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Review of the Early Cretaceous erymid lobsters (Crustacea: Decapoda) from the Western Tethys

Révision des Érymides (Crustacea : Decapoda) du Crétacé inférieur de la Téthys occidentale

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RÉSUMÉ

Les érymides (Crustacea, Decapoda, Erymidae) sont relativement courants et abondants dans les formations jurassiques (*ca* 70 espèces) mais sont beaucoup moins courants dans le Crétacé inférieur où une vingtaine d'espèces sont recensées en Europe, en Amérique du Nord, en Amérique du Sud, en Australie, en Antarctique, au Japon et à Madagascar. Une révision des douze espèces d'érymides du Crétacé inférieur d'Europe (France, Royaume-Uni) est ici présentée. Basés sur de nouvelles observations, les concepts de plusieurs genres d'érymides sont actualisés et de nouvelles diagnoses sont proposées pour *Eryma* Meyer, 1840, *Enoploclytia* M'Coy, 1849, *Palaeastacus* Bell, 1850, *Pustulina* Quenstedt, 1857, et *Stenodactylina* Beurlen, 1928, incluant le tracé des sillons de la carapace, la première paire de péréiopodes et aussi une nouvelle structure –la zone post-orbitaire– située à l'avant de la région céphalique. Le nouveau genre *Tethysastacus* est établi avec *Tethysastacus tithonius* n. comb. (Valanginien, France) comme espèce-type. Cinq nouvelles espèces sont aussi décrites : *Eryma vocontii* n. sp. (Albien, France), *Enoploclytia augustobonae* n. sp. (Barrémien, France), *Enoploclytia gigantea* n. sp. (Albien, Texas), *Pustulina occitana* n. sp. (Berriasien, France), et *Pustulina colossea* n. sp. (Hauterivien, France).

MOTS CLÉS

Crustacea, Erymidae, Europe occidentale, France, homard, Mésozoïque, Royaume-Uni.

ABSTRACT

Erymid lobsters (Crustacea, Decapoda, Erymidae) are relatively common and abundant in Jurassic rocks (*ca* 70 species) but are far less common in the Early Cretaceous with about 20 species only listed in Europe, North America, South America, Australia, Antarctic, Japan, and Madagascar. A study of the twelve species of erymid lobsters from the Early Cretaceous of Europe (France, United Kingdom) is here presented. Based on new observations, the concepts of some erymid genera are updated and new diagnoses are proposed for *Eryma* Meyer, 1840, *Enoploclytia* M'Coy, 1849, *Palaeastacus* Bell, 1850, *Pustulina* Quenstedt, 1857, and *Stenodactylina* Beurlen, 1928, including carapace groove pattern, first pereiopods and also a new structure –the post-orbital area– located in front of the cephalic region. The new genus *Tethysastacus* is erected with *Tethysastacus tithonius* n. comb. (Valanginian, France) as type species. Five new species are described: *Eryma vocontii* n. sp. (Albian, France), *Enoploclytia augustobonae* n. sp. (Barremian, France), *Enoploclytia gigantea* n. sp. (Albian, Texas), *Pustulina occitana* n. sp. (Berriasian, France), and *Pustulina colossea* n. sp. (Hauterivian, France).

KEY WORDS
Crustacea, Erymidae, lobster, Mesozoic, France, United Kingdom, Western Europe.

INTRODUCTION

Erymid lobsters are typical Mesozoic crustaceans exhibiting a worldwide distribution with occurrences in Europe (*e.g.*, Mantell 1833; Bell 1850, 1863; Oppel 1861, 1862; Lahusen 1894; Van Straelen 1925; Beurlen 1928; Glaessner 1931; Bachmayer 1959; Förster & Rieber 1982; Garassino 1996; Jagt & Fraaije 2002; Garassino & Krobicki 2002; Bravi *et al.* 2014), in the Middle East (Roger 1946; Förster & Seyed-Emani 1982; Garassino 1994; Charbonnier *et al.* in press), in North Africa (Secrétan 1984), in Western Africa (Joleaud & Hsu 1935), in Madagascar (Secrétan 1964; Charbonnier *et al.* 2012a), in North America (Rathbun 1923, 1926; Stenzel 1945; Feldmann & McPherson 1980; Schweitzer & Feldmann 2001; Feldmann & Titus 2006; Feldmann & Haggart 2007), in Latin America (Aguirre Urreta & Ramos 1981; Aguirre Urreta 1982, 1989; Vega *et al.* 2013), in Australia (Woodward 1877; Etheridge Jr. 1914; Woods 1957), in Antarctic (Taylor 1979; Aguirre Urreta 1989), and in Japan (Karasawa *et al.* 2008).

Despite their wide distribution, fossils of erymid lobsters remain sparse and fragmentary. This is a consequence of the low fossilization potential of decapod crustaceans (scavenging, decortication, disarticulation, carapace fragmentation) and of collection and reporting biases (Plotnick 1986; Bishop 1986; Plotnick *et al.* 1988; Tshudy *et al.* 1989; Müller *et al.* 2000; Stempien 2005; Mutel *et al.* 2008; Krause *et al.*

2011). So about twenty erymid species, mainly supported by a unique or a few number of fragments, are currently reported in the Early Cretaceous.

The carapace groove pattern of these decapod crustaceans is the main feature used for genera and species distinction (Van Straelen 1925; Förster 1966; Glaessner 1969). However, the diagnoses of erymid genera are not still consistent with each other, in particular for *Eryma* Meyer, 1840 and *Palaeastacus* Bell, 1850, both including the greatest number of species (Hyžný *et al.* 2015). The present contribution aims to give a new look on Early Cretaceous erymid faunas around the world, especially on European taxa which benefits from new diagnoses and descriptions. This review is also an occasion to clarify some generic concepts in Erymidae based on carapace groove pattern, first pereiopods, and carapace regions (Fig. 1).

MATERIAL AND METHODS

The entire studied material includes 160 specimens (Table 1). They were mostly studied using a CETI Belgium MEDO binocular microscope. Line drawings were prepared by the first author. Most of the studied specimens consist of isolated carapaces and first chelipeds. Most of the European species come from southeastern France and were collected from the Early Cretaceous deposits of the South-East Basin (Fig. 2), including the Vocontian Basin and its peripheral platforms (Arnaud-Vanneau *et al.* 1982; Friès & Parize 2003), which was part of the western margin of the Tethys Ocean (Savostin *et al.* 1986; Masse *et al.* 1993).

INSTITUTIONAL ABBREVIATIONS

BM	Booth Museum of Natural History, Brighton (United Kingdom).
MHNG	Muséum d'Histoire naturelle de Genève, département de géologie et paléontologie (Switzerland).
MNHN.F	Muséum national d'Histoire naturelle, Paris (France).
MHNC	Muséum d'Histoire naturelle, Chambéry (France).
NHMUK	Natural History Museum, London (United Kingdom).
OSUG	Observatoire des Sciences de l'Univers de Grenoble (France).
SM	Sedgwick Museum of Earth Sciences, Cambridge (United Kingdom).

ANATOMICAL TERMINOLOGY AND ABBREVIATIONS

Post-orbital area. — Taylor (1979) observed firstly in the cephalic region of *Palaeastacus foersteri* Taylor, 1979, a complex structure behind the ocular incision (Fig. 3A). He briefly described it: "a deeply incised and almost vertical groove parallel to the orbital margin probably represents the forward extension of the antennal groove". We propose to name this complex structure "post-orbital area" and we provide a detailed description. The post-orbital area is a slightly bulged area limited by the carinated anterior margin of cephalic region and a S-shaped anterior groove joined ventrally to antennal groove (Fig. 3B).

P1 chelipeds. — In extant representatives of lobsters, P1 chelae are laterally inclined, so the palms are almost in the horizontal plan. Thus, in this configuration the occlusal openings are in the horizontal plane. In this paper we follow this natural configuration for the description of the chelae (Fig. 3C): the palms are the widest sides and correspond to the ventral and dorsal surfaces of the chelae; similarly, the longitudinal margins correspond to inner and outer margins with dactylus located on the inner margin and index on the outer margin. Most of the time, the fingers are curved downside in lateral view.

Abbreviations.

CL	Carapace length excluding rostrum.
CH	Carapace height.
ω	Attachment site of mandibular muscle.
χ	Attachment site of adductor testis muscle.
P1-P5	Pereiopods 1 to 5.
s1-s3	Somites 1 to 3.

SYSTEMATIC PALAEONTOLOGY

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 varies throughout the literature. For a long time the family has been included within the Astacidea Latreille, 1802 (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), whereas some more recent contributions recognised the family to belong to 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 by Charbonnier *et al.* (2015) questioned the assignment of Erymidae to Glypheidea. 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. Following Schram & Dixon (2004), we only include the Erymidae in a separate clade named Erymida.

Genus *Eryma* Meyer, 1840

(Fig. 1A-C)

Eryma Meyer, 1840a: 587.

Klytia Meyer, 1840b: 19.

Eryma — Oppel 1862: 20. — Zittel 1885: 693. — Van Straelen 1925: 233. — Rathbun 1926: 127. — Secrétan 1964: 61. — Förster 1966: 88. — Glaessner 1969: 455. — Aguirre Urreta & Ramos 1981: 609. — Secrétan 1984: 516. — Aguirre Urreta 1989: 513. — Crônier & Courville 2004: 1004. — Feldmann & Titus 2006: 63. — Feldmann & Haggart 2007: 1792. — Hyžný *et al.* 2015: 375. — Feldmann *et al.* 2015: 1.

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

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 and branchiocardiac grooves subparallel; postcervical groove joined medially to branchiocardiac groove (with a short ventral extension); branchiocardiac groove strongly inclined, joined to hepatic groove; concavo-convex hepatic groove, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove; marked ω bulge; cephalic region with two divergent rows of tubercles: orbital row with strong distal spine 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.

COMMENTS. — Some species show short P1 fingers such as *Eryma modestiforme* or *E. punctatum* Oppel, 1861, and other species show long P1 fingers such as *E. bedeltum* (Quenstedt, 1857) or *E. ventrosum* (Meyer, 1840). Following Hyžný *et al.* (2015), we distinguish two forms chelae. Form I (Fig. 1B) has a short rectangular propodus with straight fingers slightly longer than the propodus; form II (Fig. 1C) has an elongate subrectangular or trapezoidal propodus with long fingers which are usually curved inward.

Eryma vocontii n. sp.

(Fig. 4A-F)

ETYMOLOGY. — The specific epithet refers to the Voconces, a prealpine federation of Gaul people.

TYPE MATERIAL. — Holotype MNHN.F.A57457 (carapace) ; paratype MNHN.F.A57458 (P1 chela) (Clément coll.).

TYPE LOCALITY. — Rosans, Hautes-Alpes department, Provence-Alpes-Côte d'Azur region, southeastern France.

TYPE AGE. — Albian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (holotype: CL= 23 mm, CH= 10 mm); rostrum not preserved; subvertical cervical groove, dorsally wide and deep, strongly narrowing under gastro-orbital groove, joined to antennal groove; cephalic region with oblique orbital row of tubercles (antennal row poorly preserved); narrow, curved antennal groove; short, wide gastro-orbital groove, originating as a slight median inflexion of cervical groove; straight, wide and deep postcervical groove, joined to dorsal margin and joined medially to branchiocardiac groove, extended with a short ventral extension; straight, strongly inclined branchiocardiac groove with narrow dorsal part, joined to dorsal margin and to hepatic groove; narrow and shallow hepatic groove, concavo-convex; strongly raised ω and χ bulges; sub-rectangular χ bulge dorsally limited by shallow depression running between hepatic and branchiocardiac grooves; rounded ω bulge; inferior groove poorly preserved; carapace uniformly covered with fine tubercles preceded by crescent-shaped pits (pits deeper in branchial region); P1 chela with compressed trapezoidal propodus; dorsal surface of P1 palm with median longitudinal bulge surrounded by two longitudinal depressions parallel to lateral margins; P1 palm with narrow dactylar bulge, posteriorly delimited by a shallow groove; long, straight fingers, gradually narrowing to distal extremity; index wider than dactylus; dactylus with small basal depression; occlusal margins slightly denticulate; propodus covered with fine tubercles; fingers covered with punctations. P1 belongs to claw form II.

DISCUSSION. — Paratype MNHN.F.A57458 (Fig. 4E, F) corresponds to an isolated right P1 chela collected in the same bed than the carapace MNHN.F.A57457 (Fig. 4A-D). Based on this report, we suggest that the association carapace-chela comes from the same species and we include the chela in the specific description.

Eryma vocontii n. sp. is assigned to *Eryma* Meyer, 1840 based on its typical carapace groove pattern and its tuberculate orbital row in cephalic region. *Eryma vocontii* n. sp. differs from the three other Early Cretaceous species, *Eryma glaessneri* (Van Straelen, 1936), *Eryma nippon* Karasawa *et al.*, 2008, and *Eryma sulcatum* Harbort, 1905 by its carapace groove pattern with (1) subvertical cervical groove (strongly inclined in the three other species), (2) straight, deep postcervical groove, slightly inclined and joined to dorsal margin (sinuous and strongly inclined in *E. glaessneri*; shallow, slightly convex forward and not joined to dorsal margin in *E. sulcatum*), (3) straight, shallow and strongly inflected branchiocardiac groove (sinuous in *E. glaessneri*; slightly inflected in *E. sulcatum*), and (4) short gastro-orbital groove (long in *E. glaessneri*). Moreover, *E. glaessneri* exhibits a relatively massive carapace with inflated branchial region (not inflated in *Eryma vocontii* n. sp.) and a flat attachment site of adductor testis muscle (inflated in *Eryma vocontii* n. sp.), and *Eryma sulcatum* exhibits a post-orbital area (absent in *Eryma vocontii* n. sp.). *Eryma nippon* has a circular χ bulge while it is sub-rectangular in *Eryma vocontii* n. sp. *Eryma vocontii* n. sp. has a carapace with uniform fine ornamentation whereas the carapaces of *E. glaessneri* and *E. sulcatum* show heterogeneous ornamentation (coarse tubercles in cardiac and cephalic regions in *E. glaessneri*; smaller and more dense ornamentation in branchial region with regard to the rest of carapace and row of coarse tubercles parallel to intercalated plate in *E. sulcatum*). *E. nippon* has a homogeneous ornamentation but it is made of coarse tubercles (small tubercles in *Eryma vocontii* n. sp.).

Other Cretaceous *Eryma* species were described from North America (*Eryma americanum* Rathbun, 1923, *Eryma flectum* Rathbun, 1926, and *Eryma stantoni* Rathbun, 1935) and from Lebanon (*Eryma 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 (largely based on fragmentary specimens) are not representatives of Erymidae. As for the Lebanese species, we follow Charbonnier *et al.* (in press) with the placement in *Pustulina*. In conclusion, *Eryma vocontii* n. sp. is the hitherto youngest occurrence of the genus *Eryma*.

Eryma glaessneri (Van Straelen, 1936)
(Fig. 4G-H)

Enoploclytia glaessneri Van Straelen, 1936: 10-11, pl. 3, fig. 1.

Enoploclytia glaessneri — Secrétan 1964: 35, 94. — Schweitzer *et al.* 2010: 22.

Eryma glaessneri — Förster 1966: 123, fig. 22 (non pl. 17, fig. 3). — Feldmann & Titus 2006: 63. — Karasawa *et al.* 2008: 104.

TYPE MATERIAL. — Holotype MNHG GEPI 28369 housed in MHNG (Van Straelen coll.) (cast MNHN.F.R10204).

TYPE LOCALITY. — Escragnolles, Alpes-Maritimes department, Provence-Alpes-Côte d'Azur region, southeastern France.

TYPE AGE. — Hauterivian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (holotype: CL= 55 mm, CH= 36 mm); rostrum not preserved; intercalated plate present but poorly preserved; wide cardiac region and inflated branchial region; deep cervical groove, joined to dorsal margin and to antennal groove, straight and strongly inclined above gastro-orbital groove, straight and subvertical under gastro-orbital groove; cephalic region with oblique orbital row of tubercles (antennal not preserved); deep antennal groove, as wide as cervical groove, strongly curved and delimiting raised antennal lobe, shallowest in its anterior end; long, wide gastro-orbital groove originating as deep and large inflexion of cervical groove; wide postcervical groove, dorsally deep, curved forward, strongly inclined, joined to dorsal margin and joined medially to branchiocardiac groove, extended with a long, shallow ventral extension; shallow branchiocardiac groove, shallowest at carapace mid-height, subparallel to postcervical groove, strongly inclined, joined to dorsal margin in posterior-most part of branchial region; narrow, deep hepatic groove, posteriorly concave, anteriorly slightly convex, joined to cervical groove; slightly inflated ω bulge, delimited ventrally by a narrow and shallow depression extending between antennal and hepatic grooves; flat attachment site of adductor testis muscle (χ bulge); deep inferior groove; carapace covered with shallow depressions between small tubercles; cardiac region with an oblique row of coarse tubercles; gastric region with two rows of coarse tubercles parallel to intercalated plate.

DISCUSSION. — This species was originally assigned to *Enoploclytia* M'Coy, 1849 by Van Straelen (1936). Later, Förster (1966) placed it in *Eryma*; this act was followed by all successive authors until the work by Schweitzer *et al.* (2010) who re-established Van Straelen's opinion. The re-examination of the holotype leads us to concur with Förster's proposition. Indeed, the carapace groove pattern (postcervical and branchiocardiac grooves joined medially) is diagnostic of *Eryma*.

We note that Förster (1966: pl. 17, fig. 3) figured a specimen which is clearly not *Eryma glaessneri*, because it exhibits carapace groove pattern (branchiocardiac groove interrupted in carapace mid-height; sinuous postcervical groove) typical of *Enoploclytia*.

Eryma sulcatum Harbort, 1905
(Fig. 4I-L)

Eryma sulcata Harbort, 1905: 15, pl. 1, fig. 11, pl. 11, fig. 4.

Astacodes falcifer (pars.) — Bell 1863: pl. 9, fig. 7-8.

Eryma sulcata — Glaessner 1929: 159. — Woods 1930: 80, pl. 22, fig. 5-7. — Van Straelen 1936: 9. — Förster 1966: 124, fig. 23, pl. 17, fig. 2 and 4. — Taylor 1979: 34. — Feldmann & Titus 2006: 64.

Eryma cf. *sulcata* — Aguirre-Urreta & Ramos 1981: 610, pl. 1, fig. a.

Eryma sulcatum — Schweitzer *et al.* 2010: 25. — Karasawa *et al.* 2013: 102.

TYPE MATERIAL. — Neotype herein designated SM B11437, specimen figured by Woods (1930: pl. 22, fig. 5a, b). After Harbort (1905), the original type material was composed of at least 3 specimens from the Hauterivian of Stadthagen near Schaumburg (Lower Saxony, Germany). After Förster (1966: 124) and Morris (1980: 7), these specimens were destroyed during World War II and only poorly preserved casts are housed at the NHM, London (see Woods 1930: 80 and Förster 1966: 124). Förster (1966) designated a lectotype based on a cast corresponding to the carapace figured by Harbort (1905: pl. 1, fig. 11a, b). After examination, the quality of this cast is not good enough to be used and we consider important to select a neotype for *Eryma sulcatum*.

We select the historical specimen SM B11437, which is three-dimensionally preserved and fits the original diagnosis according to Woods (1930), Förster (1966) and to our own observations (Fig. 4I, K). The new type locality is Speeton in northern England. After Woods (1930), the specimen was collected in the C4 bed of the Speeton Clay, which corresponds to the Hauterivian after Fletcher (1969).

TYPE LOCALITY. — Speeton, Yorkshire, United Kingdom.

TYPE AGE. — Hauterivian, Early Cretaceous (Speeton Clay C Beds).

DESCRIPTION. — Subcylindrical carapace (neotype: CL= *ca* 32 mm, visible CH= *ca* 12 mm); short rostrum; fusiform, tuberculate intercalated plate limited by a row of coarse tubercles; almost smooth post-orbital area; cephalic region with oblique orbital row of tubercles ending by strong orbital spine (antennal row absent); deep cervical groove, intercepting dorsal margin at *ca* 66° angle, joined to antennal groove; short gastro-orbital groove originating as a slight median inflexion of cervical groove; postcervical groove slightly convex forward, interrupted before joining dorsal margin, joined medially to branchiocardiac groove; deep branchiocardiac groove, strongly inclined, interrupted before joining dorsal margin, joined to hepatic groove; concavo-convex hepatic groove; slightly inflated ω bulge, delimited ventrally by a narrow and shallow depression extending between antennal and hepatic grooves; slightly inflated χ bulge; inferior groove curved forward; carapace showing dense ornamentation of small tubercles and pits; branchial region with finer tubercles; pleon densely covered with small numerous tubercles and pits; s1-s3 pleura with pointed ventral margin; pleonal somites with terga densely covered by small pits; longitudinal bulge above pleura basis; subtriangular pleura with pointed ventral margin, wide and short in s2, narrower and longer in s3 and s4, densely covered with small pits; chelate P1; massive P1 propodus, longer than wide, relatively thick with rounded inner and outer margins; P1 palm densely covered with small tubercles and deep pits; fingers not preserved; short P1 carpus, showing coarser ornamentation than propodus, distal extremity of external margin bearing a strong spine; P1 merus with the same ornamentation than P1 carpus, with spines on the dorsal margin and a spine on the distal extremity of external margin; slender, P2-P5 with a small punctation.

DISCUSSION. — *Eryma sulcatum* shows a heterogeneous ornamentation (branchial region with fine tubercles, cardiac and cephalic regions with coarser tubercles). This observation is not common among most of the representatives of *Eryma*, which exhibits more homogeneous and fine ornamentation on the whole carapace. It is worth mentioning that several Early Cretaceous species of *Eryma* exhibit the same heterogeneous and/or coarse ornamentation such as *E. glaessneri* (cephalic and cardiac regions with dorsal rows of strong tubercles; branchial region with fine tubercles) or *E. nippon* (coarse ornamentation).

Genus *Stenodactylina* Beurlen, 1928
(Fig. 1D-F)

Stenodactylina Beurlen, 1928: 175.

Erymastacus Beurlen, 1928: 171.

Erymastacus — Secrétan 1964: 71. — Glaessner 1969: 456. — Hyžný *et al.* 2015: 375.

Stenodactylina — Glaessner 1969: 456. — Schweigert 2013: 411.

TYPE SPECIES. — *Stenodactylina liasina* Beurlen, 1928, by monotypy.

DISCUSSION. — Beurlen (1928) defined two genera based on of chelipeds, namely *Erymastacus* and *Stenodactylina*. Later, *Erymastacus*, with *Glyphea ornati* Quenstedt, 1857 as type species (subsequent designation by Glaessner 1929) was regarded by many authors as a junior synonym of *Eryma* (Förster 1966, Glaessner 1969, Schweitzer *et al.* 2010) while other authors considered it as a distinct genus (Secrétan 1964, Schweigert *et al.* 2000, Schweigert & Garassino 2003, Hyžný *et al.* 2015). Hyžný *et al.* (2015) provided arguments in favor of the resurrection of *Erymastacus*, once considered as junior subjective synonym of *Eryma*, and the synonymisation of *Stenodactylina* with *Erymastacus*. Their study was based on new material of *Erymastacus lagardettei* Hyžný *et al.* 2015 (Middle Jurassic of Belmont, France), which was considered to be the only record in which *Stenodactylina*-type chelipeds are associated with their carapaces.

Careful examination of the lectotype of *Glyphea ornati* Quenstedt, 1857, leads us to a different conclusion. Indeed, this species clearly exhibits *Eryma*-like chelae (near-isochelous) instead of *Stenodactylina*-like chelae (distinctly heterochelous). In conclusion, we agree with Förster (1966), Glaessner (1969), and Schweitzer *et al.* (2010), we maintained the synonymy between *Erymastacus* and *Eryma*, and the combination *Eryma ornatum* (Quenstedt, 1857) is reinstalled. Finally, the concept of "*Erymastacus*" based on carapace and chelipeds proposed by Hyžný *et al.* (2015) is correct and should be renamed as "*Stenodactylina*".

SYSTEMATIC IMPLICATIONS. — According to Hyžný *et al.* (2015), we consider that several species fit the concept of *Stenodactylina* (ex *Erymastacus*) such as:

(1) *Eryma insignis* Oppel, 1862; this species shows P1 chela with length and shape close to that of *Eryma anisodactyla* Krause, 1891. We consider that *E. anisodactyla* is a junior synonymous of *E. insignis* and we propose the new combination *Stenodactylina insignis* (Oppel, 1862).

(2) *Erymastacus australis* Secrétan, 1964; this species shows P1 chela exhibiting a rectangular propodus, a wide inflated dactylar bulge and slender fingers. These features support the placement in *Stenodactylina*. We propose the new combination *Stenodactylina australis* (Secrétan, 1964).

(3) *Eryma falsani* Dumortier, 1867; this species is known by a P1 chela showing a rectangular propodus, long and slender fingers and a row of coarse tubercles on dorsal

surface of propodus. These characters support the assignment to *Stenodactylina*. Hence, we propose the new combination *Stenodactylina falsani* (Dumortier, 1867).
(4) *Stenodactylina lagardettei* (Hyžný *et al*., 2015) n. comb. exhibits P1 chelae typical of *Stenodactylina*.

Contrary to Hyžný *et al*. (2015), we consider that several species do not fit the concept of *Stenodactylina* (ex *Erymastacus*) such as:
(1) *Eryma babeaui* Étallon, 1861; this species possesses P1 chela typical of *Eryma* with trapezoidal propodus showing two longitudinal depressions and fingers curved inward and gradually narrowing distally.
(2) *Eryma major* Oppel, 1861; this species was synonymized with *Eryma modestiforme* (Schlotheim, 1822) by Garassino & Schweigert (2006). However, the holotype exhibits a dentition of the fingers different from that in *E. modestiforme*. *Eryma punctatum* Oppel, 1861 has the same dentition, so *E. major* is probably a large specimen of *E. punctatum*.
(3) *Erymastacus quenstedti* Beurlen, 1928; this species exhibits P1 chela typical of *Eryma* with trapezoidal propodus and fingers curved inward and gradually narrowing distally. According to Schweitzer *et al*. (2010), we maintain the placement in *Eryma*.
(4) *Eryma aalensis* (Quenstedt, 1857); this species exhibits P1 chela typical of *Eryma* with trapezoidal propodus showing two longitudinal depressions and fingers curved inward and gradually narrowing to distal extremity.

Hyžný *et al*. (2015) did not list several species, which we consider here to be representatives of *Stenodactylina* such as:
(1) *Enoploclytia armata* Secrétan, 1964; this species shows P1 chela exhibiting a strong rectangular propodus, with inner margin more compressed than outer margin, rows of coarse tubercles in dorsal and ventral surfaces and on inner margin, and a wide inflated dactylar bulge. These features support the placement in *Stenodactylina*. We propose the new combination *Stenodactylina armata* (Secrétan, 1964).
(2) *Enoploclytia triglypta* Stenzel, 1945; this species exhibits a carapace groove pattern with postcervical groove not joined to branchiocardiac groove and interrupted in hepatic region. These features support the placement in *Stenodactylina*. We propose the new combination *Stenodactylina triglypta* (Stenzel, 1945).
(3) *Eryma burgundiacum* Crônier & Courville, 2004; this species exhibits a carapace groove pattern with postcervical groove not joined to branchiocardiac groove and interrupted in hepatic region. These features support the placement in *Stenodactylina*. We propose the new combination *Stenodactylina burgundiaca* (Crônier & Courville, 2004).
(4) *Eryma granuliferum* Secrétan, 1964; this species exhibits a carapace groove pattern with postcervical groove not joined to branchiocardiac groove and interrupted in hepatic region (see Charbonnier *et al*. 2012a: fig. 10). These features support the placement in *Stenodactylina*. We propose the new combination *Stenodactylina granulifera* (Secrétan, 1964).
(5) *Eryma villersi* Morière, 1883; the carapace groove pattern (postcervical groove not joined to branchiocardiac groove, interrupted in hepatic region) and the P1 chelae (elongate propodus, elongated, slender fingers) support the assignment to

Stenodactylina. Hence, we proposed the new combination *Stenodactylina villersi* (Morière, 1883).

(6) *Erymastacus strambergensis* Bachmayer, 1959; this species shows P1 chela exhibiting a propodus with inner margin more compressed than outer margin, a row of coarse tubercles on inner margin, an inflated dactylar bulge, and a slender index basis. These features support the placement in *Stenodactylina*. We proposed the new combination *Stenodactylina strambergensis* (Bachmayer, 1959).

(7) *Eryma walkerae* Feldmann & Haggart, 2007; this species exhibits a carapace groove pattern with postcervical groove not joined to branchiocardiac groove and interrupted in hepatic region. These features support the placement in *Stenodactylina*. We propose the new combination *Stenodactylina walkerae* (Feldmann & Haggart, 2007).

(8) *Eryma deslongchampsi* Van Straelen, 1925; this species exhibits a carapace groove pattern with postcervical groove not joined to branchiocardiac groove and interrupted in hepatic region associated with a P1 chela with an elongate propodus and elongated, slender fingers. These features support the placement in *Stenodactylina*. We propose the new combination *Stenodactylina deslonchampsi* (Van Straelen, 1924).

EMENDED DIAGNOSIS. — Fusiform intercalated plate; very wide, 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 and branchiocardiac grooves nearly parallel; narrow postcervical groove, not joined to branchiocardiac groove and interrupted in hepatic region; branchiocardiac groove strongly inclined, joined to hepatic groove; concavo-convex hepatic groove, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove; chelate P1; P1 propodus rectangular or trapezoidal, adorned with rows of spines and tubercles; P1 propodus with inner margin more compressed than outer margin; wide P1 dactylar bulge; P1 with extremely long and slender fingers, equal in length; P1 chela (form I; Fig. 1E) with strong, rectangular or trapezoidal propodus, with straight or sinuous fingers, strongly narrowing immediately after their basis; outer margin convex at the base of fixed finger; P1 chela (form II; Fig. 1F) with trapezoidal propodus, outer margin straight or convex, straight fingers, narrowing gradually to their distal extremity.

Stenodactylina delphinensis (Moret, 1946) n. comb.
(Fig. 5A-B)

Eryma delphinensis Moret, 1946: 49-51, fig. 3.

Eryma delphinensis — Förster 1966: 122-123. — Schweitzer *et al.* 2010: 23.

TYPE MATERIAL. — Holotype (OSUG.UJF-ID 11152, Touchon coll.).

TYPE LOCALITY. — Noyarey, Isère department, Rhône-Alpes region, southeastern France.

TYPE AGE. — Berriasian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (holotype: CL= 36 mm; CH= 17 mm); short toothless rostrum; fusiform intercalated plate; slightly curved ocular incision; narrow tuberculate post-orbital area; wide cephalic region, extending at almost half of carapace length; wide, deep cervical groove, strongly inclined, joined to dorsal margin and to antennal groove; narrow antennal groove; short gastro-orbital groove originating as a slight median inflexion of cervical groove; postcervical and branchiocardiac grooves subparallel; deep and narrow postcervical groove, strongly inclined and curved forward, intercepting dorsal margin, interrupted in hepatic region; shallow branchiocardiac groove, as wide as postcervical groove, deeper towards its junction to hepatic groove, not joined to dorsal margin, joined to hepatic groove; narrow, hepatic groove, shallow, concave posteriorly, slightly convex anteriorly, joined to cervical groove; flat attachment site of adductor testis muscle (χ bulge); wide and deep inferior groove, convex posteriorly, joined to hepatic groove; carapace ornamentation made of small tubercles delimited anteriorly by shallow depressions; ornamentation growing more dense towards branchial region.

DISCUSSION. — The examination of the holotype reveals the absence of a junction between postcervical and branchiocardiac grooves which remain subparallel until postcervical groove interrupts in hepatic region. This carapace groove pattern is typical of *Stenodactylina*. *Stenodactylina delphinensis* (Moret, 1946) n. comb. is the only representative of the genus for the Early Cretaceous.

In addition, the holotype presents a carapace in butterfly-like position with a strong dorsoventral flattening along the dorsal midline (Fig. 5A). This layout is characteristic of a lobster molt (Glaessner 1969; Charbonnier *et al.* 2012b). A rupture of the dorsal midline is observed with a slight rotation of the two halves of carapace. This suggest a probable hinge-type opening during ecdysis (Charbonnier *et al.* 2012b).

Genus *Palaeastacus* Bell, 1850
(Fig. 1G-H)

Palaeastacus Bell, 1850: 344.

Palaeastacus — Zittel 1885: 695. — Beurlen 1928: 180. — Förster 1966: 126. — Taylor 1979: 26. — Aguirre-Urreta & Ramos 1981: 606. — Aguirre-Urreta 1989: 509. — Schweitzer & Feldmann 2001: 174. — Hyžný *et al.* 2015: 375. — Feldmann *et al.* 2015: 3.

Enoploclytia (Palaeastacus) — Mertin 1941: 161. — Glaessner 1969: 455.

TYPE SPECIES. — *Astacus sussexiensis* Mantell, 1824, by subsequent designation of Glaessner (1929).

EMENDED DIAGNOSIS. — Fusiform intercalated plate with tubercles; 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 and branchiocardiac grooves nearly parallel, both joined to hepatic groove; concavo-convex hepatic groove, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove; longitudinal rows of sub-spiny tubercles in gastric region, diagonal rows of tubercles on cardiac region; massive chelate P1; P1 propodus short, thick, slightly globose, inner margin more compressed than outer margin, longitudinal rows of spiny tubercles on dorsal and ventral surfaces, inner margin bearing strong spines; P1 palm with narrow dactylar bulge; wide fingers, slightly longer than propodus, gradually narrowing to distal extremity; index with basally curved occlusal margin.

Palaeastacus sussexiensis (Mantell, 1824)
(Fig. 6, 7A-E)

Astacus sussexiensis Mantell, 1824: 11, pl. 29, fig. 15.

Enoploclytia imagei M'Coy, 1849: 331.

Enoploclytia brevimana M'Coy, 1849: 332.

Palaeastacus dixoni Bell, 1850: 344, 345, pl. 38, fig. 1-5.

Hoploparia scabra Bell, 1863: 28, pl. 7, fig. 3-7.

Phlyctisoma granulatum Bell, 1863: 36, pl. 11, fig. 9-10.

Palaeastacus plauensis Geinitz, 1875: 291, pl. 64, fig. 9.

Astacus leachii (pars) — Mantell 1822: 223, pl. 30, fig. 3.

Astacus sussexiensis — Mantell 1833: 124, 373, 379, fig. 2. — Mantell 1844: 238, fig.4. — Quenstedt 1852: 269. — Quenstedt 1885: 411, fig. 129.

Glyphea sussexiensis — Roemer 1841: 105.

Enoploclytia imagei — M'Coy 1854: 136. — Reuss 1854: 3. — Woodward 1877: 9. — Glaessner 1929: 146. — Schweitzer *et al.* 2010: 22.

Enoploclytia brevimana — M'Coy 1854: 137. — Reuss 1854: 3. — Bronn 1851-1852: 352. — Woodward 1877: 9. — Schweitzer *et al.* 2010: 22.

Enoploclytia sussexiensis — Morris 1854: 108. — Willet 1871: 42-43. — Woodward 1877: 10. — Woodward 1878: 377, pl. 38, fig. 1-4. — Schlüter 1879: 602. — Van Straelen 1936: 12.

Palaeastacus dixoni — Geinitz 1875: 292. — Schlüter 1879: 602.

Palaeastacus sussexiensis — Glaessner 1929: 200. — Rathbun 1935: 23. — Förster 1966: 133, fig. 24, pl. 17, fig. 6. — Aguirre Urreta 1981: 609, fig. 4c. — Morris 1987: 196, pl. 42, fig. 4-5. — Aguirre Uretta

1989: 510, fig. 8-10. — Wittler 1998: 18, fig. 5. — Garassino & Schweigert 2006: 11. — Schweitzer *et al*. 2010: 26. — Karasawa *et al*. 2013: 79, 102.

Hoploparia scabra — Glaessner 1929: 221.

Palaeastacus ? *plauensis* — Glaessner 1929: 290.

Phlyctisoma granulatum — Glaessner 1929: 314. — Monaco & Garassino 2000: 297.

Enoploclytia dixoni — Woods 1930: 83, pl. 23, fig. 9-12, pl. 24, fig. 1-3. — Van Straelen 1936: 11.

Enoploclytia (Palaeastacus) sussexiensis — Mertin 1941: 161, fig. 4a.

Enoploclytia (Palaeastacus) imagei — Roberts 1962: 164.

Palaeastacus scaber — Förster 1966: 132, fig. 26, pl. 17, fig. 7-9. — Schweitzer & Feldmann 2001: 174. — Garassino & Schweigert 2006: 11. — Schweitzer *et al*. 2010: 25. — Karasawa *et al.* 2013: 102.

Palaeastacus cf. *sussexiensis* — Taylor 1979: 30, fig. 10e, pl. 4 fig. d-f.

Palaeastacus dixoni — Schweitzer *et al*. 2010: 25.

Palaeastacus ? *plavensis* — Schweitzer *et al*. 2010: 25.

Pustulina granulata — Schweitzer *et al*. 2010: 26.

Pustulina scabra — Schweitzer *et al*. 2010: 26.

TYPE MATERIAL. — According to Morris (1980), Förster (1966: 134) selected as a lectotype of *Palaeastacus sussexiensis* one of the syntypes of *Palaeastacus dixoni* Bell, 1850; obviously the selection should have been made on the original type material of Mantell (1824). So the specimen NHMUK 5601, from the original type material of Mantell, is herein designated as lectotype. 13 paralectotypes are also considered: NHMUK 5024, 5584, 5586, 5589, 5600, 5602, 5608, 5613, 5618, 5624, 5626, 5629, 10760.

TYPE LOCALITY. — Sussex, United Kingdom (precise type locality not indicated on the original labels).

TYPE AGE. — Cenomanian, Late Cretaceous.

DESCRIPTION. — Carapace sub-cylindrical (lectotype: CL= 82 mm, CH= 41 mm); long spiny rostrum; fusiform and tuberculate intercalated plate; ridge on dorsal margin of branchial region; deep cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove; short gastro-orbital groove originating as a slight median inflexion of cervical groove; postcervical and branchiocardiac grooves subparallel; dorsally deep, sinuous postcervical groove, shallowing ventrally, not joined to dorsal margin, joined to hepatic groove; narrow branchiocardiac groove, strongly inclined, shallower than postcervical groove, not joined to dorsal margin, joined to hepatic groove; concavo-convex, narrow hepatic groove, joined to cervical groove; inflated ω bulge; flat attachment site of adductor testis muscle (χ bulge); deep inferior groove, joined to hepatic groove; carapace densely covered with rounded tubercles in branchial region and widely spaced coarse tubercles in gastric, hepatic and cephalic regions; row of coarse tubercles parallel to dorsal margin in cardiac and branchial regions; two oblique rows of coarse tubercles in cardiac region; two rows of tubercles parallel to the intercalated plate in gastric region; pleonal somites with terga ornamented by three pairs of strong dorsal spines and by rounded, coarse tubercles on the remaining surface; subtriangular pleura, with pointed ventral margin, ornamented with strong spines; telson with rounded extremity; telson with longitudinal median ridge flanked by two wide lateral ridges interrupted at telson mid-length; telson covered with coarse rounded tubercles; uropods as long as telson, covered by tubercles; uropodal endopod with longitudinal carina; uropodal exopod with diaeresis; chelate P1; short, trapezoidal, slightly globose P1 propodus, with two divergent rows of spines on ventral and dorsal surfaces; inner margin with strong spines; wide fingers, slightly longer than propodus; occlusal margins with short, spaced teeth; index wider than dactylus; dactylus adorned with spines; spiny P1 carpus and merus.

DISCUSSION. — The original type material of *Astacus leachii* Mantell, 1822 was heterogeneous and composed of a set of P1 chelae and fragments of carapaces. Among these chelae, Mantell (1824) distinguished *Astacus sussexiensis* (short, spiny chelae with short fingers) from *A. leachii* (chelae with long fingers). Later, numerous authors regarded *A. sussexiensis* as a representative of *Enoploclytia* (Morris 1854; Willet 1871; Woodward 1877, 1878; Van Straelen 1936; Mertin 1941). Bell (1850) described *Palaeastacus dixoni* which type material is composed of an isolated pair of P1 chelae, some P1 chelae connected with carapaces and a complete carapace preserved in connection with a complete pleon (Fig. 6F, Bell 1850: pl. 38, fig. 1). The latter specimen was designated by Woods (1930) as the lectotype of *Enoploclytia dixoni* (Bell, 1850). Woods (1930) also considered *A. sussexiensis*, *Enoploclytia brevimana* M'Coy, 1849, *Hoploparia scabra* Bell, 1863 (Fig. 7B-C), and *Phlyctisoma granulatum* Bell, 1863 (Fig. 7D-E) as junior synonyms of *E. dixoni*. Förster (1966), recently followed by Karasawa *et al*. (2013), distinguished *Palaeastacus sussexiensis* (Mantell, 1824) (including as synonyms: *A. sussexiensis*, *Enoploclytia imagei* M'Coy, 1849, *E. brevimana*, *P. dixoni* and *Palaeastacus plauensis* Geinitz, 1875) and *Palaeastacus scaber* (Bell, 1863) (including as synonyms: *H. scabra* and *P. granulatum*). Lastly Schweitzer *et al*. (2010) re-established the distinction between *E. brevimana*, *E. imagei*, *P. granulatum*, *P. plauensis*, *P. dixoni*, *P. scaber* and *P. sussexiensis*.

Our re-examination of the type specimens reveals that the P1 chelae of *P. sussexiensis* and *P. dixoni* are similar (short, spiny P1 propodus with narrow dactylar bulge and bearing wide fingers). Moreover, the carapaces of *P. dixoni*, *P. granulatum* and *H. scabra* show the same groove pattern (nearly parallel postcervical and branchiocardiac grooves joined to hepatic groove and not joined to dorsal margin) and the same ornamentation (branchial region densely covered with tubercles; widely spaced tubercles in gastric, hepatic and cephalic regions; row of coarse tubercles parallel to dorsal margin in cardiac and branchial regions; oblique rows of coarse tubercles in cardiac region). Thus, we follow Woods (1930) and consider *A. sussexiensis*, *P. dixoni*, *H. scabra* and *P. granulatum* as a unique species: *Palaeastacus sussexiensis* (Mantell, 1824). *E. brevimana* (Fig. 6E) and *E. imagei* (Fig. 7A) have not been figured until now. Both have spiny P1 chelipeds; short P1 propodus with short and wide fingers as *P. sussexiensis*. Moreover, a syntype of *E. imagei* includes a carapace (Fig.7A) with a long rostrum, a groove pattern and an ornamentation close to *P. sussexiensis*. The type material of *P. plauensis* is an incomplete P1 propodus and fragments of wide fingers coarsely ornamented close to those of *P. sussexiensis*. Finally our review leads us to recognise *P. dixoni*, *E. imagei*, *E. brevimana*, *H. scabra*, *P. granulatum* and *P. plauensis* as junior synonyms of *P. sussexiensis*.

In addition, *Palaeastacus sussexiensis* (Mantell, 1824) had a wide geographic distribution and a stratigraphic range from the Aptian to the Turonian. Indeed, this species has been reported (1) from the Aptian of Alexander Island (Antarctic; Taylor 1979) and Patagonia (Argentina; Aguirre-Urreta 1989), (2) the Albian of England (Bell, 1863; Woods, 1930; Förster 1966), (3) the Cenomanian of England (Bell 1850; Förster 1966; Morris 1987), Germany (Mertin 1941) and France (Van Straelen 1936; Förster 1966), and (4) the Turonian of England (Mantell 1822, 1833, 1844; Morris 1987) and Germany (Wittler 1998).

Palaeastacus loryi (Van Straelen, 1923) n. comb.

(Fig. 7F, G)

Eryma loryi Van Straelen, 1923: 93.

Eryma loryi — Glaessner 1929: 155. — Van Straelen 1936: 7-8, pl. 1, fig. 6. — Moret 1946: 50, fig. 1. — Roger 1946: 42. — Secrétan 1964: 69. — Förster 1966: 123. — Feldmann & Titus 2006: 64. — Schweitzer *et al.* 2010: 24.

TYPE MATERIAL. — Holotype (OSUG, probably lost).

TYPE LOCALITY. — Malleval, Isère department, Rhône-Alpes region, southeastern France.

TYPE AGE. — Valanginian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (holotype: CL= 60 mm, CH= 30 mm); deep cervical, postcervical and branchiocardiac grooves; short gastro-orbital groove originating as a slight median inflexion of cervical groove; short antennal groove; postcervical groove parallel to branchiocardiac groove, not joined to dorsal margin, joined to hepatic groove; branchiocardiac groove, joined to dorsal margin, slightly sinuous dorsally, joined to hepatic groove; concavo-convex hepatic groove, poorly preserved; carapace homogeneously and densely covered with small tubercles following crescent-shaped pits.

DISCUSSION. — The holotype was not found in the palaeontological collections of OSUG at Grenoble, France. Our review of the species is based on the line drawing and the figure presented by Van Straelen (1923: fig. 93) and Van Straelen (1936: pl.1, fig. 6) respectively. Firstly, the line drawing is misleading by exhibiting intercalated plate not visible on the figure. Indeed, the cephalic part clearly appears to be crushed. Moreover, the carapace grooves seem to be incompletely reported. The examination of the figures leads us to identify the postcervical groove parallel to the branchiocardiac groove and joined to the hepatic groove. This pattern is typical of *Palaeastacus*. Hence, the new combination *Palaeastacus loryi* (Van Straelen, 1923) is proposed herein.

Other species of *Palaeastacus* are known from the Early Cretacous such as *Palaeastacus foersteri* Taylor, 1979 (Barremian of Alexander Island, Antarctic; Fig. 3A-B), *Palaeastacus tenuidigitatus* (Woods, 1957) n. comb. (Aptian of Queensland, Australia; see comments about *Enoploclytia*), and *Palaeastacus terraereginae* (Etheridge Jr., 1914) (Barremian of Patagonia, Argentina; Aptian of Alexander Island, Antarctic; Aptian of Queensland, Australia).

A short, spiny P1 chela from the Albian of Texas was assigned tentatively to a new species *Paramithrax* H. Milne Edwards, 1834 by Whitfield (1883): ?*Paramithrax walkeri*. Merril (1905) and Adkins (1928) followed Whitfield, but Rathbun (1935) emended his description and assigned this species to *Palaeastacus*. Rathbun (1935: pl. 3, figs 7-9) figured the holotype of *P. walkeri* (Whitfield, 1883) and included new material in this species (carapace, P1 chela, left P1 cheliped). Stenzel (1945) assigned *P. walkeri* to *Enoploclytia* and refigured the carapace added by Rathbun (1935). He also figured new material (complete right P1 cheliped, left P1 dactylus, two pleons). Following Stenzel (1945), Richardson Jr. (1955) figured a right P1 cheliped under the name *Enoploclytia walkeri* (Whitfield, 1883) but in a new variety: *E. walkeri*, var. *schmidti*. In his review, Förster (1966), later followed by Schweitzer *et al*. (2010), re-assigned the species to *Palaeastacus*.

Our review of the all the figured specimens reveals that the holotype of *P. walkeri* fits the concept of *Palaeastacus* (short, rectangular propodus, strong spines on dorsal and ventral surfaces and on dactylus, narrow dactylar bulge). Furthermore, the P1 chelae figured by Rathbun (1935: pl. 5, figs 1-3) and by Stenzel (1945: pl. 38, fig.1), the P1 dactylus figured by Stenzel (1945: fig. 8), and the P1 chelipeds figured by Rathbun (1935: pl. 5, fig. 4) and Richardson Jr. (1955: fig. 108) are similar to the holotype of *P. walkeri*. The two pleons figured by Stenzel (1945: fig. 9, pl. 38, fig. 2) probably also belong to *P. walkeri*. However, the carapace figured by Rathbun (1935: pl. 4, figs 1-2) and by Stenzel (1945: pl. 39, fig. 1) exhibits a long gastro-orbital groove, a sinuous postcervical groove joined to hepatic groove and a short branchiocardiac groove. This groove pattern is typical of *Enoploclytia* so this carapace cannot be regarded as *P. walkeri* but as a new species of *Enoploclytia* (see section *Enoploclytia*).

In conclusion, with six species, *Palaeastacus* is the erymid genus including the most species for the Early Cretaceous.

Genus *Enoploclytia* M'Coy, 1849
(Fig. 1I-J)

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.

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

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

EMENDED 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 branchiocardiac 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 ω and χ 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.

PRELIMINARY REMARKS. — Out of numerous species of *Enoploclytia* listed by Schweitzer *et al.* (2010), five are known from the Early Cretaceous. Among these species, two are from the Hauterivian of France: *Enoploclytia glaessneri* Van Straelen 1936, which belongs to *Eryma* (see comments about *Eryma glaessneri*), and *Enoploclytia salviensis* (Robineau-Desvoidy, 1849). The type material of *E. salviensis* is lost for a long time and the species is only known by the figures presented by Robineau-Desvoidy (1849): some fragments of P1 fingers and a carapace. The fragments of fingers are curved with numerous short and close teeth, while fingers of *Enoploclytia* are straight with long, slender and spaced teeth. Furthermore, the illustrations of the carapace is not clear enough to assign it to any genus of decapod crustaceans.

Two other species come from the Albian of Texas. *Enoploclytia wintoni* Stenzel, 1945 is known by a pair of chelae with globose and coarsely tuberculate propodus and slender denticulate fingers typical of *Enoploclytia*. *Enoploclytia wenoensis* Rathbun, 1935, is known by a single pleon with terga without relief, densely covered with small pits and rounded pleura. Usually species of *Enoploclytia* have a pleon with more relief (longitudinal bulges on pleura basis; coarse, widely spaced ornamentation) and triangular, sharp pleura. Then, following Stenzel (1945) and Förster (1966), we conclude that *E. wenoensis* is probably not a representative of *Enoploclytia* but maybe a representative of *Astacodes* Bell, 1863, *Hoploparia* M'Coy, 1849, or *Homarus* Weber, 1795.

Enoploclytia tenuidigitata Woods, 1957 (Aptian of Queensland, Australia) is known by some fragments of carapace, P1 chelae and pleon. The carapace groove pattern with postcervical and branchiocardiac grooves joined to hepatic groove is typical of *Palaeastacus*. So *E. tenuidigitata* should be assigned to *Palaeastacus*; thus a new combination *Palaeastacus tenuidigitatus* (Woods, 1957) is proposed herein.

Taylor (1979), Aguirre Urreta (1982) and Garassino *et al.* (2009) reported fragments of chelae attributed to *Enoploclytia* sp. from the Aptian of Alexander Island (Antarctic), the Barremian of Patagonia (Argentina) and the Aptian of Catalonia (Spain), respectively. Finally, *E. wintoni* and the fragments of chelae discussed above have until now been the only reports of *Enoploclytia* from the Early Cretaceous.

Enoploclytia augustobonae n. sp.

(Fig. 8A-D)

ETYMOLOGY. — The specific epithet refers to *Augustobona*, the Latin name of Troyes, the regional capital near the type locality.

TYPE MATERIAL. — Holotype MNHN.F.B14557.

TYPE LOCALITY. — Amance, Aube department, Champagne-Ardennes region, East France.

TYPE AGE. — Barremian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (holotype: CL= 63 mm, CH= 33 mm); rostrum not preserved; intercalated plate not preserved but underlined by a slight deviation of dorsal margin in cephalic region; deep cervical groove, joined to dorsal margin and to antennal groove, strongly inclined above gastro-orbital groove, subvertical under gastro-orbital groove; deep, shallow antennal groove, strongly curved; wide, shallow gastro-orbital groove originating as large median inflexion of cervical groove, with two divergent branches, delimiting two gastro-orbital lobes (flat upper lobe, slightly prominent lower lobe); sinuous postcervical groove, dorsally deep and ventrally shallow, joined to dorsal margin and to hepatic groove, with ventral extension at carapace mid-height; short, shallow branchiocardiac groove, joined to dorsal margin and not to postcervical groove; concavo-convex hepatic groove, joined to cervical groove; inflated ω bulge; slightly inflated χ bulge; shallow inferior groove; cephalic region without antennal row of tubercles; carapace covered with small, widely spaced tubercles; cardiac region with a dorsal row of coarse tubercles; gastric region with a row of coarse tubercles parallel to intercalated plate and an oblique row of coarse tubercles.

DISCUSSION. — The new species is assigned to *Enoploclytia* based on its typical carapace groove pattern: wide gastro-orbital groove, postcervical groove joined to hepatic groove, short branchiocardiac groove not joined to postcervical nor to hepatic grooves. It is also the oldest occurrence of *Enoploclytia*.

Enoploclytia augustobonae n. sp. cannot be compared to *Enoploclytia wintoni*, which is only known by its P1 chelae.

Enoploclytia augustobonae n. sp. differs from *Enoploclytia gigantea* n. sp. by its carapace groove pattern with (1) a non-sinuous cervical groove, (2) a less incurved antennal groove, (3) a shorter and shallower gastro-orbital groove and (4) a longer ventral extension of postcervical groove. Furthermore the ornamentation of these two species is different: *Enoploclytia augustobonae* n. sp. exhibits fine tubercles on all the carapace surface and coarse tubercles along dorsal margin and in gastric region, while *E. gigantea* n. sp. has coarse tubercles in the upper half of carapace, fine tubercles in the lower half of carapace, and a row of strong spines along dorsal margin.

Our review leads us to consider the Hauterivian species *E. glaessneri* as a representative of *Eryma* and to exclude *E. salviensis* from the Erymidae. In conclusion *Enoploclytia augustobonae* n. sp. is currently the oldest occurrence of the genus.

Enoploclytia gigantea n. sp.

(Fig. 8E-H)

ETYMOLOGY. — The specific epithet refers to the Latin *giganteus*, *-a*, *-um* (= enormous) alluding to the exceptional size of the carapace.

TYPE MATERIAL. — Holotype n°201 stored in the collections of the Bureau of Economic Geology, Texas (after Rathbun 1935).

TYPE LOCALITY. — Fort Worth, Texas (United States of America).

TYPE AGE. — Albian, Early Cretaceous.

DESCRIPTION. — Carapace subrectangular in lateral view (holotype: CL= 175 mm, CH= 110 mm); rostrum not preserved; deep, sinuous cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove, strongly curved and delimiting a slightly raised antennal lobe; long gastro-orbital groove, originating as a deep median inflexion of cervical groove, with two divergent branches delimiting two gastro-orbital lobes (flat upper lobe, slightly prominent lower lobe); deep, sinuous postcervical groove (strong sinuosity at carapace mid-height), joined to dorsal margin and to hepatic groove, with short ventral extension; short, shallow branchiocardiac groove, strongly inclined, joined to dorsal margin and not to postcervical groove; sinuous hepatic groove, joined to cervical groove; strongly inflated ω bulge; flat attachment site of adductor testis muscle (χ bulge); deep inferior groove; carapace covered with widely spaced tubercles; coarse tubercles in upper half of carapace and small tubercles in lower half of carapace; gastric region with a row of coarse tubercles parallel to intercalated plate; row of spines directed forward along dorsal margin.

DISCUSSION. — The present carapace was initially identified as *Palaeastacus walkeri* by Rathbun (1935), who was followed by Stenzel (1945; see discussion about *Palaeastacus*). Our examination of the type material of *P. walkeri* leads us to a different conclusion. Indeed, this carapace shows groove pattern typical of *Enoploclytia* (long gastro-orbital groove, postcervical groove joined to hepatic groove, short branchiocardiac groove not joined to postcervical nor to hepatic grooves).

As for *Enoploclytia augustobonae* n. sp., *Enoploclytia gigantea* n. sp. (known by its carapace) cannot be compared to *Enoploclytia wintoni* (only known by P1 chelae). For a comparison, see discussion on *E. augustobonae* n. sp.

In conclusion, *Enoploclytia gigantea* n. sp. possesses the biggest carapace currently known among all erymid lobsters.

Genus *Pustulina* Quenstedt, 1857
(Fig. 1K-L)

Pustulina Quenstedt, 1857: 807.

Phlyctisoma Bell, 1863: 34.

Phlyctisoma — Zittel 1885: 695. — Secrétan 1964: 74. — Förster 1966: 135.

Pustulina — Feldmann *et al.* 2015: 3.

TYPE SPECIES. — *Pustulina suevica* Quenstedt, 1857, by monotypy.

EMENDED DIAGNOSIS. — Fusiform intercalated plate; inflated hepatic, cardiac and branchial regions; deep cervical groove, joined to dorsal margin and to antennal groove; deep, long gastro-orbital groove, originating as a slight median inflexion of cervical groove, with two divergent incurved branches, delimiting two gastro-orbital lobes; strongly inclined postcervical groove, inflected before joining hepatic groove, not joined to dorsal margin; short and shallow branchiocardiac groove, joined to dorsal margin and not joined to postcervical groove; concave hepatic groove, joined to cervical groove; shallow cardiac groove, straight, inclined forward, rising from postcervical groove, joined to dorsal margin; cephalic region with strongly tuberculate antennal row and distal antennal spine; carapace with tuberculate ornamentation; chelate P1-P3; P1 with strongly tuberculate ornamentation; short P1 propodus with fingers barely longer; P1 dactylus longer than P1 index.

COMMENTS. — *Pustulina* shares some features with *Enoploclytia*. Both have an inflated branchial region, a well-developed gastro-orbital groove, usually divided in two branches, a short branchiocardiac groove not joined to the postcervical groove, a tuberculate antennal row, and usually a heterogeneous coarse ornamentation.

Pustulina occitana n. sp.

(Fig. 9A-D)

ETYMOLOGY. — The specific epithet refers to Occitània, the historical region in southern Europe where Occitan was the main language spoken.

TYPE MATERIAL. — Holotype MNHN.F.A57460 (Leroy coll.).

TYPE LOCALITY. — Laciterne-Boisset near Moulès-et-Baucels, Hérault department, Languedoc-Roussillon region, South France.

TYPE AGE. — Berriasian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (holotype: CL= 28 mm, CH= 15 mm); dorsal line inclined downward in cephalic region; inflated cardiac, hepatic and branchial regions; deep cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove, twice as narrow as cervical groove; long gastro-orbital groove, originating as a slight median inflexion of cervical groove, with two divergent branches, delimiting two tuberculate gastro-orbital lobes (flat upper lobe, prominent lower lobe); deep, straight postcervical groove, wider than cervical groove, strongly inclined, not joined to dorsal margin, forming a faint notch in upper hepatic region; shallow branchiocardiac groove, interrupted in upper third of carapace height, joined to dorsal margin and not joined to postcervical groove; concave hepatic groove, joined to cervical groove; deep inferior groove, joined to hepatic groove; short cardiac groove, inclined forward, rising from postcervical groove, joined to dorsal margin; cephalic region with convex antennal row of strong tubercles; carapace with scabrous surface, entirely covered with rounded tubercles, coarse and widely spaced in antennal and gastric regions, becoming gradually smaller and nearby towards posterior and ventral parts of branchial region.

DISCUSSION. — The new species is assigned to *Pustulina* based on its typical carapace groove pattern: long gastro-orbital groove with two divergent branches, strongly inclined postcervical groove joined to hepatic groove, short and shallow branchiocardiac groove not joined to postcervical or to hepatic grooves, concave hepatic groove, and cardiac groove.

Pustulina occitana n. sp. differs from the other four Early Cretaceous species, mainly by its ornamentation and its carapace groove pattern. Compared to *Pustulina victori* (Van Straelen, 1936) n. n., the cardiac groove of *P. occitana* n. sp. is narrower, shallower and less inclined forward, the gastro-orbital groove is longer and the ornamentation is denser. *Pustulina tuberculata* (Bell, 1863) possesses a cephalic region with straight dorsal margin in lateral view, whereas in *P. occitana* n. sp., the dorsal margin is inclined downward. Moreover, the carapace ornamentation in *P. tuberculata* is composed of homogeneous evenly spaced tubercles, whereas it is heterogeneous in *P. occitana* n. sp. (cephalic region with coarse and more widely spaced tubercles; branchial region with nearby and smaller tubercles). *P. occitana* n. sp. shows some differences from *Pustulina colossea* n. sp. in its carapace groove pattern: its cervical groove is not as sinuous as in *P. colossea* n. sp., its gastro-orbital groove is narrower, with a shorter upper branch, its postcervical groove is not gradually curved and its inferior groove is more strongly curved forward. Moreover *P. occitana* n. sp. is devoid of prominent upper gastro-orbital lobe and its ornamentation is denser than in *P. colossea* n. sp. *Pustulina spinulata* Secrétan, 1964 (Valanginian-Hauterivian, Madagascar) is the only extra-European *Pustulina* species for the Early Cretaceous. As *P. tuberculata*, also *P. spinulata* possesses a straight dorsal margin in cephalic region (inclined downward in *Pustulina occitana* n. sp.). In addition, *P. spinulata* differs from *P. occitana* n. sp. by its more inflated and spiny hepatic region and its homogeneous ornamentation in branchial region.

Pustulina victori nomen novum
(Fig. 9E-F)

Eryma tuberculata Van Straelen, 1936: 9, pl. 2, fig. 3.

Eryma tuberculata — Roger 1946: 42. — Secrétan 1964: 69.

Phlyctisoma sp. – Förster 1966: 144.

Eryma tuberculatum – Schweitzer *et al.* 2010: 25.

ETYMOLOGY. — The specific epithet honors Victor Van Straelen, who identified the new species.

TYPE MATERIAL. — Holotype (MHNC collection, probably lost).

TYPE LOCALITY. — Leysse, Savoie department, Rhône-Alpes region, southeastern France.

TYPE AGE. — Berriasian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (CL= *ca* 46 mm with incomplete cephalic region, CH= 24 mm); inflated cardiac, hepatic and branchial regions; wide, deep cervical groove, straight, narrowing ventrally, joined to dorsal margin and to antennal groove; wide gastro-orbital groove; very wide, deep postcervical groove, straight, dorsally strongly inclined, narrowing under its inflexion, not joined to dorsal margin, joined to hepatic groove; wide, concave hepatic groove, joined to cervical groove; deep inferior groove, joined to hepatic groove; wide, straight cardiac groove, strongly inclined forward, rising from postcervical groove, probably joined to dorsal margin; carapace ornamented with coarse, widely spaced, rounded tubercles.

DISCUSSION. — The holotype is probably lost and the present description is based on the figure proposed by Van Straelen (1936). Its low resolution does not allow to see the branchiocardiac groove. If this groove is present, it is too shallow and narrow to be distinguished.

Initially assigned to *Eryma* by Van Straelen (1936), the species was reassigned to *Phlyctisoma* sp. (now *Pustulina* sp.) by Förster (1966) based on its typical groove pattern (long gastro-orbital groove, strongly inflected postcervical groove joined to hepatic groove, concave hepatic groove, cardiac groove). Our examination of the original figure leads us to confirm Förster's placement. Moreover, the ornamentation and the well-developed cardiac groove are substantial enough to maintain the validity of the species described by Van Straelen (1936). Consequently, this situation leads to a case of secondary homonymy. To solve this problem and according to ICZN (1999: articles 53.3, 57.3), we propose herein the replacement name *Pustulina victori* pro *P. tuberculata* (Van Straelen, 1936) non *P. tuberculata* (Bell, 1863).

Pustulina colossea n. sp.

(Fig. 9G-H)

ETYMOLOGY. — The specific epithet refers to the massive size and appearance of the carapace for a representative of *Pustulina*.

TYPE MATERIAL. — Holotype MNHN.F.A57459 (Leroy coll.).

TYPE LOCALITY. — Castellane, Alpes-de-Haute-Provence department, Provence-Alpes-Côte d'Azur region, southeastern France.

TYPE AGE. — Hauterivian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (holotype: CL= *ca* 50 mm with incomplete branchial region, CH= 29 mm); rostrum not preserved; cephalic region with dorsal line strongly inclined downward; strongly inflated cardiac, hepatic and branchial regions; wide, deep cervical groove, subvertical, slightly sinuous at level of gastro-orbital groove, narrowing above its junction to hepatic groove, joined to dorsal margin and to antennal groove; narrow, shallow antennal groove, strongly curved towards anterior margin; wide, deep gastro-orbital groove, originating as a median inflexion of cervical groove, with two divergent branches delimiting two inflated gastro-orbital lobes; wide postcervical groove, strongly inclined in dorsal branchial region and arcuate before joining hepatic groove, forming a notch in upper hepatic region; deep, concave hepatic groove, joined to cervical groove; inferior groove joined to hepatic groove; shallow, straight cardiac groove, rising from postcervical groove, slightly inclined forward, joined to dorsal margin; carapace entirely covered with rounded tubercles, coarser and more widely spaced forward postcervical groove, thinner and closer in branchial and pterygostomial regions; row of coarse tubercles parallel to intercalated plate; cephalic region with convex antennal row of tubercles and distal antennal spine.

DISCUSSION. — *Pustulina colossea* n. sp. is assigned to *Pustulina* based on its typical carapace groove pattern: long gastro-orbital groove with two branches, postcervical groove joined to hepatic groove, concave hepatic groove and cardiac groove.

Pustulina colossea n. sp. differs from *Pustulina tuberculata* and *Pustulina spinulata* by the cephalic region with dorsal margin strongly inclined downward (straight in the latter), its postcervical groove curved in dorsal branchial region (straight in the latter), its prominent upper gastro-orbital lobe (flat in the latter), and its heterogeneous ornamentation (homogeneous in in the latter). The differences between *P. colossea* n. sp. and *Pustulina occitana* n. sp. are described in the discussion about *P. occitana* n. sp.

Among *Pustulina* species, *P. colossea* n. sp. is the only one showing a curved postcervical groove and a raised upper gastro-orbital lobe. Furthermore, some morphological characters of *P. colossea* n. sp., in particular the width of cervical and gastro-orbital grooves and the massive appearance of the carapace, are also encountered in *Enoploclytia*.

Pustulina tuberculata (Bell, 1863)
(Fig. 9I-L)

Phlyctisoma tuberculatum Bell, 1863: 35, pl. 11, fig. 1-8.

Phlyctisoma tuberculata — Glaessner 1929: 314. — Förster 1966: 145, pl. 18, fig. 11-12.

Enoploclytia tuberculata — Woods 1931: 82, pl. 23, fig. 4-8.

Eryma tuberculata — Woods 1957: 156.

Pustulina tuberculata — Schweitzer *et al.* 2010: 26.

TYPE MATERIAL. — Lectotype SM B22368 designated by Förster (1966); 7 paralectotypes SM B22364, B22365, B22366, B22367, B22369, B22370, B22371 (Carter coll.).

TYPE LOCALITY. — Cambridge, Cambridgeshire, United Kingdom.

TYPE AGE. — Albian, Early Cretaceous.

DESCRIPTION. — Subcylindrical carapace (lectotype: CL= 52 mm, CL= 24 mm); fusiform, tuberculate intercalated plate; inflated cardiac, hepatic and branchial regions; deep, inclined cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove, strongly curved; long gastro-orbital groove, originating as a slight median inflexion of cervical groove, with two divergent branches delimiting two gastro-orbital lobes (inflated lower lobe, flat upper lobe); wide postcervical groove, strongly inclined, inflected at carapace mid-height, not joined to dorsal margin, joined to hepatic groove; shallow, short branchiocardiac groove, joined to dorsal margin, not joined to postcervical groove; concave hepatic groove, narrow, joined to cervical groove; deep inferior groove; shallow, narrow cardiac groove, straight, rising from postcervical groove, slightly inclined forward, joined to dorsal margin; carapace uniformly covered with rounded tubercles, small tubercles are between coarse tubercles; cephalic region with a row of tubercles subparallel to intercalated plate, an oblique row of tubercles in gastric region, a convex antennal row of tubercles with antennal spine; pleonal somites poorly preserved; terga with two pairs of dorsal tubercles; pleura with rounded ventral margins, covered by small tubercles; telson and uropods poorly preserved; chelate P1; short P1 propodus, almost longer than wide, covered with rounded and coarse tubercles; P1 carpus with rounded and coarse tubercles; P1 merus poorly preserved.

REMARKS. — *Pustulina tuberculata* is close to *Pustulina spinulata* from Madagascar. The latter is only distinguished by its more prominent lower gastro-orbital lobe, its more inflated hepatic region and its denser tuberculation.

Genus *Tethysastacus* n. gen.
(Fig. 1M)

ETYMOLOGY. — A combination of Tethys, the vast Mesozoic ocean, and the Latin *astacus* (“marine crayfish” or “escrevisse” in Old French).

TYPE SPECIES. — *Eryma tithonia* Van Straelen, 1936, by monotypy.

DIAGNOSIS. — Fusiform intercalated plate; straight ocular incision; wide post-orbital area; wide and deep cervical groove; no gastro-orbital groove; wide postcervical groove, straight, strongly inclined, joined to hepatic groove; concave hepatic groove, joined to cervical groove; dense heterogeneous ornamentation, branchial region with small tubercles and small depression, gastric region with pits, frontal region with strong tubercles and pits.

DISCUSSION. — *Tethysastacus* n. gen. is assigned to the Erymidae based on the presence of the intercalated plate. It differs from all other erymid genera of erymid lobsters by its extremely simple carapace groove pattern and the absence of branchiocardiac and gastro-orbital grooves. The postcervical groove is straight, whereas it is inflected in all other genera.

Tethysastacus tithonius (Van Straelen, 1936) n. comb.

(Fig. 10A-D)

Eryma tithonia Van Straelen, 1936: 8-9, pl. 2, fig. 1-2.

Eryma tithonia — Roger 1946: 42. — Secrétan 1964: 68. — Förster 1966: 123. — Feldmann & Titus 2006: 64.

Eryma tithonium — Schweitzer *et al.* 2010: 25.

TYPE MATERIAL. — Holotype MNHN.F.J03351.

TYPE LOCALITY. — Laciterne-Boisset near Moulès-et-Baucels, Hérault department, Languedoc-Roussillon region, South France.

TYPE AGE. — Valanginian, Early Cretaceous.

DESCRIPTION. — Subrectangular carapace in lateral view (holotype: CL= 21 mm; CH= 10 mm); long, toothless rostrum; intercalated plate present; short, oblique ridge near rostrum basis; straight ocular incision; wide tuberculate post-orbital area; wide, deep cervical groove, probably joined to dorsal margin, joined to antennal groove; antennal groove shallower than cervical groove, reaching post-orbital area; gastro-orbital groove absent; straight, oblique postcervical groove, as wide and deep as cervical groove, joined to hepatic groove; slightly concave hepatic groove, narrower than cervical and postcervical grooves, joined to cervical groove; curved inferior groove, joined to ventral margin behind its junction to hepatic groove, as wide and deep as hepatic groove; branchial, cardiac and hepatic regions with small tubercles intercalated with deep circular pits; similar ornamentation in pterygostomial region but with smaller and shallower pits; cephalic region with heterogeneous ornamentation: gastric region with circular pits, frontal region with strong tubercles and small pits; dense ornamentation on the whole carapace.

COMMENTS. — The holotype presents a carapace in butterfly-like position with a strong dorsoventral flattening along the dorsal midline (Fig. 10A). This mode of preservation is characteristic of a lobster molt (Glaessner 1969; Charbonnier *et al.* 2012b). A pronounced rupture of the dorsal midline is observed with a strong rotation of the two halves of carapace. This suggest a probable hinge-type opening during the ecdysis (Charbonnier *et al.* 2012b).

CONCLUSIONS

The present study expands our knowledge on the biodiversity of erymid lobsters from the Early Cretaceous. Based on our research, the known diversity of erymid lobsters during the Early Cretaceous is four species of *Eryma* (*E. glaessneri*, *E. nippon*, *E. sulcatum*, *E. vocontii* n. sp.), three species of *Enoploclytia* (*E. augustobonae* n. sp., *E. gigantea* n. sp., *E. wintoni*), six species of *Palaeastacus* (*P. foersteri*, *P. loryi* n. comb., *P. sussexiensis*, *P. tenuidigitatus*, *P. terraereginae*, *P. walkeri*), five species of *Pustulina* (*P. colossea* n. sp., *P. occitana* n. sp., *P. victori* n. n., *P. spinulata*, *P. tuberculata*), one species of *Stenodactylina* (*S. delphinensis* n. comb.), and one species of *Tethysastacus* n. gen. (*T. tithonius* n. comb.). The re-examination of old material and of new material belonging to these twenty species has allowed us to precise the generic diagnoses of five genera (*Eryma*, *Enoploclytia*, *Palaeastacus*, *Pustulina*, *Stenodactylina*) and to create a new genus (*Tethysastacus* n. gen.), mainly based on the carapace groove pattern.

The post-orbital area is identified in different species among different genera (*Eryma sulcatum*, *Stenodactylina delphinensis*, *Palaeastacus foersteri*, *Tethysastacus tithonius*). This complex structure is not present in all other species of *Eryma*, *Palaeastacus* and *Stenodactylina* and its evolutionary significance is questionable. It may be a case of convergence or a persistent ancestral trait conserved in only some species. Only further investigations on all erymid species showing this character will provide answers to these questions.

The description of two new species associated to the revision of several fragments of crustaceans which are now not considered to belong to erymid lobsters conduct to modify the stratigraphic range of *Eryma* and *Enoploclytia*. *Eryma vocontii* n. sp. extends the stratigraphic range of *Eryma* to the Albian and is now the youngest occurrence of *Eryma*. *Enoploclytia augustobonae* n. sp. extends the stratigraphic range of *Enoploclytia* from the Maastrichtian to the Barremian; it is the oldest occurrence for the genus *Enoploclytia*.

Finally, this work indirectly emphasizes that the Early Cretaceous erymid fauna is only known by a limited number of fragmentary fossils reported around the world. Almost 45% of the Early Cretaceous species of erymid lobsters come from France and most of them were collected in the South-East Basin, including the Vocontian Basin and its peripheral platforms.

In conclusion, our knowledge of these decapod crustaceans remains superficial and the present study highlights that new data are essential to understand the evolutionary history of the whole group.

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Captions

Table 1. — List of the examined material of Early Cretaceous erymid lobsters.

Fig. 1. — Line drawings of carapaces and P1 chelae of Early Cretaceous erymid lobsters from Western Europe. **A**-**C**, *Eryma* Meyer, 1840: carapace (A), P1 chela form I (B), P1 chela form II (C); **D**-**F**, *Stenodactylina* Beurlen, 1928: carapace (D), P1 chela form I (E), P1 chela form II (F); **G-H**, *Palaeastacus* Bell, 1850: carapace (G), P1 chela (H); **I-J**, *Enoploclytia* M'Coy, 1849: carapace (I), P1 chela (J); **K-L**, *Pustulina* Quenstedt, 1857: carapace (K), P1 chela (L); **M**, *Tethysastacus* n. gen.: carapace. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; cd: cardiac groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ip: intercalated plate; PoA: post-orbital area; ω: attachment site of mandibular muscle; χ: attachment site of adductor testis muscle. Line drawings: J. Devillez and S. Charbonnier.

Fig. 2. — Geographical location of French Early Cretaceous erymids with the northern boundary of the South-East Basin during the Lower Aptian (modified after Masse *et al.* 1993).

Fig. 3. — Anatomical terminology of erymid lobsters. **A-B**: holotype BAS KG.50.4 of *Palaeastacus foersteri* Taylor, 1979 from the Barremian of Alexander Island, Antarctic: general view (A) and line drawing of the carapace (B); **C**: extant lobster *Homarus gammarus* (Linnaeus, 1758) with P1 chelae terminology. Scale bars: 10 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; c: postcervical groove; cam: carina of anterior margin; d: gastro-orbital groove; da: dactylus; db: dactylar bulge; ds: dorsal surface; e_1e: cervical groove; i: inferior groove; im: inner margin; in: index; om: outer margin: PoA: post-orbital area; Sag: S-shaped anterior groove. Photographs: Hillary Blagbrough (**A**), Bart Braun (**C**). Line drawing: J. Devillez.

Fig. 4. — Species of *Eryma* Meyer, 1840 from Western Europe. **A-D**, holotype MNHN.F.A57457 (Clément coll.) of *Eryma vocontii* n. sp. from the Albian of Rosans, France: right lateral view (A), line drawing (B), left lateral (C) and dorsal (D) views; **E-F**, paratype MNHN.F.A57458 (Clément coll.) of *Eryma vocontii* n. sp.: dorsal view of right P1 chela (E) and line drawing (F); **G-H**: cast of the holotype MNHN.F.R10204 of *Eryma glaessneri* (Van Straelen, 1936) from the Hauterivian of Escragnolles, France: left lateral view (G) and line drawing (H); **I-L**, neotype herein designated SM B11437 of *Eryma sulcatum* Harbort, 1905 from the Hauterivian of Speeton, United Kingdom: left lateral view (I), dorsal view (K) and line drawings (J, L). Scale bars: 5 mm for **A-F**;

10 mm for **G-L**. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ip: intercalated plate; PoA: post-orbital area; ω: attachment site of mandibular muscle; χ: attachment site of adductor testis muscle. Photographs: L. Cazes (**A-D**, **G**), J. Devillez (**I**, **K**). Line drawings: J. Devillez.

Fig. 5. — *Stenodactylina delphinensis* (Moret, 1946) n. comb. from the Berriasian of Noyarey, France: holotype OSUG.UJF-ID 11152. **A**, carapace in dorsal view showing the two sides; **B**, line drawing of right side. Scale bars: 5 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; PoA: post-orbital area. Photograph: L. Cazes. Line drawing: J. Devillez.

Fig. 6. —*Palaeastacus sussexiensis* (Mantell, 1824) from the Cretaceous of the United Kingdom. **A-B**, lectotype herein designated (NHMUK 5601, Mantell coll.) from the Cenomanian of Sussex: right side of carapace with parts of pereiopods (A) and line drawing of carapace (B); **C-D**, paralectotype NHMUK 5624 (Mantell coll.) from the Late Cretaceous of Southerham: dorsal view of left P1 chela (C) and line drawing (D); **E**, syntype SM B8885 of *Enoploclytia brevimana* M'Coy, 1849 from the Cenomanian of Cherryhinton: dorsal view of left P1 chela; **F**, lectotype BM 007750 (Willet coll.) of *Palaeastacus dixoni* Bell, 1850 from the Cenomanian of Glynde: dorsal view. Scale bars: 10 mm for **A-E**, 20 mm for **F**. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove. Photographs and line drawings: J. Devillez.

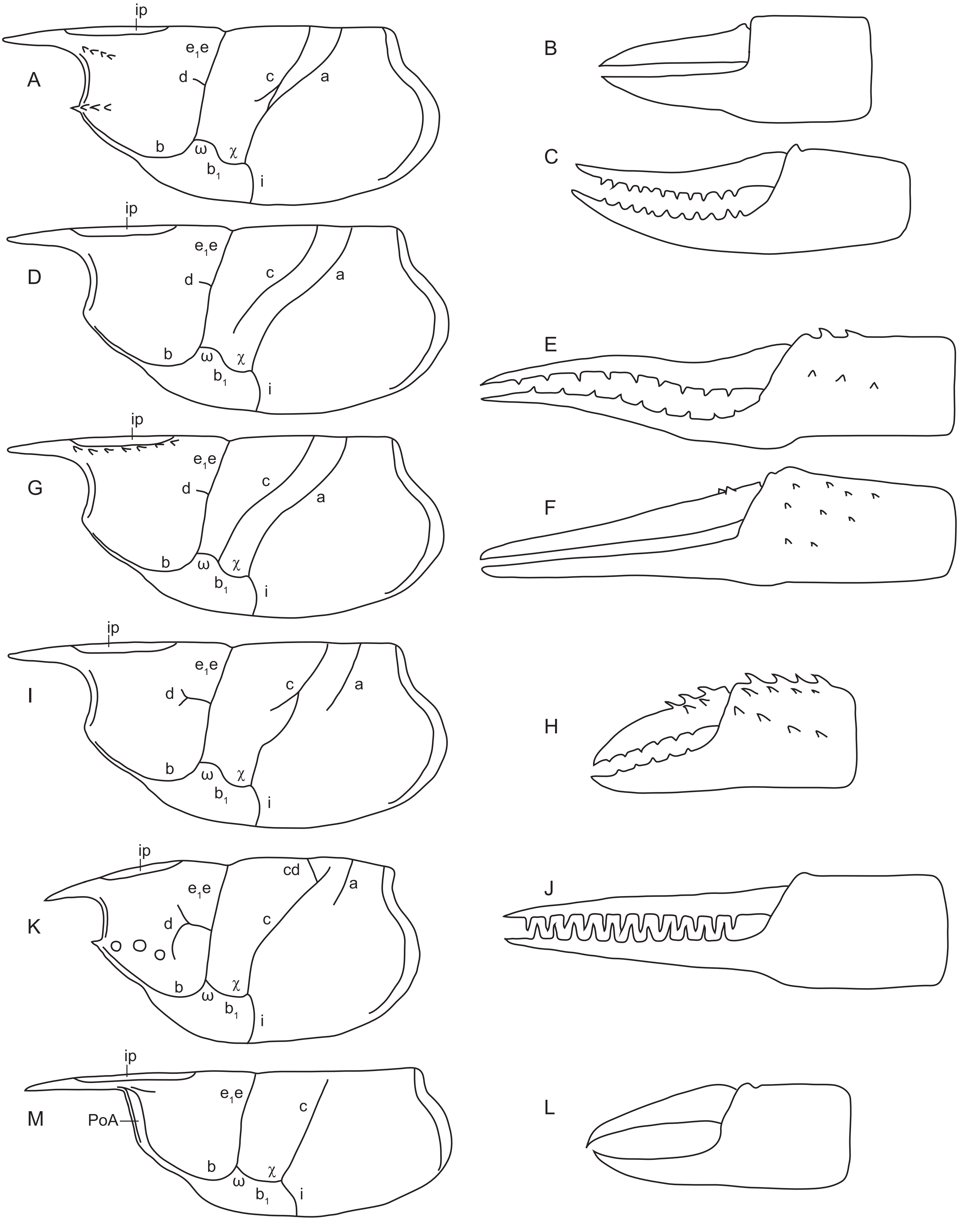
Fig. 7. — *Palaeastacus sussexiensis* (Mantell, 1824) from the United Kingdom (**A-E**) and *Palaeastacus loryi* (Van Straelen, 1923) n. comb. from France (**F-G**). **A**, syntype SM B8892 of *Enoploclytia imagei* M'Coy, 1849 from the Cenomanian of Maidstone: part of carapace with right P1 chelae; **B-C**, lectotype NHMUK 41938 of *Hoploparia scabra* Bell, 1863 from the Albian of Folkestone: right lateral view (B) and line drawing (C); **D-E**, syntype SM B22448 (Carter coll.) of *Phlyctisoma granulatum* Bell, 1863 from the Albian of Cambridge: right lateral view (D) and line drawing (E); **F-G**, holotype (probably lost) of *Palaeastacus loryi* from the Valanginian of Malleval: original figure of carapace by Van Straelen (1936: pl. 1, fig. 6) (C) and line drawing (D). Scale bars: 20 mm for **A**, 10 mm for **B-G**. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ω: attachment site of mandibular muscle. Photographs and line drawings: J. Devillez.

Fig. 8. — New species of Early Cretaceous *Enoploclytia* M'Coy, 1849. **A-D**, holotype MNHN.F.B14557 of *Enoploclytia augustobonae* n. sp. from the Barremian of Amance, France: carapace in right lateral view (A), and line drawing (B), dorsal view (C) showing the deviation of median line in cephalic region (intercalated plate) and line drawing (D); **E-H**, holotype of *Enoploclytia gigantea* n. sp. from the Albian of Fort Worth, USA: original figures of carapace by Rathbun (1935: pl. 4 figs 1-2), left lateral view (E), right lateral view (F), and line drawings (G, H). Scale bars: 10 mm for **A-D**, 20 mm for **E-H**. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ω: attachment site of mandibular muscle. Photographs: L. Cazes (**A**, **C**). Line drawings: J. Devillez.

Fig. 9. — Species of *Pustulina* Quenstedt, 1857 from Western Europe. **A-D**, holotype MNHN.F.A57460 (Leroy coll.) of *Pustulina occitana* n. sp. from the Berriasian of Laciterne-Boisset near Moulès-et-Baucels, France: carapace in right lateral view (A), dorsal view (C) and line drawings (B, D); **E-F**, holotype (probably lost) of *Pustulina victori* nomen novum from the Berriasian of Leysse, France: original figure of carapace by Van Straelen (1936: pl. 2, fig. 3) (E) and line drawing (F); **G-H**, holotype MNHN.F.A57459 (Leroy coll.) of *Pustulina colossea* n. sp. from the Hauterivian of Castellane, France: left lateral view (G) and line drawing (H); **I-L**, specimen MNHN.F.A57461 of *Pustulina tuberculata* (Bell, 1863) from the Albian of Cambridge, United Kingdom: right lateral view (I), dorsal view (K) and line drawings (J, L). Scale bars: 10 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; cd: cardiac groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove. Photographs: L. Cazes (**A**, **C**, **G**, **I**, **K**). Line drawings: J. Devillez.

Fig. 10. — Type material of *Tethysastacus* n. gen. **A-B**; holotype MNHN.F.J03351 of *Tethysastacus tithonius* (Van Straelen, 1936) n. comb. from the Valanginian of Laciterne-Boisset near Moulès-et-Baucels, France: almost complete right side of carapace and cephalic region of left side of carapace (A), detail of cephalic region showing the wide post-orbital area (B), line drawing of carapace (C) close-up of cephalic region (D). Scale bars: 5 mm. Abbreviations: b: antennal groove; b_1: hepatic groove; c: postcervical groove; cam: carina of anterior margin; e_1e: cervical groove; i: inferior groove; ip: intercalated plate; PoA: post-orbital area; Sag: S-shaped anterior groove. Photographs: L. Cazes. Line drawings: J. Devillez.

TAXA	EXAMINED MATERIAL	ANATOMY	AGES	LOCALITIES
Eryma Meyer, 1840				
Eryma babeaui Étallon, 1861	cast of holotype MNHN.F.B13231	P1 chela	Kimmeridgian	France
Eryma glaessneri Van Straelen, 1936	holotype MNHG GEPI 28369 (cast MNHN.F.R10204)	carapace	Hauterivian	France
Eryma sulcatum Harbort, 1905	—neotype SM B11437. —casts of the type material (lost): NHMUK In.27305, In.27307, In.27308, In.27309, In.27310. —3 additional specimens NHMUK In.27837, In.61410, In.61411.	carapaces with P1 chelae and pleons	Hauterivian	United-Kingdom Germany United-Kingdom
Eryma vocontii n. sp.	holotype MNHN.F.A57457, paratype MNHN.F.A57458	carapace and right P1 chela	Albian	France
Palaeastacus Bell, 1850				
Palaeastacus loryi (Van Straelen, 1923) n. comb.	holotype housed in OSUG, probably lost	carapace	Valanginian	France
Palaeastacus sussexiensis (Mantell, 1824)	—lectotype NHMUK 5601, 13 paralectotypes NHMUK 5024, 5584, 5586, 5589, 5600, 5602, 5608, 5613, 5618, 5624, 5626, 5629, 10760. —30 additional specimens NHMUK In.27682, In.36768, I.62, I.2190, I.2628, 5685, 35124, 44343, 024318,026316 46782, 59668, 59824, 59824; BM 002548, 002549, 007751, 007752, 007753, 007754, 007755, 007758, 008632, 008633, 008635, 008636, 008637, 008659, 016988, 024317, 024318, 026316.	carapaces, P1 chelae, pleons	Cenomanian - Turonian	United-Kingdom
junior synonyms of *Palaeastacus sussexiensis*				
Enoploclytia brevimana M'Coy 1849	3 syntypes SM B8884, B8885, B8886	P1 chelae	Cenomanian	United-Kingdom
Enoploclytia imagei M'Coy 1849	8 syntypes SM B8892, B8893, B8894, B8895, B8896, B8897, B8898, B8899	carapace and P1 pereiopods	Cenomanian	United-Kingdom
Hoploparia scabra Bell, 1863 partim	— lectotype NHMUK 41938, 2 paralectotypes NHMUK 39377, 39380. —4 additional specimens NHMUK In.27684, In.61022, In.27685, In. 27686.	carapaces and P1 pereiopods	Albian	United-Kingdom
Palaeastacus dixoni Bell, 1850	—lectotype BM 007750, paralectotype NHMUK I.1916. —1 additionnal specimen BM 007757.	carapaces, P1 chelae, pleon	Cenomanian	United-Kingdom
Phlyctisoma granulatum Bell, 1863	2 syntypes SM B22448, B22449	carapaces	Albian	United-Kingdom
Pustulina Quenstedt, 1857				
Pustulina occitana n. sp.	holotype MNHN.F.A57460	carapace	Berriasian	France
Pustulina victori nomen novum	holotype housed in MHNC, probably lost	carapace left side	Berriasian	France
Pustulina colossea n. sp.	holotype MNHN.F.A57459	carapace left side	Hauterivian	France
Pustulina tuberculata (Bell, 1863)	—lectotype SM B22368, 7 paralectotypes SM B22364, B22365, B22366, B22367, B22369, B22370, B22371. —3 additional specimens MNHN.F.A57461, NHMUK 34732, In.60148.	carapaces, P1 chelae, pleon	Albian	United-Kingdom
Pustulina spinulata Secrétan, 1964	holotype MNHN.F.R03961, 51 paratypes	carapaces, P1 chelae	Valanginian - Hauterivian	Madagascar
Stenodactylina Beurlen, 1928				
Stenodactylina armata (Secrétan, 1964) n. comb.	holotype MNHN.F.R03913, 3 paratypes MNHN.F.A33209, A33464, R03912	P1 chelae	Campanian	Madagascar
Stenodactylina australis (Secrétan, 1964) n. comb.	holotype MNHN.F.R03972, 3 paratypes MNHN.F.R03971, A31660, A33207	P1 chelae	Tithonian	Madagascar
Stenodactylina delphinensis (Moret, 1946) n. comb.	holotype UJF-ID 11152	carapace	Berriasian	France
Stenodactylina granulifera (Secrétan, 1964) n. comb.	holotype MNHN.F.R03975, 1 paratype MNHN.F.R3974	carapace	Kimmeridgian	Madagascar
Stenodactylina insignis (Oppel, 1862) n. comb.	holotype MNHN.F.A24613	P1 chela	Oxfordien	France
Tethysastacus n. gen.				
Tethysastacus tithonius (Van Straelen, 1936) n. comb.	holotype MNHN.F.J03351	carapace	Valanginian	France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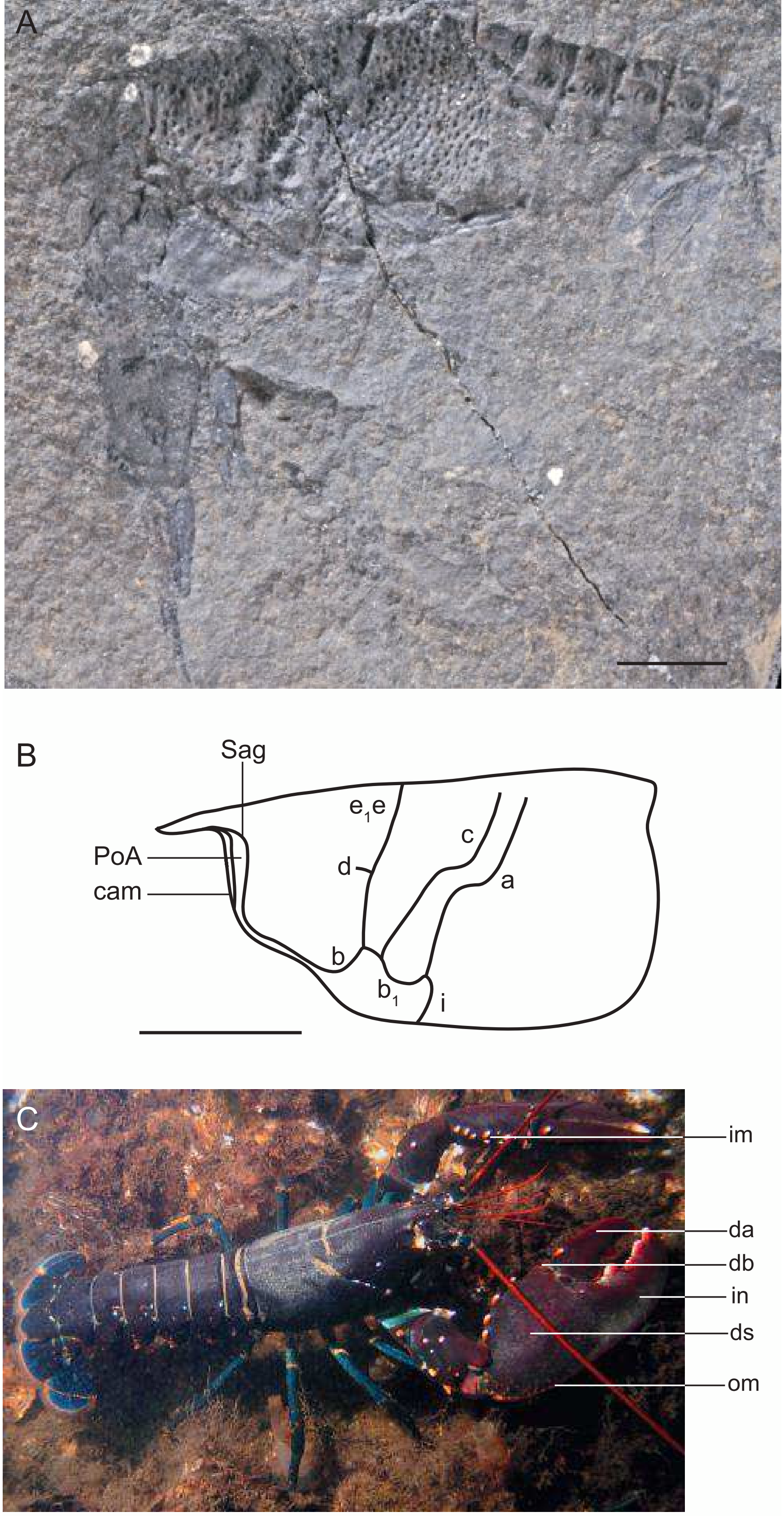
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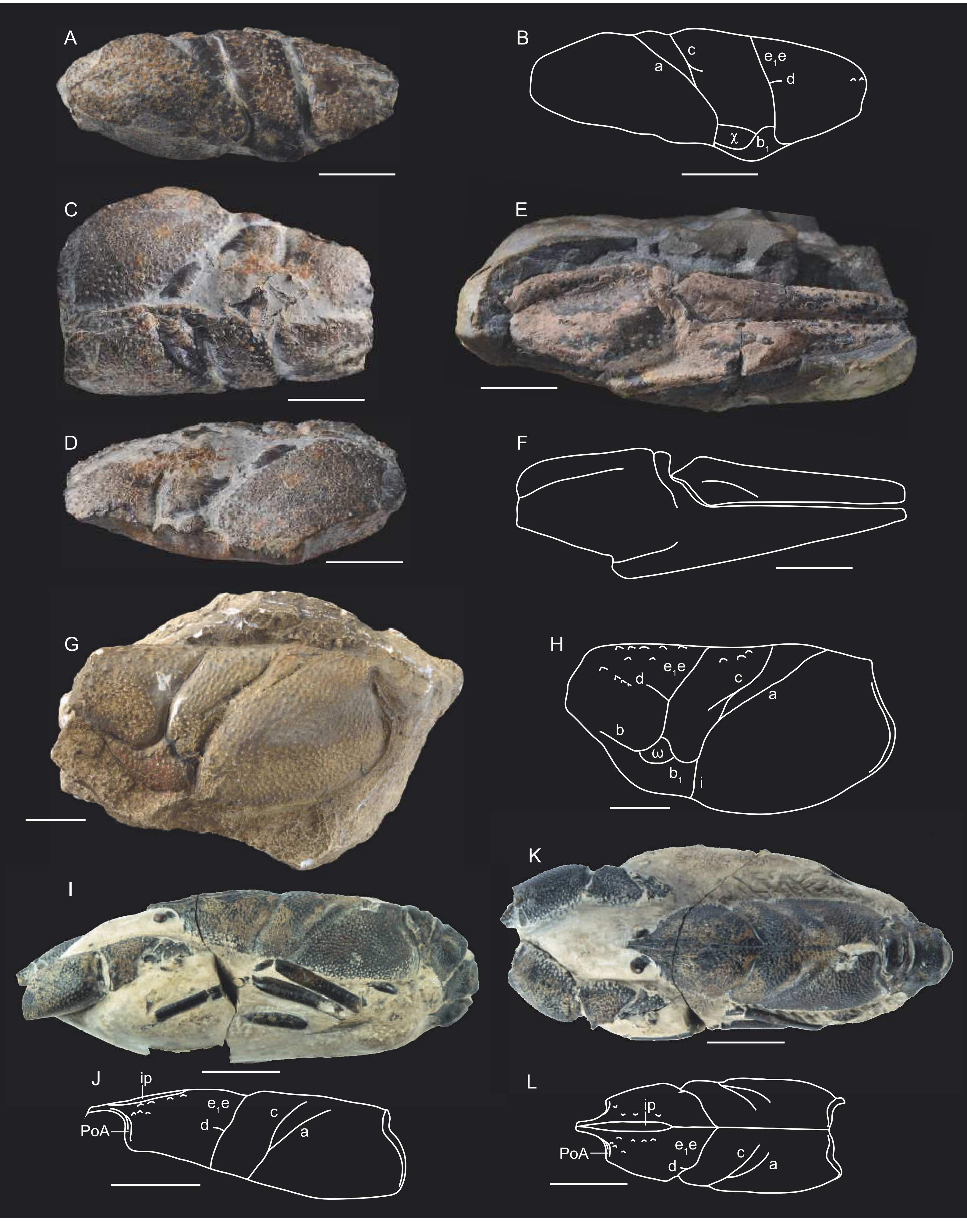
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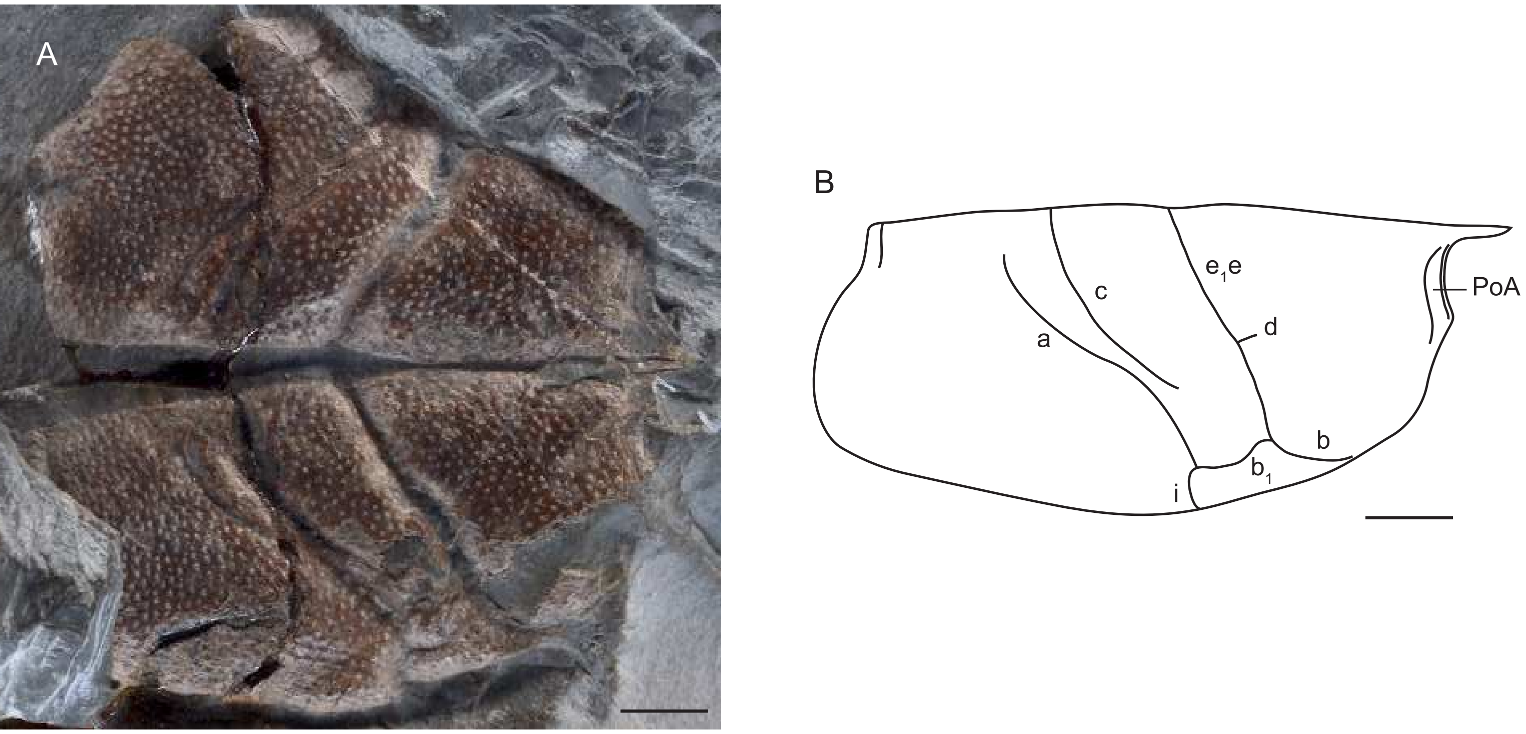
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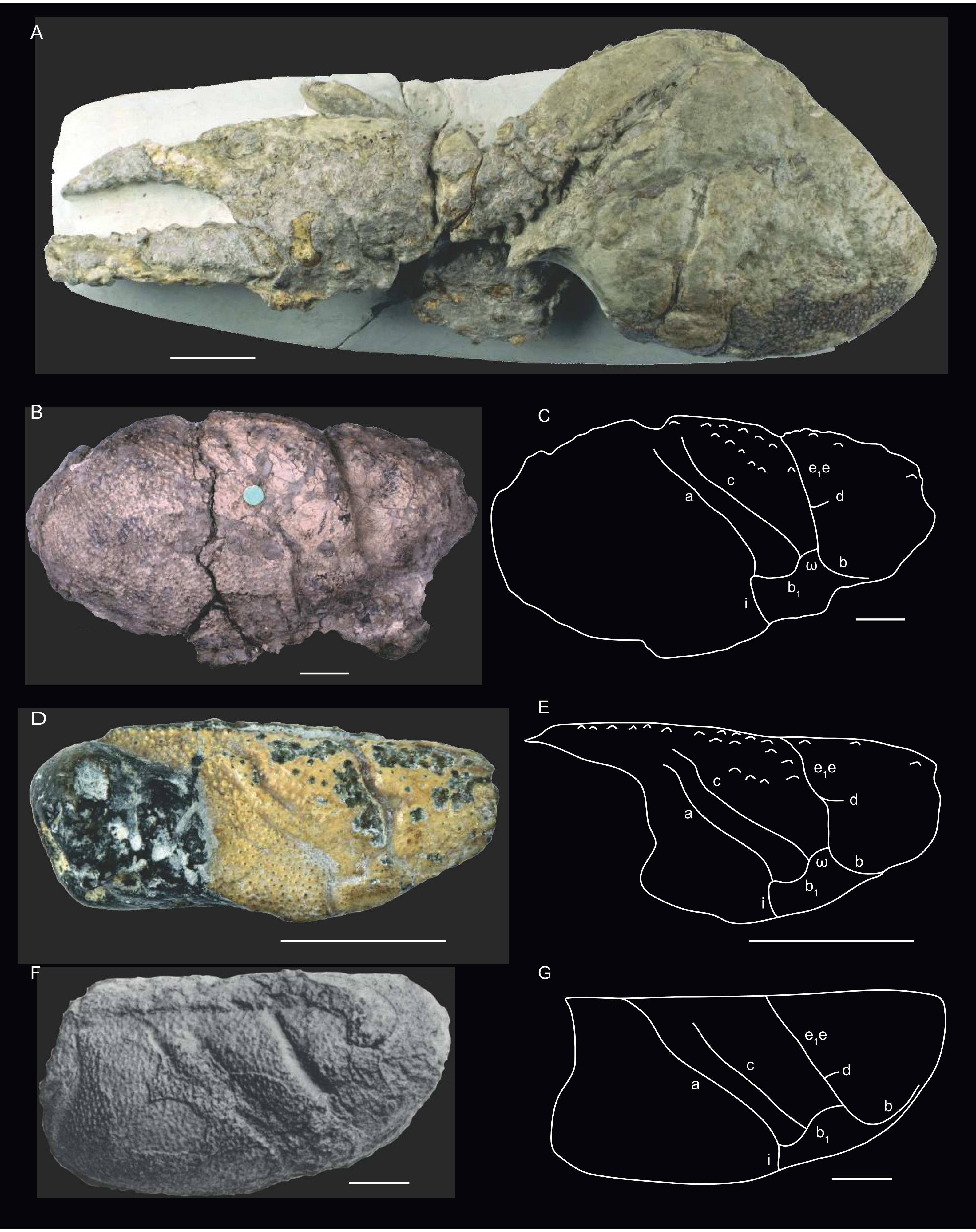
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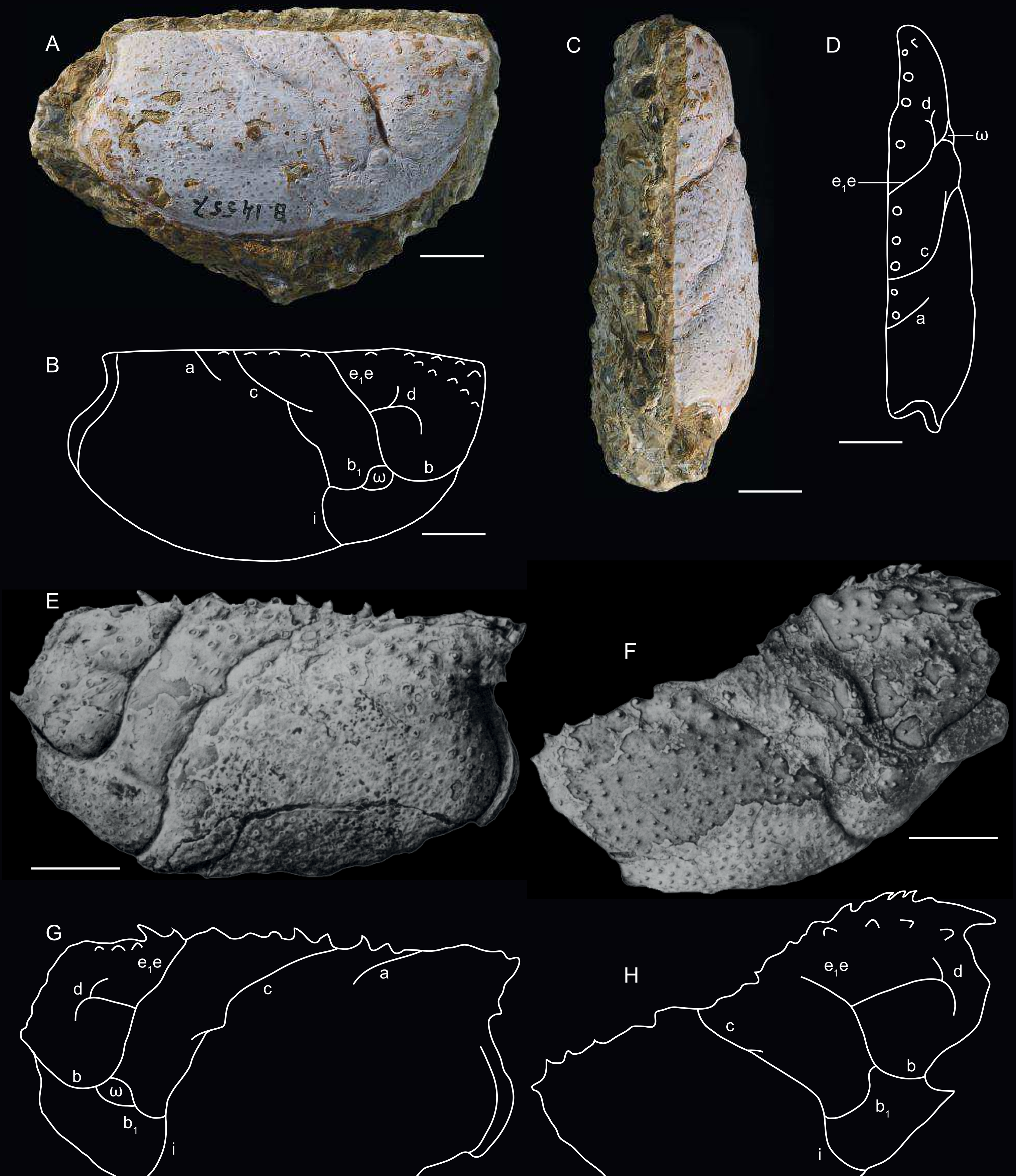
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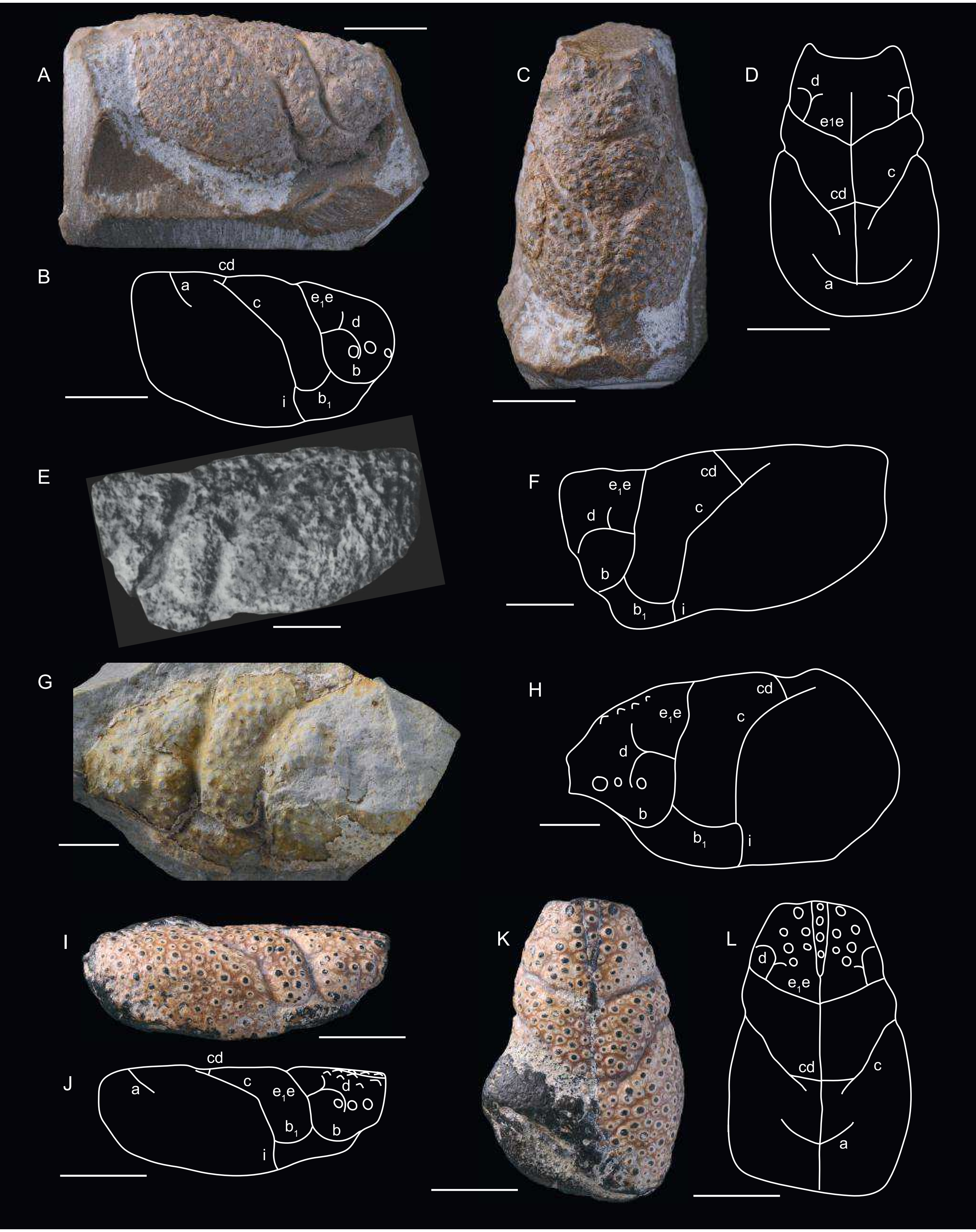
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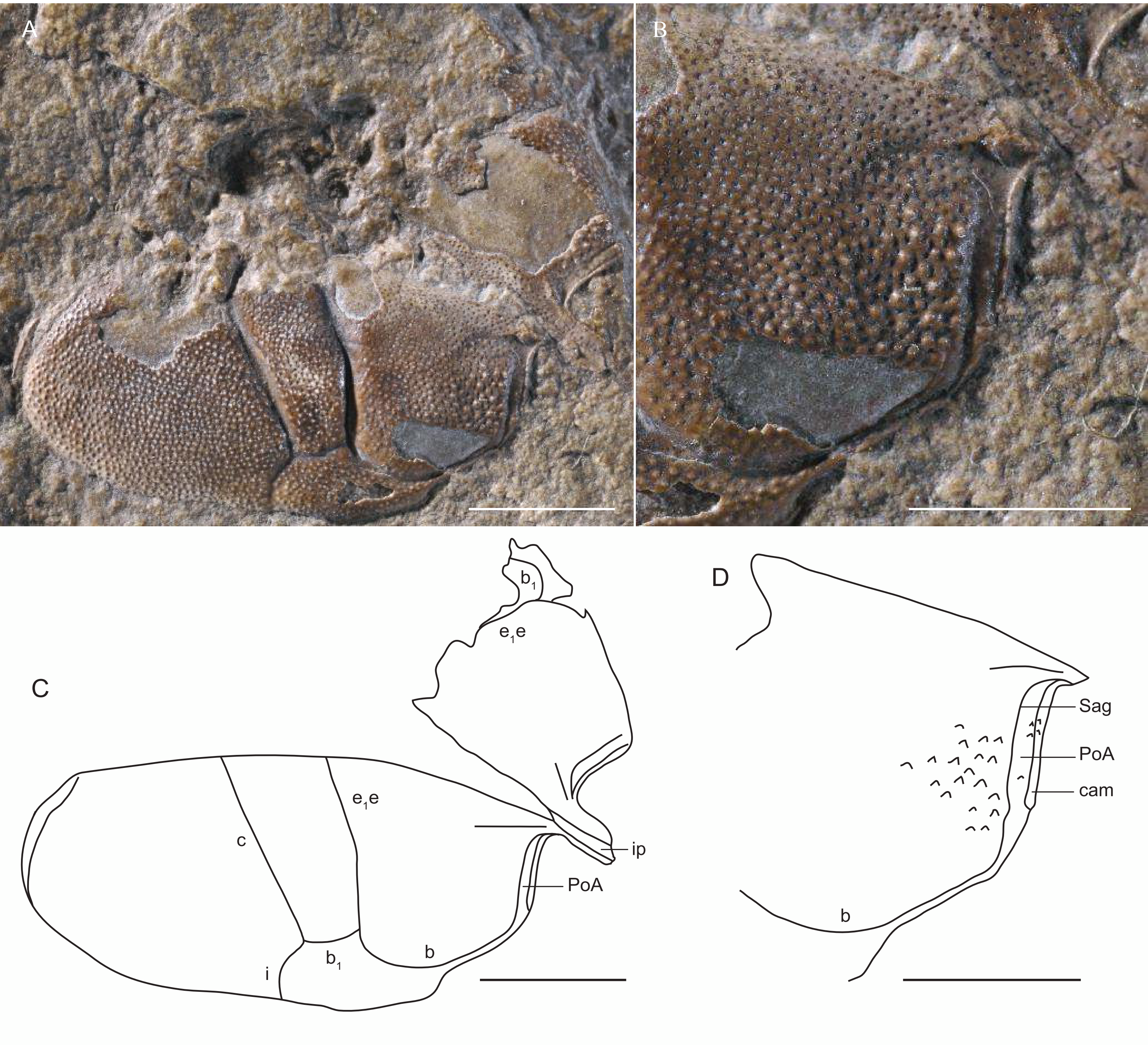
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