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Sylvain CHARBONNIER
Rémy GILARDET
Centre de Recherche en Paléontologie – Paris (CR2P, UMR 7207), MNHN, CNRS, Sorbonne Université,
Muséum national d'Histoire naturelle, 57 rue Cuvier, F-75231 Paris, cedex 05 (France)
sylvain.charbonnier@mnhn.fr (corresponding author)
remy.gilardet@gmail.com

Alessandro GARASSINO
Department of Earth and Biological Sciences,
Loma Linda University,
Loma Linda, 92350 CA (United States)
alegarassino@gmail.com

Giliane P. ODIN
Laboratoire Géomatériaux et Environnement, Université Gustave Eiffel,
F-77454 Marne-la-Vallée, (France)
giliane.odin@univ-eiffel.fr

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KEY WORDS
Crustacea,
Glypheidea,
Mecochiridae,
Mecochirus,
Cenomanian,
brood care,
eggs,
new species.

ABSTRACT
The discovery of *Mecochirus cenomanicus* n. sp. (Decapoda, Glypheoidea, Mecochiridae) from the Cenomanian stratotype (Le Mans, France) extends the biostratigraphic range of *Mecochirus* Germar, 1827 from the Early to the Late Cretaceous. The holotype preserves under the pleon about 80 large eggs carried by the pleopods, and thus represents the second record of a decapod crustacean fossilized with clusters of eggs. The size and number of eggs suggest an ontogenetic development like that of the extant decapod crustaceans with short larval stage.

MOTS CLÉS
Crustacea,
Glypheidea,
Mecochiridae,
Mecochirus,
Cénomanien,
soin de la ponte,
œufs,
espèce nouvelle.

RÉSUMÉ
Une espèce nouvelle de langouste mécochiridée du Crétacé supérieur de France préservée avec ses œufs.
La découverte de *Mecochirus cenomanicus* n. sp. (Decapoda, Glypheoidea, Mecochiridae) dans le stratotype du Cénomanien (Le Mans, France) étend la distribution biostratigraphique de *Mecochirus* Germar, 1827 du Crétacé inférieur au Crétacé supérieur. L'holotype conserve sous le pléon environ 80 gros œufs fixés aux pléopodes et représente ainsi la seconde mention d'un crustacé décapode fossilisé avec une ponte d'œufs. Le nombre et la taille des œufs suggèrent un développement ontogénétique similaire à celui des crustacés décapodes actuels au stade larvaire court.

INTRODUCTION

Brood care examples are rare in the fossil record of crustaceans; yet, they are a crucial key to understand the evolution of reproductive strategies. There are only a few examples of crustacean fossils showing direct evidence of brood care (eggs or larval stage associated with an adult) reported thus far (Early Palaeozoic arthropods: Caron & Vannier 2016; ostracods: Damotte *et al.* 1996; Lethiers *et al.* 1996; Siveter *et al.* 2007, 2014; syncarids: Perrier *et al.* 2006; peracarids: Broly *et al.* 2017; Sánchez-García *et al.* 2017; polychelidans: Jauvion *et al.* 2020). Herein we report the exquisite preservation of a mecochirid lobster (Decapoda, Glypheoidea, Mecochiridae) found with about 80 eggs attached to the pleon, preserved as a ferruginous compression at the surface of a greenish sandy clay slab from the Late Cretaceous of Le Mans (France). This exceptional specimen belongs to a new species – *Mecochirus cenomanicus* n. sp. – described herein. Moreover, it is the first clue that allows a discussion concerning the evolution of fecundity in mecochirid lobsters, comparing it to the extant glypheidean, *Neoglyphea inopinata* Forest & Saint Laurent, 1975.

MATERIAL AND METHODS

A HISTORICAL SPECIMEN

Part of the Alphonse Milne-Edwards' collection, the studied specimen MNHN.F.B16583 (part and counterpart) was collected by Jacques Triger (1801-1867), who was a French engineer geologist. He invented the process for digging through waterlogged ground using a pressurized caisson bearing his name (Martin 2004). Triger's name appears on the Eiffel Tower, whose feet were anchored by his process (Chanson 2009).

The specimen is preserved as a ferruginous compression at the surface of a greenish sandy clay slab from the Late Cretaceous of Le Mans, France (Fig. 1). It was probably collected from the middle Cenomanian Sables et Grès du Mans Formation, at La Butte, a famous quarry belonging to the Cenomanian stratotype (N. Morel, pers. comm. 2021). After Morel (2015, and references therein), the formation consists of alternating sequences of ungraded sands and sandstones and fossiliferous thin clay beds. The sand originated from the Variscan Armorican Massif, transported by rivers to the marine palaeoenvironment at the western margin of the Paris Basin during the Late Cretaceous. The studied specimen was probably collected from the clay beds, which are known for their exceptional fauna of echinoderms (Breton & Villier 2015) and crustaceans (Breton 2015). Breton (2015) provided an updated list of the decapod crustaceans from the Cenomanian stratotype area including nephropid lobsters, callianassid ghost shrimps, hermit crabs and brachyurans such as *Cenomanocarcinus inflatus* Van Straelen, 1936 and *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879. More recently, Wilson & Morel (2022) described five new species of isopods from Le Mans, and Charbonnier & Garassino (2022) also figured additional specimens housed in the historical collections of the MNHN, Paris.

IMAGING METHODS

Scanning Electron Microscopy (SEM) images were taken using a Hitachi SU 3500 Scanning Microscope, equipped with a X-ray Thermo Ultra Dry elementary probe to map chemical elements (X-ray Energy Dispersive Spectroscopy, EDS). This SEM is hosted at the PtME platform of the Muséum national d'Histoire naturelle (Paris, France). The fossil was characterized uncoated. Pictures were taken in backscatter mode, at 15 kV and 50 Pa in a variable pressure environmental chamber. For EDS analysis, the working distance was set at 10 mm.

ABBREVIATIONS

Collection acronym

MNHN.F	Muséum national d'Histoire naturelle, Paris, palaeontological collections.

Crustacean anatomy

a1	antennula;
a2	antenna;
P1-P5	pereiopods 1 to 5;
pl2-pl5	pleopods 2 to 5;
s1-s6	pleonal somites 1 to 6.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder GLYPHEIDEA Winkler, 1881
Superfamily GLYPHEOIDEA Winkler, 1881
Family MECOCHIRIDAE Van Straelen, 1925

Genus *Mecochirus* Germar, 1827

TYPE SPECIES. — *Macrourites longimanatus* Schlotheim, 1820, subsequent designation of Woods (1927: 64).

INCLUDED FOSSIL SPECIES. — *Mecochirus clypeatus* (Carter, 1898) (Bathonian, United Kingdom); *M. germari* Garassino, 1996 (Sinemurian, Italy); *M. lanceolatus* Jell, Woods & Cook, 2017 (Aptian, Australia); *M. leionoton* (Krause, 1891) (Tithonian, Germany); *M. longimanatus* (Schlotheim, 1820) (Tithonian, Germany); *M. marwicki* Glaessner, 1960 (Kimmeridgian, New Zealand); *M. mcclymontorum* Jell, Woods & Cook, 2017 (Aptian, Australia); *M. meyeri* (Roemer, 1836) (Kimmeridgian, Germany); *M. peytoni* Woodward, 1876 (Kimmeridgian, France); *M. robbianoi* Pagani, Damborenea, Manceñido & Ferrari, 2011 (Toarcian, Argentina); *M. cenomanicus* n. sp. (Cenomanian, France) (this work).

Mecochirus cenomanicus n. sp.
(Fig. 2)

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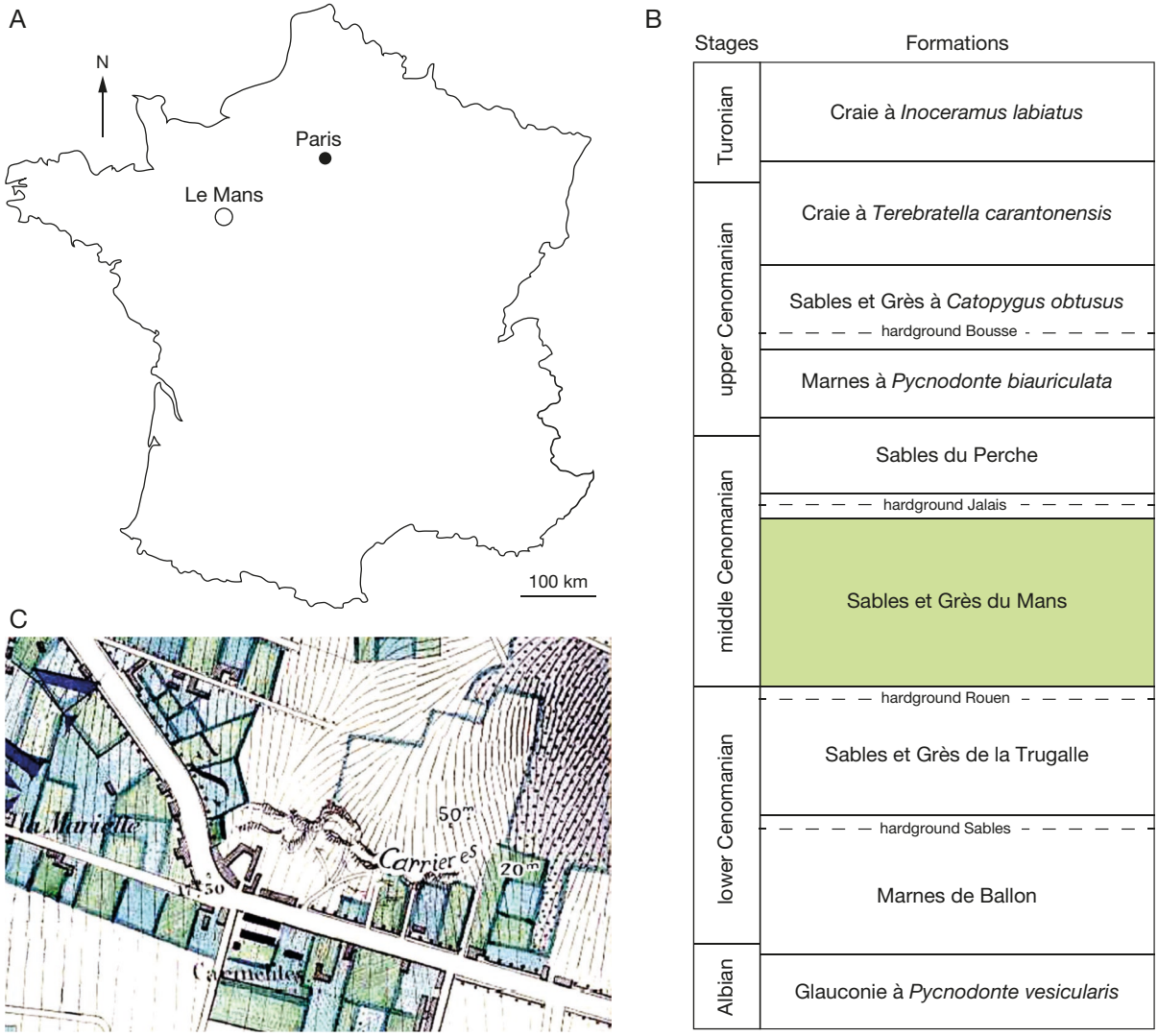

Fig. 1. — Cenomanian stratotype in France: **A**, location of Le Mans, Sarthe Department; **B**, synthetic stratigraphy of the Cenomanian stratotype with the Sables et Grès du Mans Formation (in green), where the mecochirid lobster was probably collected (modified after Morel 2015); **C**, map of the historical site of La Butte quarries (after Lombard 1839).

Etymology. — The specific epithet refers to the Cenomani, a Gallic tribe dwelling in the modern Sarthe Department, Pays de la Loire region, France, during the Iron Age and the Roman period. The Cenomani tribe is also at the origin of the name of the type locality Le Mans and of the Cenomanian stage.

Type material. — Holotype by monotypy MNHN.F.B16583 (part and counterpart, Triger coll.).

Type locality. — La Butte quarry, Le Mans, Sarthe Department, Pays de la Loire, France.

Type age. — Late Cretaceous (Cenomanian).

Description

Carapace

Subrectangular carapace (carapace length: 10 mm; carapace height: 0.5 mm).; smooth short rostrum; dorsal margin almost straight; posterior margin slightly sinuous; convex ventral margin until antennal-pterygostomial region with slightly concave ventral margin; shallow narrow orbit; cephalic region with straight raised, and tuberculate orbital and gastro-orbital carinae extending along whole length of cephalic region; deep cervical groove strongly oblique, intercepting dorsal margin at angle of *c.* 45°, ventrally joined to antennal groove, delimiting narrow cephalic region; short, weak gastro-orbital groove originating as slight median inflexion of cervical groove; shallow postcervical and branchiocardiac grooves parallel, strongly inclined, directed toward posterior margin; postcervical groove joined ventrally to branchiocardiac groove, forming one elongate, straight lobe; short, weak cardiac groove originating as slight dorsal inflexion of postcervical groove; deep hepatic groove, curved toward posterior, surrounding weak subcircular hepatic lobe; regions uniformly covered by small tubercles.

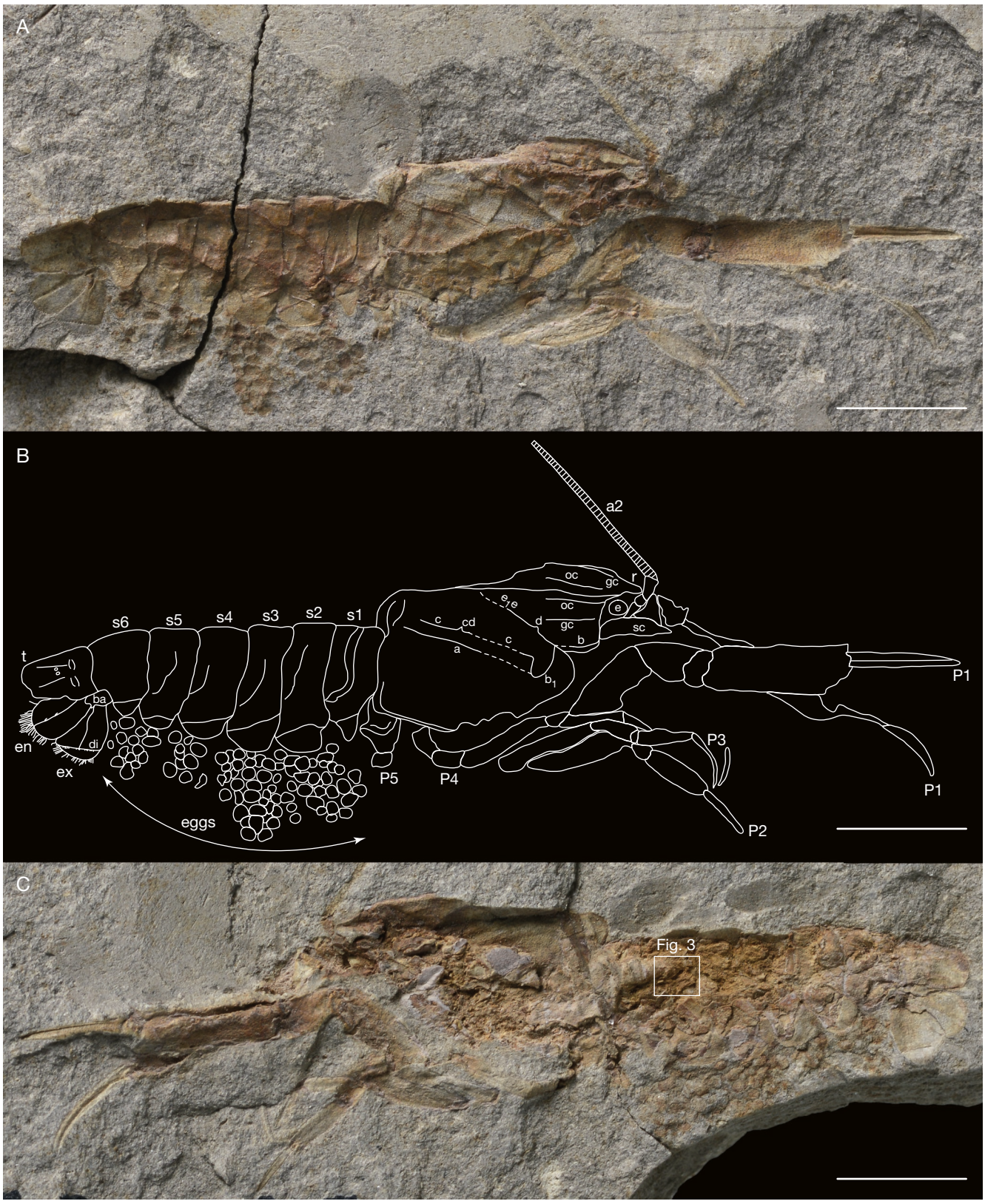

Fig. 2. — Holotype MNHN.F.B16583 (Triger coll.) of *Mecochirus cenomanicus* n. sp. from the Cenomanian of La Butte quarry, Le Mans, France: part and counterpart (**A**, **C**) and interpretative live drawing (**B**); white frame corresponds to SEM images and EDS analysis. Abbreviations: **a**, branchiocardiac groove; **a2**, antenna; **b**, antennal groove; **ba**, basipodite; **b**$_1$, hepatic groove; **c**, postcervical groove; **cd**, cardiac groove; **d**, gastro-orbital groove; **di**, diaeresis; **e**, eye; **en**, uropodal endopod; **ex**, uropodal exopod; **e**$_1$**e**, cervical groove; **gc**, gastro-orbital carina; **oc**, orbital carina; **P1**-**P5**, pereiopods 1 to 5; **r**, rostrum; **sc**, scaphocerite; s1–s6, pleonal somites 1 to 6; **t**, telson. Photographs: P. Loubry. Line drawing: R. Gilardet. Scale bars: 5 mm.

Pleon
Subrectangular s1-s6 equal in size; s1-s5 pleura with longitudinal carina on middle portion; rounded s1-s5 pleura; s1-s6 terga and pleura uniformly covered by small tubercles; subrectangular telson with subovate distal extremity and median part limited by a pair of lateral longitudinal carinae; proximal part with an axial pair of tubercles; tuberculate dorsal surface; distal extremity finely fringed; muscle fibers are preserved at level of s2 and s3.

Cephalic appendages
Small eye; eye-stalk not preserved; a1 not preserved; a2 well preserved; antennal peduncle with three segments: long thin ischiocerite; merocerite shorter than ischiocerite; long carpocerite enlarged distally to which one multi-articulate flagellum (unassessable length) is articulated; triangular scaphocerite with pointed distal extremity.

Thoracic appendages
P1-P4 complete, P5 poorly preserved; achelate P1, relatively long with a thin dactylus; subrectangular P1 merus as long as propodus; subtriangular P1 carpus; subrectangular P1 propodus as long as dactylus; P1 dactylus slightly incurved backward with rimmed ventral margin; P1 merus, carpus, and propodus with smooth dorsal and ventral margins; P1 segments covered by small tubercles; achelate P2-P4 equal in size with smooth segments.

Pleonal appendages
Pleopods covered by eggs; uropodal endopod and exopod not exceed telson length; short subtriangular basipodite; rounded uropodal endopod and exopod finely fringed distally; uropodal endopod and exopod with one longitudinal median carina; uropodal exopod with a diaeresis; diaeresis with straight serrate dorsal margin; outer margin of uropodal exopod strengthened by one row of small tubercles ending with one small distal spine at level of dorsal margin of diaeresis.

Eggs
Spherical smooth eggs (diameter: *c.* 0.5 mm); 84 eggs visible (probably an underestimated number), joined in clusters and carried by pl1-pl6, mainly pl2 and pl3.

DISCUSSION

The family Mecochiridae Van Straelen, 1925 includes four genera, *Atherfieldastacus* Simpson *in* Robin *et al.*, 2016, *Huhatanka* Feldmann & West, 1978, *Mecochirus* Germar, 1827, and *Meyeria* M'Coy, 1849. Based on the groove pattern figured by Robin *et al.* (2016: fig. 1), the studied specimen is assigned to *Mecochirus* especially for the lack of the inferior groove (joined to the ventral margin in *Atherfieldastacus* and not joined to the ventral margin in *Meyeria*) and for the very short cardiac groove not reaching the dorsal margin of the carapace (joined to the dorsal margin in *Atherfieldastacus* and *Meyeria*). Finally, *Huhatanka* exhibits a very simple carapace groove pattern, very different from the holotype.

Based on the above-mentioned list, *Mecochirus* includes ten species, recorded from the Early to the Late Jurassic, except *M. lanceolatus* and *M. mcclymontorum*, both from the Early Cretaceous (Aptian) of Queensland (Australia) (Jell *et al.* 2017). Compared to the Cretaceous species, *Mecochirus cenomanicus* n. sp. differs from *M. mcclymontorum* by relatively short P1, finely tuberculated (very elongate and with row of spines on dorsal and ventral margins in *M. mcclymontorum*) and pleonal somites uniformly covered by small tubercles (smooth in *M. mcclymontorum*). *Mecochirus cenomanicus* n. sp. differs from *M. lanceolatus* by its three cephalic carinae (only two in *M. lanceolatus*) and pleonal somites uniformly covered by small tubercles (smooth in *M. lanceolatus*). Therefore, *M. cenomanicus* n. sp. represents the youngest record of *Mecochirus*, expanding the stratigraphic range of the genus from the Early to the Late Cretaceous.

Preservation of muscle fibers (Fig. 3)
Aluminum, silicon, oxygen and iron are the main elements detected by EDS analysis on the sedimentary matrix of the fossil, evidencing a combination of aluminosilicates and iron oxy/hydroxydes. The presence of iron oxy/hydroxydes transpires visually by the rusty color. Although the specimen in strongly compressed, pleonal muscles are partially preserved and are particularly visible on pleonal somite 2. The fossilized fibers are organized in bundles probably corresponding to anterior oblique and lateral muscles. Chemical analyses indicate that calcium, phosphorus and oxygen are spatially associated on these soft tissues. Thus, we infer that these muscle fibers are made of calcium phosphate and that phosphatization is the taphonomic mode of soft tissue preservation in this case. This mode of preservation is very common within fossil malacostracans (e.g., Feldmann & Schweitzer 2010; Klompmaker *et al.* 2019 and references therein; Jauvion *et al.* 2020).

RARE PRESERVATION OF EGGS IN THE DECAPOD CRUSTACEANS

Decapod crustaceans preserving their eggs are very rare in the fossil record. Indeed only one exceptional polychelidan lobster, *Palaeopolycheles nantosueltae* Jauvion, Audo, Bernard, Daley & Charbonnier, 2020, found with hundreds of eggs attached to the pleon, was recorded from the Middle Jurassic (Callovian) of La Voulte-sur-Rhône (Ardèche, France).

Mecochirus cenomanicus n. sp. herein described represents the second record of a decapod crustacean preserving clusters of eggs carried by the pleopods.

As reported by Jauvion *et al.* (2020: fig. 1a), the decapod crustaceans with an extended planktic larval stage produce a great numbers of eggs (tens of thousands to two millions) to compensate their large loss due to predation. On the contrary, decapod crustaceans with a shorter ontogenetic development reaching a more direct adult morphology produce fewer eggs (Jauvion *et al.* 2020: fig. 1b).

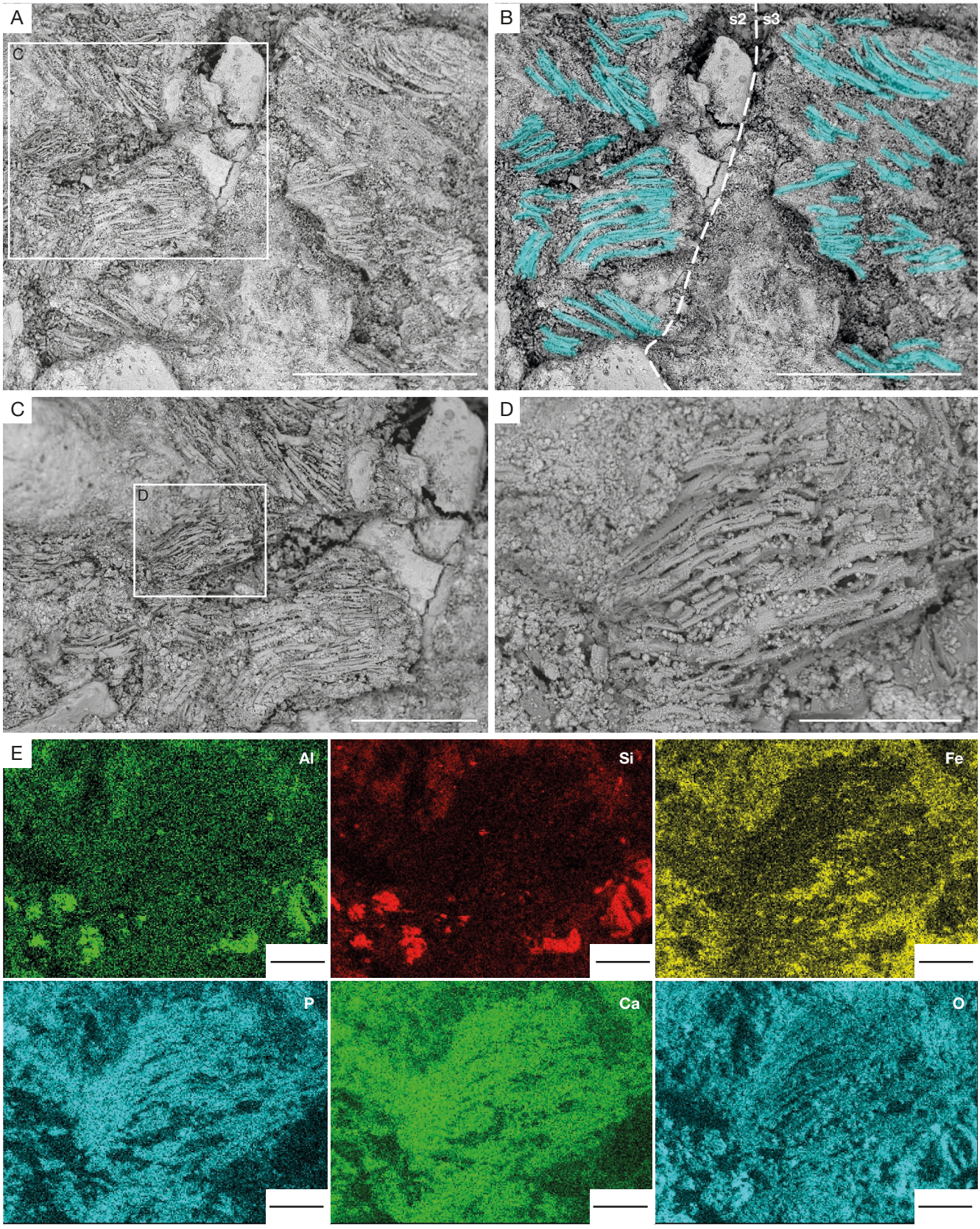

Fig. 3. — Pictures and elemental maps of preserved muscle fibers observed on holotype MNHN.F.B16583, located on pleonal somites 2 and 3: **A**-**D**, SEM images showing details of the bundles probably corresponding to anterior oblique and lateral muscles (highlighted in blue in B); **E**, EDS maps of main chemical elements corresponding to area pictured in D. Abbreviations: **Al**, aluminum; **Ca**, calcium; **Fe**, iron; **O**, oxygen; **P**, phosphorus; **Si**, silicon; **s2-s3**, pleonal somites 2 and 3. Photographs: G. P. Odin. Scale bars: A-B: 1 mm; C: 500 µm, D: 200 µm, E: 100 µm.

Based on these observations, *M. cenomanicus* n. sp., with a limited number of relatively large eggs, could be included within the second category, suggesting for this species an ontogenetic development like that of the extant decapod crustaceans with short larval stage.

One specimen of the extant glypheid lobster *Neoglyphea inopinata* (MNHN-IU-2008-14763) preserves clusters of big eggs carried by the pleopods as pointed out by Forest (2006) and figured by Charbonnier *et al.* (2012, 2013). According to Forest & Saint Laurent (1989), about 1000 eggs (diameter: *c.* 1.2-1.3 mm) are carried by long setae of proto- and endopodites, exclusively present in the females. Forest & Saint Laurent (1989) suggested a quick morphological development with the egg hatch occurring in an advanced morphological stage based on the direct observation of decapod crustaceans developing big eggs.

We could suggest a similar reproduction cycle for *Mecochirus cenomanicus* n. sp. even if the number of visible/or preserved eggs (n = 84) is low and probably underestimated. The size of the eggs (diameter *c.* 0.5 mm) is smaller than in *Neoglyphea inopinata*, but we must take into account that the new species has also a very small size (total body length: 2 cm). In conclusion, we could suppose that the reduce-sized *Mecochirus cenomanicus* developed a peculiar reproductive strategy with very limited egg-clusters bearing relatively large eggs.

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