

Exceptionally preserved crustaceans from the Oxfordian of eastern France (Terrain à Chailles Formation, Haute-Saône)

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ABSTRACT

The Oxfordian fauna from the Terrain à Chailles Formation, eastern France (Haute-Saône, Franche-Comté) is remarkable for its exceptionally preserved crustaceans found in siliceous concretions locally named “chailles”. The crustacean fauna includes 9 different species assigned to the Glypheidae, the Erymidae, the Eryonidae and the Axiidae. Glypheid and erymid lobsters are the most diversified groups with four and three different species respectively. Re-examination of numerous new specimens allows to a more modern and more complete characterization of *Glyphea regleyana* (Desmarest, 1822), *Glyphea muensteri* von Meyer, 1840 and *Eryma ventrosa* (von Meyer, 1835). New detailed anatomic descriptions of these species highlight the presence of marked sexual dimorphism in *G. regleyana* and probably in *E. ventrosa*. They reveal processes of autotomy and phenomena of ecdysis in *G. regleyana*, *E. ventrosa* and *G. muensteri*. Quantitative analyses based on 424 nodules show three dominant species: 1) *Glyphea regleyana* (50.5% of nodules); 2) *Eryma ventrosa* (24.8%); and 3) *Glyphea muensteri* (16.5%). Conver-

KEY WORDS

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Decapoda,
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Eryma,
exceptional preservation,
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gent lines of evidence from depositional environment, comparisons with others Jurassic crustaceans and modern analogues indicate that the crustacean fauna from the Terrain à Chailles Formation probably inhabited a moderately deep water setting most probably about 100-150 m (lower circalittoral zone) where light intensity was even sensitive. These crustaceans constitute a very original assemblage intermediary between the communities from the shallow carbonate platforms (e.g., Solnhofen) and those from the bathyal zone (e.g., La Voulte). This new set of data sheds new light on the colonization of the distal platforms by crustacean communities in the Mesozoic.

RÉSUMÉ

Crustacés exceptionnellement préservés de l'Oxfordien de l'Est de la France (Formation du Terrain à Chailles, Haute-Saône).

La faune oxfordienne du Terrain à Chailles, Est de la France (Franche-Comté, Haute-Saône), est remarquable pour ses crustacés exceptionnellement bien préservés dans des concrétions siliceuses appelées régionalement « chailles ». La faune de crustacés regroupe 9 espèces différentes réparties parmi les Glypheidae, les Erymididae, les Eryonidae et les Axiidae. Les glyphées et les érymidés sont les groupes les plus diversifiés avec respectivement 4 et 3 espèces différentes. Le réexamen de nombreux spécimens nouveaux permet une description plus moderne et plus complète de *Glyphea regleyana* (Desmarest, 1822), *Glyphea muensteri* von Meyer, 1840 et *Eryma ventrosa* (von Meyer, 1835). Les nouvelles descriptions anatomiques détaillées de ces espèces mettent en évidence un dimorphisme sexuel marqué chez *G. regleyana* et probablement chez *E. ventrosa*. Elles révèlent des processus d'autotomie et des phénomènes de mue chez *G. regleyana*, *E. ventrosa* et *G. muensteri*. Les analyses quantitatives basées sur 424 nodules montrent trois espèces dominantes : 1) *Glyphea regleyana* (50,5 % des nodules) ; 2) *Eryma ventrosa* (24,8 %) ; et 3) *Glyphea muensteri* (16,5 %). Un faisceau de preuves, basé sur l'environnement de dépôt et des comparaisons avec d'autres crustacés jurassiques et leurs analogues actuels, indique que la faune de crustacés du Terrain à Chailles vivait probablement dans un milieu modérément profond, autour de 100-150 m (zone circalittorale inférieure), où l'intensité lumineuse était encore sensible. Ces crustacés constituent un assemblage original intermédiaire entre les communautés de plates-formes carbonatées peu profondes (ex. : Solnhofen) et celles de la zone bathyale (ex. : La Voulte). Ces nouvelles données illustrent la colonisation des plates-formes distales par des communautés de crustacés au cours du Mésozoïque.

MOTS CLÉS

Crustacea,
Decapoda,
Glyphea,
Eryma,
conservation
exceptionnelle,
nodules,
chailles,
Haute-Saône,
Franche-Comté,
Jurassique supérieur.

INTRODUCTION

Interest in the Late Jurassic (Oxfordian) crustaceans from the Haute-Saône department (Franche-Comté, eastern France) dates back to the 19th century and the pioneer works of Desmarest (1822), Thirria (1833) and Étallon (1859) who first mentioned

the presence of glypheid and erymid lobsters three-dimensionally preserved in siliceous nodules. These nodules are locally called “chailles” (chert) and originate from a regional formation named the “Terrain à Chailles” (Lower Oxfordian, Argovian facies). The decapod crustaceans are the most diverse and abundant group of fossils contained

in the nodules. However, some trigonid bivalves, echinoids, stem ossicles of crinoids and rare fragments of corals are also present. There are very few studies on the crustaceans from the “chailles” of Haute-Saône. They were preliminarily studied by Desmarest (1822) that described the glypheid *Palinurus regleyanus* Desmarest in Brongniart & Desmarest, 1822. Since that time, several other species, mainly including glypheid and erymid crustaceans, have been described by Voltz (1835), von Meyer (1835, 1840) and Opper (1861). Étallon (1859, 1861) provided the most important contribution to the Haute-Saône crustaceans in which he listed eight different species and discussed of their sexual dimorphism. Then, Van Straelen (1925), Petitclerc (1927) and more recently Martin (1961) revised the systematics without really supplying new data.

In this paper we use the crustaceans preserved in nodules 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 the Haute-Saône department and analyze their biodiversity. For that purpose, we re-examine and modernize their systematics. Thanks to new specimens, we precise the anatomical description of three glypheid and erymid species. We also propose the first quantitative data on these crustaceans based on 424 specimens. We make detailed comparisons between the major groups represented in the siliceous nodules and their present-day analogues. These comparisons lead to discussions on the palaeobiology and the palaeoecology of the crustaceans and to interpretations concerning the palaeoenvironment.

GEOLOGICAL SETTING

The Haute-Saône department is located in the Franche-Comté region (eastern France). The present study focused on the Jurassic deposits around the town of Vesoul (*c.* 300 km east of Paris). The Vesoul area is characterized by limestone plateaux named the Plateaux de Vesoul that develop between the Saône and the Ognon Rivers (Fig. 1). The Plateaux de Vesoul dominate the region with

an average altitude of approximately 400 m. They are crossed by numerous NNE-SSW faults at the origin of an alternation of small horsts (e.g., Chariez horst) and small grabens (e.g., Andellare and Andellarot grabens). These faults are parallel to the Rhine Graben (Contini 1964, 1975). The Plateaux de Vesoul are punctually covered by a residual argileous formation called the “Argiles à chailles”. This superficial formation is composed of reddish clays that yield numerous siliceous nodules (chailles) containing three-dimensionally preserved crustaceans. These nodule-bearing clays originate from the dismantlement and the *in situ* disaggregation and alteration of an older formation called the “Terrain à Chailles”. The Terrain à Chailles Formation belongs to the Argovian facies and is mainly composed of argileous limestones and chert limestones containing centimeter-to-decimeter siliceous nodules. It is dated by some ammonites found in the nodules and belongs to the Early Oxfordian Cordatum biozone (Enay 1966; Cariou *et al.* 1997). The erosion of the Terrain à Chailles Formation originates in the emersion of the Vesoul region from the end of the Cretaceous (Contini 1976). This emersion is linked to the Alpine orogeny that, during the Oligocene-Miocene orogenic phase, led to the forming of the nodule-bearing clays by the *in situ* dismantlement of the “Terrain à Chailles” (Contini 1976). The siliceous nodules represent the most resistant elements to the dissolution and are consequently concentrated in these residual reddish clays. After this orogenic phase, these clays were both reworked *in situ* and carried along by surface runoff and solifluction to the more depressed areas such as the Andellare and Andellarot grabens (Contini 1964). The distribution of the different fossiliferous outcrops reflects the complex geological evolution of the Plateaux de Vesoul with probably multiple phases of differential emersion. Thus, in the southeast, the nodule-bearing clays (e.g., Dampierre, Rochesur-Linotte outcrops) correspond to in-place accumulations of erosional products from the Terrain à Chailles Formation (Fig. 1). From the southeast to the northwest, the nodule-bearing clays are more and more reworked, until mix with the Quaternary silts (Contini 1976). At the top of the Plateaux

de Vesoul, the nodule-bearing clays are directly deposited on the Middle Jurassic limestones. In the northwest, they are preserved into small grabens (e.g., Mailley, Levresey, Andelarre-Andelarrout outcrops) and are more reworked to the west (Fondremand-Maizières, Rosez outcrops). The duration of the reworking is relatively long but is probably very limited in distance. The present-day outcrops show an image deformed by the phenomena of concentration but remain relatively faithful to the fossiliferous content of the original deposits because the siliceous nodules resisted to the erosion. Thus each outcrop represents a more or less faithful image of an original assemblage which definitively disappeared.

MATERIAL AND METHODS

Crustaceans are the most abundant and diverse organisms from the nodules of the Haute-Saône department. They are three-dimensionally preserved in early diagenetic siliceous nodules locally named "chailles". They show generally numerous anatomical details (e.g., antennae, mandibles, and articulated appendages) that greatly facilitate their determination. Some of them show indications of a slight dislocation and flattening and might correspond to exuviae which would have less resisted to the compaction. The exceptional preservation of the Haute-Saône crustaceans coupled with the probable presence of delicate exuviae clearly indicates that they are autochthonous. As chert, siderite or phosphate nodules recorded in many Mesozoic formations, the process through which the siliceous concretions from Haute-Saône were formed is uncertain but probably results from punctual chemical conditions and microbial activity in the surroundings of the decaying carcasses (see for instance Raiswell 1976, 1987; Coleman 1993; Wilby *et al.* 1996). Their formation could also be linked to processes of sedimentary condensation governed by eustatic variations in the distal shelf (Loi *et al.* 1999; Loi & Dabard 2002).

This study is based on fossils collected during field excursions in 2009 from several outcrops of the Haute-Saône department (e.g., Frotey-lès-

Vesoul, Rosey, Maizières; see Fig. 1). This new material adds to fossil crustaceans deposited in the collections of the Muséum national d'Histoire naturelle, Paris (182 nodules), the Muséum Cuvier (Musée du Château des Ducs de Wurtemberg), Montbéliard (108 nodules), the Université Claude Bernard Lyon 1 (124 nodules) and the Institut Dolomieu of the Université Joseph Fourier Grenoble (10 nodules). The whole material consists of 424 specimens three-dimensionally preserved in siliceous nodules. We revised and updated the previous inventories made by Étallon (1859, 1861), Van Straelen (1925) and Martin (1961) in the light of personal observations and the most recent systematic studies on the Jurassic crustaceans (e.g., Garassino 1996; Crônier & Courville 2004; Garassino & Schweigert 2006). The taxonomic richness and relative abundance of crustacean species were calculated in order: 1) to establish the palaeobiodiversity; 2) to highlight the geographical distribution of the specimens; and 3) to enable comparisons with Recent crustacean communities. Biometric measurements on *Glyphea regleyana* were made on 45 complete cephalothoraces. These measurements correspond to the cephalothoracic length, excluding rostrum (CL, linear distance between the ocular incision and the dorsal posterior margin of the cephalothorax) and to the cephalothoracic height (CH, linear distance perpendicularly measured to the dorsal margin from its intersection with the branchiocardiac groove until the ventral margin). In order to compare the morphometric relationships with extant glypheids and to interpret the palaeobiology of the Haute-Saône fossil species, the results obtained were plotted graphically and regression coefficient describing the morphometric relationships was calculated using a linear model. Comparisons with extant glypheids have been realized with the specimens housed in the Collections de Zoologie from the Muséum national d'Histoire naturelle, Paris.

ABBREVIATIONS

FSL	Faculté des Sciences de Lyon, Université Claude Bernard Lyon 1;
MC-P	Collections du Muséum Cuvier, Ville de Montbéliard, Dépôt Université des Sciences de Besançon;

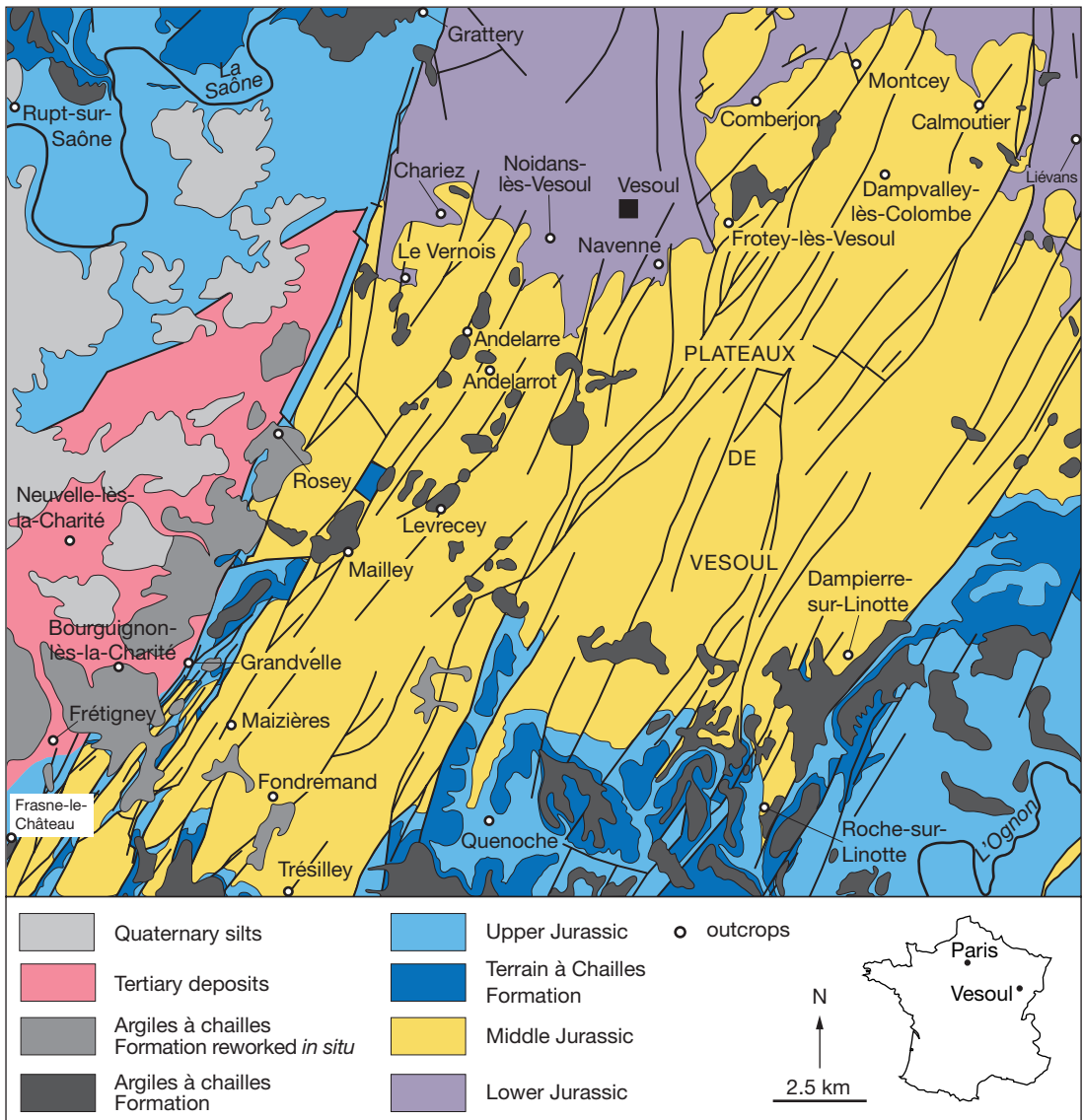


FIG. 1. — Geological map of the Vesoul area (eastern France, Franche-Comté region, Haute-Saône department) showing the main fossiliferous outcrops yielding siliceous nodules from the Terrain à Chailles Formation (composite map after Contini 1976; Dreyfuss & Kuntz 1970; Théobald *et al.* 1970).

- MNHN.F Muséum national d'Histoire naturelle, Paris, Collections de Paléontologie;
 MNHN.IU Muséum national d'Histoire naturelle, Paris, Collections de Zoologie (Crustacés);
 UJF-ID Université Joseph Fourier, Institut Dologique, Grenoble.

SYSTEMATIC PALAEONTOLOGY

The abundant material and the preparation of numerous well-preserved specimens allow new detailed anatomic descriptions of three species of macruran decapod crustaceans: *Glyphea regleyana*, *Glyphea*

muensteri and *Eryma ventrosa*. Each description begins with a synthetic presentation of the previous works, followed by our new observations. The detailed description of the well-known cephalothoracic grooves is not repeated by simplification. They will be just indicated on some illustrations. According to the more recent publications (Dixon *et al.* 2003; Ahyong & O'Meally 2004; Amati *et al.* 2004; Bracken *et al.* 2009; De Grave *et al.* 2009; Schweitzer *et al.* 2010) based in part on cladistic as well as molecular and morphological analyses, the glypheid and the erymid lobsters are grouped into the infraorder Glypheidea von Zittel, 1885 and not Winkler, 1882. Indeed, von Zittel (1885) cited Winkler (1882) as the author of the name Glyphaeidae. However, Winkler (1882) although dealing extensively with *Glyphea* did not establish a family name based on this generic name, he at most used the vernacular expression “*les glyphées*”. Von Zittel (1885) therefore must be considered the author of the family name with Latin taxonomy (for a more detailed discussion, see Holthuis [1991]).

Classe MALACOSTRACA

Latreille, 1802

Order DECAPODA

Latreille, 1802

Infraorder GLYPHEIDEA

von Zittel, 1885

Superfamily GLYPHEOIDEA

von Zittel, 1885

Family GLYPHEIDAE

von Zittel, 1885

Genus *Glyphea* von Meyer, 1835

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

Glyphea regleyana (Desmarest, 1822)
(Figs 2-6; 8-10)

SYNTHETIC DESCRIPTION

Glyphea regleyana (Fig. 2A) is the most common and the best known species of *Glyphea*. The following description is summarized after Étallon (1859, 1861), Van Straelen (1925) and Martin (1961).

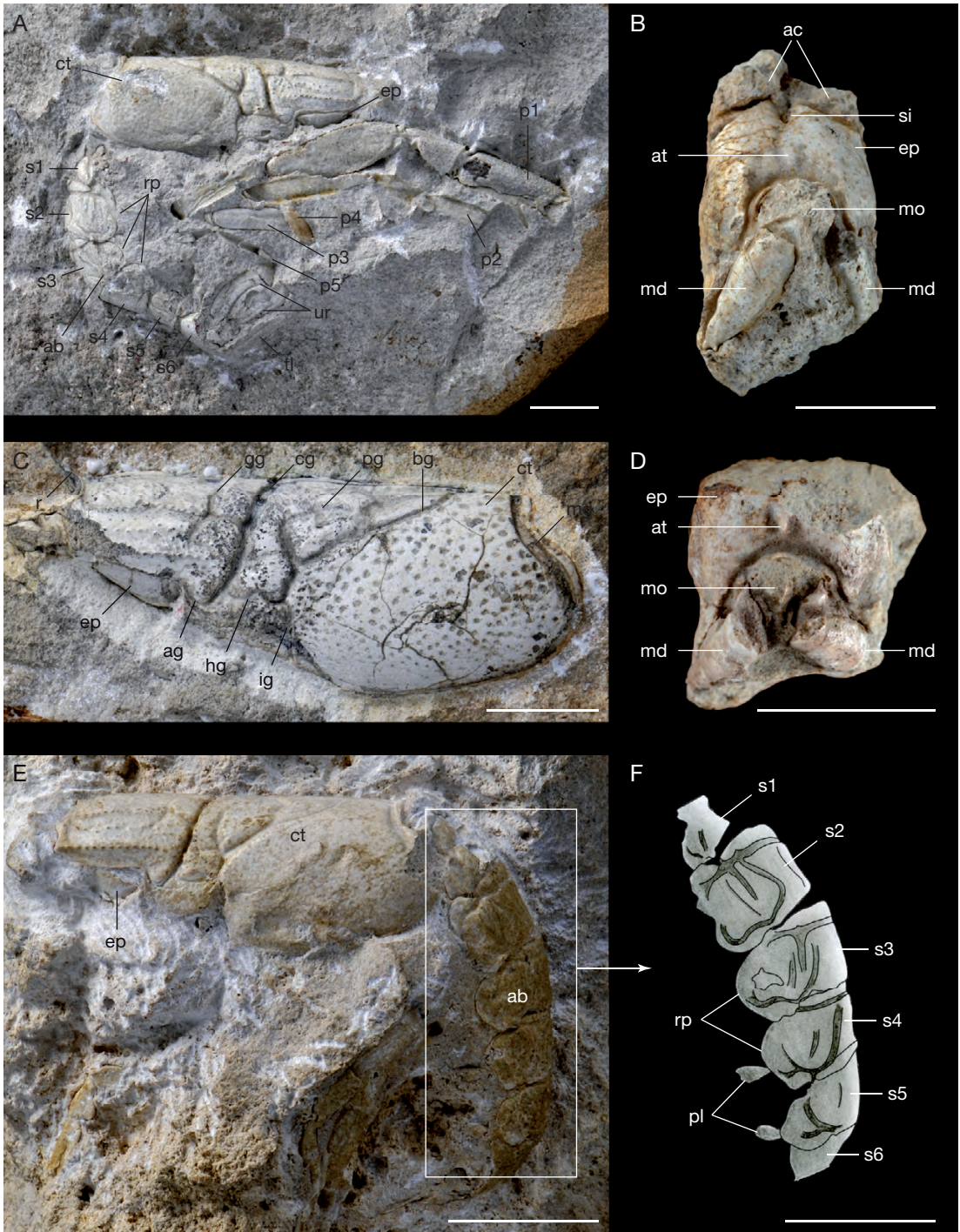
Cephalothorax subcylindrical, laterally compressed, with simple pointed rostrum straight or slightly directed downwards; cervical groove deep and steeply inclined (Fig. 2A, C); branchiocardiac groove well developed; gastro-orbital groove very characteristic with two divergent ramifications directed upwards and downwards; postcervical groove with complex ramifications; anterior cephalic margin with optical and antennal notches; cephalic region with three longitudinal tuberculated carinae on flanks (Fig. 2C); epistome large; carapace ornamentation with cupuliform punctuations posteriorly and small spines anteriorly; antennulae with two short flagella; antennae with pointed scaphocerite and long articulated flagellum; third maxillipeds very developed; first pereopods achelate, longer and slender in males shorter and more massive in females; pereopods 2 to 5 achelate, more and more short distally; abdomen relatively narrow, somites 1 and 6 short with reduced pleura, somite 2 well developed with large pleura, somites 3 to 5 more reduced; sharply pointed terminations on the abdominal pleurae in males and rounded terminations in females; telson trapezoidal; uropods with strong longitudinal groove near lateral margin, exopod with diaeresis, finely fringed.

NEW OBSERVATIONS

Epistome

Well preserved in some specimens (Figs 2B-E; 3A), large, swollen, convex and subrectangular, not

FIG. 2. — *Glyphea regleyana* (Desmarest, 1822) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A**, complete specimen (MNHN.F.A29512, Andelarrot), lateral view, note the rounded abdominal pleurae of presumed female specimen; **B**, epistome and mandibles (MNHN.F.A30229, locality unknown), ventral view; **C**, isolated cephalothorax (MNHN.F.A29496, Chariez), lateral view, note the epistome in position or slightly displaced within carapace; **D**, fragmentary epistome and mandibles (MNHN.F.A30228, locality unknown), ventral view, note the axial tubercle at the base of epistome; **E**, **F**, complete specimen (MNHN.F.A29516, Andelarre) in lateral view (**E**) and line drawing of the abdomen (**F**), note the connection between abdomen and cephalothorax, the rounded abdominal pleurae indicating a probable female specimen, the base of the pleopods, and the lateral displacement of the epistome. Abbreviations: **ab**, abdomen; **ac**, arthrodial cavity; **ag**, antennal groove; **at**, axial tubercle; **bg**, branchiocardiac groove; **cg**, cervical groove; **ct**, cephalothorax; **ep**, epistome; **gg**, gastro-orbital groove; **hg**, hepatic groove; **ig**, inferior groove; **md**, mandible; **mg**, marginal



groove; **mo**, mouth; **pg**, postcervical groove; **p1-p5**, pereopods 1 to 5; **r**, rostrum; **rp**, rounded pleura; **si**, sinus; **s1-s6**, somites 1 to 6; **ur**, uropods; **tl**, telson. Scale bars: A, C, E, 2 cm; B, D, 1 cm.

fused to the carapace but separated from it by a suture; lateral margins slightly sinuous and slightly convergent anteriorly, marked by a narrow and deep groove separating them from the edges of the carapace; anterior margin characterized by the posterior limits of the arthrodial cavities of antennae (Fig. 2B), narrow sinus between these cavities; posterior margin with large rounded depression corresponding to the front of the mouth, marked by a deep groove and a small axial tubercle posteriorly directed; ornamentation with small spinose tubercles, triangular region between the posterior margin (axial tubercle) and the anterior sinus smooth and depressed (Fig. 2D).

Abdomen (Figs 2E, F; 3C)

Somite 1 very short with large median groove; somite 2 well developed with smooth rounded tergum, tergal flanks with anterior and posterior grooves; pleura separated from tergum by small constriction connecting points of articulation; pleural margin large, arcuate, with mucronate extremity and distal groove; somites 3 and 4 similar to 2 but shorter; somite 5 very short, with smooth terga and reduced pleurae, tergal flanks with very discrete grooves; somite 6 long, narrow, pleurae absent anteriorly and replaced with large notch for the insertion of uropods; telson trapezoidal, tapering, distally rounded, proximal region transversally inflated, axial region swollen, lateral margins depressed with longitudinal grooves, ornamentation with axial ridges of small rounded tubercles.

Cephalic appendages (Figs 3A, B, D-G; 4A)

Antennulae (a1) composed of antennular peduncle with three segments: first segment (precoxopodite) short, stocky, proximally dilated and distally narrowed, dorsally sculpted, median region with strong curved carina; second segment (coxopodite) long,

cylindrical, smooth; third segment (basipodite) more slender than the second, slightly dilated distally; two short flagella articulated to the distal part of the third segment (Fig. 3E-G).

Antennae (a2) composed of antennal peduncle with three segments and long multi-articulated flagellum (Fig. 3B) and scaphocerite (Fig. 3D); antennal peduncle with short and stocky ischiocerite, thin and elongate merocerite with spinose lateral margins, and short and stocky carpocerite to which a flagellum with not assessable length (probably twice as long as the carapace) is articulated (Fig. 3E, F); scaphocerite triangular in outline, with a pointed distal extremity (Fig. 3D).

Mandibles symmetrical, strong and robust (Figs 2B, D; 4A), with a three segmented palp: both first and second segments have nearby dimensions while the third widens in an ovate palette, palp fitting behind the secant edge of the mandible (Fig. 4A).

Thoracic appendages (Figs 2A; 4B-F; 5A-D)

First maxilliped not identified; second maxilliped short, narrow with 3-4 distal segments preserved: merus long and slender, carpus short and curved, propodus short and ovate, dactylus not preserved (Fig. 4C, D); third maxilliped well developed, long (*c.* 80% CL) with 6 segments narrowing slightly towards the distal extremity (Fig. 4B-E): coxa and basis badly preserved, short and stocky; ischium long and smooth, merus long, subrectangular, lateral margins smooth, ventral margin with a row of small spines and distally a unique strong spine; carpus short, piriform, axial region swollen, lateral margins flattened (Fig. 4B, D); propodus ovate (Fig. 4E), narrow proximal articulation with carpus, axial region swollen, lateral margins flattened; dactylus short, thin.

First pereopod elongate, strong, achelate (Figs 4B-E; 5A-D); general morphology different in male

FIG. 3. — *Glypheia regleyana* (Desmarest, 1822) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A-C**, complete specimen (MNHN.F.A29507, Frotoy-lès-Vesoul), showing separation and 90 degrees rotation of abdomen, relative to the carapace and displacement of epistome (molted specimen), note the flagellum of the antennae (**B**), and the sharply pointed terminations on the abdominal pleurae suggesting a male specimen (**C**); **D**, complete scaphocerite (MNHN.F.A29502, Andelarre), lateral view; **E, F**, details of cephalic appendages (MNHN.F.A29495, Chariez), lateral view (**E**) and line drawing (**F**), note the antennal peduncles and one of the antennular peduncles showing the base of two articulated flagella; **G**, fragmentary specimen (MNHN.F.A29552, locality unknown) showing the base of cephalic appendages (antennular and antennal peduncles), dorsal view. Abbreviations: **a1**, antennula; **a1p**, antennular peduncle; **a2**, antenna; **a2p**, antennal peduncle; **ab**, abdomen; **bap**, basipodite; **cac**, carpocerite; **cop**, coxopodite; **ct**, cephalothorax;



ep, epistome; fl, flagellum; isc, ischiocerite; mec, merocerite; pp, pointed pleura; pco, precoxopodite; r, rostrum; s1-s6, somites 1 to 6; sc, scaphocerite. Scale bars: 1 cm.

(subcylindrical segments, long and slender; Figs 4E; 5C, D) and in female (stocky segments, short, massive and more flattened, Figs 2A; 3B-D; 5A, B); 6 segments: coxa, basis and ischium badly preserved, coxa and basis maybe fused, ischium with oblique articulation to the merus; merus and propodus are of equal length (*c.* 70% CL) while carpus (*c.* 30% CL) is shorter; merus laterally flattened, dorsal margin smooth with distal rows of small spines, ventral margin with rows of small spines; carpus short, conical, covered with small tubercles, ventral margin with a row of small spines; propodus characteristic of the species, subcylindrical, covered with small tubercles, ventral margin with strong forward-directed spines, the last but one of which is particularly developed (Fig. 5A, B); dactylus (*c.* 45% CL) narrow, slender, slightly curved, perpendicularly articulated to the propodus, ornamentation with small tubercles.

Pereiopods 2 to 5 of lessening size towards the posterior part, relatively thin, generally smooth, sparse spines and tubercles sometimes (Figs 2A; 4F; 5B).

Abdominal appendages (Figs 2E, F; 5B, E-H)

Pleopods with subcylindrical sympodite, stocky and smooth (flagella not preserved) (Fig. 2E, F).

Uropods composed of short coxopodite, bilobate basipodite (Fig. 5E, H), uropodal endopod and exopod rounded; endopod with distal fringe of setae (Fig. 5F), exopod with diaeresis beyond which it becomes membranous, distal fringe of setae well developed (Fig. 5H); ornamentation with sparse and very small tubercles.

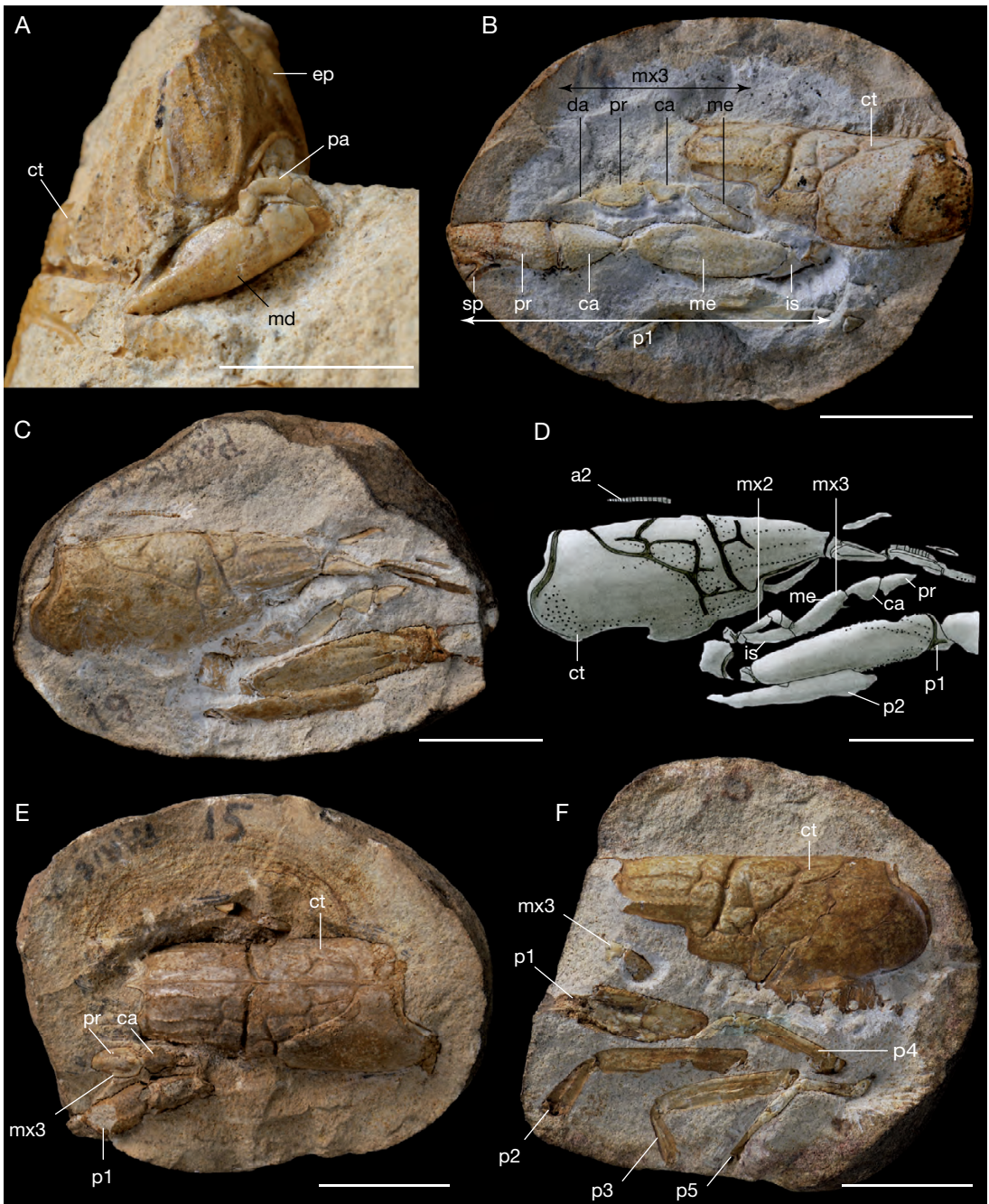
DISCUSSION AND COMPARISONS

Sexual dimorphism

Feldmann & de Saint Laurent (2002) indicate that expression of preservable secondary sexual characteristics including features of the cephalothorax and abdomen of lobsters is not particularly common. Étallon (1859) was the first to demonstrated sexual dimorphism in *Glypheg regleyana*. He highlighted

that: 1) male carapaces were twice as long as wide and female ones were smaller; 2) males possessed longer and more slender first pereiopods as opposed to stocky (Fig. 5C, D), short and more flattened first pereiopods in females (Figs. 4B; 5A, B); and 3) males presented sharply-pointed terminations on the abdominal pleurae (Fig. 3C) as opposed to rounded terminations in females (Fig. 2A, E, F). More than a century later, Forest & de Saint Laurent (1989) called attention to the work of Étallon (1859) because they recognized similar dimorphic features in the living *Neoglypheg inopinata* Forest & de Saint Laurent, 1975. In the present work, we test the three hypothesis of Étallon (1859) by biometric measurements and by the first illustrated comparisons between extant and fossil glypheids. Biometric measurements on 45 cephalothoraces including Étallon's samples show that the relation between the cephalothorax length and the cephalothorax height of *G. regleyana* is described by a linear model (Fig. 6; Bravais-Pearson test indicates significant correlation) as observed for many extant and fossil lobsters (e.g., Guégen 1997, 1998; Charbonnier 2009; Charbonnier *et al.* 2010). Our plot diagram is relatively homogenous and 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. In conclusion, the first criterion of Étallon (1859) is not convincing and could not be convincing because none of the specimens he studied shows a complete carapace associated to the first pereiopods. Regarding the morphology of the first pereiopods and the abdominal pleurae, the extant glypheid *Neoglypheg inopinata* (Fig. 7A-E) exhibits two different forms: 1) the first pereiopods of males (Fig. 7C) are longer and proportionally more slender than those of the females (Fig. 7B); and 2) the pleurae of males are quadrate and sharp (Fig. 7D) whereas those of the females are more

Fig. 4. — *Glypheg regleyana* (Desmarest, 1822) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A**, latero-ventral view of epistome and right mandible (MNHN.F.A29551, locality unknown), note the three segmented palp; **B**, incomplete specimen (MNHN.F.A29546, Andelarrot) showing cephalothorax, third maxilliped and first pereiopod with laterally flattened merus of a presumed female specimen, lateral view; **C, D**, isolated cephalothorax (MNHN.F.A29492, Fondremand) with second & third maxillipeds and pereiopods 1 & 2, note the piriform carpus and the flattened merus (female specimen), lateral view (**C**) and line drawing (**D**); **E**, dorsal



view of cephalothorax (MNHN.F.A29558, locality unknown), note the third maxilliped (ovate propodus) and fragmentary first pereiopod with cylindrical segments suggesting a male specimen; F, sub-complete specimen (MNHN.F.A29488, Grattery) showing carapace with cephalic and thoracic appendages, lateral view. Abbreviations: a2, antenna; ca, carpus; ct, cephalothorax; da, dactylus; ep, epistome; is, ischium; md, mandible; me, merus; mx2, mx3, maxillipeds 2 and 3; p1-p5, pereiopods 1 to 5; pa, palp; pr, propodus; sp, spine. Scale bars: 2 cm.

rounded (Fig. 7E). Our anatomical comparisons between the first pereiopods and abdominal pleurae of *Neoglyphea inopinata* and those of *Glyphea regleyana* confirm the presence of significant sexual dimorphism in these fossil forms. Similar evidence for sexual dimorphism demonstrable in characters of the carapace and pereiopods have been documented in only two other fossil crustacean species: *Glyphea foresti* Feldmann & de Saint Laurent, 2002 (Cenomanian, Australia) and *Meyeria pueblaensis* Feldmann, Vega, García-Barrera, Rico-Montiel & Martínez-López, 1995 (Aptian, Mexico; see Feldmann *et al.* 2007 for details).

Autotomy

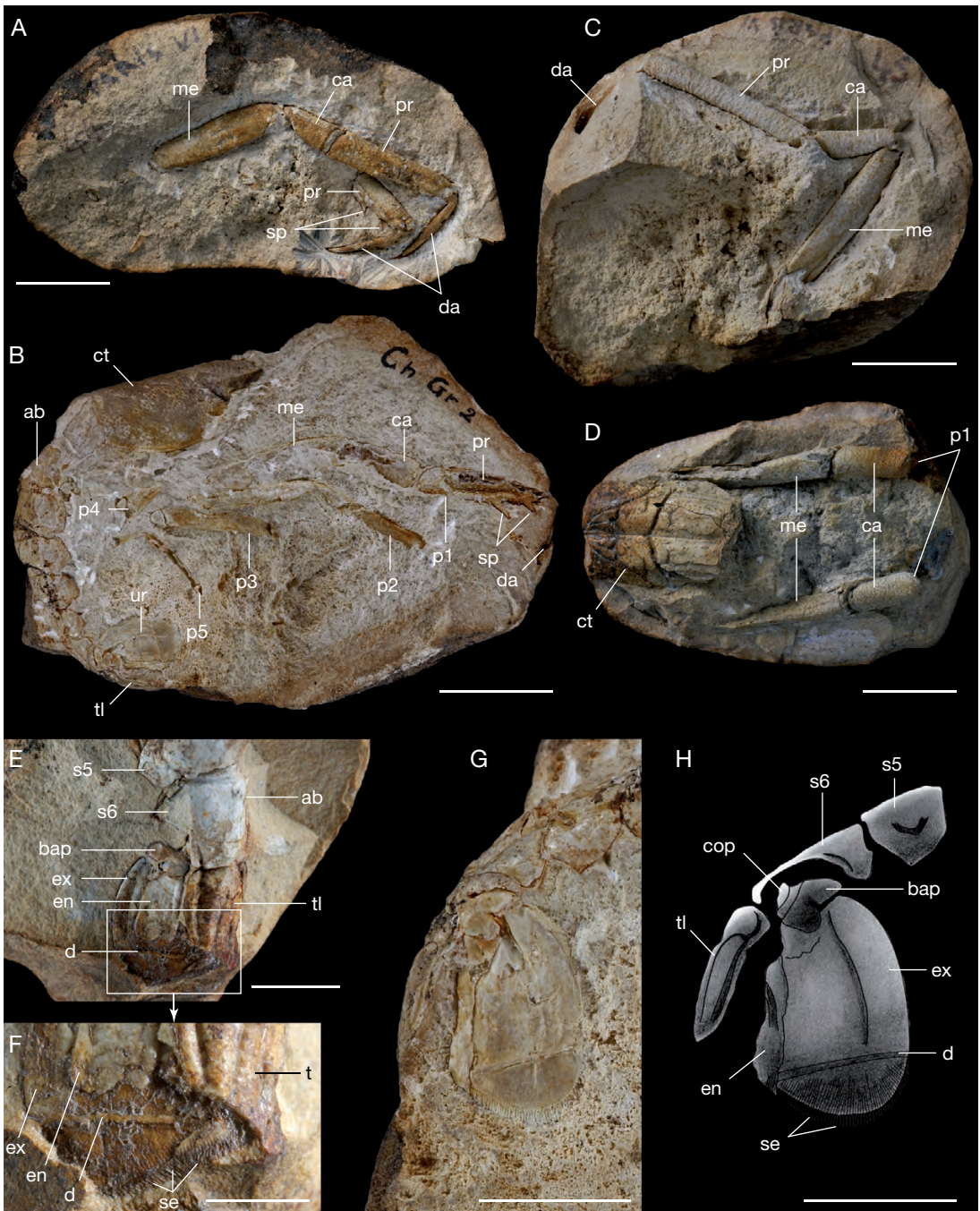
Loss and regeneration of the walking legs especially the first appendages is widespread within arthropods and well documented in extant decapod crustaceans (Maruzzo *et al.* 2005). However, autotomy, casting off an appendage in the face of predation and regeneration of the lost limb, is difficult to document in the fossil record (Förster 1969; Feldmann 2003). Forest & de Saint Laurent (1981) indicated that most of the captured specimens of the extant *Neoglyphea inopinata* had lost their first pereiopods. They indicated that the preferred breakage point was along the articulation between the basis and the ischium. They concluded that this appendotomy was probably a self-defense reflex linked to the stress of the capture. In our fossil sampling, several nodules contain isolated thoracic appendages – without associated carapaces – and that correspond only to the first pereiopods preserved either isolated (Fig. 5C) or by pair (Fig. 5A). By comparison with the living glypheids, this type of fossil preservation may be explained by a similar phenomenon of autotomy in *Glyphea regleyana*. As such, this is the first record of fossil species of glypheid, and one of the very few fossil crustaceans, in which autotomy phenomenon appears to be demonstrable.

Ecdysis

The molting process in decapod crustaceans is well documented (see Skinner 1985 for details) and fossil decapods are frequently found in molting position (Glaessner 1969). The nodules from the Haute-Saône department contain specimens of *G. regleyana* in very curious anatomical position. The body is disarticulated with a disconnection of the carapace and the abdomen that form almost a right angle (Fig. 3A), while the pereiopods are grouped in fan-shaped position pointing to the abdomen (Figs 2A; 5B). Several nodules show three-dimensionally preserved rests opposed to flattened carapaces (Fig. 5D), while others yield isolated cephalothorax dorsoventrally flattened (Fig. 8A-C) or laterally split (Fig. 8D). These positions are most probably linked to different phases of molting process in *G. regleyana*. The active phase of ecdysis in *G. regleyana* probably started with the rupture of the integument between the carapace and the first abdominal somite. The flattened carapaces and the split ones indicate that the dorsal margin worked probably as a hinge that liberated the head of the molted animal (e.g., Fig. 8A). This was followed by withdrawal of the thoracic appendages and finally the abdomen. The molted glypheid emerged, leaving the carapace displaced from the abdomen, with their axes forming almost a right angle. Relatively close molting processes are reported in *Hoploparia gammaroides* McCoy, 1849 (Eocene, England) and the same displacement and splitting of the carapace are known on the extant lobster *Homarus americanus* H. Milne Edwards, 1837 (Waddy *et al.* 1995).

The absence of small and/or juvenile specimens of *G. regleyana* may also be linked to the molting process. Indeed, at the end of the ecdysis, extant small-sized crustaceans generally eat their own exuviae in order to recycle the calcium to harden the newly formed exoskeleton (Lawton & Lavalli 1995). This observation might explicate the absence

FIG. 5. — *Glyphea regleyana* (Desmarest, 1822) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A**, isolated pair of first pereiopods (MNHN.F.A29553, locality unknown) showing laterally flattened segments (e.g., merus) of a presumed female specimen; **B**, complete specimen (MC-P-2009-6-Ch.Gr.2, Chariez) with three-dimensionally preserved cephalothorax, abdomen and pereiopods, note the first pereiopod with a propodus bearing ventral spines; **C**, isolated first pereiopod (MNHN.F.A29491, Mailley) showing sub-cylindrical segments of a presumed male specimen; **D**, fragmentary specimen (MNHN.F.A29577, Chariez) in dorsal view, note the dorsoventrally flattened carapace opposed to the subcylindrical segments of the first pereiopods (probable exuviae of male specimen); **E**, **F**, tail fan (MNHN.F.A29555, Rosey) in lateral (**E**) and detailed (**F**) views, note the trapezoidal telson and the rounded uropods with



diaeresis on exopod and well-developed distal fringe of setae; **G, H**, tail fan (detail of Fig. 5B), lateral view (**G**) and line drawing (**H**), note the reduced somite 6 with large lateral notch for the insertion of bilobate basipodite. Abbreviations: **ab**, abdomen; **bap**, basipodite; **ca**, carpus; **ct**, cephalothorax; **cop**, coxopodite; **d**, diaeresis; **da**, dactylus; **en**, endopod; **ex**, exopod; **me**, merus; **p1-p5**, pereopods 1 to 5; **pr**, propodus; **s5-s6**, somites 5 to 6; **se**, setae; **sp**, spine; **tl**, telson; **ur**, uropods. Scale bars: A-D, 2 cm; E-H, 1 cm.

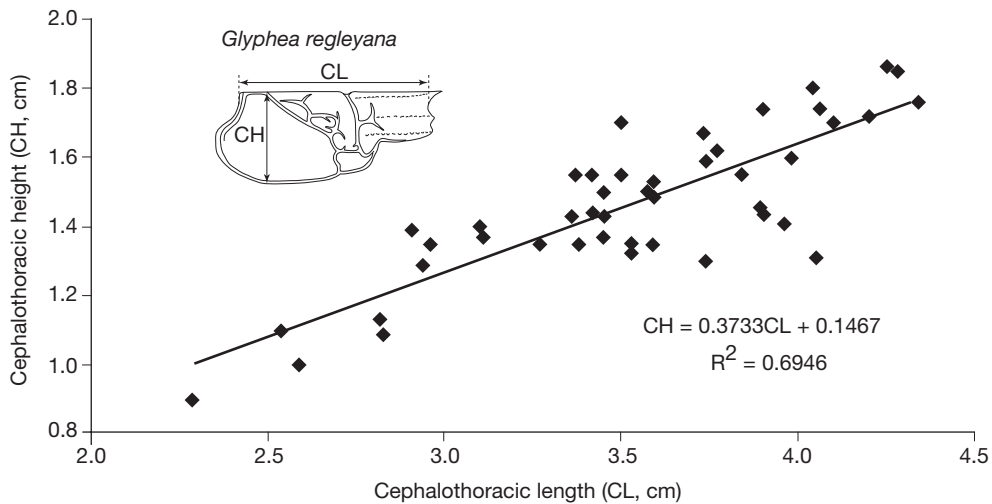


FIG. 6. — Results of biometric analyses on 45 carapaces of *Glyphea regleyana* (Desmarest, 1822): linear relation between the cephalothoracic height (CH) and the cephalothoracic length (CL), note the absence of small-sized specimens (probable juveniles). Schematic drawing indicates the measurements.

of small-sized *G. regleyana* in the nodules from Haute-Saône and more generally in the Upper Jurassic deposits.

Reconstruction

Our new observations supply more accurate description and allow a detailed iconographic reconstruction of *Glyphea regleyana* (Figs 9; 10). The general views are different from those historically proposed by Étallon (1859). They are more precise and highlight the sexual dimorphism in *G. regleyana*. The detailed views reveal new anatomical features in *G. regleyana* that provide several lines of evidence to demonstrate the relationship of fossil glypheids to the extant *Neoglyphea inopinata*.

Type material

In conclusion for all the previous remarks, we considered important to designate a neotype for *Glyphea regleyana* because the two syntypes of Desmarest (1822: 132, 133) were not found either in the collection Regley housed in the Muséum national d'Histoire naturelle, Paris or in the collection Gévril housed in the Muséum d'Histoire naturelle de Besançon. The neotype for *Glyphea regleyana* is the specimen [MNHN.FA29512](#) from Andelarrot

(Haute-Saône, Oxfordian) that shows the almost all diagnostic characters of the species and also of the genus. The new type locality is Andelarrot (Haute-Saône, eastern France).

Glyphea muensteri von Meyer, 1840 (Figs 11-13)

SYNTHETIC DESCRIPTION

Glyphea muensteri (Fig. 11A, B) is a small-sized glypheid relatively common in the Terrain à Chailles Formation. The following description is summarized after Van Straelen (1925), Petitclerc (1927), Martin (1961) and Förster & Matyja (1986).

Cephalothorax subcylindrical, stocky, laterally compressed, with simple pointed rostrum slightly directed downwards; cervical groove narrow, deep, steeply inclined, intercepting dorsal midline without interruption (Fig. 11C, D); branchicardiac groove narrow, slightly curved; gastro-orbital groove with perpendicular ramifications directed downwards (ventral branch) and upwards (dorsal branches); postcervical groove in set square; anterior cephalic margin with op-

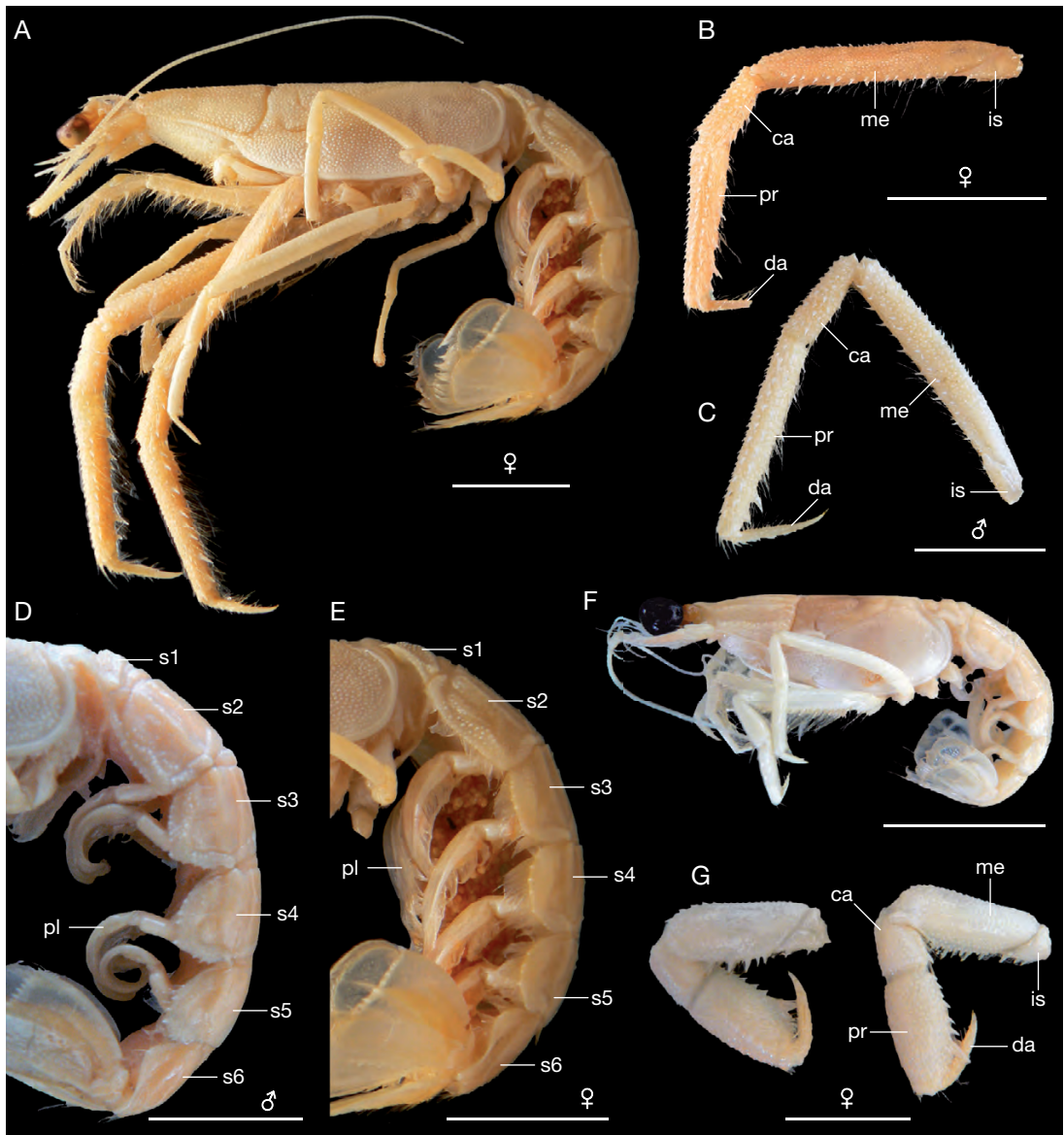


FIG. 7. — Recent glypheid lobsters *Neoglypheo inopinata* Forest & de Saint Laurent, 1975 and *Laurentaeglypheo neocaledonica* (Richer de Forges, 2006): **A**, *N. inopinata* (MNHN.IU.Pa1789, Indonesia), ovigerous female specimen, lateral view; **B**, *N. inopinata* (MNHN.IU.Pa1792, Philippines), isolated first pereiopod, female specimen; **C**, *N. inopinata* (MNHN.IU.Pa1797, Philippines), isolated first pereiopod, male specimen; **D**, *N. inopinata* (MNHN.IU.Pa1787, Philippines), abdomen with quadrate and sharp pleurae, male specimen; **E**, detail of Fig. 7A showing abdomen with rounded pleurae, note the eggs held within the pleopods; **F**, **G**, *L. neocaledonica* (holotype MNHN.IU.Pa1805, New Caledonia), female specimen, note the relatively reduced and compact first pereiopods (**G**). Abbreviations: **ca**, carpus; **da**, dactylus; **is**, ischium; **me**, merus; **pl**, pleopod; **pr**, propodus; **s1-s6**, somites 1 to 6. Scale bars: 2 cm.

tical and antennal notches; cephalic region with four longitudinal tuberculated carinae on flanks; carapace ornamentation with forward-directed

tubercles; first pereiopod well developed, achelate; other pereiopods smaller, achelate; abdomen short and narrow.

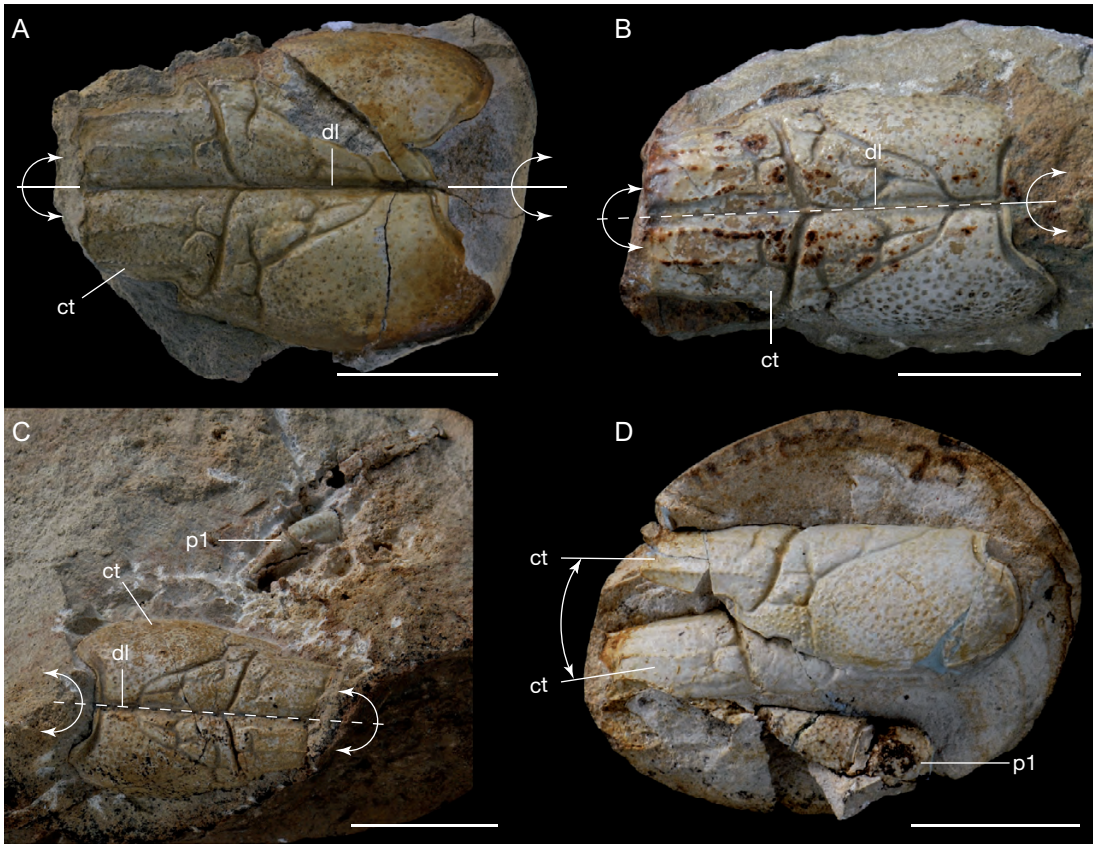


FIG. 8. — Molted specimens of *Glypheia regleyana* (Desmarest, 1822) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A**, isolated cephalothorax (UJF-ID.14030, Mailley) showing strong dorsoventral flattening along the dorsal midline, semicircular arrows suggest a probable hinge-type opening during ecdysis, dorsal view; **B**, isolated cephalothorax in dorsal view (MNHN.FA29581, locality unknown) with dorsoventral flattening, semicircular arrows and dotted line indicate that the dorsal margin worked probably as a hinge liberating the head of the molted animal; **C**, 3D-preserved specimen (MNHN.FA29522, Andelarrot), dorsal view of presumed male specimen (see subcylindrical segments of first pereopod) with dorsoventrally flattened cephalothorax (probable exuviae); **D**, isolated cephalothorax (MNHN.FA29504, Andelarrot), laterally split and divided into halves, note the longitudinal displacement (white arrows) and the rupture of the dorsal midline (presumed exuviae). Abbreviations: **ct**, cephalothorax; **dl**, dorsal midline; **p1**, pereopod 1. Scale bars: 2 cm.

NEW OBSERVATIONS

Cephalothorax (Fig. 11)

Average size for genus (CL = 2.88 cm, CH = 1.67 cm); dorsal midline interrupted by cervical groove; convex posterior margin with dorsal depression where the first abdominal somite is articulated; ventral margin with slight notch near the inferior groove, curving abruptly in the cephalic region; posterior and ventral margins with thick carina and marginal groove anteriorly fused with antennal groove; cephalic region sharply narrower than the rest of the thorax; ornamentation with large

tubercles granular (Fig. 11D, E), conical or spinose, size of tubercles decreasing from the dorsal posterior margin to the ventral margin, tubercles granular near the branchial region and more spinose at the edge of some grooves; four longitudinal cephalic carinae (Fig. 11C, D): carina 1 (dorsal position) with 10-11 spinose tubercles; carina 2 shorter, with 6-7 tubercles, two rows of small conical tubercles between carinae 1 and 2; carina 3 with 6-7 spinose tubercles; carina 4 (ventral position) well developed, with about 10 large tubercles, spinose and prominent.

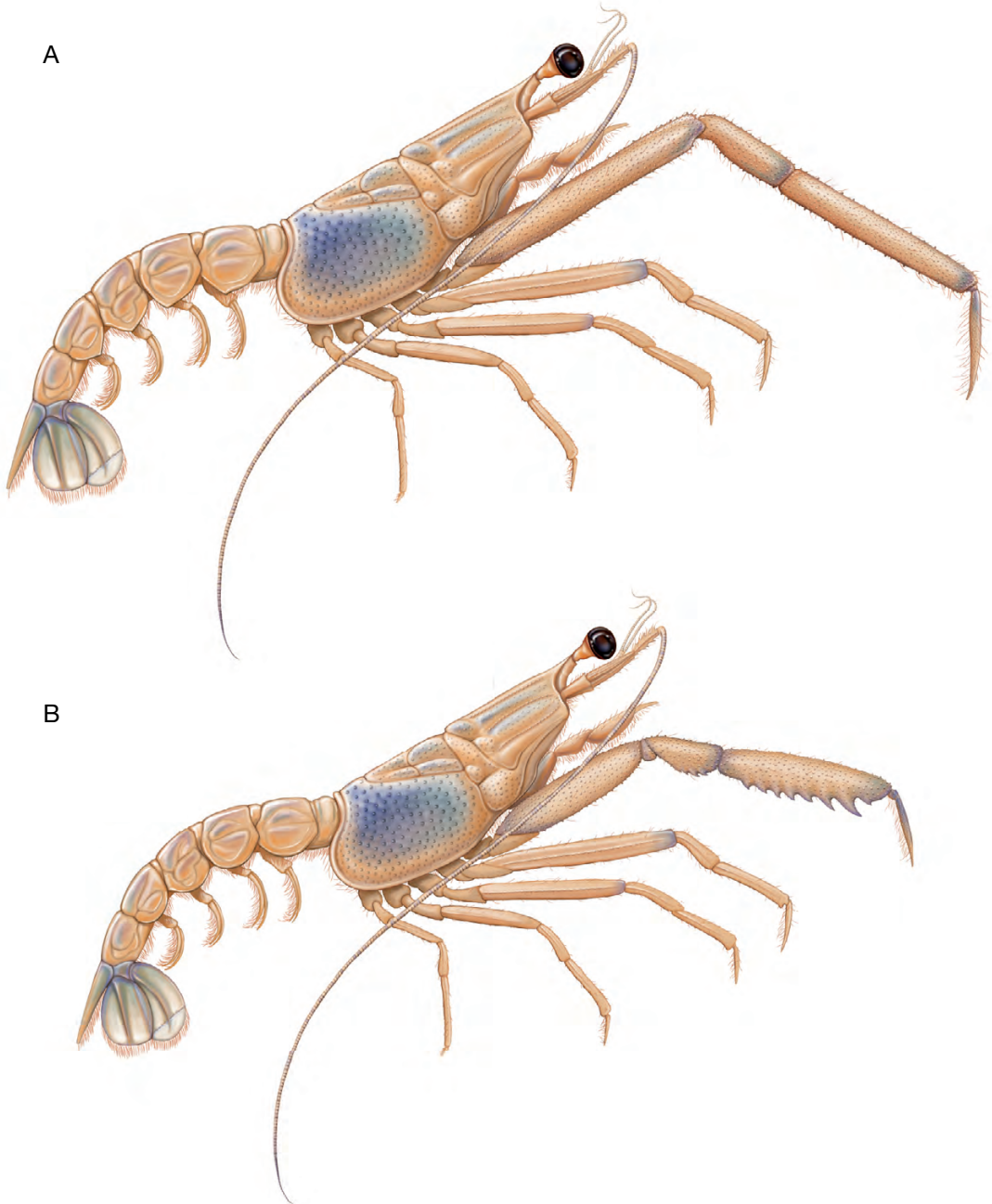


FIG. 9. — Reconstruction of *Glyphea regleyana* (Desmarest, 1822): note the differences in the morphology of the first pereiopod and the abdominal pleurae that are probably linked to sexual dimorphism (**A**, male specimen; **B**, female specimen). The proposed colors are freely inspired by those of *Neoglyphea inopinata*. Drawings: Charlène Letenneur (MNHN, scientific draughtsman).

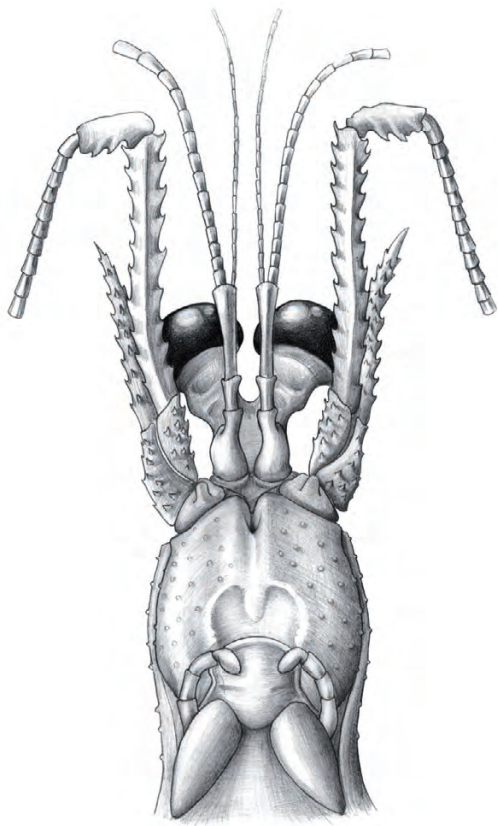


FIG. 10. — Reconstruction of *Glypheia regleyana* (Desmarest, 1822): ventral view of cephalothorax showing cephalic appendages and epistome. Drawing: Charlène Letenneur (MNHN, scientific draughtsman).

Epistome only known in lateral view in one specimen (Fig. 11E), subrectangular in outline, large, convex, not fused to the carapace and probably separates from it by a suture, lateral margins slightly sinuous; posterior margin with rounded depression where mandibles converge; ornamentation smooth.

Abdomen (Fig. 11A, B)

Somite 1 unknown; somites 2-6 decreasing in size; similar ornamentation in somites 2-5: tergum and pleura with marginal groove, tergum with one longitudinal groove in the median part and 3 transversal grooves very characteristic, pleura rounded with very small distal tubercles; somite 6 narrow, smooth, without apparent grooves, reduced pleura with large notch for the insertion of uropods; telson fragmentary, elongated and tronconical.

Cephalic appendages

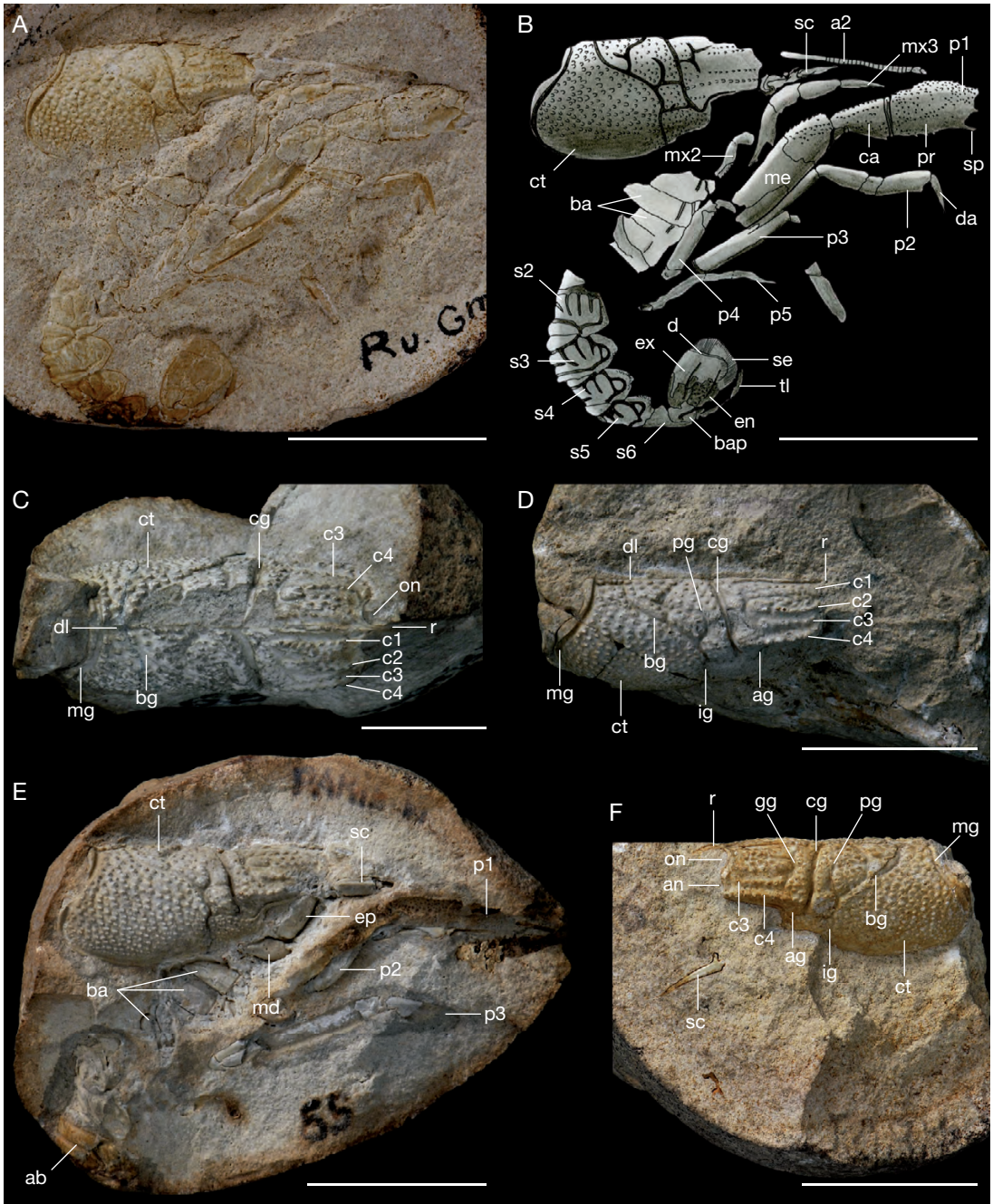
Antennulae (a1) unknown; antennae (a2) composed of antennal peduncle with multi-articulated flagellum and scaphocerite; antennal peduncle with indistinct basal segments (ischiocerite, merocerite, carpocerite?) to which a flagellum with not assessable length was articulated (Fig. 11B); scaphocerite triangular in outline with longitudinal carina and distal extremity thin and pointed (Fig. 11F).

Mandibles incompletely visible, strong and robust (Fig. 11E).

Thoracic appendages (Figs 11A, B, E; 12A, D)

First maxilliped not identified; second maxilliped short, narrow with only 3 distal segments preserved: merus long and slender, carpus short and curved, propodus short and ovate, dactylus not preserved in all our specimens, strong, curved and perpendicularly articulated to the propodus after the specimens of Förster & Matyja (1986); third maxilliped well developed, long (c. 90% CL) with 4 recognizable segments narrowing slightly towards the distal extremity: merus long, subrectangular, smooth; carpus short and pyriform; propodus ovate with narrow proximal articulation with carpus, axial region swollen, lateral margins flattened; dactylus long, flattened, pointed.

FIG. 11. — *Glypheia muensteri* von Meyer, 1840 from the nodules of the Terrain à Chailles Formation (Oxfordian): **A, B**, complete specimen (MC-P-2009-06-Ru.Grn.1, Rupt-sur-Saône), showing separation and 90° rotation of abdomen, relative to the cephalothorax and pereopods grouped in fan-shaped position pointing to the abdomen (probable exuviae of female), note fragmentary antenna (flagellum) and the second and third maxillipeds, lateral view (**A**) and line drawing (**B**); **C**, isolated cephalothorax (MNHN.F.A29532, Grandville), dorsal view, note the series of longitudinal cephalic carinae; **D**, isolated cephalothorax (MNHN.F.A29536, Chariez), lateral view, note the four longitudinal cephalic carinae and the ornamentation with forward-directed tubercles; **E**, disarticulated specimen (MNHN.F.A29531, Andelarre) showing separation and 90 degrees rotation of abdomen, relative to the cephalothorax and lateral displacement of epistome (molted specimen), note the right mandible in lateral view; **F**, small cephalothorax (MNHN.F.A29534, Grandville), lateral view, note



the thin and pointed scaphocerite. Abbreviations: **a2**, antenna; **ab**, abdomen; **ag**, antennal groove; **an**, antennal notch; **ba**, basis; **bg**, branchiocardiac groove; **bap**, basipodite; **c1-c4**, carinae 1 to 4; **ca**, carpus; **cg**, cervical groove; **ct**, cephalothorax; **d**, diaeresis; **da**, dactylus; **dl**, dorsal midline; **en**, endopod; **ep**, epistome; **ex**, exopod; **gg**, gastro-orbital groove; **ig**, inferior groove; **md**, mandible; **me**, merus; **mg**, marginal groove; **mx2**, **mx3**, maxillipeds 2 and 3; **on**, orbital notch; **p1-p5**, pereopods 1 to 5; **pg**, postcervical groove; **pr**, propodus; **r**, rostrum; **s2-s6**, somites 2 to 6; **se**, setae; **sc**, scaphocerite; **sp**, spine; **tl**, telson. Scale bars: A, B, D-F, 2 cm; C, 1 cm.

First pereopod elongate, strong, achelate and showing two different morphologies: subcylindrical segments, long and slender in very probable male specimen (Fig. 12D) and stocky segments, short, and more flattened in very probable female specimen (Figs 11A, B; 12A); 6 segments: coxa, basis and ischium smooth, coxa and basis maybe fused, ischium with oblique articulation to the merus; merus long (*c.* 70% CL), laterally flattened, dorsal margin with transversal rows of small spines distally, ventral margin with rows of small spines and distal tubercle large and rounded; carpus short (*c.* 25% CL), conical, covered by small spines; propodus characteristic of the species, long (*c.* 50% CL), subrectangular, stocky, covered with small tubercles; ventral margin with strong forward-directed spines, the last of which is particularly well developed rounded in presumed female specimen (Figs 11B; 12A); dactylus rarely preserved, straight and slender, perpendicularly articulated to the propodus (Fig. 12D).

Pereopods 2 to 5, badly preserved, of lessening size towards the posterior part, relatively thin, generally smooth, ventral margin of merus with row of small tubercles, dactylus flattened, curved and pointed (Fig. 11B).

Abdominal appendages (Fig. 11B)

Pleopods unknown. Uropods composed of short coxopodite, trilobate basipodite, rounded endopod and exopod, endopod with distal fringe of setae, exopod with diaeresis beyond which it becomes membranous, distal fringe of setae well developed, ornamentation with small tubercles and longitudinal median groove.

DISCUSSION AND RECONSTRUCTION

Sexual dimorphism in *Glyphea muensteri* is difficult to demonstrate because of a too weak number of complete specimens. However, as observed in

G. regleyana, it is possible to distinguish two types of first pereopods. We consider that the samples with long and slender first pereopod correspond to male specimens and those with short and more flattened first pereopod to female specimens. Regarding the molting process, several specimens of *G. muensteri* show appendages, internal skeleton and abdomen in very curious anatomical positions that suggest a very probable phenomenon of ecdysis with different phases during the molting process (Fig. 12). Similarly to *G. regleyana*, the body is disarticulated with the carapace and the abdomen that form almost a right angle while the pereopods, disconnected from the cephalothorax, are grouped in fan-shaped position (Figs 11A, E; 12A, B). The first abdominal somite is often absent. The cephalothorax is often longitudinally split along the dorsal midline (Fig. 12B). Some samples with two halves of cephalothorax clearly separate indicate a rupture during the molting process (Fig. 12B, C, E). Others show deformed carapaces that suggest they were very soft and demineralized before their inclusion into a nodule (Fig. 12D). The ecdysis in *G. muensteri* was probably relatively close to that of *G. regleyana* but with some variations. The active phase of ecdysis in *G. muensteri* probably started with the rupture of the integument between the carapace and the abdomen. The absence of the first abdominal somite may indicate a double rupture and its early loss. The dorsal midline split the carapace in two halves and liberated the molted animal. This was followed by withdrawal of the thoracic appendages and finally the rest of the abdomen. The molted glypheid emerged, leaving the carapace displaced from the abdomen, with their axes forming almost a right angle.

Our new observations supply more accurate description and allow a detailed iconographic reconstruction of *Glyphea muensteri* (Fig. 13). The general views are more complete than those proposed by

FIG. 12. — Molted specimens of *Glyphea muensteri* von Meyer, 1840 from the nodules of the Terrain à Chailles Formation (Oxfordian): **A**, sub-complete specimen (MNHN.F.A29530, Dampvalley-lès-Colombe) showing separation and 90° rotation of abdomen, relative to the cephalothorax (slightly split), note the well preserved first pereopod and the basis of pereopods disconnected to carapace and grouped in fan-shaped position pointing to the abdomen; **B**, complete specimen (MNHN.F.A29537, Montcey) showing separation and 90 degrees rotation of abdomen, relative to the cephalothorax, note the rupture of the dorsal midline inducing lateral split and division of the carapace into halves with longitudinal displacement (white arrows); **C**, isolated cephalothorax (MC-P-2009-6-Ca.Gm.4, Calmoutier), internal ventral view, note the dorsoventral flattening (hinge-type opening) and the rupture of the dorsal midline with slight



rotation of the two halves of carapace (white arrows); **D**, complete specimen (MNHN.F.A29533, Calmoutier) showing separation and 90° rotation of abdomen, relative to the cephalothorax, note the deformed cephalothorax opposed to the 3D-preserved first pereiopod suggesting a very soft and demineralized exoskeleton before inclusion into a nodule (probable exuviae of male specimen); **E**, nodule into parts with isolated cephalothorax (MNHN.F.B12478, locality unknown) showing lateral split and rupture of the dorsal midline with rotation of the two separate parts of the carapace (white arrows). Abbreviations: **a2**, antenna; **ab**, abdomen; **ba**, basis; **ca**, carpus; **ct**, cephalothorax; **da**, dactylus; **is**, ischium; **me**, merus; **mx3**, maxilliped 3; **p1**-**p5**, pereiopods 1 to 5; **pr**, propodus; **r**, rostrum; **sp**, spine. Scale bars: 2 cm.

Étallon (1859). They are more precise and highlight the probable sexual dimorphism in *G. muensteri*. The detailed views reveal new anatomical features in *G. muensteri* (epistome, mandibles) and provide additional evidence to demonstrate the relationship of fossil glypheids to the extant *Neoglyphea inopinata* and *Laurentaeglyphea neocaledonica* (Richer de Forges, 2006).

Superfamily ERYMOIDEA Van Straelen, 1925
Family ERYMIDAE Van Straelen, 1925

Genus *Eryma* von Meyer, 1840

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

Eryma ventrosa (von Meyer, 1835)
(Figs 14-17)

SYNTHETIC DESCRIPTION

Eryma ventrosa (Fig. 14) is a well-known species from the Terrain à Chailles Formation. The following description is summarized after Étallon (1859, 1861), Van Straelen (1925) and Petitclerc (1927).

Cephalothorax cylindrical, large with well-developed branchial region in males and more slender in females, with simple pointed rostrum straight with basal spine; dorsal midline rectilinear, anteriorly forking to form a smooth spindle-shaped surface until the base of the rostrum; cervical groove very deep, widening near the dorsal midline; gastro-orbital groove large and short; branchiocardiac groove narrow at its base and widening near the dorsal midline; postcervical groove concave, sub-parallel to the branchiocardiac groove; antennal groove narrow, deep, anteriorly fused with the marginal groove; hepatic groove with ramifications delimiting a little marked tubercle, triangular, flat, generally smooth; flanks of the cephalic region bearing two oblique carinae with distal forward-directed spines (sp1, sp2); anterior cephalic margin with orbital notch framed by sp1 and sp2; scaphocerite pointed; carapace ornamentation with areolate

tubercles slightly squamiform; first pereopods with strong and long chelae, external flank convex, heterochely very slight; second pereopods with large chelae, dactylus and index rectilinear, long; abdomen relatively large, somites 1-6 decreasing in size, somite 1 very short; somites 2-5 mucronate, somite 6 long, with reduced pleura; telson rounded; uropods with longitudinal carina and distal fringe, exopod with diaeresis.

NEW OBSERVATIONS

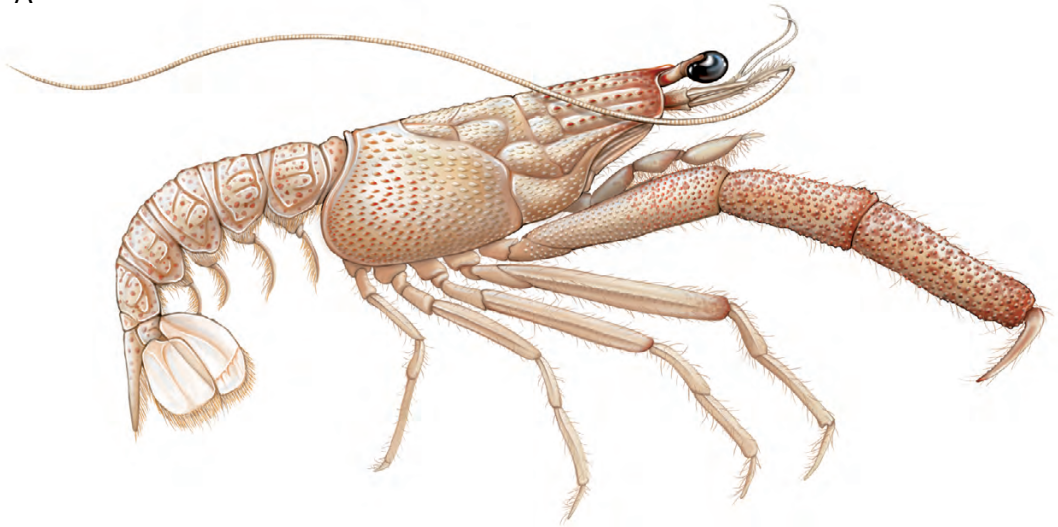
Cephalothorax

Average size for genus (CL = 3.8 cm, CH = 2.4); convex posterior margin with dorsal depression where the first abdominal somite is articulated (Fig. 14A-D); anterior margin with infra-antennal angle relatively acute; posterior and ventral margins with carina and deep marginal groove anteriorly fused with antennal groove; cephalic region showing two tuberculated lines with distal spines (sp1, sp2): first line, dorsal, oblique with 3-4 tubercles decreasing posteriorly; second line, ventral, parallel to the body axis, with 3-6 spinose tubercles decreasing posteriorly (Fig. 14A, C); ventral surface showing epistome, mandibles and fragments of thoracic sternites (Fig. D, F).

Epistome well preserved in some specimens (Fig. 14F, G), subrectangular, swollen with two convex regions separate by a triangular depression; not fused to the carapace but separates from it by a suture; lateral margins slightly sinuous, marked by a narrow and 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; ornamentation with small tubercles, triangular region between the posterior margin and the anterior sinus smooth and depressed.

Sternum partially preserved, median axis showing on both sides sections of coxae; sternites of the first two segments, corresponding to the maxillipeds, very narrow with contiguous coxae; sternites of the following segments, corresponding to pereopods 1-4, with some coxae preserved in section (Fig. 14F, G).

A



B

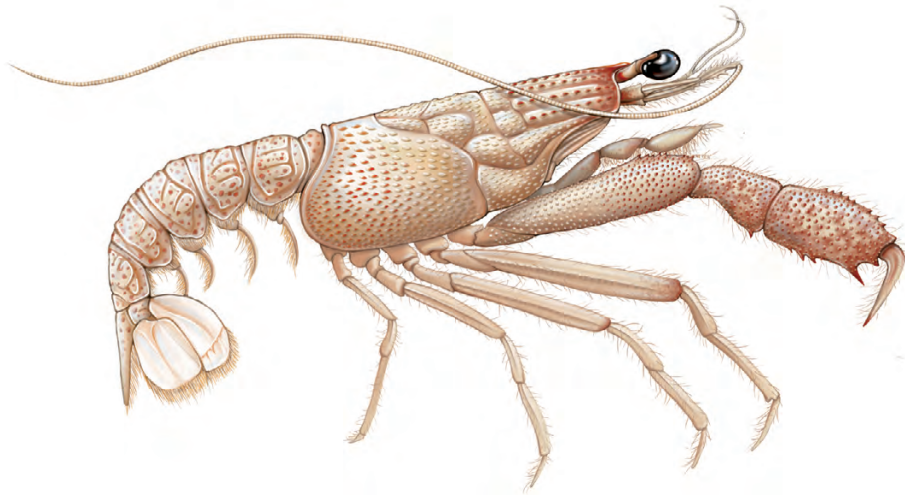


FIG. 13. — Reconstruction of *Glyphea muensteri* von Meyer, 1840: note the differences in the morphology of the first pereiopod that are probably linked to sexual dimorphism (A, male specimen; B, female specimen). The proposed colors are freely inspired by those of *Laurentaeglyphea neocaledonica*. Drawing: Charlène Letenneur (MNHN, scientific draughtsman).

Abdomen (Figs 14E; 15A, B)

Somite 1 very short, partially covered by the posterior margin of the cephalothorax, pleura reduced, rounded, with marginal groove; somites 2-5 large with terga rectilinear anteriorly and concave posteriorly; pleura large with mucronate extremity, slightly directed backwards; marginal groove on each somite;

ornamentation finely granular; somite 6 long, with reduced pleura anteriorly and replaced with large notch for the insertion of uropods, anterior tergal flank with transversal groove showing short longitudinal ramifications directed backwards (Fig. 15B); telson stocky, distally rounded, proximal region transversally inflated, ornamentation with small rounded tubercles.

Cephalic appendages

Antennulae (a1) unknown.

Antennae (a2) partially known, composed of antennal peduncle with three segments and multi-articulated flagellum (Fig. 15C) and scaphocerite; antennal peduncle with short and stocky ischiocerite, merocerite and carpocerite to which a flagellum with not assessable length (probably relatively short) is articulated; flagellum composed of cylindrical segments identical in size; antennal peduncle with scaphocerite triangular in outline, with a pointed distal extremity (Fig. 14B, F, G).

Mandibles symmetrical, strong and robust, sub-rectangular in outline (Fig. 14D), subcircular in section (Fig. 14F, G), ornamentation smooth.

Thoracic appendages

First and second maxillipeds not identified; third maxilliped well developed, long (*c.* 60% CL) with 6 segments (Fig. 14F, G); coxa and basis badly preserved, basis potentially fused with ischium; (basis-) ischium long; merus long, subrectangular with distal spine; carpus short; propodus piriform, narrow proximal articulation with carpus, axial region swollen, lateral margins flattened; dactylus not preserved.

First pereopods massive with strong chelae whose length sometimes exceeds that of the cephalothorax (Figs 15C-G; 16A, B); coxae elongate with longitudinal carina on the external surface, laterally flattened (Fig. 14D, E); basis and ischium badly preserved; merus elongate, subrectangular; carpus tronconical, short, stocky, covered with small tubercles (Fig. 15D); propodus of the chelae strong, elongate, with index as long as the dactylus, internal articulation with the dactylus, oblique, with marginal groove and distal carina (Fig. 15E); occlusal margins of dactylus and index supplied with strong tubercles; external surface of chelae convex, with small spine-shaped tu-

bercles (Fig. 15F); chelae showing two different morphologies: first one, elongate and relatively narrow (Figs 15C-E; 16C), second one, stocky and massive (Figs 15F, G; 16A).

Second pereopods partially known; chelae short, laterally flattened, with index and dactylus rectilinear, internal margins of dactylus and index supplied with small spines (Fig. 16B).

Pereopods 3-5 unknown.

Abdominal appendages (Fig. 14E)

Pleopods not preserved.

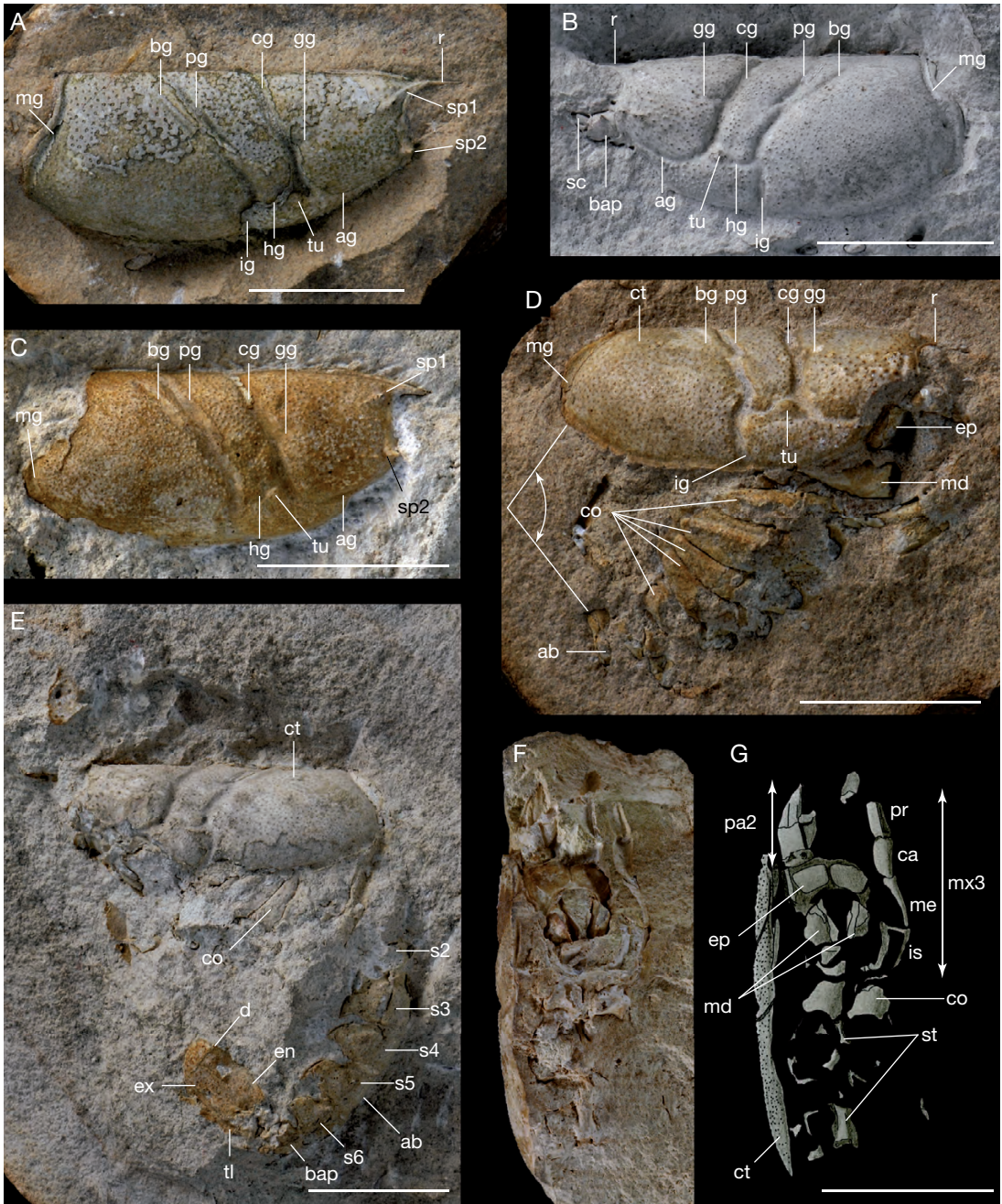
Uropods composed of rounded endopod and exopod attached to bilobate basipodite; endopod large, with distal fringe of setae and longitudinal carina; exopod ovate, with longitudinal carina and diaeresis beyond which it becomes membranous, distal fringe of setae well developed; ornamentation with sparse and small rounded tubercles.

DISCUSSION AND COMPARISONS

Sexual dimorphism

Étallon (1859, 1861) distinguished two varieties in *Eryma ventrosa*: 1) *Eryma ventrosa major* with large cephalothorax; and 2) *Eryma ventrosa minor* with shorter and elongate cephalothorax. Within the subspecies *Eryma ventrosa major*, Étallon (1859, 1861) recognized male and female specimens respectively characterized by massive and laterally compressed first pereopods with elongate chelae and more flattened first pereopods with thinner chelae. According to Van Straelen (1925), our observations lead to the conclusion that the subspecies *major* and *minor* are impossible to distinguish and that the morphological differences are more probably due to sexual dimorphism and slight heterochely. The subspecies *major* with a large cephalothorax and a well-developed branchial region may correspond to the females while the subspecies *minor* with a more elongate cephalothorax may correspond to

FIG. 14. — *Eryma ventrosa* (von Meyer, 1835) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A**, isolated cephalothorax (MNHN.FA29486, Chariez), lateral view; **B**, isolated cephalothorax (MNHN.FA29466, Montcey), lateral view, note the scaphocerite; **C**, isolated cephalothorax (MNHN.FA29469, Chariez), lateral view, note the cephalic region bearing two oblique carinae with distal forward-directed spines; **D**, sub-complete specimen (MNHN.FA29476, locality unknown) showing separation and 90° rotation of abdomen, relative to the cephalothorax and fragmentary pereopods disconnected to carapace and grouped in fan-shaped position pointing to the abdomen, note the epistome and the right mandible; **E**, complete specimen (MNHN.FA29468, Mailley) showing separation and 90 degrees rotation of abdomen, relative to the cephalothorax, lateral view; **F**, **G**, cephalothorax (MC-P-2009-6-Ch.Ev.7,



Chariez), ventral view (F) and line drawing (G), note the epistome, the mandibles in section, the third maxilliped and the sternum partially preserved. Abbreviations: **ab**, abdomen; **ag**, antennal groove; **bg**, branchiocardiac; **bap**, basipodite; **ca**, carpus; **cg**, cervical groove; **co**, coxa; **ct**, cephalothorax; **d**, diaeresis; **en**, endopod; **ep**, epistome; **ex**, exopod; **gg**, gastro-orbital groove; **hg**, hepatic groove; **ig**, inferior groove; **is**, ischium; **md**, mandible; **me**, merus; **mg**, marginal groove; **mx3**, maxilliped 3; **pg**, postcervical groove; **pr**, propodus; **pa2**, antennal peduncle; **r**, rostrum; **s1-s6**, somites 1 to 6; **sc**, scaphocerite; **st**, sternite; **sp1**, **sp2**, spines 1, 2; **tl**, telson; **tu**, tubercle. Scale bars: 2 cm.

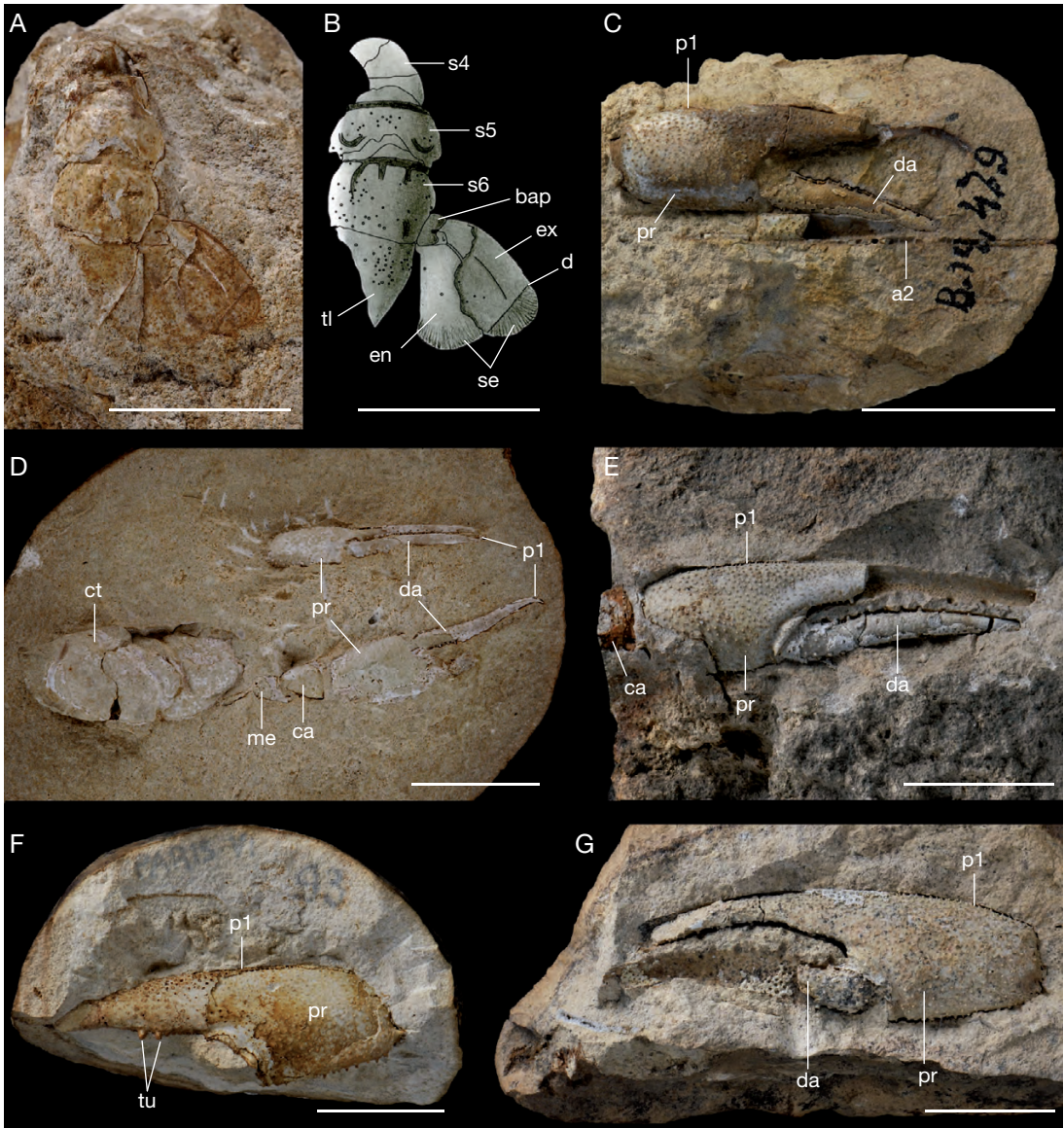


FIG. 15. — *Eryma ventrosa* (von Meyer, 1835) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A, B**, abdomen and tail fan (MC-P-2009-6-Ev.7, locality unknown), dorsal view (**A**) and line drawing (**B**), note the bilobate basipodite and the rounded uropods; **C**, left chela of pereiopod 1 and fragment of antenna (MNHN.F.B12479, locality unknown); **D**, sub-complete specimen (MC-P-2009-6-Fo.Ev.13, Fondremand), dorsal view, note the cephalothorax and the first pair of pereiopods with elongate and relatively narrow chelae; **E**, first pereiopod (MNHN.F.A29467, Mailley) showing right chela (internal view), elongate and narrow, external surface convex and covered with small spine-shaped tubercles, note the curved dactylus; **F**, massive propodus of pereiopod 1 (MNHN.F.A29560, Mailley), note the strong tubercles on the internal margin of index; **G**, massive and stocky chela of pereiopod 1 (MNHN.F.A29473, Chariez), internal view. Abbreviations: **a2**, antenna; **bap**, basipodite; **ca**, carpus; **ct**, cephalothorax; **d**, diaeresis; **da**, dactylus; **en**, endopod; **ex**, exopod; **me**, merus; **p1**, pereiopod 1; **pr**, propodus; **s4-s6**, somites 4 to 6; **se**, spine; **tl**, telson; **tu**, tubercle. Scale bars: 2 cm.

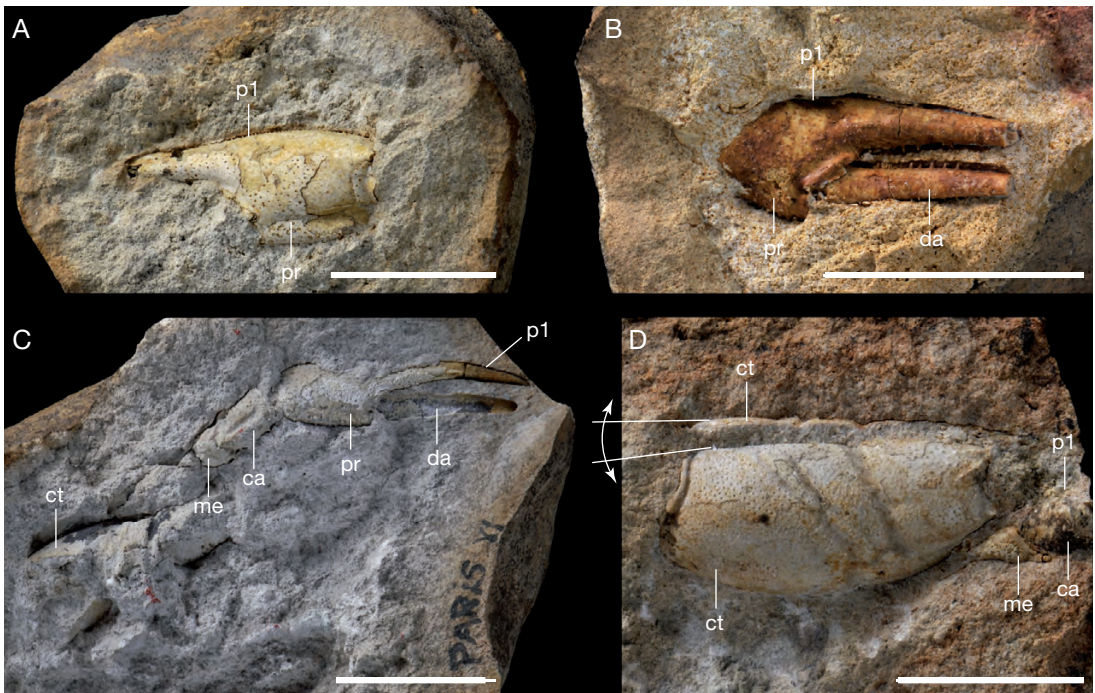


FIG. 16. — *Eryma ventrosa* (von Meyer, 1835) from the nodules of the Terrain à Chailles Formation (Oxfordian): **A**, massive and stocky chela of pereiopod 1 (MNHN.F.A29463, Rosey), internal view, note the absence of dactylus; **B**, short chela of very probable pereiopod 2 (MNHN.F.A29459, Andelarre), internal view; **C**, fragmentary specimen (MNHN.F.A29465, Frotey-lès-Vesoul) showing deformed cephalothorax and first pereiopod in connection, lateral view (molted specimen); **D**, isolated cephalothorax (MNHN.F.A29472, Montcey), note the rupture of the dorsal midline and the lateral splitting (white arrows). Abbreviations: **ca**, carpus; **ct**, cephalothorax; **da**, dactylus; **me**, merus; **p1**, pereiopod 1; **pr**, propodus. Scale bars: 2 cm.

the males. The dimensions and the morphology of the chelae are also probably link to the age of the specimens. Indeed, in the extant *Homarus americanus*, the ratio between the chelae size and the body size generally increases with the age, the growth of the chelae continuing longer than that of the rest of the body (Cadrin 1995). Thus the great variability observed in the design of the chelae of *Eryma ventrosa* may be linked to both sexual dimorphism and allometric development of the chelae.

Autotomy and ecdysis

Our fossil sampling shows several nodules bearing isolated thoracic appendages – without associated carapaces – and that correspond only to the chelae of the first pereiopods preserved either isolated or by pair (Fig. 15C, G). They indicate that the

preferred breakage point in the first pereiopods of *Eryma ventrosa* was probably along the articulation between the propodus and the carpus. This pereiopod autotomy – observed in numerous extant crustaceans – might be a self-defense reflex linked to a territory defense (Cromarty *et al.* 2000; Seidel *et al.* 2007), the establishment of dominance hierarchies (Gherardi & Daniels 2003), aggressive interactions or escape strategy (Mariappan *et al.* 2000).

Similarly to the fossil glypheid lobsters, several specimens of *E. ventrosa* are in very curious anatomical positions and suggest a probable phenomenon of ecdysis. The body is disarticulated with the carapace and the abdomen that form almost a right angle while the pereiopods are disconnected from the cephalothorax (Fig. 14D, E). Some samples, including the holotype of *E. ven-*

TABLE 1. — List of fossil crustaceans from the nodules of the Terrain à Chailles Formation (Oxfordian, Haute-Saône Department).

Decapod crustaceans	
Glypheidea	
Glypheidae	
	<i>Glyphea regleyana</i> (Desmarest, 1822)
	<i>Glyphea muensteri</i> von Meyer, 1840
	<i>Glyphea dressieri</i> von Meyer in Bronn, 1837
	<i>Glypheopsis etalloni</i> (Oppel, 1861)
Erymidae	
	<i>Eryma ventrosa</i> (von Meyer, 1835)
	<i>Eryma perroni</i> (Étallon, 1861)
	<i>Eryma insignis</i> Oppel, 1862
Polychelida	
Eryonidae	
	" <i>Eryon</i> " <i>perroni</i> Étallon, 1859
Axiidea	
Axiidae	
	<i>Etallonia</i> sp. Oppel, 1861

trota (see Oppel 1862: pl. VI, fig. 4 for instance), show cephalothoraces longitudinally split along the dorsal midline that suggest a rupture during the molting process (Fig. 16D). The ecdysis in *E. ventrosa* probably started with the rupture of the integument between the carapace and the abdomen. The dorsal midline split the carapace in two halves and liberated the molted animal. This was followed by withdrawal of the thoracic appendages and finally the rest of the abdomen. The molted erymid emerged, leaving the carapace displaced from the abdomen, with their axes forming almost a right angle. A very similar molting process is known on the extant lobster *Homarus americanus* (Waddy *et al.* 1995).

Reconstruction

Our new observations provide more accurate description and allow a detailed iconographic reconstruction of *Eryma ventrosa* (Fig. 17). The general views are more complete than those proposed by Étallon (1859). They are more precise and include the abdomen, the pereopods and some cephalic appendages. The detailed views highlight the great variability in the design of the chelae of the first pereopod. They reveal both very probable sexual dimorphism and allometric growth of the chelae.

PALAEOECOLOGY AND PALAEOENVIRONNEMENT

DIVERSITY AND RELATIVE ABUNDANCE

The Haute-Saône crustacean fauna as a whole includes 9 different species (Table 1) assigned to the glypheids, the erymids and the eryonids. The glypheid lobsters are the most diversified group with 4 species: *Glyphea regleyana*, *Glyphea muensteri*, *Glypheopsis etalloni* (Oppel, 1861) (Fig. 18A, B) and *Glyphea dressieri* von Meyer in Bronn, 1837 (Fig. 18C, D). The erymids lobsters include 3 species: *Eryma ventrosa*, *Eryma perroni* (Étallon, 1861) (Fig. 18E, F) and *Eryma insignis* Oppel, 1862 (Fig. 18G). The eryonids are represented by "*Eryon*" *perroni* Étallon, 1859 (Fig. 18H) that exhibits very unusual anatomical characters (see Van Straelen [1925] for discussion) and is temporarily maintained within the genus *Eryon* Desmarest, 1817. Moreover, according to Petitclerc (1927), some isolated propodi (Fig. 18I) are assigned to *Etallonia* Oppel, 1861 (Axiidea: Axiidae Huxley, 1879).

The quantitative analysis based on 424 nodules (Table 2, results expressed as number of specimens and percentages) shows three dominant species: 1) *Glyphea regleyana* (50.5% of nodules); 2) *Eryma ventrosa* (24.8%); and 3) *Glyphea muensteri* (16.5%). All the other crustaceans are minor elements of the fauna with relative abundances lower than 5%. Most of the remaining species are often represented by a small number of fossils (e.g., *Glyphea dressieri*, 11 specimens: 2.6%; *Eryma perroni*: 1 specimen: 0.2%).

Regarding the geographical distribution of the crustaceans from the Terrain à Chailles Formation, 29 different outcrops are identified in the literature (e.g., Étallon 1859, 1861; Van Straelen 1925; Petitclerc 1927; Martin 1961) and most of them were investigated during successive field campaigns in 2009 (Fig. 1). The very close outcrops (e.g., Andellare-Andellarot, Rosey-Mailley), often confused in the old collections, are grouped together here to facilitate the interpretations (Table 3). Thus, the results highlight 6 main localities (Table 3): Chariez (15.8% of the nodules), Calmoutier (12.3%), Mailley-Rosey (10.9%), Maizières-Fondremand-Grandvelle (9.2%), Andellare-Andellarot (6.4%) and Montcey-Comberjon (5.7%). Most of the remaining outcrops are



FIG. 17. — Reconstruction of *Eryma ventrosa* (von Meyer, 1835): note the great variability in the design of the chela of the first pereopod. The proposed colors are freely inspired by those of *Homarus gammarus* (Linnaeus, 1758). Drawing: Charlène Letenneur (MNHN, scientific draughtsman).

represented by a very small number of fossils (e.g., Le Vernois, 3 specimens: 0.7%; Rupt-sur-Saône, 1 specimen: 0.2%). The relative abundances of crustaceans, calculated for each major locality (Fig. 19), show that the assemblages from Chariez, Montcey-Comberjon and Andelarre-Andelarrot typify the composition of the crustacean fauna from the Terrain à Chailles

Formation as a whole (Table 2). By contrast, those from Calmoutier, Mailley-Rosey and Maizières-Fondremand-Grandvelle are distinct (Fig. 19). In Calmoutier, the crustacean assemblage is composed principally of *G. muensteri* (40% of nodules) followed by *G. regleyana* (27%) and *E. ventrosa* (21%). In Mailley-Rosey, the crustacean fauna includes mainly

TABLE. 2. — Crustaceans preserved in siliceous nodules from the Terrain à Chailles Formation (Oxfordian, Haute-Saône department): global results of quantitative analysis (number of nodules and percentages). Abbreviations: **MNHN.F**, Muséum national d'Histoire naturelle, Paris, collections de Paléontologie; **MC-P**, collections du Muséum Cuvier, Ville de Montbéliard, Dépôt Université des Sciences de Besançon ; **FSL**, Faculté des Sciences de Lyon, Université Claude Bernard Lyon 1; **UJF-ID**, Université Joseph Fourier, Institut Dolomieu, Grenoble.

Taxa	Collections				Total samples	Percentages (%)
	MNHN.F	MC-P	FSL	UJF-ID		
<i>Glyphea regleyana</i>	92	68	51	3	214	50.5
<i>Eryma ventrosa</i>	46	29	24	6	105	24.8
<i>Glyphea muensteri</i>	21	10	38	1	70	16.5
<i>Glypheopsis etalloni</i>	9	1	7	0	17	4.0
<i>Glyphea dressieri</i>	7	0	4	0	11	2.6
<i>Etallonia</i> sp.	4	0	0	0	4	0.9
<i>Eryma perroni</i>	1	0	0	0	1	0.2
<i>Eryma insignis</i>	1	0	0	0	1	0.2
"Eryon" <i>perroni</i>	1	0	0	0	1	0.2
Total	182	108	124	10	424	100.0

two species: *E. ventrosa* (46%) and *G. regleyana* (44%). In Maizières-Fondremand-Grandvelle, *G. regleyana* (49%) and *G. muensteri* (21%) predominate and are equally followed by *E. ventrosa* (13%) and *G. dressieri* (13%). This latter species is well represented only in this group of localities. The same observation is valid for *Glypheopsis etalloni* in Montcey-Comberjon (17% of nodules) and Calmoutier (8%).

COMPARISONS WITH RECENT AND FOSSIL CRUSTACEANS

Extant glypheid lobsters

Numerous aspects of the biology and ecology of glypheids were unknown until the discovery of the Recent glypheids *Neoglyphea inopinata* (Fig. 7A) and *Laurentaeglyphea neocaledonica* (Fig. 7F). The first species was recognized by Forest & de Saint-Laurent (1975) after a specimen collected in the Philippines in 1908 at *c.* 200 m depth by the U.S. oceanographic vessel "Albatross". Three French expeditions in the same region (Forest & de Saint-Laurent 1976, 1981, 1989; Forest 2006) and other caught by Australian fishermen in the Timor Sea (Indonesia) reveal that *N. inopinata* inhabits at depths between 180 and 260 m on bottoms composed of a compact mud with several rocky outcrops. At these depths, light penetration is even possible and *N. inopinata* that seems to reside in holes or burrows exits from it during the period of maximal light intensity of the day (Forest 2006).

The associated benthic fauna is mainly composed of gorgonians, sponges, sea urchins, large pentacrinid stalked crinoids, fishes, crabs, and hermit crabs (Forest 2006). The second Recent species was collected more recently in the deep waters of the Coral Sea from New Caledonia (Richer de Forges 2006). *Laurentaeglyphea neocaledonica* has been captured at depths between 360 and 530 m on the rocky slope of a seamount called the "Banc Capel". This seamount presents steep relief and is scoured by very strong currents. The associated fauna is composed of sponges, gorgonians, crabs and scyllarid lobsters (Richer de Forges 2006). Even though the bathymetric ranges are quite similar (depth *c.* 300 m), the rocky habitat of *L. neocaledonica* seems different from this of *N. inopinata* that is more muddy and allows the digging of burrows.

Extant crustacean faunas

Today, the distribution and abundance patterns of extant decapods, chiefly in deep waters, are clearly linked to the bathymetric zonation (Abelló *et al.* 1988; Fariña *et al.* 1997). The parameters that control the community structure are mainly the depth but also the submarine topography, the type of substrate and the seasonal fluctuations of water temperature (Fariña *et al.* 1997; Fanelli *et al.* 2007). The differences observed in the composition of the fossil crustacean assemblages of the six major localities from the Terrain à Chailles Formation may be linked to

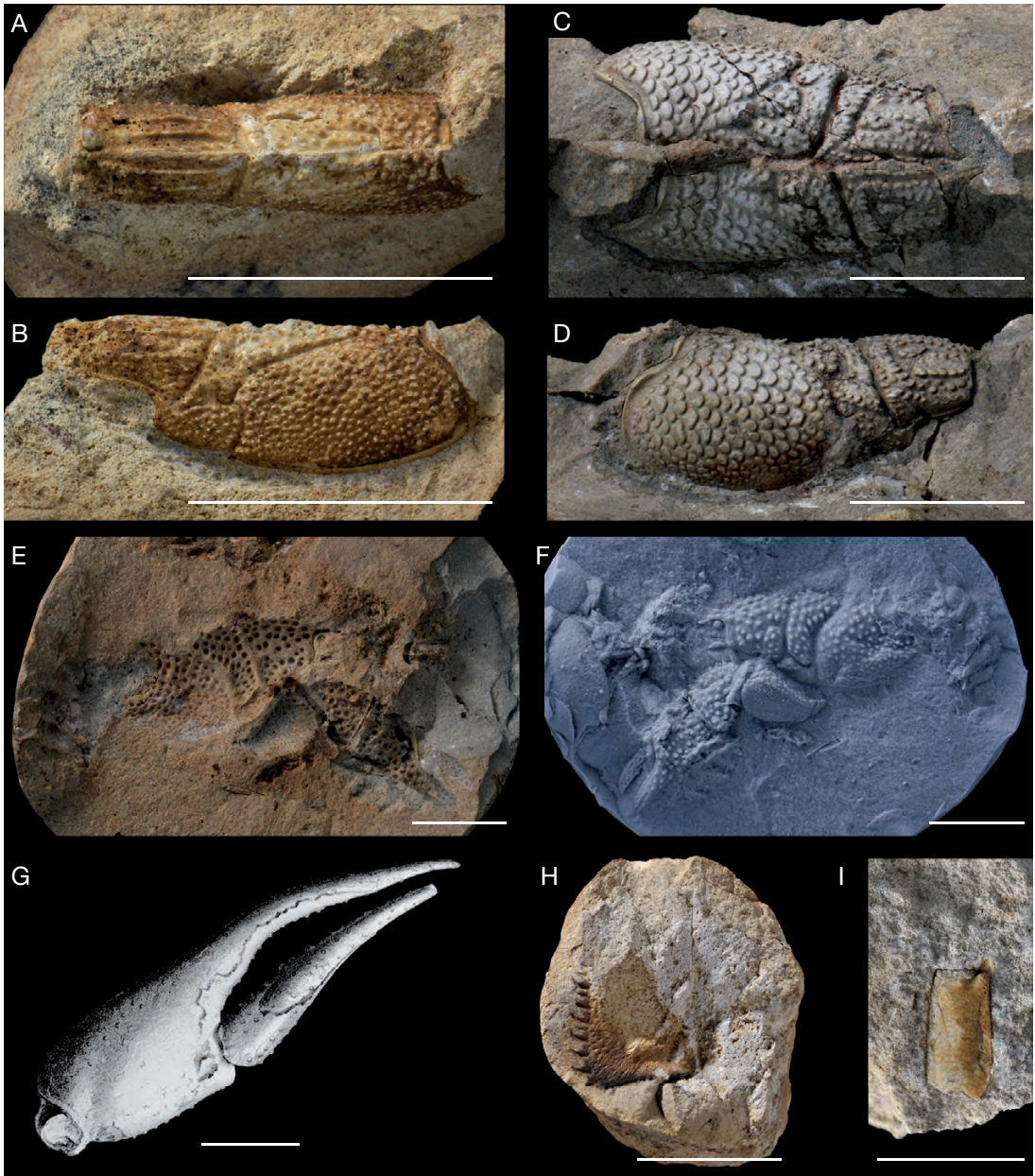


FIG. 18. — Crustaceans from the nodules of the Terrain à Chailles Formation (Oxfordian): **A, B**, *Glypheopsis etalloni* (Oppel, 1861) (MNHN.FA29541, Andelarrot), isolated cephalothorax in dorsal (**A**) and lateral (**B**) views, note the longitudinal cephalic carinae; **C, D**, *Glyphea dressieri* von Meyer in Bronn, 1837 (MNHN.FA29540, Grandvelle), isolated cephalothorax in dorsal (**C**) and lateral (**D**) views, note the scale-like ornamentation; **E, F**, *Eryma perroni* (Étallon, 1861) (syntype MNHN.FB12485, Frasne-le-Château), original specimen (**E**) and latex cast (**F**), note the tuberculated ornamentation; **G**, *Eryma insignis* Oppel, 1862 (MNHN.FA24613, cast of the holotype), drawing of the very long chela (modified after Oppel 1862); **H**, “*Eryon*” *perroni* Étallon, 1859 (holotype MNHN.FA31486, Calmoutier), ventral view of the internal carapace; **I**, *Etallonia* sp. Oppel, 1861 (MNHN.FA29572, Le Vernois), propodus in lateral view. Scale bars: A-H, 2 cm; I, 1 cm.

TABLE. 3. — Relative abundances and geographical distribution of the crustaceans from the Terrain à Chailles Formation: detailed results of quantitative analysis (number of nodules and percentages) with regard to the different studied outcrops (very close outcrops are grouped together).

Outcrops	<i>Glyphea regleyana</i>	<i>Eryma ventrosa</i>	<i>Glyphea muensteri</i>	<i>Glypheopsis etalloni</i>	<i>Glyphea dressleri</i>	<i>Etallonia</i> sp.	<i>Eryma perroni</i>	<i>Eryma insignis</i>	"Eryon" perroni	Total samples	%
Chariez	44	18	4	0	0	1	0	0	0	67	15.8
Calmoutier	14	11	21	4	1	0	0	0	1	52	12.3
Mailley, Rosey	20	21	2	2	1	0	0	0	0	46	10.9
Maizières, Fondre- mand, Grandvelle	19	5	8	1	5	1	0	0	0	39	9.2
Andelarre, Andelarro t Montcey, Comberjon	18	5	2	1	1	0	0	0	0	27	6.4
Frétigney	10	6	4	4	0	0	0	0	0	24	5.7
Frotéy-lès-Vesoul	11	2	5	0	0	0	0	0	0	18	4.3
Levrecey	10	5	0	0	0	0	0	0	0	15	3.5
Noidans-lès-Vesoul	2	1	0	2	1	0	0	0	0	6	1.4
Quenoche	4	0	0	0	0	0	0	0	0	4	0.9
Le Vernois	1	1	0	0	0	0	0	0	0	2	0.5
Trésilly	1	1	0	0	0	1	0	0	0	3	0.7
Navenne	0	0	0	0	2	0	0	0	0	2	0.5
Vesoul	1	0	0	1	0	0	0	0	0	2	0.5
Rupt-sur-Saône	1	0	0	0	0	0	0	0	0	1	0.2
Roche-sur-Linotte	0	0	1	0	0	0	0	0	0	1	0.2
Neuveville-lès-la- Charité	1	0	0	0	0	0	0	0	0	1	0.2
Liévans	1	0	0	0	0	0	0	0	0	1	0.2
Grattery	1	0	0	0	0	0	0	0	0	1	0.2
Frasne-le-Château	0	0	0	0	0	0	1	0	0	1	0.2
Dampvalley-lès- Colombe	0	0	1	0	0	0	0	0	0	1	0.2
Bourguignon-lès- La Charité	1	0	0	0	0	0	0	0	0	1	0.2
Dampierre-sur- Linotte	0	1	0	0	0	0	0	0	0	1	0.2
unknown outcrop	53	28	22	2	0	1	0	1	0	107	25.24
Total samples	214	105	70	17	11	4	1	1	1	424	100.0

palaeoenvironmental conditions slightly different. The surface of the studied area (Haute-Saône department) is relatively limited and the differences in water depth between the localities were probably not very significant. Thus, the submarine topography and the type of substrate constitute probably the determinant parameters. The sedimentological reconstructions proposed by Contini (1975, 1976) for the Haute-Saône supposed basin deposits characterized by muddy substrates with more or less detrital particles that might explicate the differences in the crustacean assemblages.

Other Jurassic crustacean faunas

The fauna from the Terrain à Chailles Formation is particularly rich in glypheid and erymid lobsters. The high proportions of these lobsters made this fauna one of the most original of the Jurassic. The diversity of the glypheid species is the main characteristic of the Haute-Saône fauna. Such a diversity is only found in the Solnhofen Lithographic Limestones (Late Jurassic, Germany) (see Schweigert & Garassino [2005: table 1]). In the Solnhofen Lithographic Limestones, there are many crustaceans preserved as molts from many different environments washed into the lagoons,

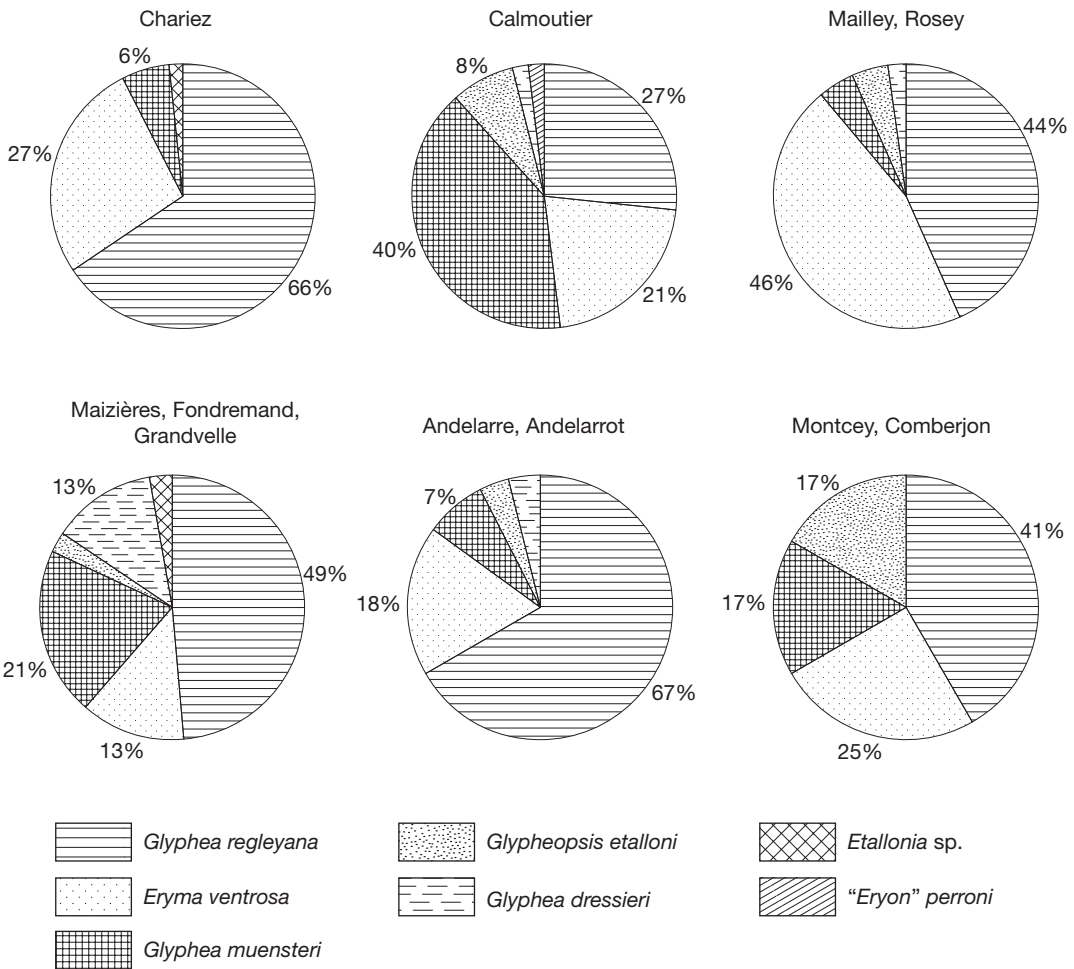


FIG. 19. — Pie-diagrams showing the crustacean relative abundances in the 6 main outcrops yielding siliceous nodules. Sampling: Chariez, 67 nodules; Calmoutier, 52 nodules; Mailley, Rosey, 46 nodules; Maizières, Fondremand, Grandvelle, 39 nodules; Andellarre, Andellarrot, 27 nodules; Montcey, Comberjon, 24 nodules. Results expressed in percentages of specimens.

so that the different outcrops are hardly comparable to the autochthonous crustaceans from the Oxfordian Terrain à Chailles Formation (G. Schweigert, pers. comm. 2011). Thus, the crustacean fauna from the Terrain à Chailles Formation is very distinct from those of Solnhofen (*c.* 70 crustacean species; Frickhinger 1999; Schweigert & Garassino 2004; Garassino & Schweigert 2006) and La Voulte (*c.* 30 crustacean species; Charbonnier 2009; Charbonnier *et al.* 2010). These differences of taxonomic richness and relative abundance reflect probably major differences in pal-

aeoecological and palaeoenvironmental conditions. Indeed, the Late Jurassic lithographic limestones of southern Germany (Solnhofen, Eichstätt, Nusplingen; Frickhinger 1994; Garassino & Schweigert 2006) were deposited in very shallow carbonate platforms and coastal lagoons where high biodiversity is commonly observed. The fauna from the La Voulte Lagerstätte (Callovian, France) corresponded very probably to a bathyal community and the biodiversity might be linked to hydrothermal processes (Charbonnier 2009; Charbonnier *et al.* 2007, 2010). However, the fauna

from the “Terrain à Chailles” can be compared to other crustacean associations that suggest also relatively deep water settings such as those of the Osteno Lagerstätte (Sinemurian, Italy) and Central Polish Uplands (Oxfordian, Poland). The Osteno fauna is particularly rich in glypheids, erymids (Garassino 1996), penaeoid shrimps (Garassino & Teruzzi 1990) and eryonoids (Pinna 1967, 1968, 1969, 1985; Teruzzi 1990). These crustaceans are preserved in sediments very rich in spicules of siliceous sponges (25% of the rock after Garassino 1996) and are thus considered to have inhabited relatively deep areas bordering the basin of the Moltrasio Limestone (Garassino pers. comm. [2009]). The crustaceans from the Central Polish Uplands (Polish Jura, Holy Cross Mountains) are mainly composed of glypheoid lobsters and erymids (Förster & Matyja 1986; Garassino & Krobicki 2002). These crustaceans lived on the soft bottom areas located below the sponge/microbialite circalittoral bioherms that classically developed at depths exceeding 80-100 m (Gwinner 1976; Gaillard 1983; Pisera 1997; Beresi 2003).

IMPLICATIONS FOR THE PALAEOENVIRONMENT OF THE HAUTE-SAÔNE CRUSTACEANS

Convergent palaeoenvironmental evidence obtained from both ecological parameters of the present-day glypheids and the fossil crustacean faunas from Osteno and Central Polish Uplands support the hypothesis that the crustaceans from the Terrain à Chailles Formation corresponded to a relatively deep water fauna. Similarly to *Neoglyphea inopinata*, the fossil glypheids from the Haute-Saône may develop at depths about 100-150 m where light penetration was even possible. They probably lived in burrows dug into soft or firm substrates that correspond today to the argileous limestones of the Terrain à Chailles Formation. This type of substrate is corroborated by the associated organisms founded in the siliceous nodules that all needed soft bottoms such as stalked crinoids (*Millericrinus* d’Orbigny, 1841), burrowing bivalves (*Trigonia* Bruguière, 1789) or irregular echinoids (*Collyrites* Desmoulins, 1835). The bathymetric range possibly exceeded 100-150 m and allowed the formation of the siliceous nodules that are often interpreted as concretions formed in low-energy environment such as the distal platforms

or the domains around the transition platform-basin (e.g., Migaszewski *et al.* 2006).

The numerous spicules of siliceous sponges in the Osteno deposits and the proximity of sponge bioherms in the Central Polish Uplands constitute convergent evidence in favor of relatively deep water setting for the crustaceans from the Terrain à Chailles Formation. Indeed, these crustaceans are contemporaneous to numerous sponge-microbialite bioherms that developed in the Franche-Comté region and in the nearby Jura platforms during the Late Jurassic (Enay 1966; Gaillard 1983; Olivier *et al.* 2004). They probably lived in an environment of distal platform. This hypothesis is also supported by palaeogeographical interpretations that place the Haute-Saône area in a small gulf prolonging southwards the Souabe basin during the Oxfordian (Contini & Bourquin 1969; Contini 1972). Moreover, the biodiversity and the richness in glypheids and erymids of the Terrain à Chailles Formation are only observed within the crustacean fauna from Osteno that is also interpreted to have flourished very probably in relatively deep water palaeoenvironment.

CONCLUSIONS

The study of the crustaceans three-dimensionally preserved in siliceous nodules from the Terrain à Chailles Formation (Haute-Saône, Franche-Comté) shows that the glypheid and the erymid lobsters are major components of the fauna. Represented by 9 different species, these crustaceans constitute a relatively original assemblage that contrasts with the decapod crustacean faunas of the celebrated Lagerstätten of La Voulte or Solnhofen. Quantitative analysis of the nodule contents shows three dominant species: *Glyphea regleyana*, *Eryma ventrosa* and *Glyphea muensteri*. New detailed descriptions of these species confirm the presence of a sexual dimorphism and reveal phenomena of autotomy in *G. regleyana* and probably in *E. ventrosa*. They also reveal different phenomenon of ecdysis in *G. regleyana*, *E. ventrosa* and *G. muensteri* and highlight several phases during the molting process. Detailed comparisons with modern morphological and ecological analogues and similar Jurassic fossil

faunas, support the hypothesis that the Haute-Saône crustaceans inhabited moderately deep water setting most probably about 100-150 m (lower circalittoral zone) where light intensity was even sensitive. If our interpretations are correct, the crustaceans from the Terrain à Chailles Formation may be considered as reliable indicators of distal platform setting. They constitute a very original assemblage, intermediary between the communities from the shallow carbonate platforms (e.g., Solnhofen) and those from the bathyal zone (e.g., La Voulte) and, thus provide key-information on the marine palaeobiodiversity of the distal platforms during the Mesozoic.

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