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## **Première occurrence d'*Enoploclytia* M'Coy, 1849 (Crustacea : Decapoda : Erymidae) dans le Jurassique**

## **First occurrence of *Enoploclytia* M'Coy, 1849 (Crustacea: Decapoda: Erymidae) in the Jurassic**

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### RÉSUMÉ

Parmi les Erymidae Van Straelen, 1925, connus dès le Permien supérieur (Changhsingien) et répandus au Jurassique, le genre *Enoploclytia* M'Coy, 1849 passe pour être apparu tardivement en raison de son absence avant le Crétacé. Jusqu'à présent, le plus ancien représentant était *E. augustobonae* Devillez, Charbonnier, Hyžný & Leroy, 2016 du Crétacé inférieur (Barrémien) de l'est du bassin de Paris (France). Cependant, un nouveau fossile récolté en Normandie (France), présentant une architecture des sillons de la carapace typique d'*Enoploclytia*, atteste de la présence du genre dès le Jurassique supérieur (Oxfordien).

### MOTS CLÉS

Crustacé, Erymidae, France, homard, Jurassique, Mésozoïque, Normandie.

### ABSTRACT

Among the Erymidae Van Straelen, 1925, known as early as the Late Permian (Changhsingian) and widespread in the Jurassic, the genus *Enoploclytia* M'Coy, 1849 seems to have a late appearance because of its lack before the Cretaceous. Until now, the oldest representative was *E. augustobonae* Devillez, Charbonnier, Hyžný & Leroy, 2016 from the Early Cretaceous (Barremian) of the eastern Paris basin (France). However, a new fossil collected in Normandy (France), showing the typical carapace groove pattern of *Enoploclytia*, attests the presence of the genus in the Late Jurassic (Oxfordian).

### KEY WORDS

Crustacea, Erymidae, France, lobster, Jurassic, Mesozoic, Normandy.

## 1. INTRODUCTION

The oldest known representative of the erymid lobsters (Decapoda, Erymidae Van Straelen, 1925) was found in the Late Permian (Changhsingian: Birshtein 1958; Glaessner 1969; Feldmann *et al.* 2015; Devillez & Charbonnier 2017) and fossils of erymids are common around the world during the Jurassic, mainly the representatives of *Eryma* Meyer, 1840 (Oppel 1862; Van Straelen 1925; Förster 1966; Charbonnier *et al.* 2012b).

Another genus, *Enoploclytia*, was erected by M'Coy (1849) who observed the “peculiar branchial furrows and ridges” and the ornamentation of carapace and chelae on fossils from the Cretaceous chalk of the United Kingdom previously assigned to *Astacus* Fabricius, 1775 (Mantell 1822, 1824, 1833, 1844). Furthermore, fossils from the Cretaceous Bohemian Basin of the Czech Republic described as *Astacus* (Geinitz 1839) or as *Klytia* Meyer, 1840 (Reuss 1845) also fit the description of M'Coy's genus. Later, additional representatives of *Enoploclytia* were reported around the world: in Europe (Reuss 1854; Quenstedt 1852; Schlüter 1862, 1879; Fritsch & Kafka 1887; Wanderer 1908; Woods 1930; Glaessner 1932; Van Straelen 1936; Mertin 1941; Förster 1966; Morris 1987; Jagt & Fraaije 2002; Garassino *et al.* 2009; Devillez *et al.* 2016), in North America (Woodward 1900; Rathbun 1935; Stenzel 1945; Feldmann & McPherson 1980; Vega *et al.* 2007, 2013), in South America (Aguirre-Urreta 1982), in Africa (Joleaud & Hsu 1935), in Madagascar (Secrétan 1964; Charbonnier *et al.* 2012a), and in Antarctica (Taylor 1979; Feldmann 1984). All the occurrences were reported from the Cretaceous. The oldest species occurs in Early Cretaceous (Barremian: Devillez *et al.* 2016), but *Enoploclytia* became the most diversified erymid genera in Late Cretaceous (Devillez *et al.* 2017) and persisted beyond the Cretaceous-Paleogene boundary (Vega *et al.* 2007; Devillez & Charbonnier 2017). Because *Enoploclytia* occurs only from the second half of Early Cretaceous, the genus was therefore supposed to have appeared late in the erymid evolutionary history.

The purpose of this paper is to describe a fossil collected in the Late Jurassic deposits of western France. The specimen shows morphological features characteristic of *Enoploclytia* and suggest an earlier appearance of this genus.

## 2. GEOLOGICAL SETTING

The studied specimen comes from the Jurassic deposits at Cricqueboeuf, Normandy, France (Fig. 1A). The Jurassic is here represented by upper Oxfordian and lower Kimmeridgian deposits (Guyader 1968, Guyader *et al.* 1968; Fig. 1B). In this area, the original monoclinical structure of the deposits is included within the landslide of the “Fosses du Macre” (Lissak 2012). So, the deposits described below are not really in situ and they were observed at the bottom of the slope, on the foreshore when it was not buried in sand.

The Oxfordian is represented by the clays and the ferruginous sandstones of Villerville which encompass the *Ringsteadia pseudocordata* ammonite biozone. The most basal part corresponds to the Black Clays of Villerville. We distinguish the inferior part made of fossiliferous black clays overlain by a marly limestone deposit and by greenish sands. The sands are under fossiliferous silty black clays, including tree trunks covered by oysters. Above some pebble beds, the second half of Oxfordian deposits are dominated by an alternance of brown clays, beds of sandstones (sometime oolitic and ferruginous), and a fossiliferous puddingstone.

The basis of the Kimmeridgian deposits corresponds to the *Pictonia baylei* ammonite biozone. The most basal part is marked by a bed of limestone with ferruginous debris and includes ammonites, nautilus and numerous gastropods and bivalves. This limestone is immediately overlain by a deposit of brown clays intercalated with a bed of oysters (*Liostrea* Douvillé, 1904) surrounded by pebble beds. The top of the Kimmeridgian deposits is made of limestones which correspond to the *Rasenia cymodoce* ammonite biozone. The top of these limestones is eroded by a post-Jurassic emersion surface and yields fossil gastropods (*Harpagodes* Gill, 1870).

The studied fossil crustacean comes from the slided Oxfordian deposits (*R. pseudocordata* zone) on the foreshore. Because of the shift of the deposits, the outcrop shows them with some disturbances. Moreover, the outcrop is partially covered by sand and the series was not entirely observed. Although the characteristics of the outcrop prevent to know precisely the stratigraphic position of the fossil, it is included within a nodule similar to those of the fossiliferous and ferruginous puddingstone and of the oolitic ferruginous sandstone (Fig. 1B).

### 3. MATERIAL AND METHODS

The specimen presented here was studied using a binocular microscope. It is included in a black silicified carbonate nodule. This dark color makes difficult the observation of anatomic features on photographs. Then, to reveal the characters we whitened the specimen with ammonium chloride.

This fossil is stored in the palaeontological collections of the Muséum national d'Histoire naturelle of Paris (MNHN.F.A66892).

### 4. SYSTEMATIC PALAEOLOGY

MALACOSTRACA Latreille, 1802  
DECAPODA Latreille, 1802  
ERYMIDA *sensu* Schram & Dixon, 2004  
Superfamily ERYMOIDEA Van Straelen, 1925  
Family ERYMIDAE Van Straelen, 1925

PRELIMINARY REMARK. — The phylogenetic position of Erymidae is debated in the literature. This family was included within Astacidea Latreille, 1802 by many authors (Van Straelen 1925; Glaessner 1969; Aguirre-Urreta 1989; Schweigert *et al.* 2000; Garassino & Krobicki 2002; Crônier & Courville 2004; Garassino & Schweigert 2006; Feldmann & Titus 2006; Schweigert 2013; Charbonnier *et al.* 2013) or within Glypheidea Zittel, 1885 (De Grave *et al.* 2009; Schweitzer *et al.* 2010; Wahle *et al.* 2012; Karasawa *et al.* 2013; Feldmann *et al.* 2015). However, the latest phylogenetic analysis of Charbonnier *et al.* (2015) focusing on Glypheidea reject this assignment. In conclusion, we consider the phylogenetic position of Erymidae to be uncertain and, following Hyžný *et al.* (2015) and according to Schram & Dixon (2004), we do not list taxonomic rank beyond superfamily. Then we therefore include Erymidae within a separate clade: Erymida.

Genus *Enoploclytia* M'Coy, 1849  
(Fig. 2A-B)

*Enoploclytia* M'Coy, 1849: 330.

*Enoploclytia* — M'Coy 1854: 137. — Zittel 1885: 694. — Fritsch & Kafka 1887: 27. — Van Straelen 1925: 278. — Beurlen 1928: 164. — Rathbun 1926: 128. — Secrétan 1964: 81. — Förster 1966: 146. — Taylor 1979: 25. — Aguirre-Urreta 1989: 514. — Feldmann *et al.* 2015: 3. — Devillez *et al.* 2016: 530. — Devillez *et al.* 2017: 786.

*Enoploclytia* (*Enoploclytia*) — Mertin 1941: 160. — Glaessner 1969: 455.

TYPE SPECIES. — *Astacus leachii* Mantell, 1822, by original designation.

INCLUDED SPECIES. — **Jurassic:** *Enoploclytia* sp. (present work). — **Cretaceous:** *E. augustobonae* Devillez *et al.*, 2016 (Barremian; France); *E. collignoni* Secrétan, 1964 (Campanian; Madagascar); *E. gigantea* Devillez *et al.*, 2016 (Albian; USA); *E. leachi* (Mantell, 1822) (Cenomanian – Campanian; Belgium, Czech Republic, France, Germany, United Kingdom); *E. minor* Woodward, 1900 (Maastrichtian; Canada); *E. seitzii* Glaessner, 1932 (Albian – Cenomanian; Germany, United Kingdom); *E. tepeyacensis* Vega *et al.*, 2013 (Campanian; Mexico); *E. tumimana* Rathbun, 1935 (Maastrichtian; USA); *E. wintoni* Stenzel, 1945 (Albian; USA) (after Devillez *et al.* 2016; Devillez *et al.* 2017). — **Paleogene:** *E. gardnerae* (Rathbun, 1935) (Thanetian – Ypresian; USA and Mexico).

DIAGNOSIS. — Fusiform intercalated plate; wide, deep cervical groove, joined to dorsal margin and to antennal groove; long, wide gastro-orbital groove originating as median inflexion of cervical groove, delimiting two gastro-orbital lobes; sinuous postcervical groove, joined to dorsal margin and to hepatic groove, with ventral extension at carapace mid-height; short branchio-cardiac groove, interrupted in upper part of carapace, joined to dorsal margin, not joined to postcervical groove; concavo-convex hepatic groove, joined to cervical groove; prominent  $\omega$  and  $\chi$  bulges; inferior groove

convex posteriorly, joined to hepatic groove; carapace with heterogeneous coarse ornamentation; massive globose P1 propodus, rounded in transversal section; long and thin P1 fingers (straight in dorsal view); occlusal margins armed with sharp and slender tooth; P1 merus with strong, prominent distal process at external side of its ventral extremity (after Devillez *et al.* 2017).

***Enoploclytia* sp.**

(Fig. 2C-E)

MATERIAL. — Specimen MNHN.F.A66892 (Pezy coll.) from the Oxfordian of Cricqueboeuf, France.

DESCRIPTION. — Subcylindrical carapace; rostrum and intercalated plate not preserved; wide cervical groove, slightly inclined, joined to antennal groove; deep antennal groove; long gastro-orbital groove, with two divergent branches delimiting two gastro-orbital lobes (inflated lower lobe, flat upper lobe); slightly sinuous postcervical groove, with a ventral extension at carapace mid-height, joined to posterior extremity of hepatic groove; narrow branchiocardiac groove, interrupted in branchial region; concavo-convex hepatic groove, joined to cervical groove; inflated attachment site of mandibular muscle; inflated and elongated attachment site of adductor testis muscle; inferior groove partially preserved, joined to posterior extremity of hepatic groove; strong antennal spine; oblique row of tubercles in antennal region; elongated merus of first chelipeds, subtriangular in section; wide carpus of first chelipeds.

DISCUSSION. — The specimen discussed herein preserves the merus and carpus of the left first pereopod connected to the carapace and a pleonal somite. The carapace groove pattern is relatively well-preserved with: the inferior half of the cervical groove, the posterior part of the antennal groove, the elongated and bifurcated gastro-orbital groove, the postcervical groove, the branchiocardiac groove, the hepatic groove and the dorsal part of the inferior groove. The shape of the carapace and this combination of grooves is typical of the Erymidae. Among this family, the absence of connection between the branchiocardiac and the hepatic groove (present in *Eryma* Meyer, 1840, *Palaeastacus* Bell, 1850 and *Stenodactylina* Beurlen, 1928), the sinuous hepatic groove (concave in *Pustulina* Quenstedt, 1857 and *Tethysastacus* Devillez *et al.*, 2016), the shape of the post-cervical groove and its connection to the posterior extremity of hepatic groove are typical of *Enoploclytia*. The poor preservation of the specimen does not allow the observation of the ornamentation, which is an important character used in specific identification of erymid lobsters. This prevents therefore identification at the species level. Furthermore, comparison with other species are limited to some details of the groove pattern, the presence of some inflated areas and the presence of a row of tubercles in antennal region. The dorsal part of the postcervical groove is less inflected than *E. tepeyacensis* and the development of the inferior branch of the gastro-orbital groove is similar to those of *E. augustobonae* and *E. gigantea* from the Early Cretaceous. The specimen also shares well-marked antennal row and inflated

attachment sites of mandibular muscle and of adductor testis muscle with *E. collignoni* and *E. leachi* from the Late Cretaceous.

BIOSTRATIGRAPHIC IMPLICATIONS. — *Enoploclytia* is considered to be typical of the Cretaceous because of its supposed absence in Jurassic deposits and the numerous fossils found in Europe, particularly in Cenomanian – Turonian deposits (Devillez *et al.* 2017). The fossil described here is the first report of *Enoploclytia* in the Jurassic and demonstrates that the supposed absence of the genus before the Cretaceous was related to collect bias. This new occurrence in the Jurassic supports an earlier appearance of the genus in erymids evolutionary history.

The gap of almost 25 million years between this occurrence (Oxfordian) and the next occurrence, *E. augustobonae* (Barremian), the gap of almost 50 million years between the two oldest species of *Eryma*, *E. antiquum* (Birshtein, 1958) (Changhsingian), and *E. sinemuriana* (Garassino, 1996) (Sinemurian; Devillez & Charbonnier 2017), and the gap of almost 50 million years between the two oldest Cretaceous occurrences of *Stenodactylina*, *S. delphinensis* (Berriasian) and *S. triglypta* (Coniacian; Devillez *et al.* 2017), are all examples that clearly demonstrate the strong discontinuities and fragmentation in the fossil record of erymid lobsters.

## 5. CONCLUSION

Despite a poor preservation, most of the carapace grooves of the fossil presented here are preserved. Carefull examination of the specimen has allowed us to identify the typical groove pattern of *Enoploclytia*, but the almost complete lack of preservation of the ornamentation prevents identification at the species level. So, we identify this specimen as *Enoploclytia* sp.

This fossil, found in Oxfordian deposits of Normandy (Western France), is the first occurrence of the genus in the Jurassic and demonstrates that the supposed absence of *Enoploclytia* before the Cretaceous was due to collecting bias. Furthermore, the lack of occurrences of *Enoploclytia* between its two oldest occurrences is another example of the strong discontinuities in the fossil record of erymid lobsters.

In conclusion, we noticed that the locations of the oldest occurrences of *Enoploclytia* (Oxfordian of France, present work; Barremian of France; Devillez *et al.* 2016; Aptian of Spain, Garassino *et al.* 2009) might indicate an European origin of this genus, even if its fossil record is probably too scarce to be completely affirmative.

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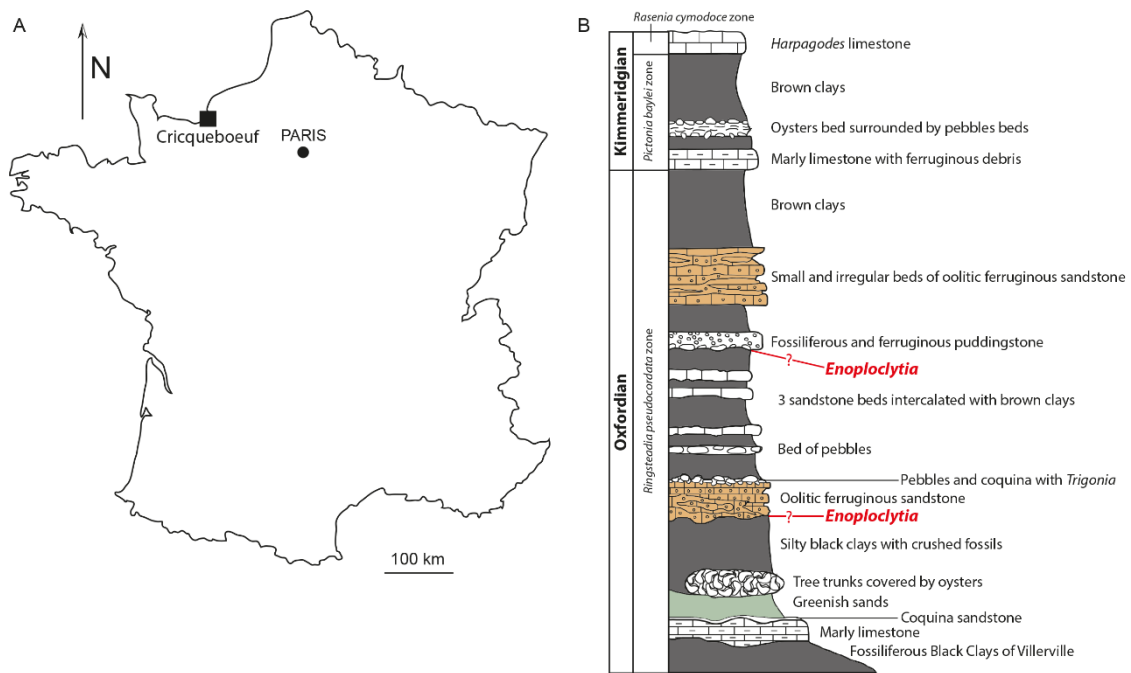


FIG. 1. — Cadre géographique et géologique. **A**, localisation de l’affleurement; **B**, colonne stratigraphique de la succession Oxfordien supérieur - Kimméridgien à Cricqueboeuf (d’après Guyader 1968) avec les possibles localisations du fossile d’*Enoploclytia* M’Coy, 1849.

Geographic and geological settings. **A**, location of the outcrop; **B**, stratigraphic log of the Upper Oxfordian - Kimmeridgian succession of Cricqueboeuf (after Guyader 1968) with the possible stratigraphic locations of the specimen of *Enoploclytia* M’Coy, 1849.

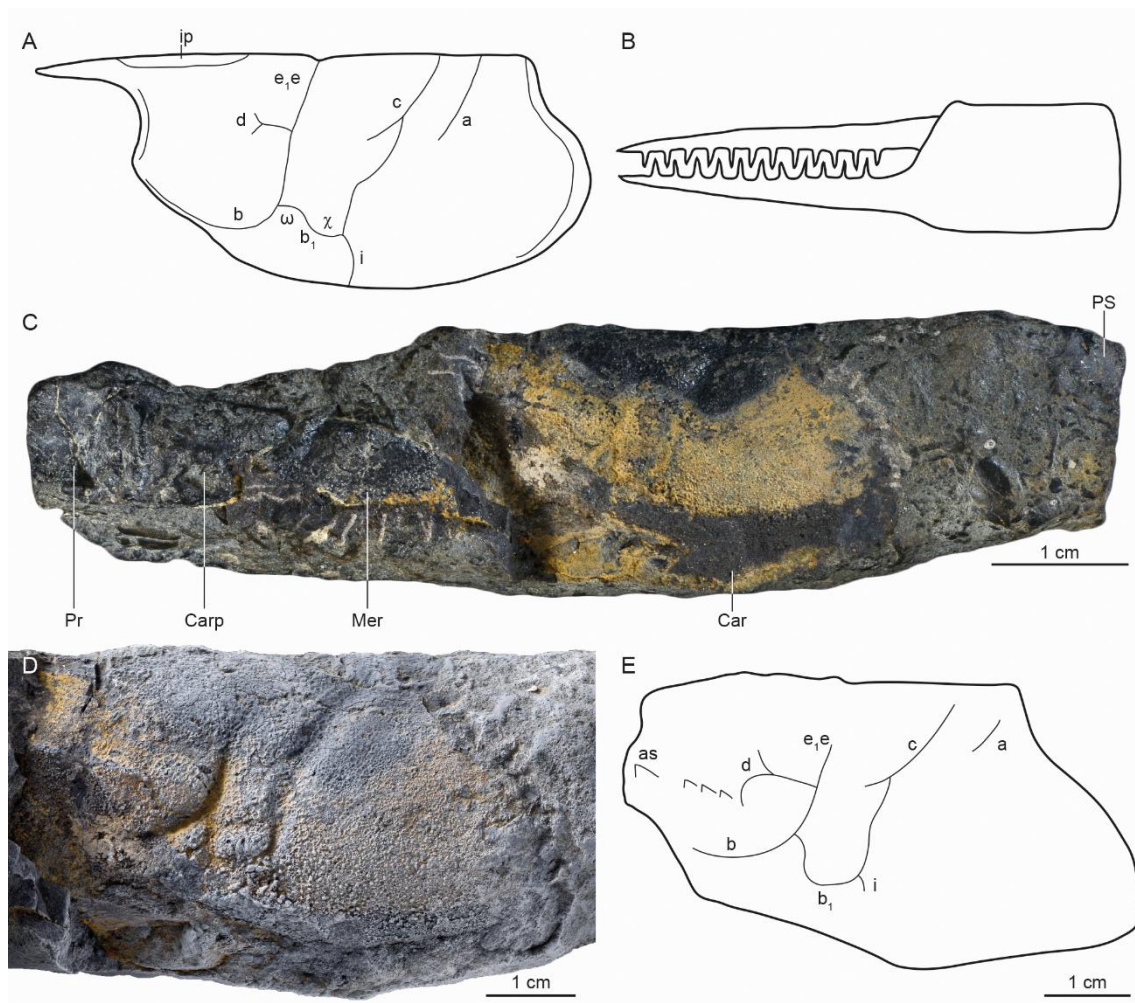


FIG. 2. — *Enoploclytia* M'Coy, 1849. **A**, architecture générale des sillons de la carapace; **B**, pince caractéristique de la première paire de péréiopodes; **C-E**, spécimen MNHN.F.A66892 (coll. Pezy) d'*Enoploclytia* sp. de l'Oxfordien de Cricqueboeuf, Normandie, France: vue latérale gauche de la carapace et du premier chélipède (**C**), détail de la carapace blanchie au chlorure d'ammonium (**D**) et schéma des sillons (**E**). Abréviations : a : sillon branchio-cardiaque ; as : épine antennaire ; b : sillon antennaire ; b<sub>1</sub> : sillon hépatique ; c : sillon post-cervical ; Car : carapace ; Carp : carpus ; d : sillon gastro-orbitaire ; e<sub>1</sub>e : sillon cervical ; i : sillon inférieur ; ip : plaque intercalaire ; Mer : mérus ; Pr : propode ; PS : somite du pléon ; ω : site d'attache des muscles mandibulaires ; χ : site d'attache des muscles adducteurs. Photographies : P. Loubry (**C**) et L. Cazes (**D**). Dessins au trait : J. Devillez.

*Enoploclytia* M'Coy, 1849. **A**, general carapace groove pattern; **B**, chela characteristic of the first pair of pereiopods; **C-E**, specimen MNHN.F.A66892 (Pezy coll.) of *Enoploclytia* sp. from the Oxfordian of Cricqueboeuf, Normandy, France: left lateral view of carapace and first cheliped (**C**), detail of the carapace covered by ammonium chloride (**D**) and line drawing of the grooves (**E**). Abbreviations: a: branchiocardiac groove; as: antennal spine; b: antennal groove; b<sub>1</sub>: hepatic groove; c: postcervical groove; Car: carapace; Carp: carpus; d: gastro-orbital groove; e<sub>1</sub>e: cervical groove; i:

inferior groove; ip: intercalated plate; Mer: merus; Pr: propodus; PS: pleonal somite;  $\omega$ : attachment site of mandibular muscle;  $\chi$ : attachment site of adductor testis muscle. Photographs: P. Loubry (C) and L. Cazes (D). Line drawings: J. Devillez.