The genus *Eryma* Meyer, 1840 (Crustacea: Decapoda: Erymidae): new synonyms, systematic and stratigraphic implications

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Abstract – Among Erymidae Van Straelen, 1925 (Van Straelen V. 1925. Contribution à l'étude des crustacés décapodes de la période jurassique. *Mémoires de la Classe des Sciences de l'Académie royale de Belgique* 7: 1–462), typical Mesozoic crustaceans, the genus *Eryma* Meyer, 1840 (Meyer H. von. 1840a. Briefliche Mittheilungen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkunde* 576–587) includes the largest number of species, mainly from Jurassic deposits. However, the lack of clear diagnoses for erymid genera has led to mistakes in generic assignments and to the establishment of redundant genera. The review of the concept of *Eryma* herein presents an attempt to clarify its diagnosis, mainly supported by the carapace groove pattern and the morphology of chelae of the first pair of pereopods, and to emphasize its systematic implications. Thus, we maintain the synonymy of *Klytia* Meyer, 1840, *Bolina* Münster, 1839 (Münster G. 1839. Decapoda Macrura. Abbildung und Beschreibung der Fossilen Langschwänzigen Krebse in den Kalkschiefern von Bayern. *Beiträge zur Petrefactenkunde* 2: 1–88) (sensu Étallon [Étallon A. 1859. Description des crustacés fossiles de la Haute-Saône et du Haut-Jura. *Bulletin de la Société géologique de France* 16: 169–205]), and *Erymastacus* Beurlen, 1928 (Beurlen K. 1928. Die Decapoden des Schwäbischen Jura mit Ausnahme der aus den oberjurassischen Plattenkalken stammenden. *Palaeontographica* 70: 115–278) with *Eryma*. Moreover, a review of the genera *Protoclytiopsis* Birshtein, 1958 (Birshtein JA. 1958. Ein Vertreter der ältesten Ordo der Crustacea Decapoda *Protoclytiopsis antiqua* gen. nov. sp. nov. aus dem Permo West-Sibiriens. *Doklady Akademii Nauk, SSSR* 122: 477–480), and *Galicia* Garassino and Krobicki, 2002 (Garassino A, Krobicki M. 2002. *Galicia marianae* n. gen., n. sp. (Crustacea, Decapoda, Astacidea) from the Oxfordian (Upper Jurassic) of the Southern Polish Uplands. *Bulletin of the Mizunami Fossil Museum* 29: 51–59), reveals the presence of a junction between the postcervical and branchiocardiac grooves. This feature is diagnostic of *Eryma* and supports the integration of these genera into the synonymy of *Eryma*. The addition of *Protoclytiopsis* to the synonymy of *Eryma* makes *Eryma antiquum* (Birshtein, 1958) nov. comb. the oldest representative of the genus and of the family, extending its stratigraphic range to the Late Permian (Changhsingian). Thus, this work also emphasizes that Erymidae crossed the Permian-Triassic boundary.

Keywords: lobsters / Mesozoic / new synonyms / Permian / Poland / Russia

Résumé – Le genre *Eryma* Meyer, 1840 (Crustacea: Decapoda: Erymidae): nouveaux synonymes, implications systématique et stratigraphique. Parmi les Erymidae Van Straelen, 1925 (Van Straelen V. 1925. Contribution à l'étude des crustacés décapodes de la période jurassique. *Mémoires de la Classe des Sciences de l'Académie royale de Belgique* 7: 1–462), crustacés typiques du Mésozoïque, *Eryma* Meyer, 1840 (Meyer H. von. 1840a. Briefliche Mittheilungen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkunde* 576–587) est le genre regroupant le plus grand nombre d'espèces principalement dans les dépôts jurassiques. Cependant, le manque de clarté des diagnoses des genres d'Erymidae a mené à des erreurs dans les identifications génériques ainsi qu'à l'instauration de genres redondants. La révision du concept du genre *Eryma* présentée ici est donc l'occasion de proposer une diagnose clarifiée, reposant essentiellement sur l'architecture des sillons de la carapace et la

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morphologie des pinces de la première paire de péréiopodes, et d'en souligner les implications systématiques. Ainsi, la mise en synonymie avec *Eryma* des genres *Klytia* Meyer, 1840, *Bolina* Münster, 1839 (Münster G. 1839. Decapoda Macrura. Abbildung und Beschreibung der Fossilen Langschwänzigen Krebse in den Kalkschiefern von Bayern. *Beiträge zur Petrefaktenkunde* 2: 1–88) (sensu Étallon [Étallon A. 1859. Description des crustacés fossiles de la Haute-Saône et du Haut-Jura. *Bulletin de la Société géologique de France* 16: 169–205]) et *Erymastacus* Beurlen, 1928 (Beurlen K. 1928. Die Decapoden des Schwäbischen Jura mit Ausnahme der aus den oberjurassischen Plattenkalken stammenden. *Palaeontographica* 70: 115–278) est ici confirmée. De plus, la révision des genres *Protoclytiopsis* Birshtein, 1958 et *Galicia* Garassino and Krobicki, 2002 (Garassino A, Krobicki M. 2002. *Galicia marianae* n. gen., n. sp. (Crustacea, Decapoda, Astacidea) from the Oxfordian (Upper Jurassic) of the Southern Polish Uplands. *Bulletin of the Mizunami Fossil Museum* 29: 51–59) révèle la présence d'une jonction entre les sillons postcervical et branchiocardiaque. Ce caractère diagnostique d'*Eryma* justifie l'intégration de ces deux genres dans la synonymie d'*Eryma*. L'ajout de *Protoclytiopsis* à la synonymie d'*Eryma* fait d'*Eryma antiquum* (Birshtein, 1958) nov. comb. le plus ancien représentant du genre et de la famille, repoussant son extension stratigraphique à la fin du Permien (Changhsingien). Ainsi, ce travail met en lumière le fait que les Erymidae ont franchi la limite Permien-Trias.

Mots clés : homards / Mésozoïque / nouveaux synonymes / Permien / Pologne / Russie

1 Introduction

Eryma Meyer, 1840 is a genus of typical Mesozoic crustaceans. It is known by many fossils supporting the greatest number of described species among Erymidae Van Straelen, 1925 (Schweitzer *et al.*, 2010; Hyžný *et al.*, 2015). *Eryma* is well known in European Jurassic and Early Cretaceous deposits (Carter, 1886; Étallon, 1859, 1861; Oppel, 1861, 1862; Ferry, 1865; Krause, 1891; Lahusen, 1894; Harbort, 1905; Van Straelen, 1920, 1925; Hée, 1924; Beurlen, 1928; Woods, 1925–1931; Birshtein, 1956; Förster, 1965, 1966; Martill, 1991; Garassino, 1996; Schweigert *et al.*, 2000; Fischer, 2003; Etter, 2004; Carpentier *et al.*, 2006; Garassino and Schweigert, 2006; Charbonnier, 2009; Schweitzer *et al.*, 2009; Charbonnier *et al.*, 2010, 2012, 2014, in press; Bravi *et al.*, 2014; Devillez *et al.*, 2016), and some occurrences are also reported throughout the world: in Middle East (Roger, 1946; Förster and Seyed-Emani, 1982; Garassino, 1994), in Africa (Beurlen, 1933; Secrétan, 1984), in North America (Rathbun, 1923, 1926; Feldmann and Titus, 2006) in Latin America (Aguirre-Urreta and Ramos, 1981; Aguirre-Urreta, 1989; J. Luque, pers. com.), in Antarctic (Taylor, 1979) and in Japan (Karasawa *et al.*, 2008; Kato *et al.*, 2010; Devillez *et al.*, 2016).

Currently, the carapace groove pattern of erymid lobsters is the main feature used for genera and species distinction (Van Straelen, 1925; Förster, 1966; Glaessner, 1969). However, the lack of clear generic diagnoses in the works of the nineteenth century and the different states of preservations of crustaceans has led to confusions about the concept of *Eryma*, and descriptions of redundant genera as consequences (*Bolina* Münster, 1839, *Eryma* and *Klytia* Meyer, 1840 sensu Étallon [1859]). Such confusions persist nowadays but some recent works have attempted to bring clear elements for erymid lobsters discrimination (Hyžný *et al.*, 2015; Devillez *et al.*, 2016).

This work aims to clarify the concept of *Eryma* on the basis of the carapace groove pattern and the morphology of the first pereopod chelae. It also emphasizes systematic and stratigraphic implications of such clarification.

2 Material and methods

The studied material includes 42 specimens from the palaeontological collections of European institutions (Tab. 1). Except fossils from the Solnhofen Lithographic Limestones, most of the studied specimens are fragmentary with only isolated carapaces or chelae preserved. They were mostly studied using a CETI Belgium MEDO binocular microscope. Line drawings were prepared by the first author.

3 Systematic palaeontology

MALACOSTRACA Latreille, 1802

DECAPODA Latreille, 1802

ERYMIDA sensu Schram and Dixon, 2004

Superfamily ERYMOIDEA Van Straelen, 1925

Family ERYMIDAE Van Straelen, 1925

Preliminary remark. – Throughout the literature Erymidae has been included within Astacidea Latreille, 1802 (Van Straelen, 1925; Glaessner, 1969; Aguirre-Urreta, 1989; Schweigert *et al.*, 2000; Garassino and Krobicki, 2002; Crônier and Courville, 2004; Feldmann and Titus, 2006; Garassino and Schweigert, 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). Recent phylogenetic analysis of Charbonnier *et al.* (2015) questioned the assignment of Erymidae to Glypheidea. Then, following Hyžný *et al.* (2015), we consider the systematic position of the Erymidae as uncertain and do not list the taxonomic rank beyond the superfamily. Hence, following Schram and Dixon (2004), we only include the Erymidae in a separate clade, Erymida.

Genus *Eryma* Meyer, 1840

(Fig. 1A–C)

Eryma Meyer, 1840: 587.

Klytia Meyer, 1840: 19.

Bolina Münster, 1839 sensu Étallon (1859: 192) (non Mertens, 1833).

Table 1. List of the examined material.

Taxa	Examined material	Ages	Localities
<i>Eryma</i> Meyer, 1840			
<i>Eryma antiquum</i> (Birshtein, 1958) nov. comb.	holotype PIN 1453	Changhsingian	Russia
<i>Eryma modestiforme</i> (Schlotheim, 1822)	MNHN.F.B13446, 13450, A33507	Tithonian	Germany
<i>Eryma ornati</i> (Quenstedt, 1857)	MNHN.F.A32408	Kimmeridgian	
<i>Eryma sinemuriana</i> (Garassino, 1996)	lectotype GPIT/CU/00349	Callovian	Germany
	holotype MSNM il3517, 3 paratypes MSNM i9887, il0357, il0450	Sinemurian	Italy
<i>Eryma sulcatum</i> Harbort, 1905	neotype SM B11437	Hauterivian	United Kingdom
<i>Eryma ventrosum</i> (Meyer, 1835)	holotype lost, cast MNHN.F.B12484	Oxfordian	France
	— 13 additional specimens MNHN.F.A29459, A29463, A29465, A29466, A29467, A29468, A29469, A29472, A29473, A29476, A29486, A29560, NHMUK In.27134, In.27146		France, United Kingdom
	— 3 additional specimens MNHN.F.B12479, A29484, A29584 (syntypes of <i>Bolina ventrosa major</i> Étallon, 1859)		France
	— 4 additional specimens OSUG UJF-ID 11906 and 11895 (figured as <i>Eryma cumonti</i> by Charbonnier <i>et al.</i> [2010: figs 3b, 4e]); OSUG UJF-ID 11543 (figured as <i>Eryma mandelslohi</i> by Charbonnier <i>et al.</i> [2010: fig. 4d]), 11544.	Callovian	France
	— 2 additional specimens KSGRA/AGH/K/4 (holotype of <i>Galicja marianae</i> Garassino and Krobicki, 2002), KSGRA/AGH/K/5 (holotype of <i>G. marianae</i>)	Oxfordian	Poland
<i>Eryma vocontii</i> Devillez <i>et al.</i> , 2016	holotype MNHN.F.A57457, paratype MNHN.F.A57458	Albian	France
<i>Bolina</i> Münster, 1839			
<i>Bolina girodi</i> Étallon, 1859	syntype MNHN.F.A29783	Bathonian	France
<i>Palaeastacus</i> Bell, 1850			
<i>Palaeastacus meyeri</i> (Garassino, 1996) nov. comb.	holotype MSNM i7606, 3 paratypes MSNM i9871, i9893, i9895	Sinemurian	Italy
<i>Incertae sedis</i>			
<i>Erymastacus</i> (?) <i>hoerstgenensis</i> Bachmayer & Malzahn, 1983	holotype GPANM 1982/106	Late Permian	Germany

Protoclytiopsis Birshtein, 1958: 477. nov. syn.
Galicja Garassino and Krobicki, 2002: 55. nov. syn.
Eryma — Oppel (1862: 20). — Zittel (1885: 693). — Méchin (1901: 74). — Van Straelen (1925: 233). — Rathbun (1926: 127). — Secrétan (1964: 61). — Förster (1966: 88). — Glaessner (1969: R455). — Aguirre-Urreta and Ramos (1981: 609). — Secrétan (1984: 516). — Aguirre-Urreta (1989: 513). — Crônier and Courville (2004: 1004). — Feldmann and Titus (2006: 63). — Feldmann and Haggart (2007: 1792). — Hyžný *et al.* (2015: 375). — Feldmann *et al.* (2015: 1).
Clytia — Beurlen (1928: 165).
Protoclytiopsis — Förster (1966: 86). — Feldmann *et al.* (2015: 10).
Klytia — Glaessner (1969: R456).
Galicja — Feldmann *et al.* (2015: 3).
Type species.—*Macrourites modestiformis* Schlotheim, 1822, by subsequent designation of Glaessner (1929).

Included species. — A list of fossil species of *Eryma*, including 60 species, has been done by Schweitzer *et al.* (2010). However, this work is a compilation, and the species of *Eryma* need a careful review as suggested by Bravi *et al.* (2014) and Hyžný *et al.* (2015). Such review requires the examination of the type material of all included species, so the proposition of a new list is beyond the aims of the present contribution.

Emended diagnosis.—Fusiform intercalated plate; deep cervical groove, joined to dorsal margin and to antennal groove; short gastro-orbital groove originating as a slight median inflexion of cervical groove; postcervical groove joined medially to branchiocardiac groove; branchiocardiac groove strongly inclined, joined to hepatic groove; concavo-convex hepatic groove, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove and to ventral margin; inflated ω area; cephalic region with two divergent rows of tubercles: orbital row with strong distal spine

Fig. 1. Line drawings of carapaces and P1 chelae of erymid lobsters. A–C, *Eryma* Meyer, 1840: carapace (A), P1 chela form I (B), P1 chela form II (C); D, carapace of *Palaeastacus* Bell, 1850; E, carapace of *Stenodactylina* Beurlen, 1928; F, carapace of *Enoploclytia* M'Coy, 1849; G, carapace of *Pustulina* Quenstedt, 1857. Abbreviations: a: branchiocardiac groove; b: antennal groove; b₁: hepatic groove; c: postcervical groove; cd: cardiac groove; d: gastro-orbital groove; e,e: cervical groove; i: inferior groove; ip: intercalated plate; ω: attachment site of mandibular muscle; χ: attachment site of adductor testis muscle. Line drawings: J. Devillez and S. Charbonnier.

and antennal row with strong distal antennal spine; chelate P1-P3; P1 chelipeds without prominent spines and with homogeneous ornamentation; P1 propodus dorso-ventrally compressed with narrow inner and outer margins; P1 with narrow dactylar bulge; fingers longer than P1 propodus, equal in length, narrowing gradually to distal extremity; index wider than dactylus (modified after Devillez *et al.*, 2016).

Comments. – According to Hyžný *et al.* (2015), followed by Devillez *et al.* (2016), we distinguish two forms of P1 chelae: form I (Fig. 1B) with short rectangular propodus and straight fingers, slightly longer than the propodus; form II (Fig. 1C) with an elongate sub-rectangular or trapezoidal propodus bearing elongated fingers, usually curved inward.

The most recent diagnoses of *Eryma* proposed by Feldmann and Titus (2006), Hyžný *et al.* (2015) and Feldmann *et al.* (2015) are relatively broad, particularly about the characteristics of the groove pattern. So, among the erymid lobsters, *Eryma* is the only genus exhibiting a junction between postcervical and branchiocardiac grooves. Other erymids such as *Enoploclytia* M'Coy, 1849 (Fig. 1F) and *Pustulina* Quenstedt, 1857 (Fig. 1G) show a reduced branchiocardiac groove only joined to dorsal margin, while it is well-developed and joined to the posterior extremity of the hepatic groove in *Palaeastacus* Bell, 1850 (Fig. 1D) and *Stenodactylina* Beurlen, 1928 (Fig. 1E) (Devillez *et al.*, 2016).

Discussion. – Meyer (1840) established two genera: (1) *Eryma* for small crustaceans from the Solnhofen Lithographic Limestones, previously assigned to *Glyphea* Meyer, 1835 by Münster (1839) (Fig. 2A), and (2) *Klytia* with *Klytia ventrosa* (Meyer, 1835) (Oxfordian, Haute-Saône, France) (Fig. 2C–D), and *Klytia mandelslohi* Meyer, 1840 (Oxfordian, Baden-Württemberg, Germany). According to Étallon (1859), the different states of preservation between the strongly compressed fossils from Solnhofen and the three-dimensionally preserved ones from Haute-Saône and Baden-Württemberg probably prevented Meyer (1840b) to assign them to the same genus. However, *Klytia* was clearly established based on the junction between postcervical and branchiocardiac grooves (see Meyer [1840b: 20]), which supports the synonymy between *Eryma* and *Klytia*. This synonymy was followed by numerous subsequent authors (*e.g.*, Oppel, 1862; Van Straelen, 1925; Förster, 1966) even if some authors maintained the distinction between the two genera (*e.g.*, Beurlen, 1928; Glaessner, 1929). After some hesitation, Glaessner (1969: R626) re-established the synonymy, which has been commonly accepted since then.

Münster (1839) erected *Bolina* with two new species from the Solnhofen Lithographic Limestones: *Bolina pustulosa* and *Bolina angusta*. Later, Étallon (1859) proposed an emended description for *Bolina*. He described the groove pattern as follows: there are three oblique, wide and deep transverse grooves; the first (cervical groove) is inflected forward and the two others (postcervical and branchiocardiac grooves) are dorsally close, joining each other at carapace mid-height. The carapace groove pattern of *Bolina* sensu Étallon (1859) clearly fits the diagnosis of *Eryma* and does not fit the descriptions of *Bolina pustulosa* and *Bolina angusta*, which are clearly not erymid lobsters. Moreover, Oppel (1861) proposed the new genera *Stenochirus* (type species: *Bolina angusta*) and *Pseudastacus* (type species: *Bolina pustulosa*) and remarked that *Bolina* Münster, 1839 was preoccupied by *Bolina* Mertens, 1833 (Cnidaria).

Fig. 2. *Eryma* representatives from Late Permian and Jurassic. A, specimen MNHN.F.B13450 of *Eryma modestiforme* (Schlotheim, 1822) from the Tithonian of Solnhofen, Germany; B, P1 chelae of the lectotype GPIT/CU/00349 (Quenstedt coll.) of *Eryma ornatum* (Quenstedt, 1857) from the Callovian of Gammelshausen, Germany ; C–D, cast of the holotype MNHN.B.12484 of *Eryma ventrosum* (Meyer, 1840) from the Oxfordian of Calmoutier, France: carapace (C) and line drawing (D); E–F, holotype PIN 1453 of *Protoelytiopsis antiqua* Birshtein, 1958 from the Changhsingian of Ust-Jenisseisk, Russia: carapace (E) and line drawing (F); G–H, holotype KSGR/AGH/K/4 of *Galicia marianae* Garassino and Krobicki, 2002 from the Oxfordian of Rudno, Poland: carapace (after Garassino and Krobicki: fig. 7) (G) and line drawing (H). Abbreviations: a: branchiocardiac groove; b: antennal groove; b₁: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e₁e: cervical groove; i: inferior groove; ip: intercalated plate; ω: attachment site of mandibular muscle; χ: attachment site of adductor testis muscle. Scale bars = 10 mm. Photographs: L. Cazes (A), G. Schweigert (B), J. Devillez (C), F. Schram (E). Line drawing: J. Devillez.

Beurlen (1928) established the genus *Erymastacus* to accommodate erymid lobsters only known by P1 chelae bearing very long fingers, and previously assigned to *Eryma*. Later, Glaessner (1929) subsequently designated *Glyphea ornati* Quenstedt, 1857 as type species for *Erymastacus*. Throughout the literature this genus was regarded as a junior synonym of *Eryma* (Förster, 1966; Glaessner, 1969; Schweitzer *et al.*, 2010; Feldmann *et al.*, 2015) or as a distinct genus (Secrétan, 1964; Schweigert *et al.*, 2000; Schweigert and Garassino, 2003; Hyžný *et al.*, 2015). Careful examination of the lectotype of *Glyphea ornati* (Fig. 2B) leads us to regard it as P1 chelae of *Eryma*, belonging to form II because of the trapezoidal shaped propodus, the inward curvature of fingers and the index width greater than that of dactylus. In conclusion, we agree with Förster (1966), Glaessner (1969), Schweitzer *et al.* (2010), Feldmann *et al.* (2015) and Devillez *et al.* (2016), by maintaining the synonymy between *Erymastacus* and *Eryma*.

Birshtein (1958) erected the new genus *Protoclytiopsis* with *Protoclytiopsis antiqua* (Changhsingian, Siberia, Russia) as the type species. This species is known by a single laterally crushed carapace. Förster (1966) pointed out the close similarity between the carapace groove pattern of this species and that of *Eryma* spp. Finally, he included *Protoclytiopsis* within the subfamily Eryminae Beurlen, 1928. Förster's opinion was followed by Glaessner (1969) but not by Karasawa *et al.* (2013), Feldmann *et al.* (2012) and Feldmann *et al.* (2015), who assigned *Protoclytiopsis* within the family Clytiopsidae Beurlen, 1927 (*pro* Clytiopsinae Beurlen, 1927, which was elevated to family rank by Amati *et al.* [2004]).

Our examination of the photograph of the holotype of *Protoclytiopsis antiqua* reveals the presence of the typical grooves of the Erymidae: deep cervical groove, gastro-orbital groove present, postcervical and branchiocardiac grooves almost parallel. Moreover, the postcervical and branchiocardiac grooves are joined medially, as in *Eryma* (Fig. 2E-F). In conclusion, we consider *Protoclytiopsis* as a junior synonym of *Eryma* and the new combination *Eryma antiquum* (Birshtein, 1958) is herein proposed.

Garassino and Krobicki (2002) erected the new genus *Galicja* with *Galicja marianae* (Oxfordian; southern Poland) as the type species. Most of the authors assigned this genus to the family Erymidae (Garassino and Krobicki, 2002; Schweitzer *et al.*, 2010; Karasawa *et al.*, 2013; Feldmann *et al.*, 2015) while others included it in the family Clytiopsidae because of the absence of intercalated plate (Feldmann *et al.*, 2012). Our review of the holotype indicates a carapace shape and a groove pattern typical of an Erymidae (subcylindrical carapace, deep cervical groove, gastro-orbital groove present, postcervical and branchiocardiac grooves almost parallel). Moreover, the carapace groove pattern exhibits the junction between the postcervical and the branchiocardiac grooves which is diagnostic of the genus *Eryma* (Fig. 2G-H). Hence, we consider *Galicja* to be a junior synonym of *Eryma*.

In addition, *Galicja marianae* exhibits a carapace with the following morphological characters: a wide branchial region, a well-marked gastro-orbital groove, subparallel postcervical and branchiocardiac grooves, slightly concave forward, a short branch extends the postcervical groove under its junction with branchiocardiac groove, a slightly inflated ω area and a flat χ area, an ornamentation made of fine tubercles. The carapace

groove pattern and ornamentation are very similar to those of the well-known *Eryma ventrosum* (Meyer, 1835) from the Terrain à Chailles Formation (Oxfordian, Haute-Saône, France) (Meyer, 1840b; Bronn, 1851–1852; Étallon, 1859; Van Straelen, 1925; Charbonnier *et al.*, 2012) (Fig. 2C-D). Hence, we consider *G. marianae* to be a junior synonym of *E. ventrosum*.

4 Stratigraphic implications

Until now, *Eryma* extended from Sinemurian (Early Jurassic), with *E. meyeri* Garassino, 1996, to Albian (Early Cretaceous), with *E. vocontii* Devillez *et al.*, 2016.

However, our examination of the holotype MSNM i7606 of *E. meyeri* (Osteno, Italy) reveals morphological characters diagnostic of *Palaeastacus* Bell, 1850: postcervical groove not joined medially to branchiocardiac groove but joined ventrally to hepatic groove, short and stout P1 chelae covered by spines (Fig. 3A-B). Thus, we propose the new combination: *Palaeastacus meyeri* (Garassino, 1996). Our review of the holotype MSNM i13517 of *Pustulina sinemuriana* Garassino, 1996, from the same locality (Osteno, Italy) reveals morphological characters diagnostic of *Eryma*: postcervical and branchiocardiac grooves joined medially, elongate P1 chelae (Fig. 3C-D). Thus, we propose the new combination: *Eryma sinemuriana* (Garassino, 1996).

Most of the described species of *Eryma* occurs in Jurassic (Fig. 2A-D, 2G-H, 3C-D) while only four species occurs in Early Cretaceous (Devillez *et al.*, 2016): *Eryma glaessneri* (Van Straelen, 1936) and *Eryma sulcatum* Harbort, 1905 in Hauterivian (Fig. 3I-L), *Eryma nippon* Karasawa *et al.*, 2008 in Barremian and *E. vocontii* Devillez *et al.*, 2016, in Albian (Fig. 3E-H). Other *Eryma* species found in Late Cretaceous deposits were described from North America (*E. americanum* Rathbun, 1923, *E. flectum* Rathbun, 1926, *E. stantoni* Rathbun, 1935) and Lebanon (*E. cretaceum* Roger, 1946). After careful examination of the figures presented by Rathbun (1923, 1926, 1935) and according to Förster (1966: 125), we consider that the American species, only represented by fragments of specimens, are not representatives of Erymidae. As for the Lebanese species, we follow Charbonnier *et al.* (in press) with the placement in *Pustulina* Quenstedt, 1857.

Addition of *Protoclytiopsis* Birshtein, 1958 to the synonymy of *Eryma* extends the stratigraphic range of the genus *Eryma* to the Late Permian (Changhsingian). Previously, Bachmayer and Malzahn (1983) had doubtfully assigned to *Erymastacus* a poorly preserved P1 chela from the Late Permian of Germany: *Erymastacus* (?) *hoerstgenensis*. As Schweitzer *et al.* (2010) regarded *Erymastacus* as synonymous with *Eryma*, they listed the species within representatives of *Eryma*. Later, Karasawa *et al.* (2013) removed the species from Erymidae because of its angular propodus and the shape of its fingers. Examination of the figure of the holotype of *E. hoerstgenensis* leads us to support the opinion of Karasawa *et al.* (2013).

Thus, *Eryma antiquum* (Birshtein, 1958) nov. comb., is the only erymid lobster reported in the Paleozoic and the oldest known representative of *Eryma* and Erymidae.

Finally, it is worth pointing out that the gap of almost 50 million years without reported *Eryma* between its two oldest representatives (*E. antiquum* nov. comb. from the Changhsingian and *E. sinemuriana* nov. comb. from the Sinemurian) shows the lack of fossils in the record of *Eryma* during the Trias.

Fig. 3. Erymid lobsters from Early Jurassic and Early Cretaceous. A–B, holotype MSNM i7606 of *Palaeastacus meyeri* (Garassino, 1996), originally described as *Eryma*, from the Sinemurian of Osteno, Italy: whole specimen (A) and line drawing of the carapace and of the P1 chelae (B); C–D, holotype MSNM il3517 of *Eryma sinemuriana* (Garassino, 1996), originally described as *Pustulina*, from the Sinemurian of Osteno, Italy: whole specimen (C) and line drawing of the carapace and of the P1 chela (D); E–G, holotype MNHN.F.A57457 (Clément coll.) of *Eryma vocontii* Devillez *et al.*, 2016, from the Albian of Rosans, France: carapace in lateral view (E), line drawing (F) and carapace in dorsal view (G); H, paratype MNHN.F.A57458 (Clément coll.) of *Eryma vocontii* from the Albian of Rosans, France; I–L, Neotype SM B11437 of *Eryma sulcatum* Harbort, 1905 from the Hauterivian of Speeton, United Kingdom: specimen in lateral view (I), specimen in dorsal view (J), line drawing of the carapace in lateral view (K) and line drawing of the carapace in dorsal view (L). Scale bars = 10 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b₁: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e₁e: cervical groove; i: inferior groove; ip: intercalated plate; χ: attachment site of adductor testis muscle. Photographs: A. Garassino (A, B), L. Cazes (E, F), J. Devillez (G, H). Line drawings: J. Devillez.

5 Conclusions

A review of erymid genera leads us to consider *Proto-clytiopsis* Birshtein, 1958, and *Galicia* Garassino and Krobicki, 2002, as junior synonyms of *Eryma*. Moreover, *Galicia marianae* Garassino and Krobicki, 2002, is herein considered to be a junior synonym of *Eryma ventrosum* (Meyer, 1835) on the basis of its carapace groove pattern and ornamentation. These additions into the synonymy of *Eryma* result in the extension of its stratigraphic range to Changhsingian (Late Permian). Thus, *Eryma* survived the Permian-Triassic mass extinction, commonly considered as the biggest of all major extinctions (Raup, 1979; Erwin, 1994; Stanley and Yang, 1994), with the occurrence of *Enoploclytia gardnerae* (Rathbun, 1935) in Mexican Paleocene deposits (Vega *et al.*, 2007), it is worth noting that Erymidae also survived the Cretaceous-Paleogene mass extinction. However, *E. gardnerae* is the last occurrence of erymid lobsters in the fossil record so they are considered to be extinct. The presence of an intercalated plate, an exclusive character of Erymidae, was recognized by Schram and Dixon (2004) in members of the extant family Enoplometopidae (Saint Laurent, 1988). This observation leads us to question the link between Erymidae and Enoplometopidae.

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Abbreviations

GPANM	Naturhistorisches Museum, Wien (Austria)
KSGR	Department of Stratigraphy and regional geology of the University of mining and metallurgy, Kraków (Poland)
MNHN.F	Muséum national d’Histoire naturelle, Paris (France)
MSNM	Museo di Storia Naturale di Milano (Italy)
NHMK	Natural History Museum, London (United Kingdom)

OSUG	Observatoire des Sciences de l’Univers, Grenoble (France)
PIN	Palaeontological Institute, Moscow (Russia)
SM	Sedgwick Museum, Cambridge (United Kingdom)
ω	Attachment site of mandibular muscle
χ	Attachment site of adductor testis muscle
P1-P3	Pereiopods 1 to 3

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