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Couverture / *Cover*:
Reconstitution de *Glyphea dressieri* Meyer in Bronn, 1837/*Reconstitution of* Glyphea dressieri *Meyer in Bronn, 1837* (Charlène Letenneur, CR2P, MNHN).

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Middle Jurassic lobsters (Crustacea, Decapoda) from Normandy, France

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ABSTRACT
The Middle Jurassic (Callovian) fauna from Sainte-Scolasse-sur-Sarthe (Normandy, France) is remarkable for its exceptionally preserved crustaceans in arenaceous limestone beds. The crustacean fauna includes five species assigned to the Glypheidae, Erymidae and Longodromitidae. Glypheid lobsters are the most diversified and abundant group. A new detailed anatomic description leads to the first reconstruction of *Glyphea dressieri* Meyer *in* Bronn, 1837, and to highlight a marked sexual dimorphism. Similar observations are made in *Glyphea regleyana* (Desmarest, 1822). A quantitative analysis based on 149 specimens shows two dominant species: *Glyphea regleyana* (47.0 % of specimens) and *G. dressieri* (46.3 %). The palaeoenvironment is interpreted as subtidal mud flats largely open to offshore conditions. More precisely, the sedimentary facies and the associated fauna are indicators of a distal platform setting (upper circalittoral zone). The Sainte-Scolasse fauna is relatively close to that of the Oxfordian of Haute-Saône (eastern France) and thus forms an intermediate assemblage between the communities from the shallow carbonate platforms (e.g., Solnhofen Lithographic Limestone Lagerstätten) and those from the bathyal zone (e.g., La Voulte-sur-Rhône Lagerstätte).

KEY WORDS
Mesozoic,
Callovian,
Glypheidae,
Erymidae,
Longodromitidae,
Glyphea,
Eryma,
Abyssophtalmus,
exceptional preservation.

RÉSUMÉ
Crustacés (Crustacea, Decapoda) du Jurassique moyen de Normandie, France.
La faune du Jurassique moyen (Callovien) de Sainte-Scolasse-sur-Sarthe (Normandie, France) est remarquable par ces crustacés exceptionnellement conservés dans des niveaux de calcaire gréseux. La faune de crustacés est composée de cinq espèces appartenant aux Glypheidae, Erymidae et Longodromitidae. Les glyphées constituent le groupe le plus diversifié et abondant. Une description anatomique détaillée permet de proposer la première reconstitution de *Glyphea dressieri* Meyer *in* Bronn, 1837, et de mettre en évidence un dimorphisme sexuel marqué. Des observations similaires sont faites chez *Glyphea regleyana* (Desmarest, 1822). Une analyse quantitative basée sur 149 spécimens montre que deux espèces sont dominantes : *Glyphea regleyana* (47,0 % des spécimens) et *G. dressieri* (46,3 %). Le paléoenvironnement est interprété comme une vasière côtière largement ouverte sur la mer franche. Plus précisément, le faciès sédimentaire et la faune associée indiquent un milieu de plateforme distale (zone circalittorale supérieure). La faune de Sainte-Scolasse est relativement proche de celle de l'Oxfordien de Haute-Saône (Est de la France) et forme donc aussi un assemblage intermédiaire entre les communautés de plateformes carbonatées peu profondes (ex : Lagerstätten du Calcaire Lithographique de Solnhofen) et celles de la zone bathyale (ex : Lagerstätte de La Voulte-sur-Rhône).

MOTS CLÉS
Mésozoïque,
Callovien,
Glypheidae,
Erymidae,
Longodromitidae,
Glyphea,
Eryma,
Abyssophtalmus,
conservation
exceptionnelle.

INTRODUCTION

Jurassic crustaceans are particularly diverse and abundant in the fossil record of Europe, especially in Konservat-Lagerstätten, which are sedimentary deposits known for the exceptional preservation of organisms, including many lightly mineralized ones. Exceptionally preserved crustacean faunas are for instance known from the Early Jurassic Osteno Lagerstätte, Italy (e.g., Garassino 1996), the Middle Jurassic La Voulte-sur-Rhône Lagerstätte, France (e.g., Van Straelen 1922a, 1925; Charbonnier 2009; Charbonnier *et al.* 2010; Audo *et al.* 2014b; Jauvion *et al.* 2020), the Middle Jurassic Monte Fallano Lagerstätte, Italy (Bravi *et al.* 2014), as well as the Late Jurassic Lagerstätten of the Solnhofen Lithographic Limestones, Germany (Solnhofen, Eichstätt, Nusplingen: e.g., Münster 1839; Oppel 1862; Garassino & Schweigert 2006, Charbonnier & Garassino 2012; Schweigert *et al.* 2016; Odin *et al.* 2019), and from the Cerin and Canjuers plattenkalks, France (Van Straelen 1922b; Audo *et al.* 2014a).

Jurassic deposits of "intermediate" nature also exist: they provide fossil crustaceans that are relatively well preserved in volume within siliceous or carbonate concretions, without reaching a Lagerstätten-type preservation. These intermediate deposits still provide high-quality anatomical details as well as new palaeobiological information on sexual dimorphism, allometry growth, and phenomena of moulting and autotomy. A few of these are known from the Jurassic. This is the case for the crustaceans found in siliceous concretions in the Terrain à Chailles Formation, Eastern France (Oxfordian; Charbonnier *et al.* 2012).

In Normandy, several Jurassic outcrops yielded crustaceans preserved in nodules and nodular limestones. The littoral outcrops along the English Channel (e.g., Vaches Noires cliffs) or historical quarries (e.g., La Caine, Ranville) yielded diverse crustacean faunas studied by pioneers such as Eudes-Deslongchamps (1835, 1842), Morière (1864), Hée (1924), and Van Straelen (1925) (see historical synthesis by Gendry 2020). In the 2000s, new studies were carried out on occasional but important discoveries in the Early Jurassic (e.g., hermit crabs: Schweigert *et al.* 2013), Middle Jurassic (e.g., isopods: Guinot *et al.* 2005; homolodromioid crabs: Fraaije *et al.* 2013; galatheoid anomurans: Fraaije *et al.* 2019; erymid lobsters: Devillez & Charbonnier 2019), and Late Jurassic (e.g., erymid lobsters: Devillez *et al.* 2018; glypheid lobsters: Charbonnier *et al.* 2013).

In the interior of Normandy, outcropping conditions are generally less favorable and discoveries of fossil crustaceans are rarer. The area of Sainte-Scolasse-sur-Sarthe (Orne department) is an exception since it yielded numerous decapod crustacean remains (lobsters, crabs), the study of which has remained preliminary since Eudes-Deslongchamps (1842). This regional palaeontologist was the first to describe and figure specimens he had received from L.-M. Bachelier, a landowner on the commune of Sainte-Scolasse-sur-Sarthe. About thirty specimens were collected "among the fragments, broken by the roadmenders for daily repairs". Based on this material, Eudes-Deslongchamps (1842) described two species he considered as new: the squammiferous lobster *Palinurus squamifer* and the long-arm lobster *Palinurus longebrachiatus*. Later, Bachelier (1850) described the deposits, which had delivered the crustaceans, as belonging to the Callovian, but did not locate any outcrops precisely. All fossil crustaceans collected in the middle of the 19th century at Sainte-Scolasse-sur-Sarthe are now housed in different historical collections and have not been revised for more than 170 years.

In the present study, these crustaceans are used as an important source of information to investigate the structure of a Jurassic arthropod community and to reconstruct key aspects of its marine palaeoenvironment. We present the updated faunal inventory of the crustaceans from Sainte-Scolasse-sur-Sarthe and analyze their biodiversity. For that purpose, we re-examine their systematics in the light of modern standards. Thanks to new specimens, we improve the anatomical description of the glypheid lobster *Glyphea*

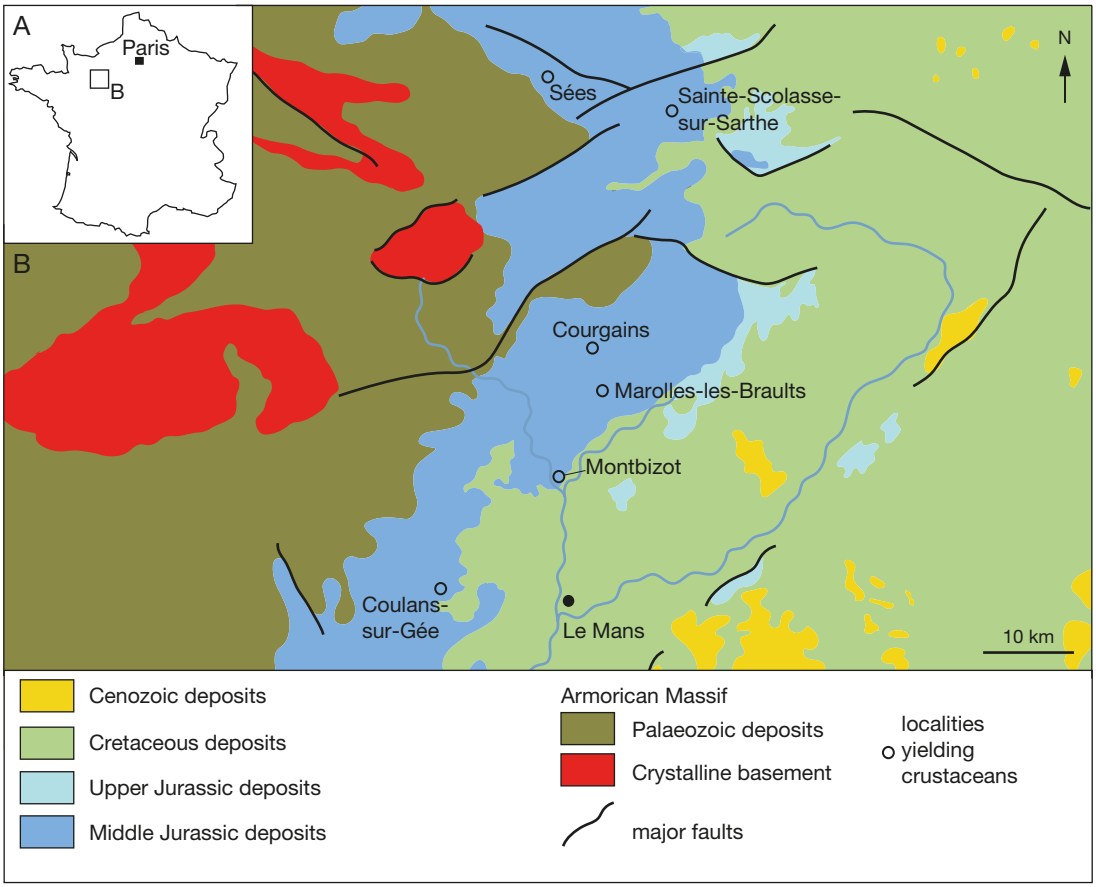


FIG. 1. — Geological map of the Perche region (Normandy, France) and location of the different Callovian outcrops yielding decapod crustaceans of the Ste-Scolasse fauna (modified after Carte géologique de la France 1/1 000 000).

dressieri Meyer *in* Bronn, 1837. We also analyze its palaeobiogeographical distribution. We propose quantitative data based on 149 specimens, allowing detailed palaeoecological and palaeoenvironmental comparisons with other Jurassic crustacean faunas.

GEOLOGICAL SETTING

Sainte-Scolasse-sur-Sarthe (later noted as Ste-Scolasse) is located in the Orne department in Normandy (north-west of France) at about 50 kilometres north of Le Mans (Fig. 1). This locality belongs to the natural region of Perche, a transitional zone between the western margin of the Paris Basin to the east, and the Hercynian crystalline Armorican Massif to the west. The area is mainly covered by Mesozoic sediments. The oldest formations are of Middle-Late Jurassic age with the Upper Callovian Assise des Carreaux and the Callovian-Oxfordian Marnes à Pernes formations (Moguedet *et al.* 1998). In the east, the Cretaceous (Albian-Cenomanian) transgressive glauconitic sands disconformably overlie the Jurassic sediments. Since the Late Cretaceous, the region is in emersion and undergoes continental weathering. Several Hercynian basement faults (70°N and 160°N) affect the Jurassic-Cretaceous series.

The studied crustaceans were collected in the Assise des Carreaux Formation, which was first succinctly described by Bachelier (1850), later formally defined by Bizet (1884, 1885), and revised by Dangeard (1950). After Moguedet *et al.* (1998), this formation is 15 to 25 meters thick and is composed of fine-grained sands and silts with interbedded decametric sandy limestones. The sandy and silty levels are not very fossiliferous, whereas the more indurated beds are rich in fossils. Fossil crustaceans are clearly concentrated in the arenaceous limestone beds. The Assise des Carreaux Formation is dated to the upper Callovian by abundant ammonites: the basal beds yielded species – *Peltoceras* cf. *baylei* Prieser, 1937, *Hecticoceras rursicostatum* (Buckman, 1924) – characteristic of the Athleta biozone, while the upper beds yielded species – *Kosmoceras dunkani* (Sowerby, 1817), *Quenstedtoceras lamberti* (Sowerby, 1819) – characteristic of the Lamberti biozone.

The associated benthic fauna, in addition to crustaceans, was composed of rhynchonellid brachiopods, diverse endobenthic bivalves, stalked crinoids, and solitary corals (d'Orbigny 1850; Bachelier 1850). According to Moguedet *et al.* (1998), the fine-grained deposits are characteristic for subtidal mud flats that were largely open to offshore conditions, as indicated by the abundant pelagic fauna, especially ammonites. A thin section in the matrix of one of the Ste-Scolasse crustaceans reveals a wackestone facies with abundant micrite and some bioclasts

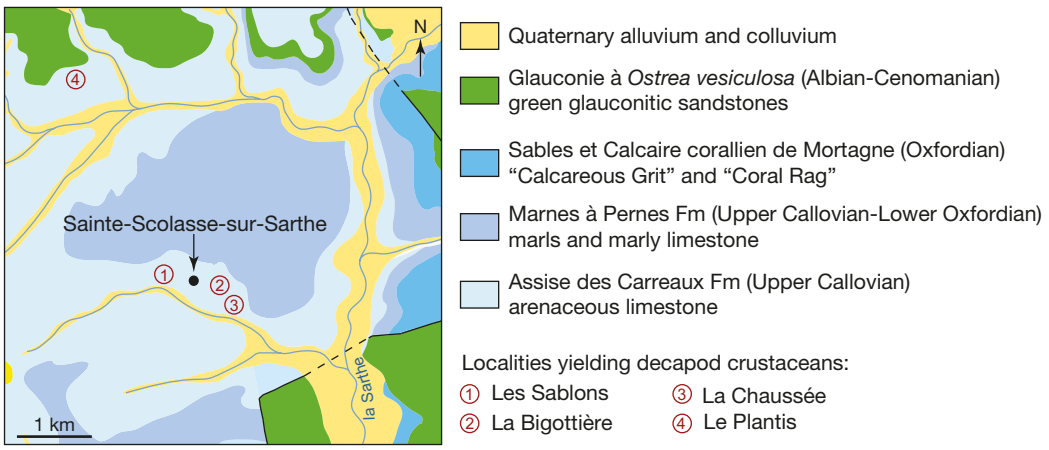


FIG. 2. — Detailed geological map of the Sainte-Scolasse-sur-Sarthe area with the different historical outcrops yielding decapod crustaceans (modified after Moguedet *et al*. 1998).

(including gastropods, bryozoans). Ooids and peloids are absent. Quartz and feldspath grains are abundant and their granulometry is about 120 to 250 micrometers. They are angular and suggest a relatively close origin: all these detrital minerals, associated with phtanite grains (M.-P. Dabard, comm. pers., 2017) were related to the erosion of the emerged crystalline Armorican Massif.

MATERIAL AND METHODS

The material consists of 149 three-dimensionally preserved specimens in fine-grained calcaro-siliceous nodules. The crustacean cuticle is completely silicified and has a particular bluish-grey colour (appearing black after preparation and sandblasting). In most cases, the specimens correspond to molts visible on the dorsal and lateral sides. The carapaces or cephalothoraces are sometimes articulated and linked to pereiopods. Some rare cephalothoraces are preserved articulated with the cephalic, thoracic and pleonal appendages.

Among the material, 135 specimens are from Ste-Scolasse and its surroundings. Indeed, according to the few historical handwritten notes available, some specimens originate from at least four localities a few hundred metres away: the places known as Les Sablons, La Bigottière and La Chaussée located on the commune itself, and an outcrop in the Le Plantis village, just north Ste-Scolasse (Fig. 2). The other specimens come from five localities to a few tens of kilometers: Sées, Marolles-les-Braults, Courgains, Montbizot and Coulans-sur-Gée (Fig. 1).

All the material originates from historical collections housed at the Muséum d'Histoire naturelle du Mans – Musée Vert, the Muséum national d'Histoire naturelle, Paris, and the Institut de Géologie de Rennes. During this study, some of the type material of crustaceans (*Palinurus squamifer* and *P. longebrachiatus*) described by Eudes-Deslongchamps (1842) was rediscovered at MNHN in Alphonse Milne Edwards' collection. Considered as destroyed during the World War II bombing of the city of Caen (Bigot 1945), these specimens were actually spared.

The taxonomic richness and relative abundance of crustacean species were calculated in order to estimate the palaeobiodiversity, and to enable comparisons with other Jurassic crustacean communities. Biometric measurements on glypheid lobsters were made on 78 complete carapaces. These measurements correspond to the carapace length (CL) and carapace height (CH). In order to compare the morphometric relationships with other fossil glypheids and to interpret the palaeobiology of Ste-Scolasse fossil species, the results obtained were plotted graphically and regression coefficient describing the morphometric relationships was calculated using a linear model.

ABBREVIATIONS

Institutional abbreviations

IGR	Institut de Géologie de Rennes, Université de Rennes 1, Rennes;
MNHN.F	Muséum national d'Histoire naturelle, collection de Paléontologie, Paris;
MNHN.Gg	Muséum national d'Histoire naturelle, collection de Géologie, Paris;
MHNLM	Muséum d'Histoire naturelle du Mans – Musée Vert, Le Mans;
NHMW	Naturhistorisches Museum Wien, Austria;
UCBL-FSL	Université Claude Bernard Lyon 1, Villeurbanne;
UCBL-EM	collection of the École nationale supérieure des Mines de Paris (ENSM), housed at the Université Claude Bernard Lyon 1 (Villeurbanne);
USTL	Université Sciences Technologies Lille (Villeneuve d'Ascq).

Anatomical abbreviations

CL	carapace (cephalothoracic shield) length, excluding rostrum: linear distance between ocular incision and dorsal posterior margin;
CH	cephalothoracic height: linear distance perpendicularly measured to dorsal margin from its intersection with branchiocardiac groove until ventral margin;
Mxp2	second maxilliped (thoracopod 2);
Mxp3	third maxilliped (thoracopod 3);
P1-P5	pereiopods 1 to 5 (thoracopods 4 to 8);
s1-s2	pleonal somites 1 to 6.

SYSTEMATIC PALAEONTOLOGY

The systematic arrangement used in the present paper follows the classifications proposed by Charbonnier *et al.* (2015) for the glypheid lobsters and Devillez *et al.* (2019) for the erymid lobsters.

Class MALACOSTRACA Latreille, 1802
Order DECAPODA Latreille, 1802
Infraorder GLYPHEIDEA Zittel, 1885
Superfamily GLYPHEOIDEA Zittel, 1885
Family GLYPHEIDAE Zittel, 1885

Genus *Glyphea* Meyer, 1835

TYPE SPECIES. — *Palinurus regleyanus* Desmarest, 1822, by monotypy.

DIAGNOSIS (by Charbonnier *et al.* 2013). — Subcylindrical carapace, laterally compressed; short pointed rostrum, spineless, straight or slightly downward-inclined; cephalic region with longitudinal spiny carinae; very deep cervical groove, steeply inclined, ventrally joined to antennal groove, delimiting narrow cephalic region; ventral margin of antennal-pterygostomial region strongly concave; antennal groove strongly rounded ventrally, forming raised antennal lobe; antennal groove joined with carinate ventral margin of cephalic region; deep gastro-orbital groove joined to cervical groove at level of gastro-orbital carina, with two transverse divergent branches strongly incurved, delimiting two tuberculated gastro-orbital lobes; deep postcervical groove joined dorsally, medially (laterocardiac groove) and ventrally to branchiocardiac groove, forming two elongate lobes separated by laterocardiac groove; straight cardiac groove, upward-inclined and joined posteriorly to postcervical groove and anteriorly to dorsal margin; deep intercervical groove progressively shallow from postcervical to cervical grooves; deep, straight branchiocardiac groove, strongly inclined, joined to dorsal margin of carapace; deep hepatic groove, convex ventrally at intersection with branchiocardiac groove and straight at intersection with antennal groove; inflated adductor muscle insertion area; deep, sinuous inferior groove, joined to hepatic groove; subchelate P1-P4; achelate P5; uropodal exopod with diaeresis.

Glyphea dressieri Meyer *in* Bronn, 1837
(Figs 3-9)

Glyphea dressieri Meyer *in* Bronn, 1837: 480.

Palinurus squamifer J.-A. Eudes-Deslongchamps, 1842: 55, pl. 4, figs 4, 5.

For detailed list of synonymy see Charbonnier *et al.* (2013: 52, 53)

TYPE MATERIAL. — ***Glyphea dressieri***: holotype by monotypy NHMW 1847/0051/1133 (d'Udressier coll.). In their monograph, Charbonnier *et al.* (2013) designated a neotype (MNHN.F.A29540, Petitclerc coll.), just before the holotype was rediscovered in the Natural History Museum in Vienna, Austria, by Feldmann *et al.* (2015). An historical cast of this holotype was identified in Paris in Alexandre Brongniart's collection (MNHN.F.A59982). — ***Palinurus squamifer***: 16 syntypes (A. Milne-Edwards coll., *ex* Eudes-Deslonchamps coll.) from the Upper Callovian of Ste-Scolasse, Normandy, France.

TYPE LOCALITY. — Quenoche, Haute-Saône department, France.

TYPE AGE. — Late Jurassic, early Oxfordian (Terrain à Chailles Formation).

ADDITIONAL EXAMINED MATERIAL. — See Table 1.

DISTRIBUTION. — Late Bathonian-late Oxfordian.

DESCRIPTION

Carapace (Fig. 4)

Subcylindrical carapace (cephalothoracic shield), laterally compressed (holotype: CL = 42 mm, CH = 22 mm); short pointed rostrum, without spine and straight; anterior cephalic margin with optical and antennal notches; cephalic region covered by raised scales, aligned to form four longitudinal subparallel carinae: orbital, gastro-orbital, supra-antennal, and antennal carinae; gastro-orbital and supra-antennal carinae stronger than orbital carina; antennal carina strongly raised, with large spines directed forward; very deep cervical groove, steeply inclined, intercepting dorsal margin at angle of *c*. 80° at a distance of one-third of total length of dorsal margin from anterior; cervical groove ventrally joined to a shallow antennal groove, delimiting a narrow cephalic region; ventral margin of antennal-pterygostomial region strongly concave; antennal groove slightly rounded ventrally, forming slightly raised antennal lobe; antennal groove parallel to carinate ventral margin of cephalic region; sinuous gastro-orbital groove joined to cervical groove at the level of gastro-orbital carina, with two transverse branches parallel to cervical groove, extending from the dorsal margin to antennal carina, delimiting two raised gastro-orbital lobes; gastro-orbital lobes composed of three to four vertical rows of tubercles, one of which extends and forms antennal carina; deep postcervical groove joined dorsally, medially and ventrally to branchiocardiac groove, forming two raised squamose lobes separated by laterocardiac groove; anterior lobe wider than posterior one; shallow cardiac groove, upward-inclined, joined posteriorly to postcervical groove and anteriorly to dorsal margin; deep intercervical groove progressively shallower from postcervical to cervical grooves, slightly backward-directed; deep straight branchiocardiac groove not reaching dorsal margin of carapace; branchiocardiac groove, strongly inclined (*c*. 60°), at distance four-fifths of total length of dorsal margin from anterior; deep hepatic groove, strongly convex ventrally at intersection with branchiocardiac groove, straight and backward-directed in the intersection with antennal groove; strongly inflated adductor muscle insertion area; shallow inferior groove, convex posteriorly, joined to hepatic groove; carapace with large raised scales sub-aligned in cardiac and branchial regions and small raised scales in cephalic and hepatic regions; posterior and ventral margins bordered by very small tubercles; dorsal midline limited on each side by row of small rounded tubercles.

Epistome

Large epistome, swollen, convex, and subrectangular, not fused to the carapace but separated from it by a suture; lateral margins slightly sinuous; anterior margin characterized by the posterior limits of the arthrodial cavities of antennae, narrow sinus between these cavities; posterior margin with

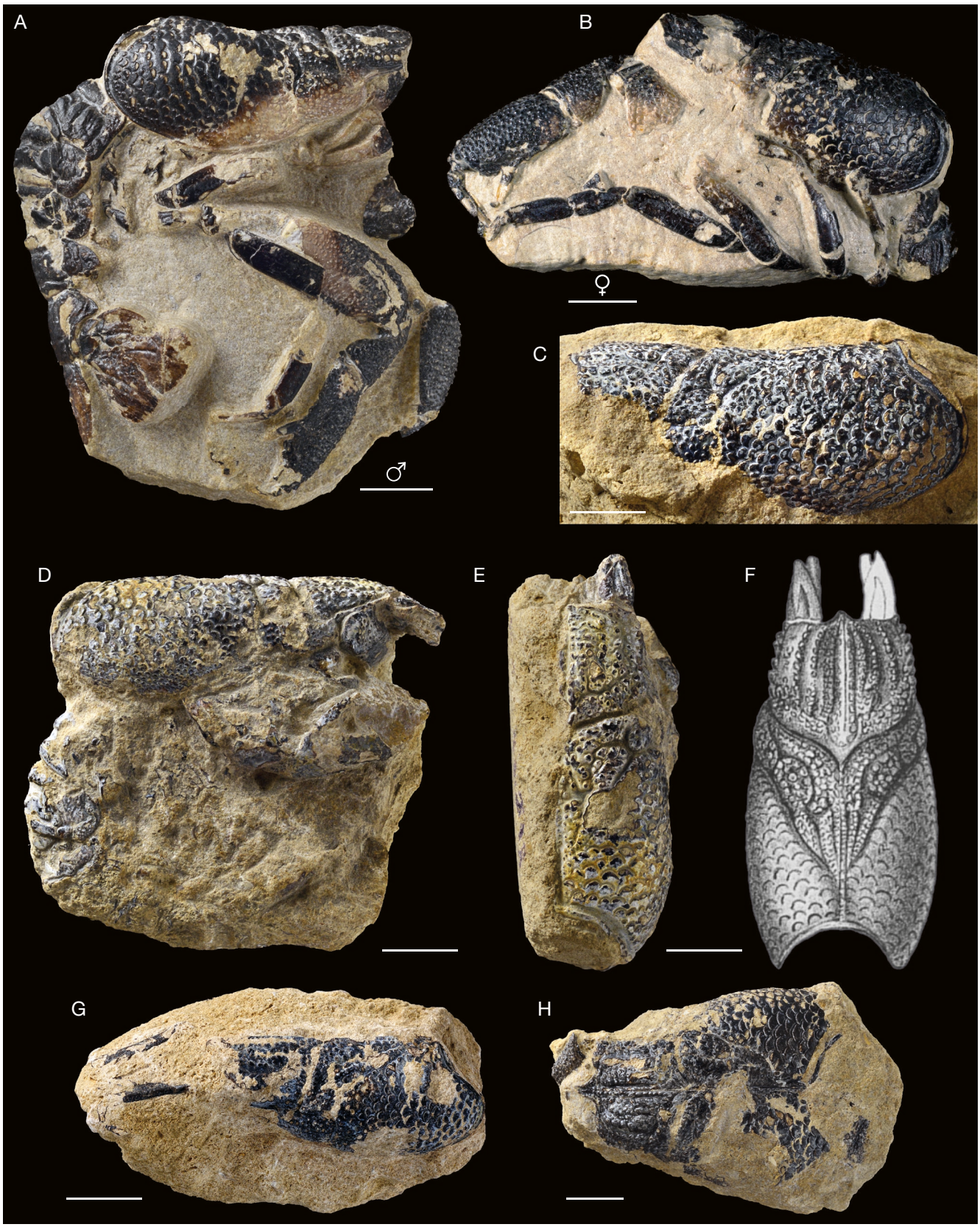


FIG. 3. — *Glyphea dressieri* Meyer *in* Bronn, 1837 from the Upper Callovian of Sainte-Scolasse-sur-Sarthe: **A**, MNHN.GG.Gg2004-19049 (Bachelier coll), almost complete specimen, right lateral view; **B**, MHNLM 2008.12.612.5 (Bachelier coll), subcomplete specimen, left lateral view; **C**, MNHN.F.A59325, syntype of *Palinurus squamifer* Eudes-Deslongchamps, 1843, isolated carapace, left lateral view; **D**-**F**, MNHN.F.B11048, syntype of *P. squamifer*, carapace and pleon in right lateral view (**D**), carapace in dorsal view (**E**) and original figure (**F**) by Eudes-Deslongchamps (1842: pl. 4, fig. 5); **G**, MHNLM 2008.12.612.6 (Bachelier coll), carapace and antennal peduncles; **H**, MNHN.F.A59328, syntype of *P. squamifer*, butterfly-shaped carapace (exuvia). Photographs: A, C-E, G, H, L. Cazes; B, J. Falconnet. Scale bars: 1 cm.

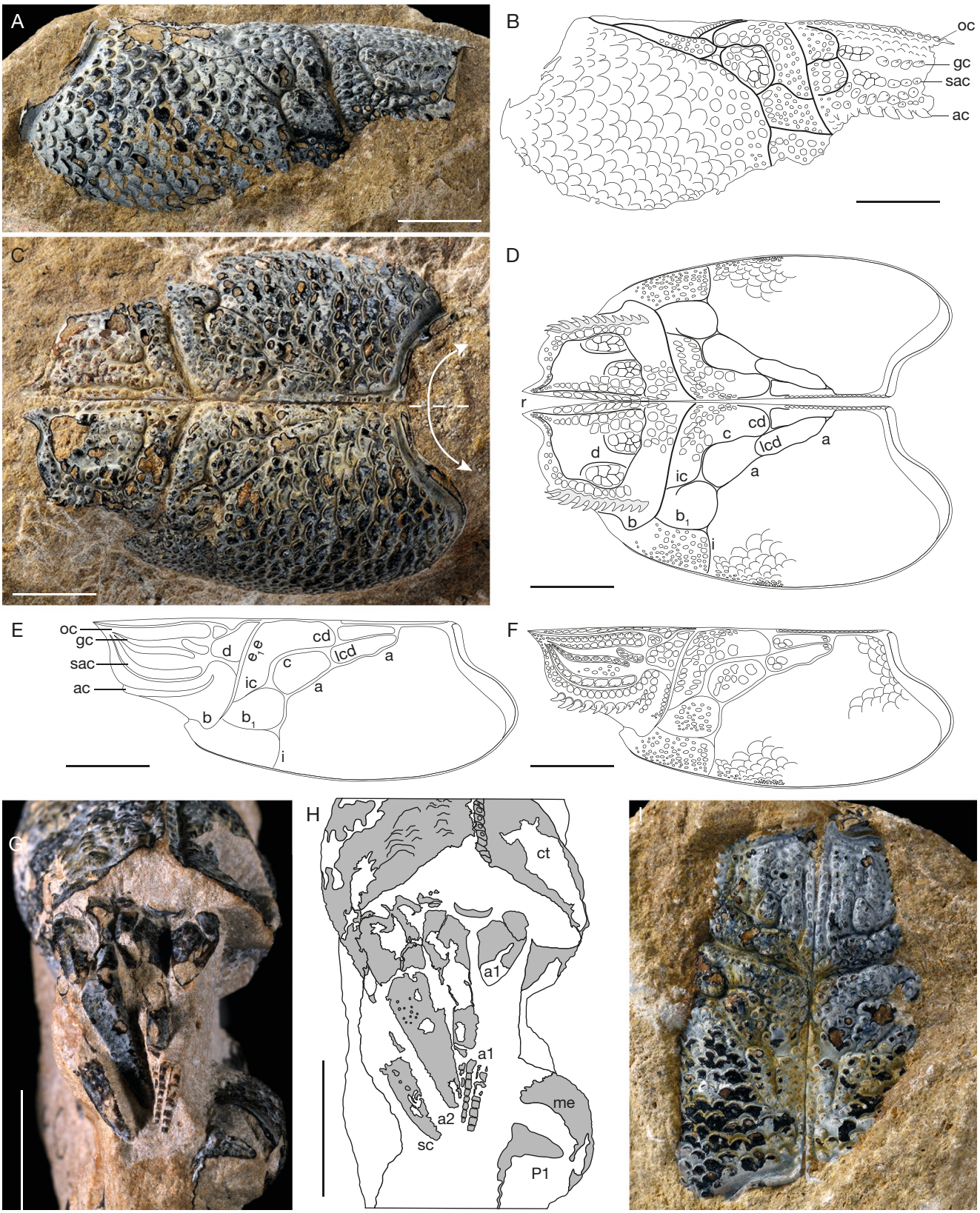


FIG. 4. — *Glyphea dressieri* Meyer *in* Bronn, 1837 from the Upper Callovian of Sainte-Scolasse-sur-Sarthe (Bachelier coll.): **A**, **B**, MHNLM 2008.12.613.5, isolated carapace, right lateral view and line drawing; **C**-**F**, MHNLM 2008.12.612.2, butterfly-shaped carapace (exuvia) and line drawings with and without scaly ornamentation in order to highlight carapace groove pattern and cephalic carinae; **G**, **H**, MHNLM 2008.12.613.7, detail of frontal region with cephalic appendages (**G**) and line drawing (**H**); **I**, MHNLM 2008.12.612.3, butterfly-shaped carapace (exuvia). Abbreviations: **a**, branchiocardiac groove; **ac**, antennal carina; **a1**, antennula; **a2**, antenna; **b**, antennal groove; **b_1**, hepatic groove; **c**, postcervical groove; **cd**, cardiac groove; **ct**, carapace; **d**, gastro-orbital groove; **e_1e**, cervical groove; **gc**, gastro-orbital carina; **i**, inferior groove; **ic**, intercervical groove; **lcd**, laterocardiac groove; **me**, merus; **oc**, orbital carina; **P1**, pereiopod 1; **sac**, supra-antennal carina; **sc**, scaphocerite. Photographs: A, C, I, P. Loubry; G, J. Falconnet. Line drawings: C. Chény. Scale bars: 1 cm.

large rounded depression corresponding to front of mouth, marked by deep groove and small axial tubercle posteriorly directed; ornamentation with small tubercles, circular region between the posterior margin (axial tubercle) and anterior sinus smooth and depressed.

Cephalic appendages
Antennulae (a1) composed of antennular peduncle with three segments: pyriform precoxopodite; long, cylindrical, coxopodite; subrectangular basipodite; two short flagella articulated to distal part of basipodite; antennae (a2) composed of an antennal peduncle with three segments (short, stocky ischiocerite; thin, elongate merocerite with spinose lateral margins, and short, stocky carpocerite), a long multi-articulated flagellum, and an elongate, triangular, pointed scaphocerite; symmetrical, strong, and robust mandibles, with three-segmented palp: the third widens in ovate palette, palp fitting behind secant edge of mandible.

Pleon (Fig. 5)
s1-s6 with rounded tergum, tergal flanks with anterior and posterior grooves and tergopleuron separated from tergum by small constriction connecting points of articulation; short s1 with trapezoidal tergopleura; very large s2 tregopleuron with subrectilinear ventral margin and proximal part more elongate forwards, partially covering s1 tergopleuron; s2-s5 tergopleura with outer surface bearing two to three longitudinal lobes limited by a system of grooves and tuberculated ventral margin; s3-s5 tergopleura with ventral margin pointed in male and rounded in female; s6 with subtrapezoidal tergum and pointed to rounded tergopleura with distal notched for uropodal insertions; subrectangular telson with two deep lateral grooves; dorsal surface with two longitudinal carinae converging to a pair of flattened tubercles in proximal part; large scale located proximally to one pair of tubercles.

Thoracic appendages (Fig. 6)
Short Mxp2 with thin and elongate merus, short incurved carpus and short ovoid propodus; elongate Mxp3 (*c.* 80 %CL) with smooth elongate ischim, subrectangular merus; elongate, strong, and subchelate P1, short quadrate P1 ischium, long P1 merus, laterally flattened, with small scales dorsally and small tubercles ventrally, spiny ventral margin with strong distal spine; trapezoidal P1 carpus, covered by small tubercles with spiny ventral margin; P1 propodus and dactylus showing two different morphologies: long and slender propodus and large and elongate dactylus in male specimens; short and laterally flattened propodus and short, thin dactylus in female specimens; P1 propodus, strongly tuberculated, ventral margin with very strong and elongate spine (located in the first third anteriorly) followed by four small spines and one longer distal spine neighbouring an inflated tubercle at the articulation with dactylus; strong and elongate P1 dactylus, very large proximally and slender distally with a median longitudinal groove dorsally, covered by small tubercles, inner margin of P1 dactylus with setal pores; achelate P2-P5, relatively thin, uniformly covered by very small pits; elongate P2-P5 dactyli, with a median longitudinal groove dorsally.

Pleonal appendages
Only basal parts of pleopods 2-5 preserved; rounded uropods as long as telson; uropodal exopod with fringed diaeresis and longitudinal median carina slightly spiny, reaching ventral margin of the diaeresis and flanked by outer tuberculated ridge, shorter and stopped at level of the dorsal margin of the diaeresis; outer lateral margin with small distal spine; uropodal endopod with longitudinal median carina slightly spiny, reaching the ventral margin and flanked by an outer tuberculated ridge, shorter, not reaching the ventral margin and stopped at three quarters of the uropod height.

Discussion

The configuration of the cephalothoracic grooves follows precisely that given in the diagnosis of *Glyphea* (see Charbonnier *et al.* 2013: 35 & fig. 11). The morphology of P1 propodus, and the scaly ornamentation of the specimens from Ste-Scolasse are diagnostic characters of *Glyphea dressieri*.

Following Bigot (1945: 20), Charbonnier *et al.* (2013) indicated that the type material of *Palinurus squamifer* was destroyed during the bombardment of Caen during the World War II. However, the careful examination of specimens in Alphonse Milne-Edwards' collection leads us to identify the type material, probably sent to him or to his father Henri Milne Edwards by J.-A. Eudes-Deslongchamps himself. We ignore the precise history of these specimens, which were fortunately not destroyed but forgotten for about 150 years. After checking all the available syntypes, we confirm that *P. squamifer* is a junior synonym of *G. dressieri*.

Examination of the well-preserved specimens from Ste-Scolasse leads us to describe anatomical details that were unknown until today for this species: cephalic appendages, dorsal midline with rows of tubercles, ornamentation of first pereiopods, telson.

Sexual dimorphism
Étallon (1859) was the first to evoke sexual dimorphism in *G. dressieri*, but he had unfortunately only very few specimens and his hypothesis stemmed mainly from his observation of *G. regleyana*, for which he had numerous specimens.

Based upon 70 specimens, the present analysis is the first to allow the identification of a potential sexual dimorphism in *Glyphea dressieri*. Following Charbonnier *et al.* (2012), we made biometric measurements on 37 carapaces. The relation between the carapace length and height of *G. dressieri* is described by a linear model (Fig. 7; Bravais-Pearson test indicates a significant correlation) as already observed in *G. regleyana* (see Charbonnier *et al.* 2012: fig 6). Our plot diagram does not show separate clusters that might be interpreted as being due to sexual dimorphism. The measured specimens form a relatively homogenous assemblage with a wide range of carapace sizes, although small and/or juvenile glypheids seem to be absent.

Forest & Saint Laurent (1989) recognized dimorphic features in the extant glypheid lobster *Neoglyphea inopinata* Forest & Saint Laurent, 1975, in which the first pereiopods of males are longer and proportionally thinner than in

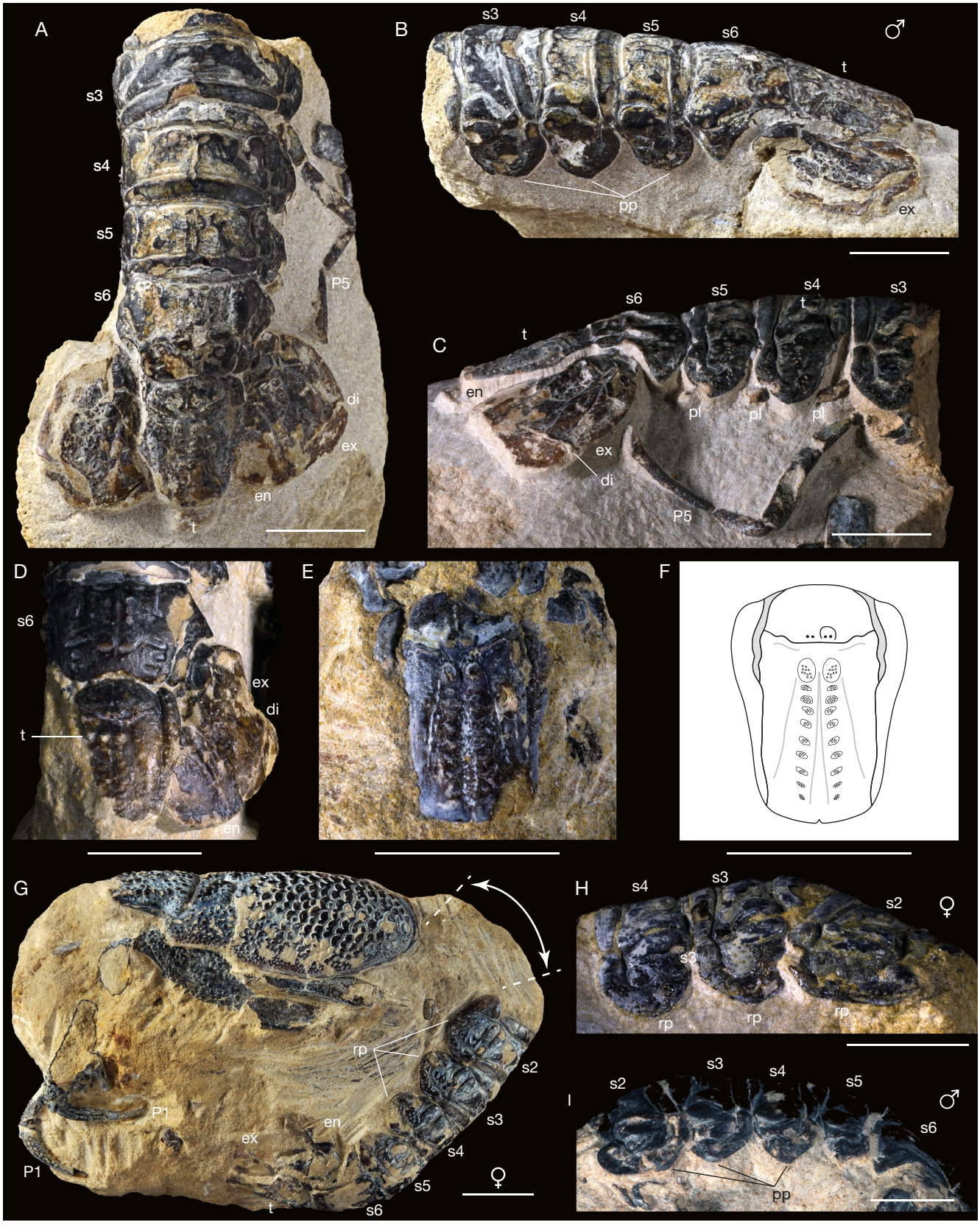


FIG. 5. — *Glyphea dressieri* Meyer *in* Bronn, 1837 from the Upper Callovian of Sainte-Scolasse-sur-Sarthe: **A**-**C**, MNHN.F.A59896, syntype of *Palinurus squamifer*, isolated pleon, dorsal, left and right lateral views; **D**, MNHN.F.GG.Gg2004.19049 (Bachelier coll.), detail of tail fan, dorsal view; **E**, MHNLM 2008.12.612.16 (Bachelier coll.), detail of telson, dorsal view; **F**, line drawing of telson; **G**, UCBL-EM 80055, subcomplete specimen (exuvia) showing disarticulation between carapace, pleon and pereiopods, left lateral view; **H**, MHNLM 2008.12.613.22 (Bachelier coll.), detail of female pleon, right lateral view; **I**, MHNLM 2008.12.613.2 (Bachelier coll.), detail of male pleon, left lateral view. Abbreviations: **di**, diaeresis; **en**, uropodal endopod; **ex**, uropodal exopod; **P1**-**P5**, pereiopods 1 to 5; **pl**, pleopod; **pp**, pointed tergopleuron; **rp**, rounded tergopleuron; **s2**-**s6**, pleonal somites 2 to 6; **t**, telson. Photographs: A-C, L. Cazes; D, E, H, I, J, Falconnet; G, C. Lemzaouda. Line drawing: C. Chény. Scale bars: 1 cm.

Fig. 6. — *Glyphea dressieri* Meyer *in* Bronn, 1837 from the Upper Callovian of Sainte-Scolasse-sur-Sarthe (Bachelier coll.): **A**, **B**, MHNLM 2008.12.612.5, female specimen, detail of P1 showing short propodus and dactylus and line drawing; **C**, **D**, MHNLM 2008.12.613.2, male specimen, detail of P1 showing elongate propodus and dactylus and line drawing; **E**, MHNLM 2008.12.613.2, male specimen, showing elongate P1 propodus and dactylus and pleonal somites with pointed tergopleura; **F**, MNHN.GG.Gg2005-8347c, female specimen, showing short P1 propodus and dactylus and pleonal somites with rounded tergopleura; note the brachyuran crab carapace (white arrow). Abbreviations: **ca**, carpus; **da**, dactylus; **me**, merus; **P1**-**P5**, pereiopods 1 to 5; **pr**, propodus; **sp**, spine. Photographs: A, C, E, Falconnet; F, L. Cazes. Line drawings: C. Chény. Scale bars: 1 cm.

females, and the pleonal somites show quadrate and sharp tergopleura in males, whereas they are more rounded in females. We therefore also examined the morphology of the first pereipods and tergopleura of pleonal somites. In the present sample, we identified specimens of *G. dressieri* with elongate P1 propodus and large and stocky P1 dactylus associated with sharply pointed (mucronate) s2-s5 tergopleura. They are probably male specimens. Other specimens show shorter P1 propodus and dactylus associated with rounded s2-s5 tergopleura. They are probably female specimens. This interpretation concurs with those proposed by Charbonnier *et al.* (2012) for *G. regleyana* and *G. muensteri*. We note that the secondary sexual characters in P1 and pleonal somites are less visible in *G. dressieri* than in other fossil glypheids, probably due to its overall strongly tuberculated and scaly ornamentation.

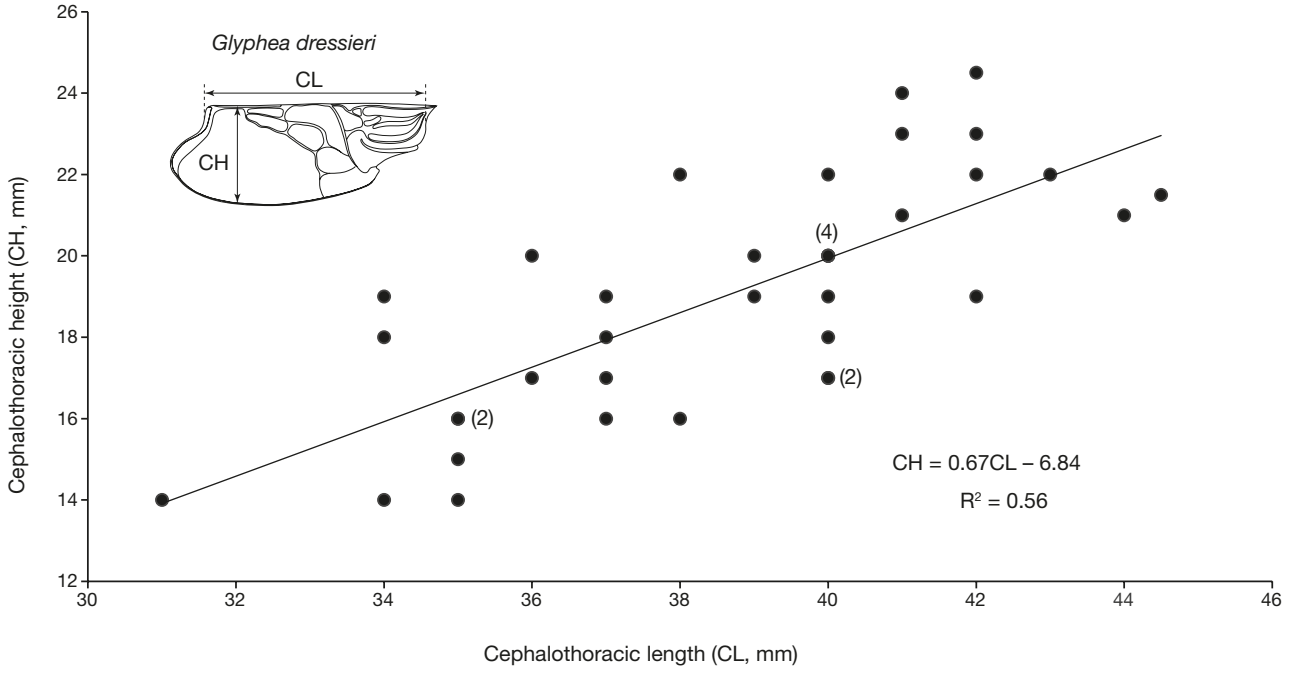


Fig. 7. — Biometric analysis (Bravais-Pearson test) on 37 carapaces in *Glyphea dressieri* Meyer *in* Bronn, 1837: linear relationship between length (**CL**) and height (**CH**) of carapace. Schematic drawing indicates the measurements. Numbers in brackets correspond to overlapping measurements.

Similar evidence of sexual dimorphism have been documented in other fossil glypheoid species: *Mecochirus longimanatus* (Schlotheim, 1820) (Kimmeridgian-Tithonian, Germany; Garassino & Schweigert 2006; Charbonnier *et al.* 2021), *Angarestia foresti* (Feldmann & Saint Laurent, 2002) (Cenomanian, Australia; Feldmann & Saint Laurent 2002) and *Atherfieldastacus magnus* (M'Coy, 1849) (Aptian, Mexico; see Feldmann *et al.* 2007 for details). To summarize, secondary sexual characteristics including features of the first pereiopods and/or tergopleura of pleonal somites seem to be relatively frequent in fossil glypheoid lobsters when their preservation allows their observation.

Ecdysis (Figs 5G; 8)

Some specimens of *G. dressieri* are fossilized in very particular anatomical positions: the body is disarticulated with a disconnection between the carapace and pleon which form almost a right angle, while the pereiopods are grouped in a fan pointing to the pleon. Several specimens also correspond to isolated carapaces, which are dorsoventrally flattened (butterfly-shaped carapace) and sometimes split along the dorsal midline. All these positions are typical of different phases of molting process in glypheid lobsters (e.g., *G. regleyana*, *G. muensteri*) as already described by Charbonnier *et al.* (2012). The active phase of ecdysis in *G. dressieri* probably started with the rupture of the integument between the carapace and the first pleonal somite. The butterfly-shaped carapaces indicate that the dorsal margin worked probably as a hinge that liberated the head of the molted animal. This was followed by extraction of the thoracic appendages and finally the pleon. The molted glypheid emerged, leaving the carapace displaced from the pleon, with their axes forming almost a right angle.

Reconstruction (Fig. 9)

Our new observations supply more accurate description and allow a detailed iconographic reconstruction of *G. dressieri*. The general views differ from those historically proposed by Eudes-Deslongchamps (1842) and Étallon (1859), but are a continuation of the work of Charbonnier *et al.* (2012). The reconstructions are more precise and highlight the sexual dimorphism in *G. dressieri*.

Biostratigraphy and palaeobiogeography

The first occurrence of *Glyphea dressieri* dates backs to the late Bathonian of United Kingdom. Woods (1927) figured specimens from the Cornbrash of Bedford and Kirtlington (Discus ammonite biozone after P. Taylor, comm. pers., 2017). Sellwood (1971) reported subtidal *Thalassinoides* burrow containing *G. dressieri* from the Bathonian, Great Oolite Group, White Limestone Formation of Oxfordshire. Van Straelen (1925) mentioned the species in the Bathonian of Courgains (Sarthe, France) but this age was wrong and the specimen from this locality is actually late Callovian in age and belongs to the Ste-Scolasse assemblage. *Glyphea dressieri* is a major component of the late Callovian Ste-Scolasse crustacean fauna (present work). It is also present in the early Oxfordian (Terrain à Chailles Formation) of Haute-Saône, France (Charbonnier *et al.* 2012) and in the middle Oxfordian of Malton, United Kingdom (Woods 1927). Recently, Charbonnier *et al.* (2013) figured an historical specimen (UCBL-EM 80056, Dolfuss coll.) from Trouville-sur-Mer and dated to the Kimmeridgian (Argiles à Ammonites Formation *sensu* Dollfus 1863). Actually, this formation is equivalent to the Argiles brunes de Villerville Formation,

FIG. 8. — *Glyphea dressieri* Meyer *in* Bronn, 1837 from the Upper Callovian of Sainte-Scolasse-sur-Sarthe: **A**, MNHN.F.B11047, syntype of *Palinurus squamifer*, subcomplete specimen (exuvia) showing disarticulation between carapace, pleon and pereiopods, right lateral view; **B**, MHNLM 2008.12.613.4 (Bachelier coll.), disarticulated carapace and pleon (exuvia); **C**, MHNLM 2008.12.612.4 (Bachelier coll.), disarticulated carapace, pereiopods and tail fan (pleon not preserved) (exuvia) ; **D**, MNHN.F.A59898, syntype of *P. squamifer*, butterfly-shaped carapace (exuvia), dorsal view, **E**, MNHN.F.A59893, syntype of *P. squamifer*, butterfly-shaped carapace (exuvia), dorsal view; **F**, MHNLM 2008.12.612.8 (Bachelier coll.), butterfly-shaped carapace (exuvia), dorsal view; **G**, MHNLM 2008.12.613.6 (Bachelier coll.), butterfly-shaped carapace and isolated P1 propodus and dactylus (exuvia), dorsal view; **H**, MNHN.F.A59894, syntype of *P. squamifer*, butterfly-shaped carapace (exuvia), dorsal view. Photographs: A, D, E, H, L. Cazes; C, Falconnet; B, F, G, P. Loubry. Scale bars: 1 cm.

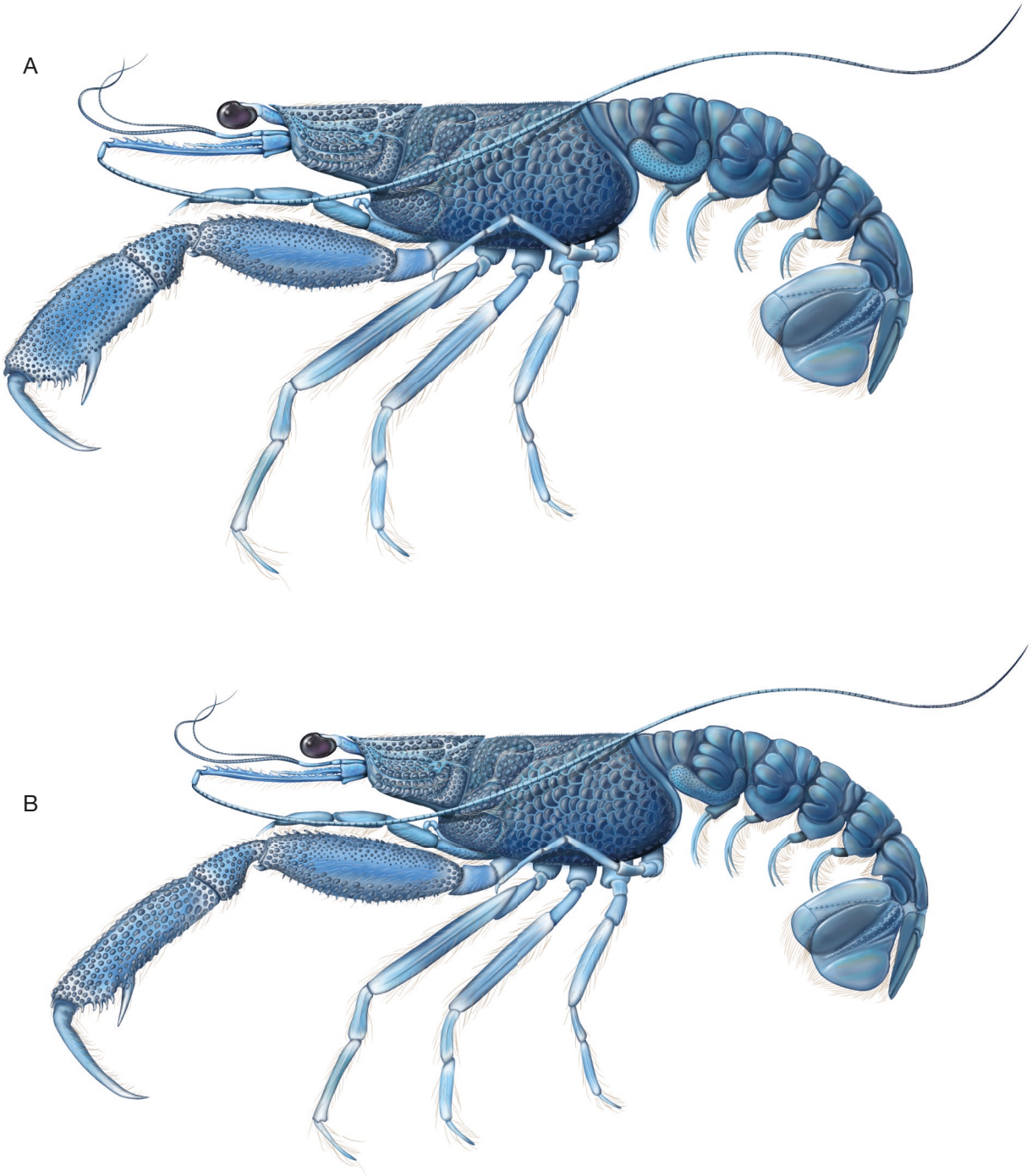


FIG. 9. — Reconstruction of *Glyphea dressieri* Meyer *in* Bronn, 1837: **A**, female specimen with short P1 propodus and dactylus associated with rounded s2-s5 tergopleura; **B**, male specimen with elongate P1 propodus and dactylus associated with sharply pointed (mucronate) s2-s5 tergopleura. Reconstructions: C. Letenneur.

which is late Oxfordian in age, even if the upper part is sometimes confused with Kimmeridgian deposits (Guyader *et al.* 1968). Thus, *Glyphea dressieri* seems limited to the Anglo-Paris Basin and has probably occupied distal platform palaeoenvironments from the upper circalittoral zone (Bathonian; Sellwood 1971) to lower circalittoral zone (Oxfordian; Charbonnier *et al.* 2012).

Glyphea regleyana (Desmarest, 1822)
(Figs 10; 11)

Palinurus regleyanus Desmarest, 1822: 132-133, pl. 11, fig. 3.

Palinurus longebrachiatus Eudes-Deslongchamps, 1842: 58, 60, pl. 4, figs 6, 7.

For detailed list of synonymy see Charbonnier *et al.* (2013: 37).

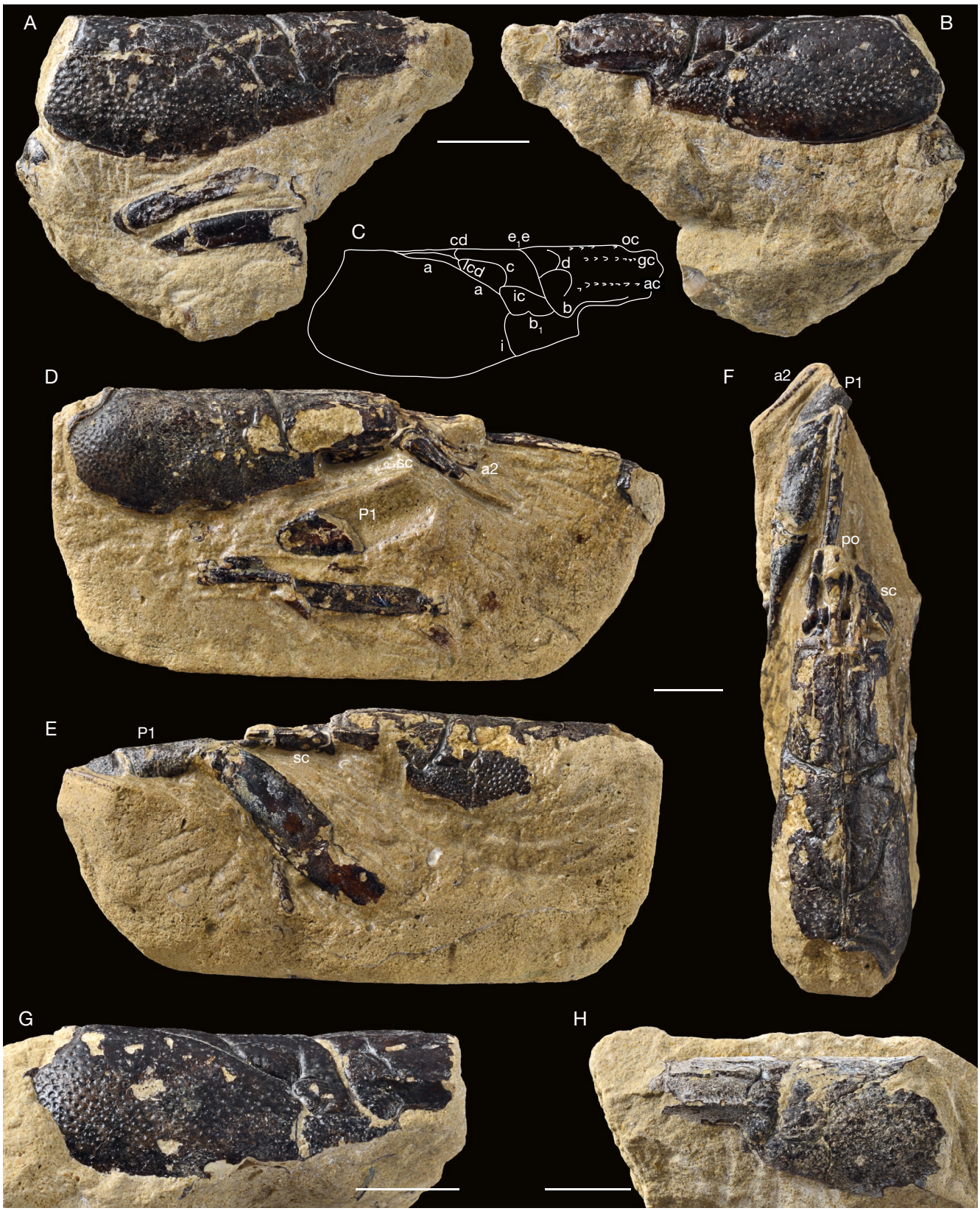


FIG. 10. — *Glyphea regleyana* (Desmarest, 1822) from the Upper Callovian of Sainte-Scolasse-sur-Sarthe: **A**-**C**, MNHN.F.A59331, syntype of *Palinurus longebrachiatus*, carapace, right and left lateral views, line drawing (**C**); **D**-**F**, MNHN.F.B11043, syntype of *P. longebrachiatus* (figured by Eudes-Deslongchamps 1842: pl. 4, figs 6, 7), carapace, cephalic and thoracic appendages, right, left and dorsal view; **G**, MNHN.F.A59332, syntype of *P. longebrachiatus*, isolated carapace, right lateral view; **H**, MNHN.F.A59334, syntype of *P. longebrachiatus*, isolated carapace, left lateral view. Abbreviations: **a**, branchiocardiac groove; **ac**, antennal carina; **a1**, antennula; **a2**, antenna; **b**, antennal groove; **b_1**, hepatic groove; **c**, postcervical groove; **cd**, cardiac groove; **ct**, carapace; **d**, gastro-orbital groove; **e_1e**, cervical groove; **gc**, gastro-orbital carina; **i**, inferior groove; **ic**, intercervical groove; **lcd**, laterocardiac groove; **me**, merus; **oc**, orbital carina; **P1**, pereiopod 1; **po**, ocular peduncle; **sc**, scaphocerite. Photographs: L. Cazes. Line drawing: S. Charbonnier. Scale bars: 1 cm.

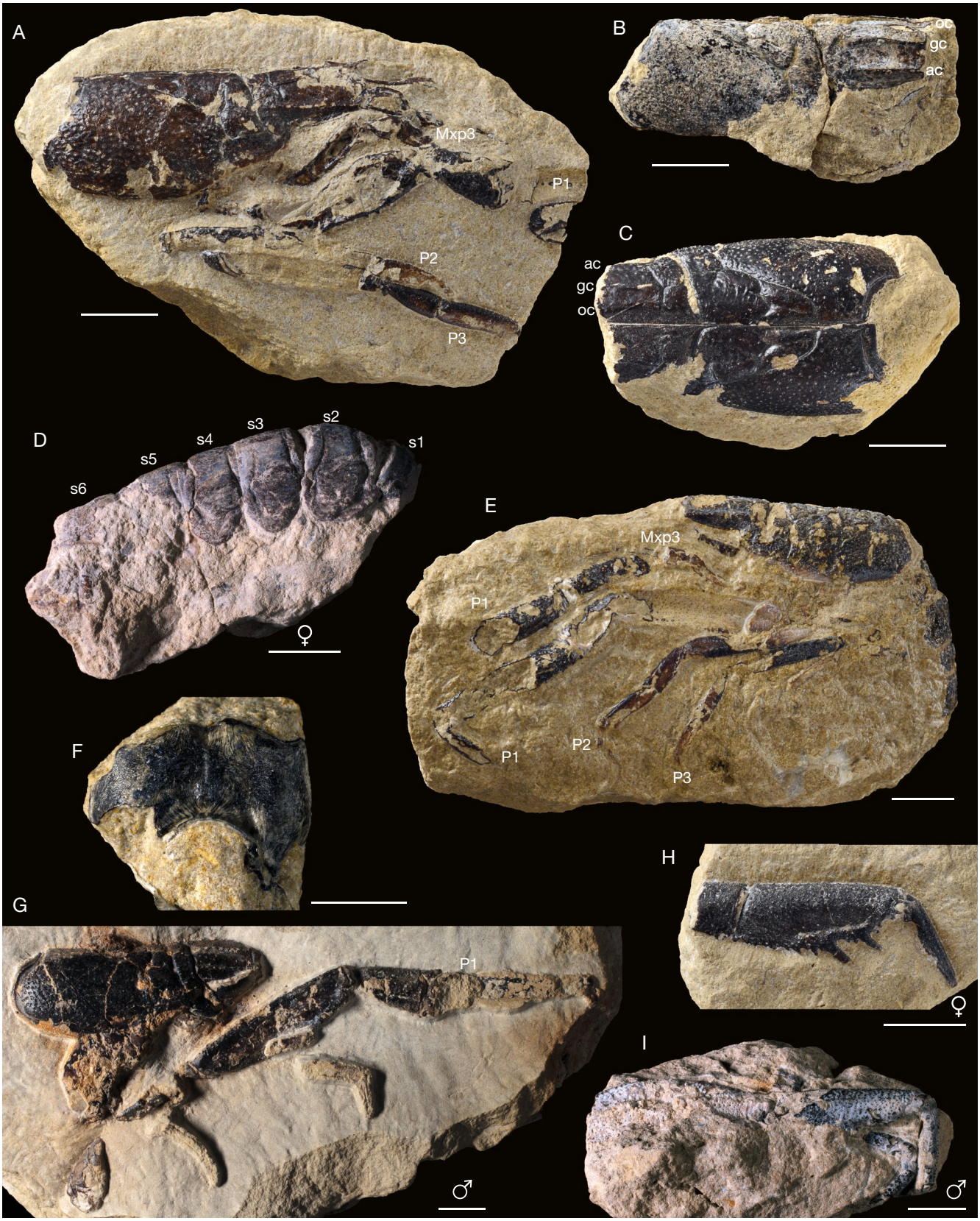


FIG. 11. — *Glyphea regleyana* (Desmarest, 1822) from the Upper Callovian of Sainte-Scolasse-sur-Sarthe: **A**, MNHN.F.A59330, syntype of *Palinurus longebrachiatus*, carapace and fragments of thoracic appendages, right lateral view; **B**, MNHN.F.A59330, syntype of *P. longebrachiatus*, isolated carapace; **C**, MNHN.F.A59332, syntype of *P. longebrachiatus*, butterfly-shaped carapace (exuvia), dorsal view; **D**, MNHN.F.A59341 (A. Milne-Edwards coll.) isolated pleon, right lateral view; **E**, MNHN.F.A59888, syntype of *P. longebrachiatus*, subcomplete specimen, left lateral view; **F**, MHNLM 2003.1.3573, epistome, ventral view; **G**, MHNLM 2008.12.612 (Bachelier coll.), disarticulated specimen; **H**, MNHN.GG.Gg2005-8347b (Bachelier coll.), P1 propodus and dactylus, female specimen; **I**, MNHN.F.A59890 (A. Milne-Edwards coll.), isolated pair of cylindrical first pereiopods, male specimen. Abbreviations: **ac**, antennal carina; **gc**, gastro-orbital carina; **Mxp3**, third maxilliped; **oc**, orbital carina; **P1**-**P3**, pereiopods 1 to 3; **s1**-**s6**, pleonal somites 1 to 6. Photographs: A-E, H, L. Cazes; F, G, I, J. Falconnet. Scale bars: 1 cm (except F: 5 mm).

TYPE MATERIAL. — ***Glyphea regleyana***: neotype MNHN.F.A29512 (Milne-Edwards coll.) selected by Charbonnier *et al.* (2012). — ***Palinurus longebrachiatus***: 10 syntypes (A. Milne-Edwards coll., *ex* Eudes-Deslongchamps coll.) from the Upper Callovian of Ste-Scolasse, Normandy, France.

TYPE LOCALITY. — Andelarrot, Haute-Saône department, France.

TYPE AGE. — Late Jurassic, early Oxfordian (Terrain à Chailles Formation).

ADDITIONAL EXAMINED MATERIAL. — See Table 1.

DESCRIPTION

Carapace

Subcylindrical carapace, laterally compressed; short pointed rostrum without spine, straight or bent slightly downward; anterior cephalic margin with optical and antennal notches; cephalic region with three longitudinal spiny carinae: orbital, gastro-orbital and antennal carinae, parallel, equally spaced and strongly raised; antennal carina raised more than the others; carapace groove pattern: see diagnosis of *Glyphea*; cephalic, cardiac, hepatic, and pterygostomial regions with small spines; branchial region with pits.

Epistome

Large, swollen, convex and subrectangular, not fused to the carapace but separated from it by a suture; lateral margins slightly sinuous and slightly convergent anteriorly, marked by a narrow, deep groove separating them from the edges of the carapace; anterior margin characterized by the posterior limits of the arthrodial cavities of antennae, narrow sinus between these cavities; posterior margin with large rounded depression corresponding to the front of the mouth, marked by a deep groove and small axial tubercle posteriorly directed.

Cephalic appendages

Antennae (a2) composed of antennal peduncle with three segments and long multi-articulated flagellum and scaphocerite; antennal peduncle with short, stocky ischiocerite; thin, elongate merocerite with spinose lateral margins, and short, stocky carpocerite to which flagellum with not assessable length (probably twice as long as the carapace) is articulated; triangular scaphocerite, with pointed distal extremity.

Pleon

Short s1 with large median groove; s2-s4 with smooth rounded tergum, tergal flanks with anterior and posterior grooves; tergopleuron separated from tergum by small constriction connecting points of articulation; large, arcuate tergopleural margin; s3 and s4 similar to s2 but shorter; very short s5, with smooth tergum and reduced tergopleura, tergal flanks with very discrete grooves; s2-s5 tergopleura with sharply pointed terminations in male and rounded terminations in female; narrow, long s6, with large notch for insertion of uropods; trapezoidal telson, tapering, distally rounded, proximal region transversally inflated, axial region swollen, lateral margins depressed with longitudinal grooves, ornamentation with axial carinae of small rounded tubercles.

Thoracic appendages

Long Mxp3 with long, subrectangular merus, short, piriform carpus; ovate propodus and short, flattened dactylus; elongate, strong, P1 showing general morphology different in male (achelate P1 with long, slender subcylindrical segments) and in female (subchelate P1 with short, massive, and more flattened stocky segments; subchelate P2-P4 of lessening size toward posterior part, relatively thin, generally smooth, with sparse spines and tubercles; achelate P5.

Pleonal appendages

Rounded uropodal endopod and exopod as long as telson; exopod with diaeresis.

DISCUSSION

Following Bigot (1945: 20), Charbonnier *et al.* (2013) indicated that the type material of *Palinurus longebrachiatus* was destroyed during the bombardment of Caen during the World War II. The careful examination of specimens in Alphonse Milne-Edwards' collection leads us to identify the type material, probably sent to him or to his father Henri Milne Edwards by J.-A. Eudes-Deslongchamps himself. We ignore the precise history of these specimens: they were fortunately not destroyed but forgotten during about 150 years. After checking all the available syntypes, we confirm that *P. longebrachiatus* is a junior synonym of *G. regleyana*.

Charbonnier *et al.* (2013) provided a detailed description of the species. The configuration of the cephalothoracic grooves, the morphology of P1 propodus, and the ornamentation of the specimens from Ste-Scolasse are diagnostic characters of *Glyphea regleyana*. The study of the best-preserved specimens confirms the secondary sexual characters in P1 and pleonal somites, as already observed by Charbonnier *et al.* (2012): the P1 of males are longer and proportionally thinner than those of females, and the s2-s5 tergopleura of males are quadrate and sharp whereas those of the females are more rounded. The present sample did not provide additional anatomical details compared to the review proposed by Charbonnier *et al.* (2013). However, we note that que P1 ornamentation is relatively similar in males and females, contrary to that reported by Charbonnier *et al.* (2012), who did not have as many specimens with well-preserved P1.

Glyphea muensteri Meyer, 1840
(Fig. 12A-C)

Glyphea münsteri Meyer, 1840: 12, pl. 3, fig. 23.

For detailed list of synonymy see Charbonnier *et al.* (2013: 67).

TYPE MATERIAL. — Neotype MNHN.F.A29534 (coll. Petitclerc) selected by Charbonnier *et al.* (2012).

TYPE LOCALITY. — Grandvelle, Haute-Saône department, France.

TYPE AGE. — Late Jurassic, early Oxfordian (Terrain à Chailles Formation).

ADDITIONAL EXAMINED MATERIAL. — see Table 1.

TABLE 1. — List of the studied sample: type material, specimens from Sainte-Scolasse-sur-Sarthe (Upper Callovian, Normandy) and other localities in Normandy. Abbreviation: **S.-S.-sur-S.**, Sainte-Scolasse-sur-Sarthe (Orne).

Taxa	Material	Collections	Localities	Ages	Number of specimens
Glypheidae					
Glyphea dressieri	holotype NHMW 1847.0051.1133	d'Udressier	Quenoche (Haute-Saône)	early Oxfordian	1
	syntypes of *Palinurus squamifer* MNHN.F.A59325, A59328, A59329, A59335, A59345, A59893, A59894, A59895, A59896, A59897, A59898, A59899, A59900, A84187, B11046, B11047, B11048 (figured by Eudes-Deslongchamps 1843: pl. 4, fig. 5).	A. Milne-Edwards (ex Eudes-Deslongchamps)	Sainte-Scolasse-sur-Sarthe (Orne)	late Callovian	17
	MNHN.F.A59892, B11049	A. Milne-Edwards	S.-S.-sur-S. (Orne)	late Callovian	2
	MNHN.F.A05674, A59522	d'Orbigny	S.-S.-sur-S. (Orne)	late Callovian	2
	MNHN.F.B11050	Abbot Lambert	S.-S.-sur-S. (Orne)	late Callovian	1
	MNHN.GG.Gg2004-8084, Gg2005-8347c, Gg2004-19049	Bachelier	S.-S.-sur-S. (Orne)	late Callovian	3
	MHNLM 2008.12.612.2-6, 8, 11-13, 15-24, 26, 29, 613.2, 4-7, 9, 20, 22, 26, 27, 34, 35	Bachelier	S.-S.-sur-S. (Orne)	late Callovian	32
	MHNLM 2003.1.3573.2, 3	Fonds ancien	S.-S.-sur-S. (Orne)	late Callovian	2
	MHNLM 2003.1.3573.1	Fonds ancien	Courgains (Sarthe)	late Callovian	1
	IGR 103390, 103391, 132771, 132772	Institut de Géologie de Rennes	Marolles-les-Braults (Sarthe)	late Callovian	4
	UCBL-FSL 170650	Lioure-Faucher	S.-S.-sur-S. (Orne)	late Callovian	1
	UCBL-EM 80055 (cast MNHN.F.A59901)	ENSM	S.-S.-sur-S. (Orne)	late Callovian	1
	UCBL-EM 80190, 80191	ENSM	S.-S.-sur-S. (Orne)	late Callovian	2
	UCBL-EM 80056	Dolfuss	Trouville-sur-Mer (Calvados)	late Oxfordian	1
Glyphea regleyana	neotype MNHN.F.A29512	A. Milne-Edwards	Andelarrot (Haute-Saône)	early Oxfordian	1
	syntypes of *Palinurus longebrachiatus* MNHN.F.A59330, A59331, A59332, A59333, A59334, A59336, A59887, A59888, A59889, B11043 (figured by Eudes-Deslongchamps 1843: pl. 4, figs 6, 7)	A. Milne-Edwards (ex Eudes-Deslongchamps)	S.-S.-sur-S. (Orne)	late Callovian	10
	MNHN.F.A59337, A59338, A59339, A59340, A59341, A59342, A59343, A59344, A59346, A59347, A59890, A59891, B11044, B11045, B11051	A. Milne-Edwards	S.-S.-sur-S. (Orne)	late Callovian	15
	MNHN.F.A02690, A59521	d'Orbigny	S.-S.-sur-S. (Orne)	late Callovian	2
	MNHN.F.A47622	Hoffstetter	S.-S.-sur-S. (Orne)	late Callovian	1
	MNHN.GG.Gg2004-19318a, Gg2004-19318b, Gg2004-19318c, Gg2005-8347a, Gg2005-8347b	Bachelier	S.-S.-sur-S. (Orne)	late Callovian	5
	MHNLM 2008.12.612.1, 7, 9, 10, 14, 25, 27, 28, 30, 31, 613.1, 3, 10, 11, 13, 15, 21, 23-25, 28-33	Bachelier	S.-S.-sur-S. (Orne)	late Callovian	26
	MHNLM 2003.1.3573.4, 5	Fonds ancien	S.-S.-sur-S. (Orne)	late Callovian	2
	MHNLM 2003.1.3574	Fonds ancien	Coulans (Sarthe)	late Callovian	1
	MHNLM 2010.4.6262	Rioult	Montbizot (Sarthe)	late Callovian	2
	MHNLM 2015.9.1133	Raboeuf	Sées (Orne)	late Callovian	3
	IGR 103396	Institut de Géologie de Rennes	Marolles-les-Braults (Sarthe)	late Callovian	1
	IGR 144561	Keravel	S.-S.-sur-S. (Orne)	late Callovian	1
	UCBL-FSL 170683	Lioure-Faucher	S.-S.-sur-S. (Orne)	late Callovian	1
Glyphea muensteri	neotype MNHN.F.A29534	Petitclerc	Grandvelle (Haute-Saône)	early Oxfordian	1
	MHNLM 2008.12.613.12, 14	Bachelier	S.-S.-sur-S. (Orne)	late Callovian	2
	IGR 103397	Institut de Géologie de Rennes	Marolles-les-Braults (Sarthe)	late Callovian	1
Erymidae					
Eryma ventrosum	MHNLM 2008.12.613.8, 14, 16, 17, 19	Bachelier	S.-S.-sur-S. (Orne)	late Callovian	5
	MHNLM 2008.12.613.18	Bachelier	Marolles-les-Braults (Sarthe)	late Callovian	1
Longodromitidae					
Abyssophthalmus aff. *bellaii*	MNHN.GG.Gg2005-8347d	Bachelier	S.-S.-sur-S. (Orne)	late Callovian	1

DESCRIPTION

Carapace

Subcylindrical carapace, cephalic region with four longitudinal spiny carinae: parallel orbital, gastro-orbital, supra-antennal, and antennal carinae; orbital carina distanced from the others, and only marked by small aligned spines; gastro-orbital, supra-antennal, and antennal carinae strongly raised; antennal carina more raised than the others; carapace groove pattern similar to that observed in *Glyphea*; all regions of carapace with spiny tubercles uniformly arranged, decreasing in size ventrally in the branchial region.

Thoracic appendages

Poorly preserved Mxp3 (flattened and pointed dactylus); poorly preserved P1 (merus laterally flattened, with spiny dorsal and ventral margins) and P2 (merus laterally flattened, with spiny dorsal and ventral margins).

DISCUSSION

Charbonnier *et al.* (2013) provided a detailed description of the species. The configuration of the cephalothoracic grooves, the four cephalic carinae, and the tuberculated ornamentation of the specimens from Ste-Scolasse correspond to diagnostic characters of *Glyphea muensteri*. The sample is too small to produce a more detailed discussion.

Infraorder ASTACIDEA Latreille, 1802
Superfamily ERYMOIDEA Van Straelen, 1925
Family ERYMIDAE Van Straelen, 1925
Subfamily ERYMINAE Van Straelen, 1925

Genus *Eryma* Meyer, 1840

TYPE SPECIES. — *Macrourites modestiformis* Schlotheim, 1822, by subsequent designation of Glaessner (1929).

DIAGNOSIS (by Devillez & Charbonnier 2019). — Fusiform intercalated plate; deep cervical groove, strongly inclined dorsally, joined to dorsal margin and to antennal groove; short gastro-orbital groove, originating as a slight median inflexion of the cervical groove; postcervical groove joined to branchiocardiac groove at carapace mid-height; branchiocardiac groove usually strongly inclined, joined to the posterior extremity of hepatic groove; hepatic groove concavo-convex, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove and to ventral margin; v area usually inflated; cephalic region usually with an orbital row and with strong orbital and antennal spines; chelate P1-P3; P1 chelae without prominent spines and with an homogeneous ornamentation; P1 propodus compressed dorso-ventrally with narrow inner and outer margins, with a narrow dactylar bulge; P1 fingers usually longer than propodus, equal in length, progressively narrowing to their distal extremity; index wider than dactylus; P1 chelae (form I) with a short rectangular propodus, straight fingers, slightly longer than propodus; P1 chelae (form II) with an elongated subrectangular or trapezoidal propodus, bearing fingers quite longer than propodus, usually curved inward.

Eryma ventrosum (Meyer, 1835)
(Fig. 12E-I)

Glyphea ventrosa Meyer, 1835: 329.

For detailed list of synonymy see Devillez & Charbonnier (2021: 32).

TYPE MATERIAL. — Holotype by monotypy, not located, cast MNHN.F.B12484.

TYPE LOCALITY. — Frétigney, Haute-Saône department, France.

TYPE AGE. — Late Jurassic, early Oxfordian (Terrain à Chailles Formation).

ADDITIONAL EXAMINED MATERIAL. — See Table 1.

DESCRIPTION

Carapace

Subcylindrical carapace; spineless rostrum; fusiform intercalated plate; carapace groove pattern: see diagnosis of *Eryma*; inflated ω area; flat χ area; carapace densely covered by small tubercles preceded by crescent-shaped depressions; cephalic region with an oblique row of tubercles ended by a strong orbital spine; antennal region with an oblique row of tubercles ended by a strong antennal spine.

DISCUSSION

After Devillez & Charbonnier (2021), the carapace groove pattern, and the carapace ornamentation are diagnostic characters of *Eryma ventrosum*. One specimen (MHNLM 2008.12.613.8) corresponds to an isolated carapace, which is dorsoventrally flattened (butterfly-shaped carapace) and split along the dorsal midline. This configuration is typical of a molted specimen but the sample is too small to produce a more detailed discussion.

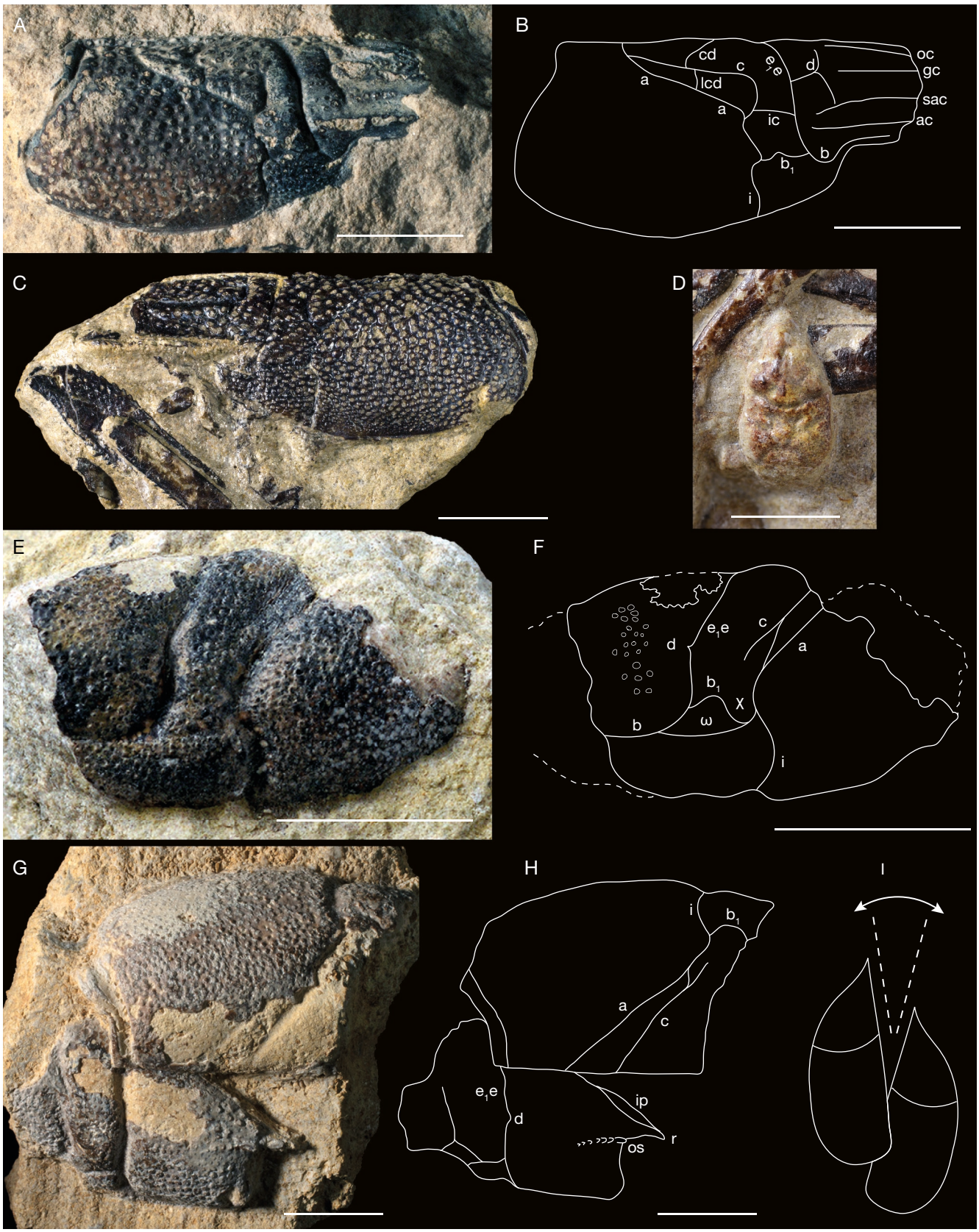
Infraorder BRACHYURA Linnaeus, 1758
Superfamily HOMOLODROMIOIDEA Alcock, 1900
Family LONGODROMITIDAE Schweitzer & Feldmann, 2009

Genus *Abyssophthalmus* Schweitzer & Feldmann, 2009

TYPE SPECIES. — *Prosopon spinosum* Meyer, 1842, by original designation of Schweitzer & Feldmann (2009).

DIAGNOSIS (by Schweitzer *et al.* 2018). — Rostrum long, straight sided, extending well beyond augenrests; augenrests deep, directed forward, bounded by intra-, outer-, and subaugenrest spines, sometimes possessing inner-augenrest spine; outer-augenrest spine long, prominent, directed forward or anterolaterally; cervical and branchiocardiac grooves well developed; postcervical groove composed of two discrete segments, nearly continuous, extending laterally and crossing axis to bound anterior margin of cardiac region, postcervical groove may be indistinct and poorly developed; lateral margins parallel sided, position of maximum width variable; subhepatic region well developed, situated below orbit.

FIG. 12. — Decapod crustaceans from the Upper Callovian of Sainte-Scolasse-sur-Sarthe area: **A**, **B**, *Glyphea muensteri* Meyer, 1840, IGR 103397 (Marolles-les-Braults), isolated carapace, right lateral view and line drawing; **C**, *Glyphea muensteri*, MHNLM 2008.12.613.14 (Ste-Scolasse, Bachelier coll.), carapace and fragments of pereiopods, left lateral view; **D**, *Abyssophthalmus* aff. *bellaii* (Crônier & Boursicot, 2009), MNHN.GG.Gg2005-8347d (Ste-Scolasse, Bachelier coll.), carapace, dorsal view; **E**, **F**, *Eryma ventrosum* (Meyer, 1835), MHNLM 2008.12.613 (Ste-Scolasse, Bachelier coll.), fragment of carapace, left lateral view and line drawing; **G-I**, *Eryma ventrosum* MHNLM 2008.12.613.8 (Ste-Scolasse, Bachelier coll.), butterfly-shaped carapace split into two half carapaces (exuvia), dorsal



view, line drawing, and schematic drawing of the molted carapace (**l**). Abbreviations: **a**, branchiocardiac groove; **ac**, antennal carina; **b**, antennal groove; **b_1**, hepatic groove; **c**, postcervical groove; **cd**, cardiac groove; **ct**, carapace; **d**, gastro-orbital groove; **e_1e**, cervical groove; **gc**, gastro-orbital carina; **i**, inferior groove; **ic**, intercervical groove; **ip**, intercalated plate; **lcd**, laterocardiac groove; **oc**, orbital carina; **r**, rostrum; **sac**, supra-antennal carina; χ, attachment site of adductor testis muscle; ω, attachment site of mandibular muscle. Photographs: A, C, E, G, J. Falconnet; D, L. Cazes. Scale bars: 1 cm (except D: 5 mm).

TABLE 2. — Decapod crustaceans from the Sainte-Scolasse-sur-Sarthe area (Upper Callovian, Normandy): number of specimens and percentages.

Taxa	Collections				Total of specimens	Percentages (%)
	MNHN	MHNLM	IGR	UCBL		
Glyphea regleyana	33	34	2	1	70	47.0
Glyphea dressieri	25	35	4	5	69	46.3
Glyphea muensteri	0	2	1	0	3	2.0
Eryma ventrosum	0	6	0	0	6	4.0
Abyssophthamus aff. *bellaii*	1	0	0	0	1	0.7
Total	59	77	7	6	149	100.0

Abyssophthalmus aff. ***bellaii*** (Crônier & Boursicot, 2009) (Figs 6F; 12D)

Nodoprosopon? *bellaii* Crônier & Boursicot, 2009: 1279, 1280, fig. 3h-j, pl. 2[figs 1-3].

TYPE MATERIAL. — Holotype by monotypy USTL 3852 (Boursicot coll.).

TYPE LOCALITY. — Montreuil-Bellay, Maine-et-Loire department, France.

TYPE AGE. — Middle Jurassic, early Callovian (Gracilis ammonite biozone).

EXAMINED MATERIAL. — One isolated carapace MNHN.GG.Gg2005-8347d, associated to specimen MNHN.GG.Gg2005-8347c of *Glyphea dressieri*.

DESCRIPTION

Carapace

Carapace longer than wide; carapace groove pattern: see diagnosis of *Abyssophthalmus*; lateral margins parallel sided; protogastric region with strong tubercle differentiated from slightly inflated hepatic region; hepatic region with strong tubercle; inflated mesogastric region; wide urogastric lobe; pentagonal cardiac lobe; inflated mesobranchial region; inflated epibranchial lobe; posterior margin strongly concave axially;

DISCUSSION

Nodoprosopon bellaii was tentatively assigned to *Abyssophthalmus* by Krobicki & Zatoń (2016), followed by Schweitzer *et al.* (2018). We concur with this interpretation. The general morphology and the ornamentation of the present carapace recall that of *Abyssophthalmus* aff. *bellaii*.

PALAEOECOLOGY AND PALAEOENVIRONMENT

DIVERSITY AND RELATIVE ABUNDANCE

The Ste-Scolasse fauna included five different species assigned to the glypheid lobsters (three species), erymid lobsters (one species), and longodromitid crabs (one species) (Table 1). The quantitative analysis based on 149 specimens shows two dominant species: *Glyphea regleyana* (47.0 % of specimens) and *G. dressieri* (46.3 %). The other crustaceans were minor elements of the fauna with relative abundances below 5 % (Table 2).

By comparison with the almost contemporaneous crustacean fauna from the early Oxfordian of Haute-Saône, France (Charbonnier *et al.* 2012; Fig. 13), the Ste-Scolasse fauna was less diversified (five species *versus* nine species in Haute-Saône). However, the samplings are not similar (149 specimens *versus* 424 in Haute-Saône) and the study areas are very different (about 12 km² *versus* 550 km² in Haute-Saône). The Ste-Scolasse fauna was particularly rich in glypheids and the high proportions of these lobsters may be compared with those of the Haute-Saône fauna. *Glyphea regleyana* was as abundant in Ste-Scolasse area (47.0 %) as in Haute-Saône (50.5 %). *Glyphea dressieri* was much more abundant in Ste-Scolasse area (46.3 %) than in Haute-Saône (2.6 %). *Glyphea muensteri* was not very abundant in Haute-Saône (16.5 %) and a minor component in Ste-Scolasse area (2.0 %). We note the absence of *Glypheopsis etalloni* (Oppel, 1861) in Ste-Scolasse area. *Eryma ventrosum* was also a minor component in Ste-Scolasse area (4.0 %), whereas it was well represented in Haute-Saône (24.8 %). In conclusion, the Ste-Scolasse fauna is remarkable, especially by the abundance of *G. dressieri*, which is so far unique in the fossil record.

PALAEOENVIRONMENT

The differences of taxonomic richness and relative abundance between the Ste-Scolasse and Haute-Saône assemblages probably reflect differences in palaeoenvironmental conditions. Indeed, the Haute-Saône crustaceans inhabited a moderately deep water setting most probably about 100-150 m (lower circalittoral zone), where light intensity was yet perceptible (Charbonnier *et al.* 2012). In the Ste-Scolasse area, the palaeoenvironment is interpreted as subtidal mud flats, however, largely open to offshore conditions. The sedimentary facies and the associated fauna are indicators of a distal platform setting (upper circalittoral zone). Thus, the Ste-Scolasse palaeoenvironment was probably slightly shallower than the one in Haute-Saône.

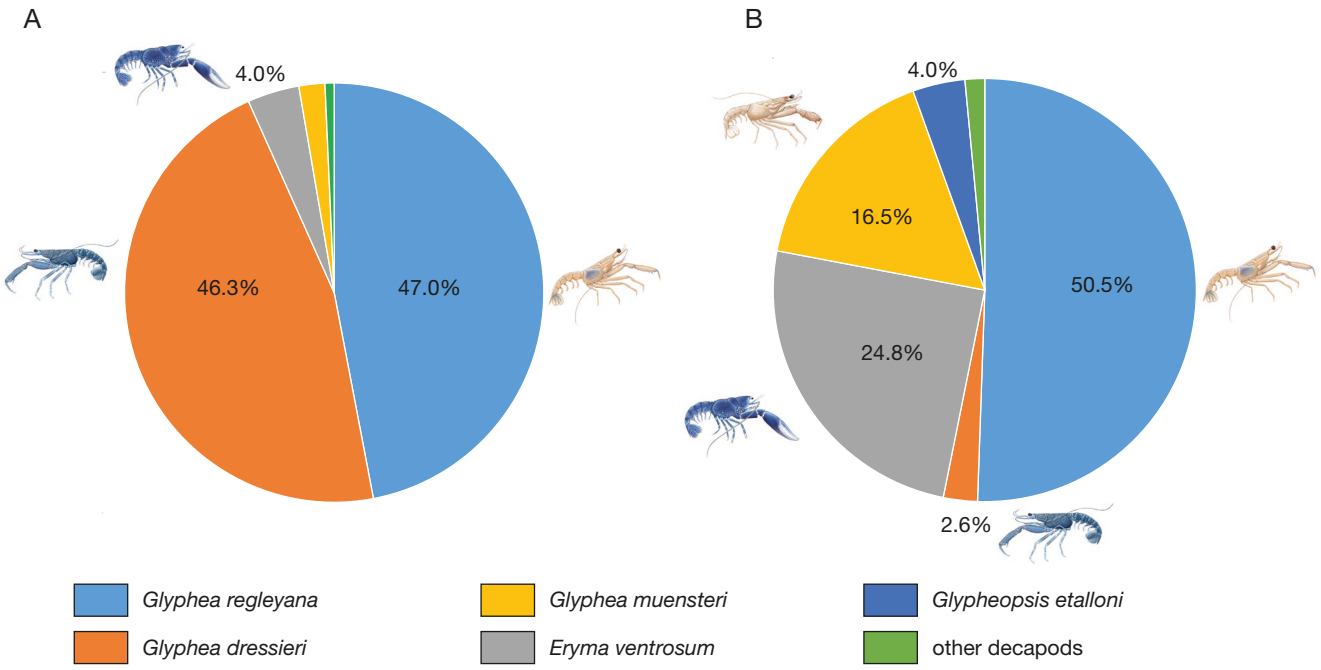


FIG. 13. — Comparison between the relative abundances of the crustacean communities from: **A**, Sainte-Scolasse-sur-Sarthe (Upper Callovian, Normandy; present work); and **B**, Haute-Saône (Lower Oxfordian, east France; after Charbonnier *et al*. 2012).

CONCLUSION

The study of the three-dimensionally preserved crustaceans from the Callovian of Sainte-Scolasse-sur-Sarthe shows that the glypheid lobsters (*Glyphea regleyana* and *G. dressieri*) are major components of the fauna. The great abundance of *G. dressieri* is so far unique in the fossil record and allow us to propose the first reconstruction of this species and to reveal the presence of a sexual dimorphism. Compared to the early Oxfordian Haute-Saône crustaceans, the crustacean assemblage of Ste-Scolasse constitutes a very original assemblage intermediate between the Jurassic communities from the shallow carbonate platforms (e.g., Solnhofen; Garassino & Schweigert 2006) and those from the bathyal zone (e.g., La Voulte-sur-Rhône; Charbonnier *et al.* 2010).

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