudodrobna kennigotti* Winkler, 2017; one specimen of *Palaeobenthonectes arambourgi* (Roger, 1946); and two specimens of *Palaeobenthescymus libanensis* (Brocchi, 1875).

Specimens are housed in Muséum national d'Histoire naturelle (MNHN.F, Paris, France), Natural History Museum (NHMUK, London, United Kingdom), Staatliches Museum für Naturkunde Stuttgart (SMNS, Baden-Württemberg, Germany). Norbert Winkler private collection (Stahnsdorf,

Brandenburg, Germany) and Roger Frattigiani private collection (Laichingen, Baden-Württemberg, Germany).

Specimens were documented with various photographic techniques allowing an increase in contrast and revealing details difficult to see with naked eye: cross-polarized macrophotography (specimens from MNHN; see Bengtson 2000 – see Fig. 1D), UV-yellow autofluorescence macrophotography (specimens from Schernfeld – figured – and MNHN – not figured, with a faint autofluorescence; see Haug *et al.* 2011, Tischlinger 2015 and Charbonnier *et al.* 2017 – see Fig. 1I-J) and simple macrophotography in diffuse light (all specimens, only this technique in the case of NHMUK specimens).

SYSTEMATIC PALAEONTOLOGY

EUCARIDA Calman, 1904

DECAPODA Latreille, 1802

DENDROBRANCHIATA Bate, 1888

Superfamily PENAEOIDEA Rafinesque, 1815

Family PENAEIDAE Rafinesque, 1815

Genus *Pseudodrobna* Winkler, 2017

TYPE SPECIES. — *Pseudodrobna kennigotti* Winkler, 2017, by monotypy.

INCLUDED SPECIES. — *Pseudodrobna kennigotti*, *Pseudodrobna natator* (Glaessner, 1945) n. comb.

Pseudodrobna natator (Glaessner, 1945) n. comb.
(Figs 1A-H; 2A)

Penaeus natator Glaessner, 1945: 700-702, fig. 3.

Penaeus libanensis – Roger 1946: 23-26, figs 16-17, pl. 1 fig. 4 not pl. 3 fig. 1 (*pro parte*).

Drobna sp. I – Roger 1944: 848; 1946: 29-31, fig. 21, pl. 1 fig. 6.

Metapenaeopsis natator – Charbonnier *et al.* 2017: 69-74, figs 121-141.



FIG. 1. — Comparison between *Pseudodrobna natator* (Glaessner, 1945) n. comb. from the Santonian of Sahel Alma, Lebanon and *P. kenngotti* Winkler, 2017 from the lower Tithonian of Schernfeld near Eichstätt, Germany: **A-H**, *Pseudodrobna natator*: holotype NHMUK 59690, right lateral view, in natural light (**A**); paratype NHMUK In 29578, dorsal view, in natural light (**B**); reconstruction (**C**); specimen MNHN.F.A30697, in cross-polarized light (**D**); specimen MNHN.F.A30702, left lateral view, detail of the rostrum, in natural light (**E**); specimen MNHN.F.A30696, right lateral view, detail of the dorsal part of the cephalothoracic shield, in natural light (**F**), detail of the eye (**G**) and detail of the scaphocerite (**H**). **I-J**, *Pseudodrobna kenngotti*: holotype SMNS 70355, lateral left view, UV-yellow autofluorescence (**I**) and specimen from N. Winkler private collection, right lateral view, UV-yellow autofluorescence (**J**). Abbreviations: **P1-P5**, pereiopods 1-5 (= thoracopods 4-8). Images: Courtesy Claire Mellish, © NHMUK (**A, B**), Denis Audo (**C, D**), Gaëlle Doitteau (**E-recolnat**) (**E-H**) and Norbert Winkler (**I, J**). Scale bars: A, B, D, H, I, 10 mm; E-H, 1 mm.

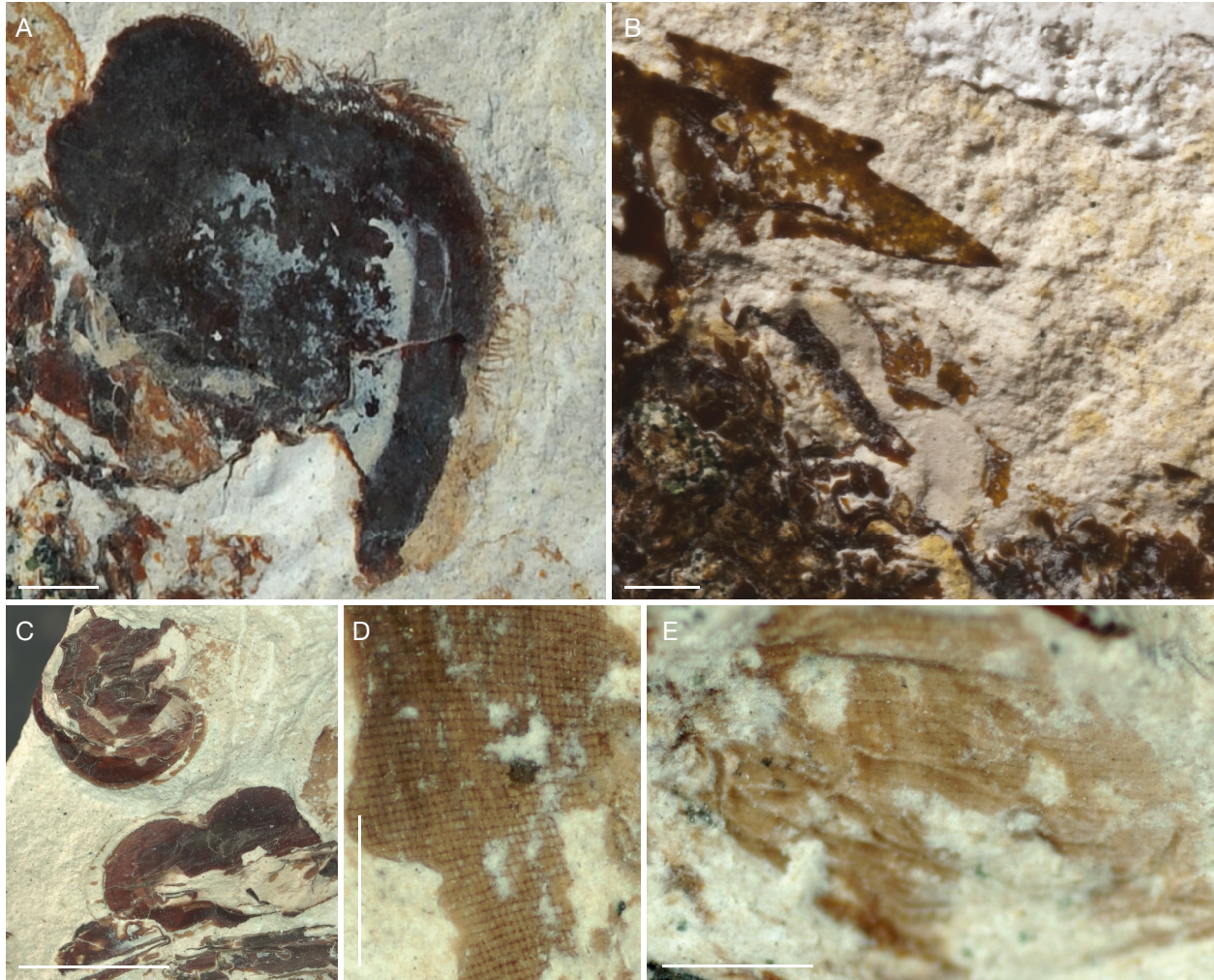


FIG. 2. — Bilobed eyes of dendrobranchiate shrimps from Sahel Alma: **A**, bilobed eye of *Pseudodrobna natator* (Glaessner, 1945) specimen MNHN.F.B18859, right lateral view, natural light; **B**, bilobed eye of *Palaebenthonectes arambourgi* (Roger, 1946), specimen MNHN.F.A30703, natural light; **C-E**, bilobed eyes of *Palaebenthescymus libanensis* (Brocchi, 1875), specimen MNHN.F.A30607 (**C**), details of the ommatidia of the anterior lobe of the eye (**D**) and ommatidia of the posterior lobe of the eye of specimen MNHN.F.A30587 (**E**) – note that **D** and **E** are reproduced at the same scale to ease comparison. Images: Christian Lemzaouda (MNHN) (**A**), Denis Audo (**B**) and Marie-Béatrice Forel (**C-E**). Scale bars: A, B, 1 mm; C, 5 mm; D, E, 0.5 mm.

TYPE MATERIAL. — Holotype NHMUK 59690 (part and counterpart, Fig. 1A); paratypes NHMUK 59511, In 29563, In 29578 (Fig. 1B). As stated by Charbonnier *et al.* (2017), the original material also included three additional paratypes, now excluded from the type series, and assigned to *Palaebenthonectes arambourgi* (Roger, 1946) (NHMUK 59688, 59689) and *Carpopenaeus septemspinatus* (Dames, 1886) (NHMUK I 148), respectively.

TYPE LOCALITY. — Sahel Alma, Kesrouane district, Lebanon.

TYPE AGE. — Late Cretaceous, late Santonian, Nannofossil biozone UC13 of Burnett (1998) - UC17 pro parte Sissingh (1977).

DISTRIBUTION. — Santonian (Lebanon).

ADDITIONAL MATERIAL. — Same as Charbonnier *et al.* (2017): five specimens MNHN.F.B18859 (Fig. 2A) (also figured by Roger 1946: pl. 1, fig. 4), MNHN.F.B18886 (figured by Roger 1946: pl. 1, fig. 6), MNHN.F.A30696 (Figs 1F-H), A30697 (Fig. 1C), A30702 (Arambourg coll., Fig. 1E). All are from Sahel Alma.

DESCRIPTION

See Appendix 1.

DISCUSSION

Pseudodrobna natator n. comb. was assigned to *Penaeus* Fabricius, 1798 without real justification by Glaessner (1945), as it has often been the case for numerous fossils (Pérez Farfante & Kensley 1997; Charbonnier *et al.* 2017). Charbonnier *et al.* (2017) justified the assignment to Penaeidae, mostly by elimination, as, unfortunately, diagnostic characters of Penaeidae are difficult to observe and mostly defined on extant species (see Pérez Farfante & Kensley 1997). Later, Charbonnier *et al.* (2017), not aware of the work by Winkler (2017), assigned *P. natator* n. comb. to *Metapenaeopsis* Bouvier, 1905 based upon the rostrum with only suprarostal teeth (Fig. 1E), the epigastric tooth separated from rostral teeth, the marked antennal and pterygostomial spines and pubescent (i.e. covered by setae) exoskeleton (Fig. 1F). However, in the light of the work by Winkler (2017), it appears that *P. natator* n. comb. is more closely allied to *Pseudodrobna* Winkler, 2017 than *Metapenaeopsis*: indeed, as *Pseudodrobna kenngotti* Winkler,

2017 (type species and only species assigned to *Pseudodrobna* by Winkler 2017 – Fig. 1I, J), *P. natator* n. comb. possesses a rather short cephalothoracic shield, almost as long as high in lateral view (vs distinctly longer in *Metapenaeopsis*), a rather short, upturned rostrum (vs longer in *Metapenaeopsis*). For these reasons, we assign *Penaeus natator* to *Pseudodrobna*.

DISCUSSION

LINKS BETWEEN JURASSIC, LATE CRETACEOUS AND EXTANT FAUNAS (TABLE 2)

As already pointed out by Charbonnier *et al.* (2017), there are several crustacean genera in common between the Late Jurassic of Solnhofen-type Fossil-Lagerstätten and the Late Cretaceous Lebanese Fossil-Lagerstätten. Lebanese Lagerstätten also yield several crustaceans prefiguring modern crustacean faunas. Along the same lines, we observe several similarities between *Metapenaeopsis* and *Pseudodrobna*, possibly due to close phylogenetic ties, highlighting, again, the progressive transition from Jurassic fauna to modern fauna.

THE BIG, BILOBED EYES OF DENDROBRANCHIATA IN SAHEL ALMA

One salient point of the morphology of *Pseudodrobna natator* n. comb. is the presence of conspicuous bilobed eyes (Fig. 2A) reminiscent of *Palaeobenthonectes arambourgi* (Roger, 1946) (Fig. 2B) and of *Palaeobenthescymus libanensis* (Brocchi, 1875) (Fig. 2C-E). These resemblances are probably due to a convergent evolution: these species belong to different families (Penaeidae for *Pseudodrobna natator* n. comb.; Benthescymidae Wood-Mason, 1891 for the other two) and each of these are related to species without bilobed eyes (e.g. species of *Benthescymus* Bate, 1881, in the case of *P. libanensis* and species of *Metapenaeopsis*, in the case of *P. natator* n. comb.). Audo & Charbonnier (2013) and Charbonnier *et al.* (2017) therefore suggested that this character could be linked to the deep environment of Sahel Alma, where these species occurred. This interpretation could be also supported, at least in the case of *P. libanensis*, by the presence of square ommatidial lenses (Audo & Charbonnier 2013; Figs 2D-E) suggesting reflecting superposition optics in the eye, which provide an increased sensitivity (see Audo *et al.* 2016, 2019). *Pseudodrobna kennigotti* from Schernfeld does not seem to possess bilobed eyes. This absence of bilobed eyes in *Pseudodrobna kennigotti* could be expected: indeed Schernfeld, as other Solnhofen-type Lagerstätten preserves mostly shallow water and terrestrial fauna (Barthel *et al.* 1990), so eyes adapted to the dim-light of deep water would not have been particularly advantageous there. This would suggest that the ancestors of *Pseudodrobna natator* n. comb. probably had ovoid, non-bilobed eyes, as other penaeids and *P. kennigotti*. *Pseudodrobna natator* n. comb. would therefore be the result of an adaptation to a deep water setting, as are *Palaeobenthescymus libanensis* and *Palaeobenthonectes arambourgi*.

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APPENDIX 1. — Descriptive matrix of *Pseudodrobna natator* (Glaessner, 1945) n. comb. and *Pseudodrobna kennigotti* Winkler, 2017. Note: the outlines of structures are described by default in lateral, as the majority of fossils are preserved in lateral compression.

Taxa		<i>Pseudodrobna natator</i> n. comb.	<i>Pseudodrobna kennigotti</i>	
Source of data		Charbonnier et al. (2017), present study	Winkler (2017), present study	
Examined material		Holotype: NHMUK 59690 (part+counterpart); three paratypes: NHMUK 59511, In 29563, In 29578, three other paratypes belonging to other species have been excluded from the type series by Charbonnier et al. (2017)	Holotype: SMNS 70355; Paratypes: 1 without coll. number (coll. N. Winkler, Stahnsdorf), 1 without coll. number (coll. Frattigiani, Laichingen) and SMNS 70356.	
Number of specimens		4	3	
Cephalothoracic shield (Carapace)	Outline	outline in lateral view	subquadrate, about as long as high	subrectangular, c. 0.6 times as high as long
		proportions height/width	Laterally flattened	Laterally flattened
		rostrum	long rostrum (about as long as carapace), reaching the tip of scaphocerite, bent slightly upward with sharp distal extremity and six long suprarostal spines	long rostrum (slightly shorter than carapace), reaching the distal margin of the third article of antennular peduncle but not the tip of scaphocerite, bent slightly upward with sharp distal extremity and three long suprarostal spines
		dorsal margin	straight and smooth, with a small epigastric spine distinctly separated from the cluster of suprarostal spines	straight, possibly with a thin carina (poorly preserved), with a small epigastric spine distinctly separated from the cluster of suprarostal spines
		ocular incision	wide and shallow	wide and shallow
		antennal spine	wide and short, poorly preserved	large and short spine
		antennal incision	wide and shallow, smaller than ocular incision	wide and shallow, smaller than ocular incision
		pterygostomian spine	narrower and longer than antennal spine	narrower and longer than antennal spine
		ventral margin	slightly convex	convex
		posterior margin, articular area	height c. 1/2 carapace height, subrectilinear	height slightly less than 1/2 carapace height, subrectilinear
posterior margin, branchial area	convex	convex		
Grooves	branchiocardiac (a)	antennal (b)	faint traces, possibly extending to the median line near posterior margin	faint traces, possibly extending to the median line near posterior margin
		hepatic (b1)	not visible/preserved	not visible/preserved
		postcervical (c)	not visible/preserved	not visible/preserved
		gastro-orbital (d)	not visible/preserved	not visible/preserved
		Cervical (e1e)	faint traces, possibly extending to the median line posterior to epigastric spine	faint traces, possibly extending to the median line posterior to epigastric spine
		inferior (i)	not visible/preserved	not visible/preserved
		intercervical (ic)	not visible/preserved	not visible/preserved
Spines and Carinae	Hepatic	posterior to antennal spine, poorly preserved	not visible/preserved	
	Branchial	not visible/preserved	not visible/preserved	
Ornamentation	Cephalic area	not visible/preserved	tubercles of irregular size	
	Branchial area	not visible/preserved	not visible/preserved	
	Above branchial area	dense cover of thin setae	tubercles of irregular size	
Pleon	Proportions	Height	slightly higher than cephalothorax	slightly higher than cephalothorax
		Width	slightly narrower than cephalothorax	Not visible on available specimens
		Length	1.5 times as long as cephalothorax (rostrum included)	about twice as long as cephalothorax (rostrum included)
	pleonite 1	Dorsal part	shorter than other pleonites, separated from tergopleuron by a midlateral hinge articulating with pleonite 2	shorter than other pleonites, poorly preserved
		Axial carina Tergopleuron	not visible/preserved forming an acute spine	not visible/preserved forming an acute spine
	pleonite 2	Dorsal part	slightly longer than s1, separated from tergopleuron by a midlateral hinge	longer than s1, poorly preserved, separated from tergopleuron by a midlateral hinge
		Axial carina Tergopleuron	not visible/preserved forming an acute spine	not visible/preserved forming an acute spine
	pleonite 3	Dorsal part	about 1.5 times longer than s2, separated from tergopleuron by a midlateral hinge	longer than s2, separated from tergopleuron by a midlateral hinge, poorly preserved
		Axial carina Tergopleuron	not visible/preserved poorly preserved	thin (poorly preserved) Subtriangular, tapering sharply to form an acute spine
		Position	Forming a bend in the pleon with s4	Forming a bend in the pleon with s4
	pleonite 4	Dorsal part	Almost as long as s2+s3 length, separated from tergopleuron by a midlateral hinge thin (poorly preserved)	Almost as long as s1+s2 length, separated from tergopleuron by a midlateral hinge thin (poorly preserved)
		Axial carina Tergopleuron	subtriangular, poorly preserved ventrally	Subtriangular, tapering sharply to form an acute spine
		Position	Forming a bend in the pleon with s3	Forming a bend in the pleon with s3

APPENDIX 1. — Continuation.

Taxa			<i>Pseudodrobna natator</i> n. comb.	<i>Pseudodrobna kenngotti</i>
	pleonite 5	Dorsal part Axial carina Tergopleuron	Almost as long as s4, separated from tergopleuron by a midlateral hinge thin (poorly preserved) subquadrate, smooth	Almost as long as s4, separated from tergopleuron by a midlateral hinge thin (poorly preserved) subquadrate, forming a spine at the postero-ventral angle
	pleonite 6	Dorsal part Axial carina Tergopleuron	longer than other pleonites thin (poorly preserved) straight	longer than other pleonites thin (poorly preserved) straight
	Ornamentation		smooth	smooth
Telson	Outline surface		subtriangular, very thin, as long as s6 lateral margin carinate	subtriangular, very thin, as long as s6 lateral margin carinate, with a row of small spines distally (poorly preserved anteriorly)
Eyes	Shape		bilobed - with anterior and posterior lobes separated by a latero-dorsal notch, large (c. 1/6 CL rostrum included)	With a short peduncle, poorly preserved, possibly with an ovoid visual surface
	Ommatidia Setae		not visible/preserved visual surface fringed with a row of setae	not visible/preserved no setae
Cephalic appendages	a1 antennula	Basis Endopod Exopod	almost as long as rostrum, poorly preserved multi-articulated, short ($\geq 1/6$ CL including rostrum), multiarticulated multi-articulated, short ($\geq 1/6$ CL including rostrum), multiarticulated	almost as long as rostrum, distal margin of third podomere not reaching the tip of scaphocerite, poorly preserved multi-articulated, short ($\geq 1/3$ CL including rostrum), multiarticulated multi-articulated, short ($\geq 1/3$ CL including rostrum), multiarticulated
	a2 antenna	Basipod Endopod Exopod (scaphocerite)	short, poorly preserved multi-articulated, ≥ 2 CL (not including rostrum), not prepared/preserved on their entire length long, with straight outer margin strengthened by longitudinal carina and lamelar, fringed and setose inner and distal margins	short, poorly preserved multi-articulated, probably long, not preserved/prepared on their entire length long, with straight outer margin strengthened by longitudinal carina and lamelar (poorly preserved) inner and distal margins
	Mandible	incisor/molar processes coxal body	not visible/preserved not visible/preserved	not visible/preserved not visible/preserved
	Maxilla 1 Maxilla 2		not visible/preserved not visible/preserved	not visible/preserved not visible/preserved
Thoracic appendages	Thoracopod 1 Thoracopod 2 Thoracopod 3	maxilliped 1 maxilliped 2 maxilliped 3	not visible/preserved Short, wide and multiarticulated exopodite Leg-like, poorly preserved	not visible/preserved not visible/preserved Leg-like, not overreaching antennal scale, merus longest, twice as long as carpus, propodus and carpus of similar length, dactylus with short spines, other articles unarmed
	Thoracopod 4	Pereiopod 1 (P1) Coxa	poorly preserved	not visible/preserved
	Thoracopod 4	P1 Basis	poorly preserved	not visible/preserved
	Thoracopod 4	P1 Ischium	poorly preserved	not visible/preserved
	Thoracopod 4	P1 Merus	short, tapering proximally	subrectangular, c. 1/6 cephalothorax length (rostrum included)
	Thoracopod 4	P1 Carpus	almost twice as long as merus, fringed with setae dorsally and ventrally	subrectangular, shorter than merus
	Thoracopod 4	P1 Propodus	shorter than carpus, forming a claw with the dactylus	tapering distally, forming a claw with dactylus, with a thin index, longer than carpus
	Thoracopod 4	P1 Dactylus	forming a claw with index of propodus, length \geq total propodus length	thin, forming a claw with index of propodus
	Thoracopod 5	Pereiopod 2	slender, with a slender chela	th5 and th6 difficult to identify; one very slender, with a thin straight claw; the other slender with a smaller claw
	Thoracopod 6 Thoracopod 7	Pereiopod 3 Pereiopod 4	slender, with a slender chela about as long as cephalothorax (excluding rostrum), achelate	about as long as cephalothorax (excluding rostrum), achelate
	Thoracopod 8	Pereiopod 5	about as long as cephalothorax (excluding rostrum), achelate	about as long as cephalothorax (excluding rostrum), achelate
Pleonal appendages	Pleopod 1	Female Male (Petasma)	not visible/preserved longer than one half of the cephalothorax length (including rostrum)	not visible/preserved not visible/preserved
	Pleopod 2		basipod slightly rounded, covered with setae, carrying two flagella also carrying setae	not visible/preserved

APPENDIX 1. — Continuation.

Taxa		<i>Pseudodrobna natator</i> n. comb.	<i>Pseudodrobna kenngotti</i>
Pleopod 3		basipod slightly rounded, covered with setae, carrying two flagella also carrying setae	not visible/preserved
Pleopod 4		basipod slightly rounded, covered with setae, carrying two flagella also carrying setae	not visible/preserved
Pleopod 5		basipod slightly rounded, covered with setae, carrying two flagella also carrying setae	not visible/preserved
Pleopod 6 (uropod)	Basipod Endopod	subtrapezoidal and stocky elongated and lanceolate, strengthened by a median longitudinal carina, fringed by a row of setae	subtrapezoidal and stocky elongated and lanceolate, strengthened by a median longitudinal carina
	Exopod	elongated and lanceolate, distally cut by a large, slightly curved diaeresis, strengthened with a two longitudinal carinae, one near the outer margin, one along outer margin which ends in a spine anterior to the diaeresis	elongated and lanceolate, distally cut by a large, slightly curved diaeresis, strengthened with a two longitudinal carinae, one near the outer margin, one along outer margin which ends in a spine anterior to the diaeresis

APPENDIX 2. — Species and genera from Lebanon also occurring in Solnhofen-type outcrops and/or modern environments. References: **1**, present work; **2**, Audo 2019; **3**, Charbonnier *et al.* 2013; **4**, Charbonnier *et al.* 2015; **5**, Charbonnier *et al.* 2017; **6**, Feldmann & Charbonnier 2011; **7**, Garassino 1994; **8**, Garassino & Schweigert 2006; **9**, Haug *et al.* 2008; **10**, Larghi 2004; **11**, Münster, 1839; **12**, Pérez Farfante & Kensley 1997; **13**, Schweigert & Garassino 2005; **14**, Schweigert *et al.* 2016; **15**, Schweitzer *et al.* 2010; **16**, Strand 1928; **17**, Winkler 2012; **18**, Winkler 2017.

Taxa	Kimmeridgian-Tithonian of Germany	Cenomanian of Lebanon	Santonian of Lebanon	Present day	References
DENDROBRANCHIATA					
Aegeridae	×	×	×	—	5, 14
<i>Acanthochirana</i>	×	×	—	—	5, 14, 16
<i>Aeger</i>	×	×	×	—	5, 11, 14
Benthescymidae	—	—	×	×	5, 12
Carpopenaeidae	×	×	×	—	5, 14
<i>Carpopenaeus</i>	—	×	×	—	5
<i>Epipenaeus</i>	×	×	—	—	5, 13
Penaeidae	×	×	×	×	5, 12, 14
<i>Libanocaris</i>	×	×	—	—	5, 7, 14, 17
<i>Pseudodrobna</i>	×	—	×	<i>Metapenaeopsis?</i>	1, 5, 18
Sergestidae	—	—	×	×	5, 12
CARIDEA					
Crangonidae	—	×	×	×	5
<i>Odontochelion</i>	—	×	×	—	5
Glyphocrangonidae	—	×	—	×	5
Hippolytidae	—	—	×	×	5
Pandalidae	—	×	—	×	5
STENOPODIDEA					
Stenopodidae	—	×	—	×	5
ASTACIDEA					
Erymidae	×	×	—	—	5, 8
<i>Eryma</i>	×	×	—	—	5, 8
<i>Pustulina</i>	×	×	—	—	5, 8
Nephropidae	—	x?	—	×	5
GLYPHEIDEA					
Glypheidae	×	×	—	×	3, 4, 5
ACHELATA					
Phyllosoma-like larvae	×	×	×	×	5
Scyllaridae	×	×	—	×	2, 5
Palinuridae	×	×	—	×	5, 8
AXIIDEA					
Axiidae	×	×	—	×	5, 8
<i>Magila</i>	×	×	—	—	5, 8
Callianassidae	—	×	—	×	5
<i>Calliaxina</i>	—	×	—	×	5
ANOMURA					
Chirostylidae	—	×	×	×	5
<i>Phalangiopsis</i>	—	×	×	—	5
Diogenidae	—	×	—	×	5
BRACHYURA					
PODOTREMATA					
Homolidae	—	×	—	×	5, 10, 15
Raninidae	—	×	x?	×	5, 15
ISOPODA					
Cirolanidae	—	—	×	×	5, 6
LOPHOGASTRIDA					
Gnathophausidae	—	—	×	×	5
STOMATOPODA					
Scudidae	×	×	—	—	5, 9
<i>Sculda</i>	×	×	—	—	5, 9