

Review of the Late Jurassic erymoid lobsters (Crustacea: Decapoda)

Julien DEVILLEZ & Sylvain CHARBONNIER



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Review of the Late Jurassic erymoid lobsters (Crustacea: Decapoda)

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ABSTRACT

Erymoid lobsters (Crustacea, Decapoda, Erymoidea) are an important component of Mesozoic crustacean faunas in Europe, especially during the Jurassic. With 36 species reported, these lobsters reach their highest diversity during the Late Jurassic. After the review presented here, 23 species belonging to *Eryma* Meyer, 1840 (11 species), *Palaeastacus* Bell, 1850 (2 species), *Pustulina* Quenstedt, 1857 (2 species) and *Stenodactylina* Beurlen, 1928 (8 species) remain valid. One new species is described: *Stenodactylina shotoverigiganti* n. sp., and *Eryma pseudoventrosa* Beurlen, 1928 is integrated to *Stenodactylina*. We also notice the oldest representative of *Enoplochytia* M'Coy, 1849, known by a single specimen unidentified at specific level. *Eryma ventrosum* (Meyer, 1835) is the most common species in Western Europe, and may be seen as emblematic of the Middle-Late Jurassic. Moreover, the lithographic limestones of Germany yield an exceptionally diversified erymoid fauna, with four genera (*Eryma*, *Palaeastacus*, *Pustulina*, *Stenodactylina*) and 11 species listed. All the Late Jurassic representatives of *Palaeastacus* were found in this lithology. Finally, the examination of some specimens allows the observation of the strong effects of the decortication on the ornamentation of the erymoids and the resulting taxonomic issues.

KEY WORDS

Mesozoic,
Erymoidea,
Erymidae,
lobster,
decortication,
Lagerstätte,
palaeobiodiversity,
Western Europe,
new synonyms,
new combination,
new species.

RÉSUMÉ

Révision des érymoïdes (Crustacea: Decapoda) du Jurassique supérieur.

Les érymoïdes (Crustacea, Decapoda, Erymoidea) sont une composante importante des faunes de crustacés au Mésozoïque en Europe, tout particulièrement au Jurassique. Avec 36 espèces recensées, le Jurassique supérieur est la période où ces homards atteignent leur plus grande diversité. À l'issue du travail de révision présenté ici, 23 espèces appartenant aux genres *Eryma* Meyer, 1840 (11 espèces), *Palaeastacus* Bell, 1850 (2 espèces), *Pustulina* Quenstedt, 1857 (2 espèces) et *Stenodactylina* Beurlen, 1928 (8 espèces) restent valides. Parmi elles nous décrivons une nouvelle espèce : *Stenodactylina shotoverigiganti* n. sp., tandis qu'*Eryma pseudoventrosa* Beurlen, 1928 est déplacée dans *Stenodactylina*. Nous relevons aussi la présence du plus ancien représentant d'*Enoploclytia* M'Coy, 1849 avec un spécimen non identifié spécifiquement. *Eryma ventrosum* (Meyer, 1835) est l'espèce la plus courante en Europe occidentale et peut être considérée comme emblématique du Jurassique moyen-supérieur. De plus, les calcaires lithographiques d'Allemagne présentent une faune d'érymoïdes exceptionnellement diversifiée avec quatre genres (*Eryma*, *Palaeastacus*, *Pustulina*, *Stenodactylina*) et 11 espèces présentes. Les représentants du genre *Palaeastacus* du Jurassique supérieur ne sont d'ailleurs connus que dans cette formation. Enfin, l'examen de certains spécimens permet aussi de visualiser l'effet important de la décortication sur l'ornementation des érymoïdes et les problèmes taxinomiques qui peuvent en résulter.

MOTS CLÉS

Mésozoïque,
Erymoidea,
Erymidae,
homard,
décortication,
Lagerstätte,
paléobiodiversité,
Europe occidentale,
synonymes nouveaux,
combinaison nouvelle,
espèce nouvelle.

INTRODUCTION

Erymoid lobsters are an important component of the Mesozoic decapod faunas, reported on every continents: in Europe (e.g., Mantell 1833; Bell 1850, 1863; Oppel 1861, 1862; Lahusen 1894; Van Straelen 1925; Beurlen 1928; Glaessner 1931; Reuss 1854; 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-Emami 1982; Garassino 1994; Charbonnier *et al.* 2017), in Africa (Beurlen 1933; Joleaud & Hsu 1935; Secrétan 1964, 1984; Charbonnier *et al.* 2012a), in North America (Rathbun 1923, 1926; Stenzel 1945; Feldmann & McPherson 1980; Aguirre-Urreta & Ramos 1981; Aguirre-Urreta 1982, 1989; Schweitzer & Feldmann 2001; Feldmann & Titus 2006; Feldmann & Haggart 2007; Vega *et al.* 2013; J. Luque pers. com.), in Japan (Karasawa *et al.* 2008; Kato *et al.* 2010), in Australia (Woodward 1877; Etheridge Jr 1914; Woods 1957), and in Antarctica (Taylor 1979; Aguirre-Urreta 1989).

Despite its importance, this group of lobster was not revised since the study of Förster (1966). With 36 species reported, the Late Jurassic erymoid fauna is the most diversified. Indeed, it is more than the number of species reported in Early and Middle Jurassic together (Devillez & Charbonnier 2019) or in Cretaceous (Devillez *et al.* 2016, 2017). So, this period is of high interest in the evolutionary history of these lobsters.

Following the recent studies of Devillez *et al.* (2016, 2017) and Devillez & Charbonnier (2017), the present contribution aims to give a new look at the Late Jurassic erymoid species, which benefit of new descriptions.

MATERIAL AND METHODS

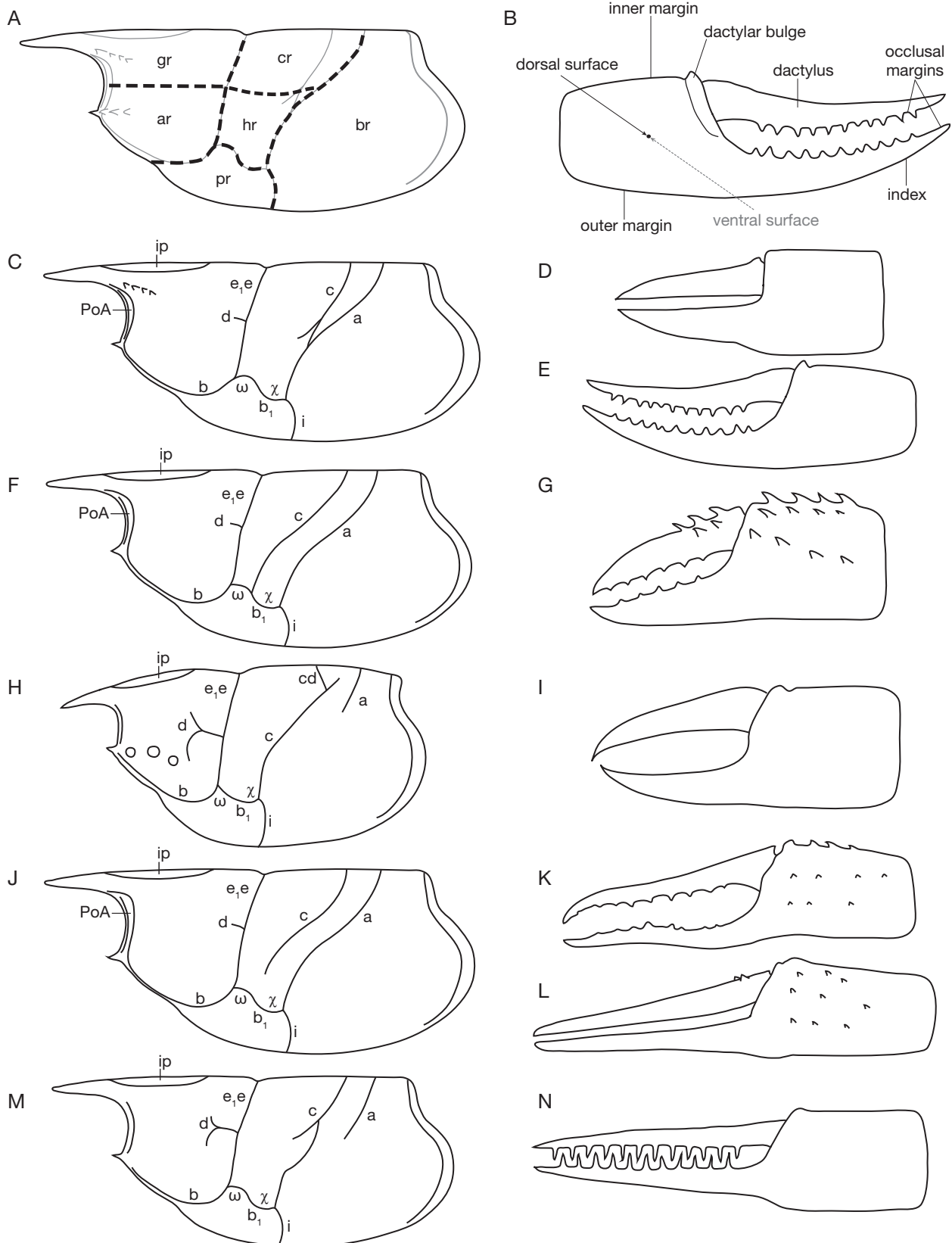
The studied material includes 498 specimens Late Jurassic in age, mainly from the palaeontological collections of European institutions (Appendix 1).

The carapace and the P1 chelae are the most commonly preserved anatomical parts in erymoid lobsters. So, most of useful characters in generic and specific identifications are located on these parts. Especially, the trajectories and connexions of the carapace grooves are of high taxonomic value because they are involved in both generic and specific identifications. The extension and inflation of the different regions of the carapace mapped in Fig. 1A were also found of importance in the identification of genera and species while the ornamentation and shape of P1 chelae are only used at specific level.

In extant 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 plan. The terminology used in this paper follows this natural configuration for the description of the chelae: 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 (Fig. 1B).

The Lagerstätte of Solnhofen is here of high interest because it provides numerous specimens almost complete on which some anatomical structures almost never preserved can be easily observed, in particular the cephalic appendages and third maxillipeds.

Fig. 1. — Carapace and P1 chela morphologies of the Late Jurassic erymoids: **A**, regions of the carapace; **B**, morphology of a chela of the first pair of pereopods; **C**, typical carapace groove pattern of *Eryma*; **D**, form I of chela of the first pair of pereopods of *Eryma*; **E**, form II of chela of the first pair of pereopods of *Eryma*; **F**, typical carapace groove pattern of *Palaeastacus*; **G**, typical chela of the first pair of pereopods of *Palaeastacus*; **H**, typical carapace groove pattern of *Pustulina*; **I**, typical chela of the first pair of pereopods of *Pustulina*; **J**, typical carapace groove pattern of *Stenodactylina*; **K**, form I of chela of the first pair



of pereiopods of *Stenodactylina*; **L**, form II of chela of the first pair of pereiopods of *Stenodactylina*; **F**, typical carapace groove pattern of *Enoploclytia*; **G**, typical chela of the first pair of pereiopods of *Enoploclytia*. Abbreviations: **a**, branchiocardiac groove; **ar**, antennal region; **b**, antennal groove; **b₁**, hepatic groove; **br**, branchial region; **c**, postcervical groove; **cr**, cardiac region; **d**, gastro-orbital groove; **e₁e**, cervical groove; **gr**, gastric region; **hr**, hepatic region; **i**, inferior groove; **ip**, intercalated plate; **PoA**, post-orbital area; **pr**, pterygostomial region; **χ**, attachment site of adductor testis muscle; **ω**, attachment site of mandibular muscle. Line drawings: J. Devillez.

ABBREVIATIONS

Institutional abbreviations

BSPG	Bayerische Staatsammlung für Paläontologie und Geologie, Munich;
FSL	Université Claude Bernard Lyon 1, Lyon;
GPIT	Fachbereichs Geowissenschaften, Eberhard Karls Universität, Tübingen;
IRSNB	Institut royal des Sciences naturelles de Belgique, Bruxelles;
MAN	Musée-aquarium, Nancy;
MFN	Museum für Naturkunde, Berlin;
MJSN	Musée jurassien des sciences naturelles, Porrentruy;
MNHLN	Muséum d'Histoire naturelle, Le Mans;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMUK	Natural History Museum, London;
NMB	Naturhistorisches Museum Basel;
OSUG	Observatoire des Sciences de l'Univers, Grenoble;
PVM	Paléospace l'Odyssée, Villers-sur-Mer;
SM	Sedgwick Museum of Earth Sciences, Cambridge;
SMNS	Staatliches Museum für Naturkunde, Stuttgart;
UR	Laboratoire de paléontologie de l'Université de Rennes, Rennes;
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington.

Anatomical abbreviations

Mxp3	Third maxilliped;
P1-5	Pereiopods 1 to 5;
s1-s6	Somites 1 to 6;
χ	Attachment site of adductor testis muscle;
ω	Attachment site of mandibular muscle.

SYSTEMATIC PALAEOLOGY

Class MALACOSTRACA Latreille, 1802
Order DECAPODA Latreille, 1802
Superfamily ERYMOIDEA Van Straelen, 1925

Genus *Eryma* Meyer, 1840
(Fig. 1C-E)

Eryma Meyer, 1840a: 587. — Oppel 1862: 20. — Zittel 1885: 693. — Méchin 1901: 74. — Van Straelen 1925: 233. — Rathbun 1926: 127. — Secrétan 1964: 61; 1984: 516. — Förster 1966: 88. — Glaessner 1969: 455. — Aguirre-Urreta & Ramos 1981: 610. — 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. — Devillez *et al.* 2016: 518. — Devillez & Charbonnier 2017: 3.

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

Klytia Meyer, 1840b: 19. — Glaessner 1969: 456.

Protylopsis Birshtein, 1958: 477. — Förster 1966: 86. — Feldmann *et al.* 2015: 10.

Galicina Garassino & Krobicki, 2002: 55. — Feldmann *et al.* 2015: 3.

Clytia – Beurlen 1928: 165.

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

DIAGNOSIS BY Devillez & Charbonnier (2019). — Fusiform intercalated plate; deep cervical groove, strongly inclined dorsally, joined to dorsal

margin and to antennal groove; short gastro-orbital groove, originating as a slight median inflexion of the cervical groove; postcervical groove joined to branchiocardiac groove at carapace mid-height; branchiocardiac groove usually strongly inclined, joined to the posterior extremity of hepatic groove; hepatic groove concavo-convex, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove and to ventral margin; ω area usually inflated; cephalic region usually with an orbital row and with strong orbital and antennal spines; chelate P1-P3; P1 chelae without prominent spines and with an homogeneous ornamentation; P1 propodus compressed dorso-ventrally with narrow inner and outer margins, with a narrow dactylar bulge; P1 fingers usually longer than propodus, equal in length, progressively narrowing to their distal extremity; index wider than dactylus; P1 chelae (form I; Fig. 1D) with a short rectangular propodus, straight fingers, slightly longer than propodus; P1 chelae (form II; Fig. 1E) with an elongated subrectangular or trapezoidal propodus, bearing fingers quite longer than propodus, usually curved inward.

DISCUSSION

In the literature, two species only known by isolated P1 chelae found in the Oxfordian of United Kingdom were wrongly assigned to *Eryma*: *Eryma pulchellum* Carter, 1886 and *Eryma stricklandi* (Phillips, 1871). The short propodus bearing short fingers slightly curved outward indicates that *E. pulchellum* does not belong to Erymoidea. Förster (1966) proposed to assign this species to *Magila* Münster, 1839. The P1 chelae of *E. stricklandi* exhibits elongated propodus and fingers, that are slender and of opposite curvatures – so their distal extremities are convergent – and an index longer than dactylus. Such morphology is not consistent with any known erymoid lobster. So, *E. stricklandi* does not belong to Erymoidea.

De Gregorio (1884) described *Eryma rinellincolum* on a P1 propodus from the Tithonian near Palermo (Italy). This specimen is not located and has never been figured. It is also insufficiently described (Förster 1966). Because it is impossible to clearly determine the genus or the family of this specimen, we consider it as *nomen dubium*.

Some specimens of *Eryma mandelslohi* (Meyer, 1840) from the Oxfordian of France and Switzerland are stored in the collections of the MNHN and the NMB. The age of this species is Callovian (Middle Jurassic). Devillez & Charbonnier (2019) have redescribed it in the review of the Early and Middle Jurassic erymids, so it will not be discussed here.

To shorten the discussions, the comparisons of the species of *Eryma* described below are restricted to the other Late Jurassic species.

Eryma georgeii Carter, 1886 (Fig. 2A-D)

Eryma georgeii Carter, 1886: 549, pl. 16, fig. 4. — Van Straelen 1925: 267. — Woods 1930: 78, pl. 21, fig. 9. — Secrétan 1964: 69. — Schweitzer *et al.* 2010: 24.

Clytia georgei – Glaessner 1929: 115.

Eryma stricklandi – Förster 1966: 111, fig. 18, pl. 15, fig. 1 (non 2-3, 6).

TYPE MATERIAL. — Holotype SM J 3247; one paratype SM J 3248.

TYPE LOCALITY. — St. Ives, Cambridgeshire, United Kingdom.

TYPE AGE. — Oxfordian.

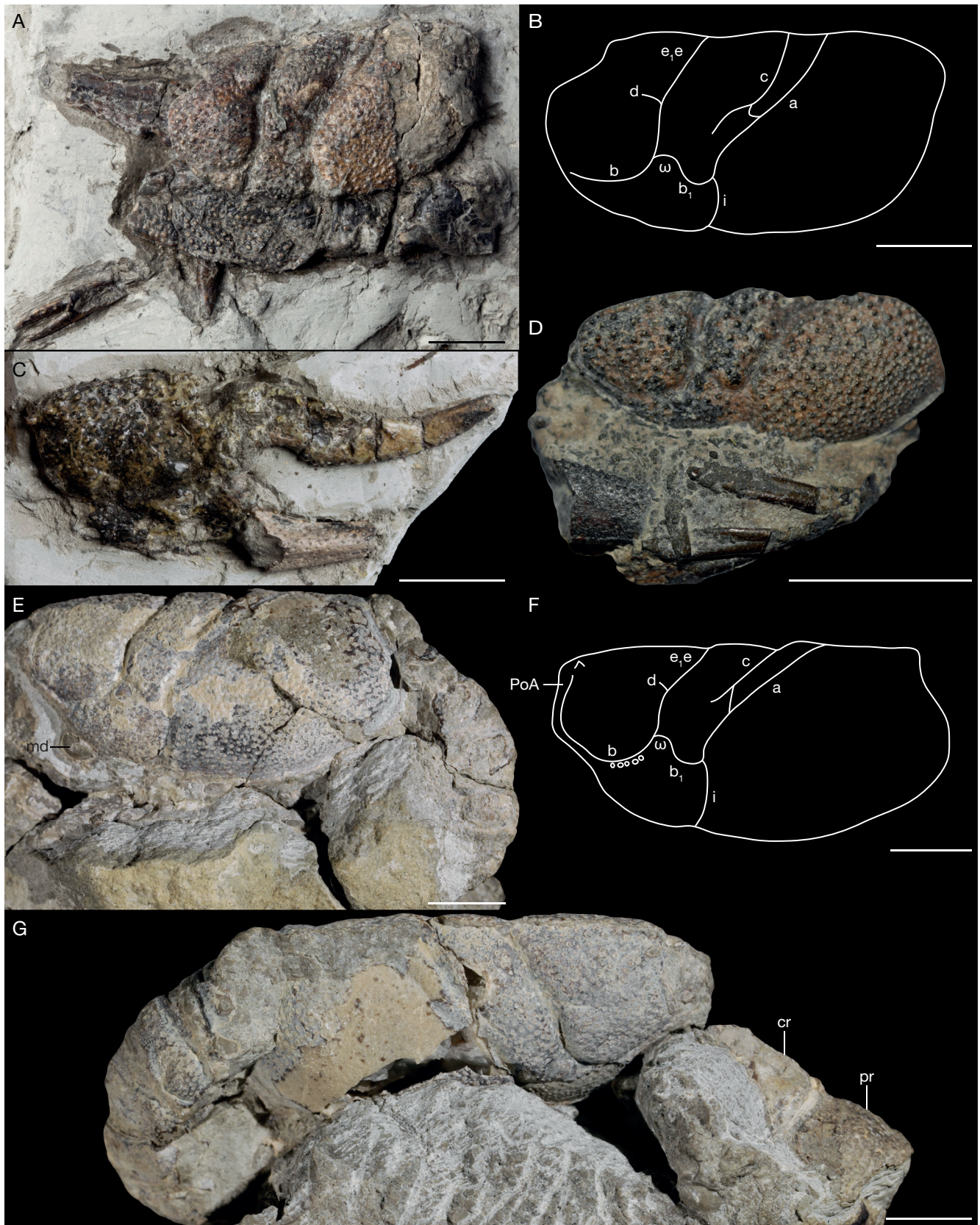


FIG. 2. — *Eryma georgeii* Carter, 1868 and *Eryma jungostricta* Feldmann & Titus, 2006 from the Oxfordian: **A, B**, holotype SM J 3247 of *E. georgeii* (St Ives, United Kingdom): general view (**A**), schema (**B**); **C**, paratype SM J 3248 of *E. georgeii* (St Ives, United Kingdom); **D**, carapace of *E. georgeii* NMB F501 (Soyhières, Switzerland), left lateral view; **E–G**, holotype USNM 530027 of *E. jungostricta* (Utah, United States): left lateral view (**E**), schema (**F**), right lateral view (**G**). Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **cr**, carpus; **d**, gastro-orbital groove; **e₁e**, cervical groove; **i**, inferior groove; **md**, mandible; **PoA**, post-orbital area; **pr**, propodus; **ω**: attachment site of mandibular muscle. Photographs: A, C, D, J. Devillez; E, G, L. O'Reilly. Line drawings: J. Devillez. Scale bars: 1 cm.

DESCRIPTION

Carapace

Sub-cylindrical carapace; deep and wide cervical groove, strongly inclined dorsally, sub-vertical under its strong median inflexion, joined to dorsal margin and to antennal groove; deep and shallow antennal groove, curved; short gastro-orbital groove, deep and wide, originating as median inflexion of cervical groove; deep postcervical groove, sinuous, joined to dorsal margin and to branchiocardiac groove at carapace mid-height, with a long and sinuous ventral extension; branchiocardiac groove slightly curved, narrow dorsally, joined to dorsal margin and to hepatic groove; shallow and narrow hepatic groove, concavo-convex, joined to cervical groove; inflated ω area; flat χ area; deep and wide inferior groove.

Thoracic appendages

Chelate P1; P1 propodus trapezoidal, inner and outer margins slightly rounded in shape, compressed dorso-ventrally; narrow dactylar bulge, posteriorly delimited by a deep groove; long P1 fingers, strongly curved inward, progressively narrowing to their distal extremity, basis of occlusal margin of the dactylus strongly curved, with small conical teeth very closely spaced.

Ornamentation

Carapace homogeneously covered by small and prominent tubercles, separated by wide rounded depressions; P1 propodus covered by small tubercles preceded by deep crescent-shaped depressions; fingers covered by depressions.

DISCUSSION

Eryma georgeii was described on a carapace and an isolated P1 chela. It is assigned to *Eryma* because of the short gastro-orbital groove, the presence of a junction between postcervical and branchiocardiac grooves at carapace mid-height, the sinuous hepatic groove and the shape of the chela (trapezoidal, compressed propodus bearing curved fingers narrowing to their distal extremity).

Förster (1966) considered this species as a junior synonym of *Eryma stricklandi* (Phillips, 1871). This latter is based on a P1 chela which has not the classical morphology of those of the erymoid lobsters (see discussion above about *Eryma* for more details). However, Carter's species is clearly an erymid, so *E. georgeii* is here considered as a valid species.

Eryma georgeii has an extremely elongated ventral extension of the postcervical groove, which is a unique feature among the genus. The ornamentation of this species made of tubercles separated by depressions is present in some species of the genus, but the tubercles of *E. georgeii* have the particularity to be strongly prominent. Moreover, the clearly trapezoidal shape of the P1 propodus of this species is distinct from that of *E. jungostrictrix*, *E. lerasi*, *E. major*, *E. mandelslohi*, *E. modestiforme*, *E. quadriverrucatum*, *E. veltheimii*, *E. ventrosum*, and *E. westphali*.

Eryma jungostrictrix Feldmann & Titus, 2006 (Fig. 2E-G)

Eryma jungostrictrix Feldmann & Titus, 2006: 64, figs 3-4. — Garassino & Schweigert 2006: 8. — Feldmann & Haggart 2007: 1792, 1794. — Schweitzer *et al.* 2010: 24. — Devillez *et al.* 2017: 792.

TYPE MATERIAL. — Holotype USNM 530027.

TYPE LOCALITY. — NE $\frac{1}{4}$, SW $\frac{1}{4}$, SW $\frac{1}{4}$, Sec. 4, T5S, R24E (Salt Lake Meridian), Utah, United States.

TYPE AGE. — Oxfordian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; short, spiny rostrum; fusiform intercalated plate; narrow, inflated post-orbital area; high pterygostomial region; deep and wide cervical groove, strongly inflected at carapace mid-height, joined to dorsal margin and to antennal groove; shallow and narrow antennal groove; short and narrow gastro-orbital groove, originating as strong median inflexion of cervical groove; deep and wide postcervical groove, almost straight, strongly inclined, joined to dorsal margin and joined to branchiocardiac groove at carapace mid-height, with a short ventral extension; deep branchiocardiac groove, subparallel to postcervical groove, almost straight dorsally, slightly curved towards its junction to the hepatic groove, strongly inclined, joined to dorsal margin and to hepatic groove; deep and wide hepatic groove, concavo-convex, joined to cervical groove; inflated ω area, strongly rounded in shape, ventrally delimited by a shallow depression extending between antennal and hepatic grooves; flat χ area; deep and wide inferior groove.

Pleon and uropods

Somites with a bulge at the basis of the pleurites.

Thoracic appendages

Chelate P1; P1 propodus subrectangular, compressed dorso-ventrally; P1 carpus short, subtriangular.

Ornamentation

Carapace densely covered by rounded tubercles; gastric region with a row of coarse tubercles parallel to the intercalated plate, and with an oblique orbital row ended by a strong antennal spine; pterygostomial region with a row of coarse tubercles under the antennal groove; pleonal tergites with small and widely spaced tubercles; pleonal pleurites densely covered by rounded depressions; P1 propodus and carpus densely covered by small tubercles.

DISCUSSION

Eryma jungostrictrix is known by only one specimen with a carapace connected to a first cheliped and most of the pleon. A mandible is also preserved (Fig. 2E). The generic assignment of this species is supported by the typical carapace groove pattern: short gastro-orbital groove, presence of a junction between postcervical and branchiocardiac grooves, and sinuous hepatic groove.

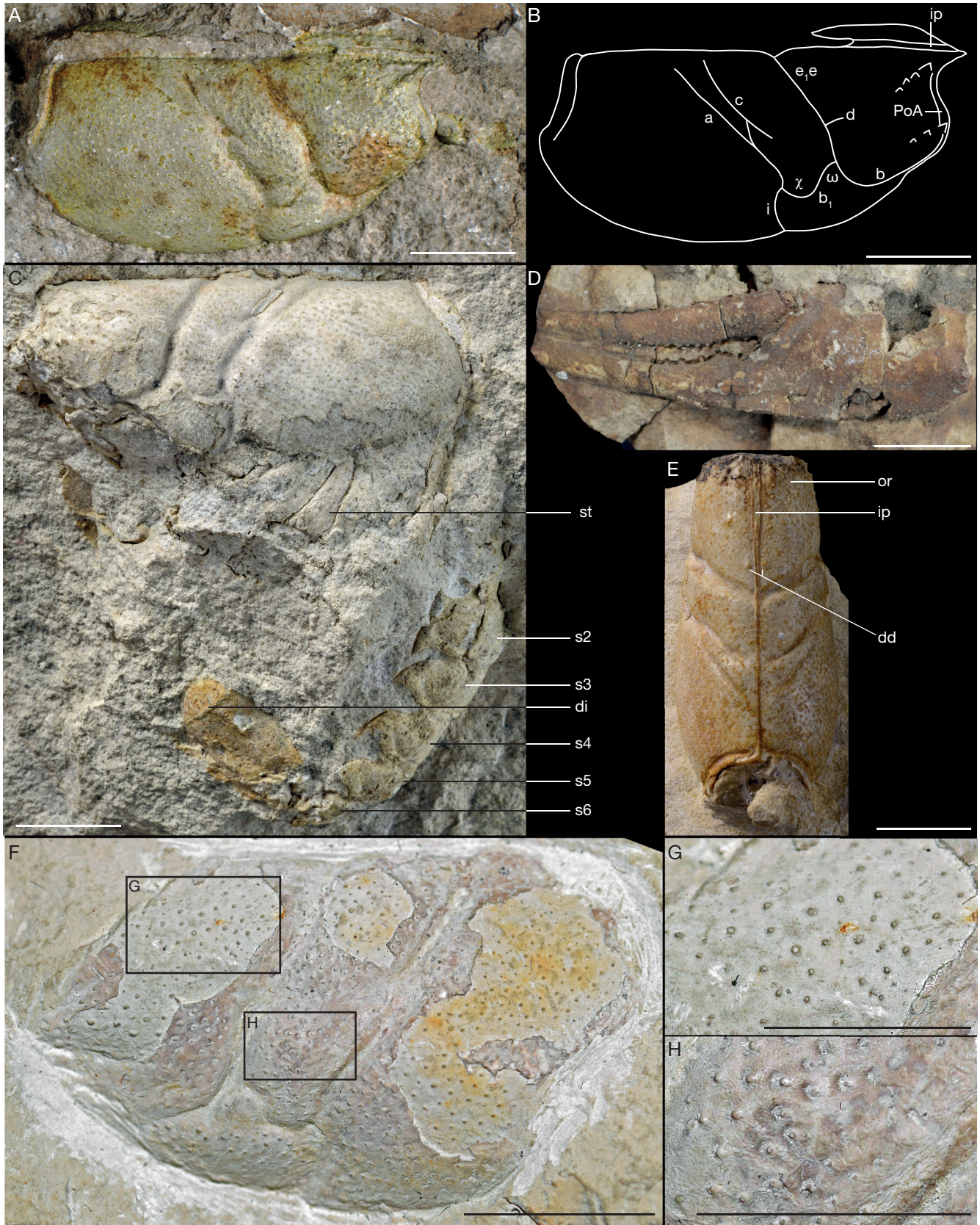


FIG. 3. — *Eryma ventrosus* (Meyer, 1835) from France: **A, B**, cast of the holotype MNHN.F.B12484 (Oxfordian, Frétille); general view (A), schema (B); **C**, specimen MNHN.F.A29468 (Oxfordian, Mailley); **D**, specimen MNHN.F.A29470 (Oxfordian, Mailley); **E**, specimen MNHN.F.A29479 (Oxfordian, Montcey); **F-H**, specimen BSPG 1961 VIII 148 (Kimmeridgian, Chablais): general view (F), detailed view of an entirely decorticated area (G), detailed view of an area non entirely decorticated (H). Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **dd**, dorsal domes; **di**, diaeresis; **e, e**, cervical groove; **i**, inferior groove; **ip**, intercalated plate; **or**, orbital row; **PoA**, post-orbital area; **s2-s6**, pleonal somites; **st**, sternum; χ , attachment site of adductor testis muscle; ω , attachment site of mandibular muscle. Photographs: A, D, F-G, J. Devillez; C, L. Cazes; E, P. Loubry. Line drawing: J. Devillez. Scale bars: 1 cm.

Eryma jungostrix is the only *Eryma* species to have a row of tubercles under the antennal groove. Some features of its carapace groove pattern support the distinction of *E. jungostrix* from other Late Jurassic species. Indeed, the strong inflexion of the cervical groove is not present in *E. mandelslohi*, *E. modestiforme*, *E. ventrosum*, and *E. westphali*. Moreover, the almost straight postcervical and branchiocardiac grooves are distinct from *E. georgeii*, *E. lerasi*, *E. mandelslohi*, *E. modestiforme*, *E. quadriverrucatum*, *E. ventrosum*, and *E. westphali*. The carapace ornamentation of *E. jungostrix* is only made of tubercles contrary to *E. georgeii*, *E. lerasi*, *E. mandelslohi*, *E. modestiforme*, *E. quadriverrucatum*, *E. ventrosum*, and *E. westphali*.

***Eryma ventrosum* (Meyer, 1835)**
(Figs 3-5)

Glypheia ventrosa Meyer, 1835: 329; 1836: 56. — Quenstedt 1857: 599, pl. 74, fig. 20.

Clytia girodi Étallon, 1857: 19 (*nomen nudum*). **n. syn.**

Bolina thirriae Étallon, 1859: 198, pl. 5, fig. 5.

Eryma greppini Oppel, 1861: 357; 1862: 27, pl. 4, figs 8-9 **n. syn.** — Trautschold 1866: 20, 21. — Quenstedt 1857: 321; 1885: 410. — Carter 1886: 549. — Krause 1891: 201. — Lissajous 1907: 66. — Van Straelen 1925: 245, fig. 114. — Secrétan 1964: 69. — Wannier & Panchaud 1977: 931. — Förster & Seyed-Emami 1982: 43. — Bravi *et al.* 2014: 94. — Charbonnier *et al.* 2014b: 333, figs 2-4. **n. syn.** — Devillez & Charbonnier 2019: 17.

Eryma radiata Oppel, 1861: 358; 1862: 31, pl. 6, figs 2-3. — Morière 1888: 143. — Lahusen 1894: 318. — Förster 1966: 113. — Etter 2004: 384. — Feldmann & Titus 2006: 64. **n. syn.**

Eryma subventrosa Étallon, 1861: 165. — Oppel 1861: 358; 1862: 33. — Van Straelen 1925: 263. — Schweitzer *et al.* 2010: 25.

Eryma rugosa Étallon, 1861: 167, pl. 8, figs 3-4. — Oppel 1861: 358; 1862: 31. — Lahusen 1894: 321. **n. syn.**

Eryma babeau Étallon, 1861: 169, pl. 8, fig. 1. — Oppel 1861: 359; 1862: 42, pl. 10, fig. 8. — Dollfus 1863: 36. — Morière 1883: 165. — Carter 1886: 548, pl. 16, fig. 3. — Krause 1891: 207. — Sauvage 1891: 92, 95, pl. 4, figs 1-2. — Van Straelen 1925: 269, fig. 125. — Woods 1930: 78. — Förster 1966: 115, pl. 16, fig. 4. — Carriol 1991: 222. — Feldmann & Titus 2006: 63. — Schweitzer *et al.* 2010: 23. — Devillez *et al.* 2016: 524, table 1.

Eryma thurmanni Étallon, 1861: 169, pl. 7, fig. 4. — Oppel 1861: 359; 1862: 42. — Étallon & Thurmann 1862: 437, pl. 60, fig. 11. — Van Straelen 1925: 268. — Schweitzer *et al.* 2010: 25.

Eryma affinis Ferry, 1865: 368, pl. 7, figs 3-4. — Lissajous 1907: 66. — Van Straelen 1925: 249, fig. 116. — Secrétan 1964: 69. — Förster 1966: 102. — Feldmann & Titus 2006: 63. — Schweitzer *et al.* 2010: 23. — Bravi *et al.* 2014: 94. — Charbonnier *et al.* 2014b: 335. **n. syn.**

Eryma villersi Morière, 1883: 166, pl. 1, figs 1-5. — Carter 1886: 548, pl. 16, fig. 3. — Hée 1924: 130. — Van Straelen 1925: 265, pl. 9, fig. 1-2. — Glaessner 1929: 163. — Woods 1930: 78. — Förster 1966: 110. — Carpentier *et al.* 2006: 624, fig. 8. — Schweitzer *et al.* 2010: 25.

Eryma falcifera Morière, 1888: 141, pl. 5, figs 1-2. — Schweitzer *et al.* 2010: 23. **n. syn.**

Eryma corbieri Morière, 1888: 142, pl. 5, fig. 3. — Krause 1891: 205. — Hée 1924: 132. — Schweitzer *et al.* 2010: 23. **n. syn.**

Eryma caraboeufi Morière, 1888: 143, pl. 5, fig. 4. — Hée 1924: 131. — Van Straelen 1925: 254. — Glaessner 1929: 162. — Förster 1966: 103. — Crônier & Courville 2004: 1007. — Feldmann & Titus 2006: 63. — Schweitzer *et al.* 2010: 23. **n. syn.**

Eryma meandrina Krause, 1891: 204, pl. 13, fig. 7. — Van Straelen 1925: 253. — Beurlen 1928: 174. — Crônier & Courville 2004: 1007. — Schweitzer *et al.* 2010: 25.

Eryma crassimanus Krause, 1891: 205, pl. 13, fig. 5. — Van Straelen 1925: 267. — Beurlen 1928: 157, 162, 163. — Glaessner 1929: 153. — Förster 1966: 113. — Feldmann & Titus 2006: 63. **n. syn.**

Eryma fossata Krause, 1891: 205, pl. 13, fig. 6. — Beurlen 1928: 157, 159, 163. — Secrétan 1964: 69. — Förster 1966: 113. — Förster & Seyed-Emami 1982: 44. — Feldmann & Titus 2006: 63. **n. syn.**

Eryma leblanci Sauvage, 1891: 90, pl. 4, fig. 6. — Carriol 1991: 224. **n. syn.**

Eryma boloniensis Sauvage, 1891: 92, pl. 3, figs 5-6. — Van Straelen 1925: 282. — Glaessner 1929: 152. — Förster 1966: 116 (non pl. 16, fig. 5). — Carriol 1991: 223. — Feldmann & Titus 2006: 63. — Schweitzer *et al.* 2010: 23. **n. syn.**

Eryma beaugrandi Sauvage, 1891: 94, pl. 4, fig. 3. — Carriol 1991: 223. **n. syn.**

Eryma cumonti Van Straelen, 1921: 139, pl. 1, figs 2-3; 1922: 983; 1925: 253, fig. 118. — Secrétan 1964: 67, 68. — Förster 1966: 103. — Fischer 2003: 241. — Crônier & Courville 2004: 1007. — Feldmann & Titus 2006: 63. — Charbonnier 2009: 15, 158, table 14. — Charbonnier *et al.* 2010: 115, tables 1-2, figs 3B, 4E; 2014a: 375. — Schweitzer *et al.* 2010: 23. **n. syn.**

Eryma morieri Hée, 1924: 128, pl. 3, fig. 2. — Schweitzer *et al.* 2010: 25.

Eryma corallina Van Straelen, 1925: 255, fig. 119, pl. 8, fig. 4. — Secrétan 1964: 69. — Förster 1966: 103. — Crônier & Courville 2004: 1007. — Feldmann & Titus 2006: 63. **n. syn.**

Galicia marianae Garassino & Krobicki, 2002: 55, fig. 5-8. — Schweitzer *et al.* 2010: 25. — Karasawa *et al.* 2013: table 1. — Hyžný *et al.* 2015: 375, 376, 379. — Devillez *et al.* 2017: 6, 8, figs 2G-H.

Klytia ventrosa — Meyer 1840b: 20, pl. 4, fig. 29. — Quenstedt 1850: 195, pl. 2, figs 18-19. — Devillez *et al.* 2017: 4, figs 2C-D.

Clytia ventrosa — Bronn 1849: 578; 1852: 425. — Reuss 1854: 4, 5. — Beurlen 1928: 168. — Glaessner 1929: 118. — Vialle 1948: 63.

Astacus ventrosus — Quenstedt 1852: 268, pl. 20, fig. 13; 1867: 320, pl. 25, fig. 13; 1885: 410, 412, pl. 32, fig. 8.

Fig. 4. — Synonyms of *Eryma ventrosum* (Meyer, 1835): **A**, original figure of Étallon (1861: pl. 8, fig. 4) of *Eryma rugosa* (Oxfordian, Eschert, France); **B**, original figure of Étallon (1861: pl. 8, fig. 4) of *Eryma thurmanni* (Kimmeridgian, Porrentruy, France); **C**, **D**, original figures of Morière (1888: pl. 5, figs 1-2) of *Eryma falcifera* (Callovian, Écouché, France); **E**, original figure of Morière (1888: pl. 5, fig. 4) of *Eryma caraboeufi* (Callovian, Troarn, France); **F**, original figure of Morière (1888: pl. 5, fig. 3) of *Eryma corbieri* (Callovian, Écouché, France); **G**, original figure of Krause (1891: pl. 8, fig. 7) of *Eryma meandrina* (Callovian, Hildesheim, Germany); **H**, original figure of Krause (1891: pl. 8, fig. 5) of *Eryma crassimanus* (Oxfordian, Galgenberg near Hildesheim, Germany); **I**, original figure of Krause (1891: pl. 8,

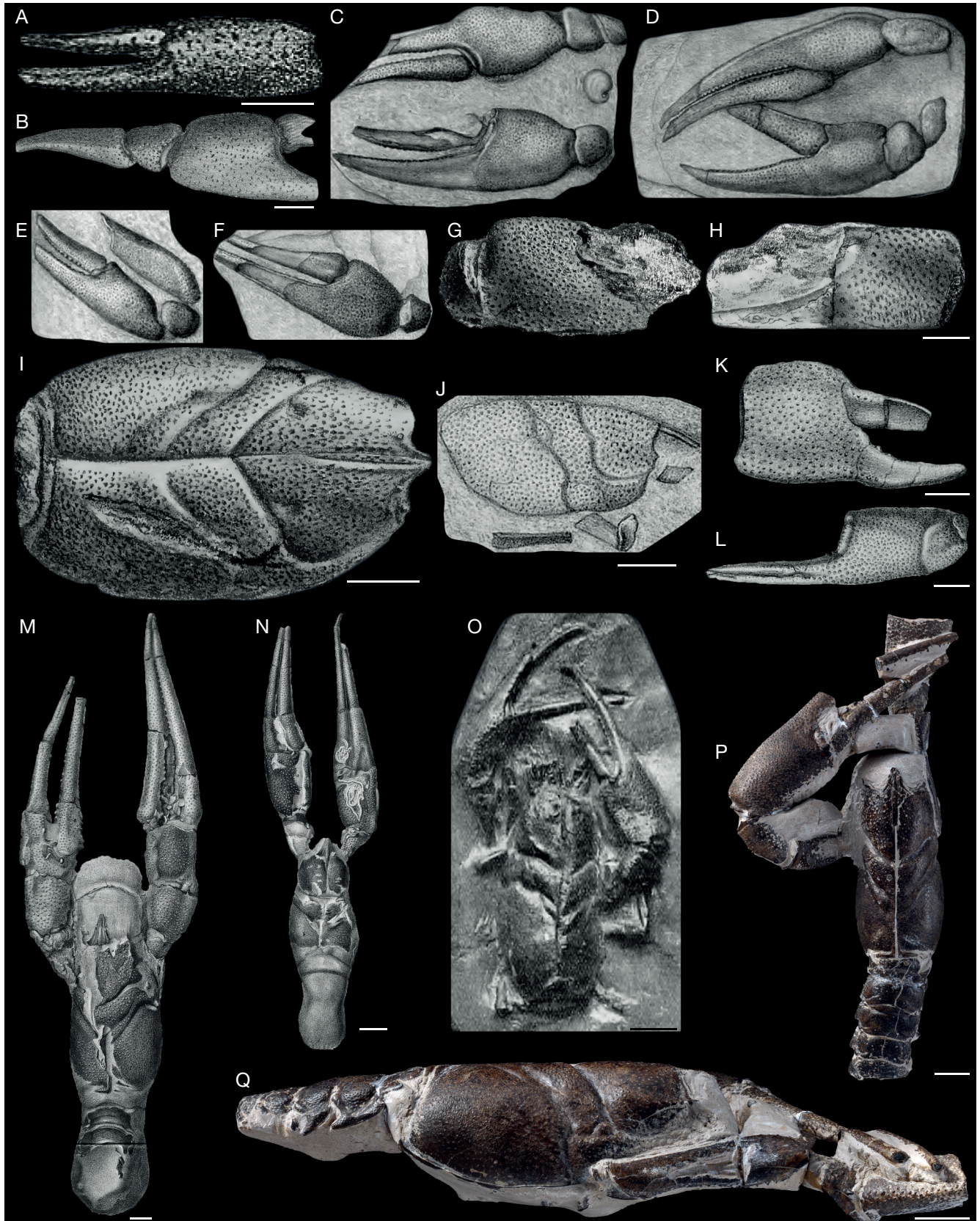


fig. 6) of *Eryma fossata* (Oxfordian, Galgenberg near Hildesheim, Germany); **J**, original figure of Sauvage (1891: pl. 4, fig. 6) of *Eryma leblanci* (Kimmeridgian, Boulogne-sur-Mer, France); **K**, original figure of Sauvage (1891: pl. 3, fig. 5) of *Eryma boloniensis* (Kimmeridgian, Boulogne-sur-Mer, France); **L**, original figure of Sauvage (1891: pl. 4, fig. 3) of *Eryma beaugrandi* (Kimmeridgian, Boulogne-sur-Mer, France); **M**, **N**, original figures of Morière (1883: pl. 1, figs 1-2) of the syntypes of *Eryma villersi* (Oxfordian, Villers-sur-Mer, France); **O**, original figure of Van Straelen (1925: pl. 9, fig. 1) of the holotype of *Eryma morieri* Hée, 1924 (Oxfordian, Villers-sur-Mer, France); **P**, **Q**, specimen from the Callovian of Villers-sur-Mer (France, private collection of J.-P. Pezy). Photographs: L. Cazes. Scale bars: 1 cm.

Bolina ventrosa – Étallon 1859: 194, 202, pl. 6, figs 1-6. — Morière 1883: 165.

Bolina ventrosa var. *major* – Étallon 1859: 194, pl. 6, figs 1-6.

Bolina girodi Étallon, 1859: 196, pl. 6, figs 7-8. — Devillez & Charbonnier 2017: table 1.

Eryma ventrosa – Étallon 1861: 164, pl. 8, fig. 7. — Oppel 1861: 358; 1862: 32, pl. 6, fig. 4. — Morière 1883: 165, 166. — Carter 1886: 547, 550. — Krause 1891: 202. — Sauvage 1891: 93, 95. — Van Straelen 1921: 141. — Hée 1924: 127. — Beurlen 1928: 156, 160. — Woods 1930: 76, pl. 21, fig. 4, figs 6-7 (non 5). — Woods 1957: 156. — Secrétan 1964: 69. — Förster 1966: 108, fig. 12, pl. 15, figs 4-5, fig. 7, pl. 16, figs 1-2. — Feldmann & Copeland 1988: 95. — Crônier & Courville 2004: 1005, 1006. — Etter 2004: 384. — Carpentier *et al.* 2006: 624, fig. 5D. — Feldmann & Titus 2006: 64. — Charbonnier *et al.* 2012b: 552, figs 14-17.

Eryma girodi – Étallon 1861: 165. — Oppel 1861: 357; 1862: 28. — Sauvage 1891: 91. — Van Straelen 1925: 248, fig. 115, pl. 8, fig. 1. — Secrétan 1964: 69. — Förster & Seyed-Emami 1982: 43.

Eryma thirriai – Étallon 1861: 168. — Oppel 1861: 359; 1862: 42. — Sauvage 1891: 91. — Van Straelen 1925: 267, fig. 124, pl. 9, fig. 3. — Secrétan 1964: 69. — Schweitzer *et al.* 2010: 25.

Eryma mandelslohi – Van Straelen 1922: 983. — Vialle 1948: 60. — Martill 1991: fig. 7.3j. — Charbonnier 2009: 15, table 14, figs 234, 242; 2010: pl. 2, fig. 7. — Charbonnier *et al.* 2010: 115, tables 1-2, fig. 4D; 2014a: 375, table 1, figs 4J.

Eryma bizeti – Van Straelen 1925: 250, fig. 117, pl. 8, figs 2-3.

Clytia greppini – Beurlen 1928: 168, 172. — Glaessner 1929: 116. — Vialle 1948: 64.

Clytia girodi – Beurlen 1928: 168. — Glaessner 1929: 115.

Clytia radiata – Beurlen 1928: 169, 170, pl. 7, fig. 18, 21.

Clytia thirriai – Beurlen 1928: 171. — Glaessner 1929: 117. — Vialle 1948: 64.

Erymastacus babeau – Beurlen 1928: 175. — Schweigert *et al.* 2000: 8, pl. 3, figs 4-5.

Clytia affinis – Glaessner 1929: 114.

Clytia corallina – Glaessner 1929: 115.

Clytia cumonti – Glaessner 1929: 115.

Clytia thurmanni – Glaessner 1929: 118.

Eryma sp. cf. *ventrosa* – Woods 1930: 77, pl. 20, fig. 8.

Eryma cf. *bedelta* – Beurlen 1933: 89, 91, fig. 1.

Eryma sp. – Förster 1966: 101, pl. 14, fig. 13 (non 7). — Etter 2004: 384, fig. 2A.

Eryma cf. *babeau* – Carpentier *et al.* 2006: 623, fig. 7.

Eryma corallinum – Schweitzer *et al.* 2010: 23.

Eryma crassimanum – Schweitzer *et al.* 2010: 23.

Eryma fossatum – Schweitzer *et al.* 2010: 24.

Eryma radiatum – Schweitzer *et al.* 2010: 24.

Eryma ventrosus – Schweitzer *et al.* 2010: 25. — Charbonnier *et al.* 2015: tables 1-2, figs 3-5a, b. — Devillez *et al.* 2016: 518; 2017: 6, 8, table 1. — Devillez & Charbonnier 2019: 5, 7, 13, 15, 17, 32.

Stenodactylina villersi – Devillez *et al.* 2016: 524.

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

TYPE LOCALITY. — Fréteigny, Haute-Saône département, Bourgogne, France.

TYPE AGE. — Oxfordian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; moderately elongated, spineless rostrum; fusiform intercalated plate; smooth post-orbital area; deep and wide cervical groove, strongly inclined dorsally, slightly inclined ventrally, joined to dorsal margin and to antennal groove; deep and narrow antennal groove; short gastro-orbital groove, originating as a median inflexion of cervical groove; deep and wide postcervical groove, almost straight or very slightly concave forward, not joined to dorsal margin, joined to branchiocardiac groove at carapace mid-height, with a straight ventral extension; deep and wide branchiocardiac groove, almost straight with a slight inflexion towards its junction with hepatic groove, not joined to dorsal margin, joined to hepatic groove; deep and narrow hepatic groove, concavo-convex, joined to cervical groove; inflated ω area; flat or slightly inflated χ area; deep and wide inferior groove, curved forward, joined to hepatic groove.

Pleon and uropods

Somites with subrectangular tergites; somites with subtriangular pleurites, directed backward, with a longitudinal elliptic bulge on their basis; s2 pleurites wider than others, s3-5 pleurites equal in length, s6 pleurites shorter; rounded telson; uropods as long as telson; uropodal endopods with a longitudinal carina; uropodal exopods with a diaeresis, and a longitudinal carina.

Eyes and cephalic appendages

Rounded stalked eyes, with numerous small rectangular ommatidia; antennae made of numerous and short cylindrical articles; short, triangular scaphocerite; wide epistome, with a linear contact with the carapace; wide, subrectangular mandibles (Charbonnier *et al.* 2012b: fig. 14F-G).

Thoracic appendages

Elongated Mxp3; chelate P1; P1 propodus subrectangular or trapezoidal, compressed dorso-ventrally; narrow dactylar bulge, inflated, posteriorly delimited by a deep and narrow groove; thin, elongated fingers, equal in length, progres-

FIG. 5. — Additional synonyms of *Eryma ventrosus* (Meyer, 1835): **A**, **B**, holotype BSPG AS VIII 114 of *Eryma radiatum* Oppel, 1861 (Oxfordian, Balingen, Germany); carapace (**A**), P1 chela (**B**); **C**, holotype IRSNB of *Eryma cumonti* Van Straelen, 1921 (Callovian, Pouques-les-Eaux, France); **D**, holotype MNHN.F.B13231 of *Eryma babeau* Étallon, 1861 (Kimmeridgian, Boulogne-sur-mer, France); **E**, syntype MNHN.F.A29782 of *Bolina thirriai* Étallon, 1859 (Kimmeridgian, Gray, France); **F**, syntype MNHN.F.A29727 of *Eryma affinis* Ferry, 1865 (Bathonian, Fuissé, France); **G**, original figure of Garassino & Krobicki (2002: fig. 7) of the



holotype of *Galiccia marianae* (Oxfordian, Rudno, Poland); **H**, syntype MNHN.F.A29783 of *Bolina girodi* Étallon, 1859 (Saint-Claude, France); **I**, lectotype MJSN Col.Del.475 of *Eryma greppini* (Oppel, 1861) (Vellerat, Switzerland); **J**, paralectotype MJSN Col.Del.1 of *E. greppini* (Vellerat, Switzerland); **K**, dorsal view of the syntype MNHN.F.A29783 of *B. girodi*; **L**, dorsal view of the lectotype MJSN Col.Del.475 of *E. greppini*; **M**, specimen MFN 2236 P1383/2 MB.A.1537 from the Late Jurassic of Tanzania. Abbreviation: **dd**, dorsal domes. Photographs: A-C, M, J, Devillez; D-F, P. Loubry; H, K, L, Cazes; I-J, L, D. Becker. Scale bars: 1 cm.

sively narrowing to their distal extremity, almost straight or curved inward, sometimes with a terminal hook; occlusal margin with small conical teeth closely spaced; P1 carpus short, subtriangular; elongated P1 merus, triangular in section, with a short process at outer side of its ventral extremity; thin P2-P5.

Ornamentation

Carapace densely covered by small tubercles preceded by crescent-shaped depressions; intercalated plate irregularly covered by small tubercles; cephalic region with an oblique row of tubercles ended by an orbital spine; antennal region with an oblique row of tubercles ended by an antennal spine; pleonal tergites and pleurites densely covered by small depressions; P1 propodus, carpus, merus and fingers densely covered by small tubercles; smooth P2-P5.

DISCUSSION

This species is based on a carapace from the Terrain à Chailles Formation (Oxfordian, France) and supported the establishment of *Klytia* Meyer, 1840^b. Careful examination of the cast of the holotype stored in the collections of the MNHN clearly shows that the groove pattern of this carapace is typical of *Eryma*: short gastro-orbital groove, presence of a junction between postcervical and branchiocardiac grooves at carapace mid-height, and sinuous hepatic groove.

The holotype of *Eryma ventrosum* is an internal mould entirely decorticated. So, the apparent ornamentation is only made of tubercles. However, a specimen stored in the collections of the BSPG is only partially decorticated (Fig. 3F). Only tubercles are present on the parts where the internal mould is exposed (Fig. 3G) while these tubercles are preceded by crescent-shaped depressions where the cuticle remains (Fig. 3H). So, the true ornamentation of *E. ventrosum* consists in tubercles and crescent-shaped depressions. This case is an illustration of the effects of the decortication on the ornamentation of the erymid lobsters. The review of *Eryma subventrosa* Étallon, 1861 is probably a concrete case of confusion resulting from the effects of the decortication on ornamentation. This species also from the Terrain à Chailles Formation (Oxfordian, France) has never been figured and the type material is not located. In the description, Étallon pointed out the proximity of this species with *E. ventrosum*, well-represented in the same formations. After Étallon (1861), the main difference is in the ornamentation. Indeed, the tubercles of *E. pseudoventrosa* are inclined forward and are preceded by depressions. Considering these elements, the distinction between *E. ventrosum* and *E. pseudoventrosa* established by Étallon (1861) is probably the consequence of different states of decortication between the holotypes of these two species. So, *E. pseudoventrosa* is here considered as a junior synonym of *E. ventrosum*.

This review results with the integration of many species described since the second half of the nineteenth century into the synonymy of *Eryma ventrosum*. The type material of some of these species could not be examined because it

is lost or destroyed. Some of them were based on P1 chelae more or less complete. Then, *Eryma rugosa* Étallon, 1861 (Oxfordian, France; Fig. 4A), *Eryma thurmanni* Étallon, 1861 (Kimmeridgian, France; Fig. 4B), *Eryma falcifera* Morière, 1888 (Callovian, France; Fig. 4C, D), *Eryma caraboeufi* Morière, 1888 (Callovian, France; Fig. 4E), *Eryma corbieri* Morière, 1888 (Callovian, France; Fig. 4F), *Eryma meandrina* Krause, 1891 (Callovian, Germany; Fig. 4G), *Eryma crassimanus* Krause, 1891 (Oxfordian, Germany; Fig. 4H), *Eryma boloniensis* Sauvage, 1891 (Kimmeridgian, France; Fig. 4K), and *Eryma beaugrandi* Sauvage, 1891 (Kimmeridgian, France; Fig. 4L) exhibit a very similar ornamentation (fine, homogeneous and dense), a subrectangular or slightly trapezoidal P1 propodus, and thin elongated fingers, longer than propodus, progressively narrowing to their distal extremity and with occlusal margins adorned by numerous short conical teeth. These morphological features are characteristics of *E. ventrosum*, so the species previously cited are considered as junior synonyms of this species.

The lost type material of *Eryma fossata* Krause, 1891 (Oxfordian, Germany; Fig. 4I) and *Eryma leblanci* Sauvage, 1891 (Kimmeridgian, France; Fig. 4J) consists of isolated carapaces. Both exhibit a dense, fine ornamentation very close to that of *E. ventrosum*. Moreover, the carapace groove patterns of *E. fossata* and *E. leblanci* are similar to that of *E. ventrosum* with a slightly inflected cervical groove, a short gastro-orbital groove, deep and wide postcervical and branchiocardiac grooves, slightly curved and joined at the level of the gastro-orbital groove. So, *E. fossata* and *E. leblanci* are also considered as junior synonyms of *E. ventrosum*.

Van Straelen (1925) described *Eryma corallina* (Callovian, France) based on a fragment of carapace poorly preserved and currently lost. The original photograph is not good enough to clearly see the specimen, but the characteristics of the species are represented on a schematic sketch (Van Straelen 1925: fig. 119). It shows the presence of orbital and antennal rows of tubercles like in *E. ventrosum*. The description also indicates a fine ornamentation with small tubercles. These features led us to consider *E. corallina* as another junior synonym of *E. ventrosum*.

The erymid fossils from the Callovian – Oxfordian of the Vaches Noires cliffs (Normandy, France) are assigned to *Eryma villersi* Morière, 1883 and *Eryma morieri* Hée, 1924 (Fig. 4O). The type material of these species figured by Morière (1883; Fig. 4M-N) was probably destroyed during the World War II but numerous fossils were found in the same locality since the nineteenth century. So, the examination of the figures of Morière (1883) and of new specimens (Fig. 4P, Q) reveals that *E. villersi* and *E. morieri* have a cervical groove slightly inflected, a short gastro-orbital groove, slightly curved postcervical and branchiocardiac grooves, joined at carapace mid-height, a ventral extension of the postcervical groove, an inflated ω area, a dense, fine ornamentation made of tubercles and crescent-shaped depressions, orbital and antennal rows of tubercles, elongated P1 chelae with a subrectangular propodus which is compressed dorso-ventrally, bearing long thin fingers armed

with numerous teeth. These species share the listed characteristics with *E. ventrosum*, so, following Förster (1966), we consider *E. villersi* and *E. morieri* as junior synonyms of *E. ventrosum*. Previously, Devillez *et al.* (2016) assigned *E. villersi* to *Stenodactylina* because the junction of the postcervical and branchiocardiac grooves is not visible on Morière's original figures and the strong length of the P1 fingers of the specimens. However, the junction of the postcervical and branchiocardiac grooves which is usually shallow. So, this could explain the absence on Morière's figure.

The holotype of *Eryma radiatum* Oppel, 1861 (Oxfordian, Germany; Fig. 5A, B) has a carapace groove pattern (short gastro-orbital groove, postcervical and branchiocardiac grooves slightly curved and joined at carapace mid-height, presence of a ventral extension of the postcervical groove), an ornamentation (dense made of small tubercles preceded by crescent-shaped depressions), and a P1 chela (slightly trapezoidal propodus, compressed dorso-ventrally, thin and elongated fingers, curved inward) very close to those of *E. ventrosum*. Both *Eryma cumonti* Van Straelen, 1921 (Callovian, France; Fig. 5C), *Eryma babeau* Étallon, 1861 (Kimmeridgian, France; Fig. 5D), *Bolina thirriae* Étallon, 1859 (Kimmeridgian, France; Fig. 5E), *Eryma affinis* Ferry, 1865 (Bathonian, France, Fig. 5F), and *Galicja marianae* Garassino & Krobicki, 2002 (Oxfordian, Poland; Fig. 5G) exhibit similar characteristics. So, considering these morphological features, we consider *E. radiatum*, *E. cumonti*, *E. babeau*, *B. thirriae*, *E. affinis*, and *G. marianae* as junior synonyms of *E. ventrosum*.

Bolina girodi Étallon, 1859 (Bathonian, France; Fig. 5H,) and *Eryma greppini* (Oppel, 1861) (Bathonian, Switzerland; Fig. 5I-J) exhibit characteristics similar to those previously listed. Charbonnier *et al.* (2014b) pointed out the presence of a pair of dorsal domes in the posterior part of the gastric region in *E. greppini* (Fig. 5L). They considered this morphological feature taxonomically significant, and supported the reinstatement of the species, previously considered as a synonym of *E. bedeltum* (Förster 1966). We noticed the presence of this pair of domes on the syntype of *B. girodi* (Fig. 5K) and some dorsally well-preserved specimens of *E. ventrosum* (Fig. 3E). So, considering these elements (carapace groove pattern, ornamentation, morphology of P1 chelae), we also add *B. girodi* and *E. greppini* to the synonymy of *E. ventrosum*.

The erymids from the La Voulte Lagerstätte were usually identified as *E. mandelslohi* (Van Straelen 1922; Vialle 1948; Martill 1991; Charbonnier 2009; Charbonnier 2010; Charbonnier *et al.* 2010; Charbonnier *et al.* 2014a). However, they are here assigned to *E. ventrosum* considering both carapace groove pattern and ornamentation. Indeed, there are tubercles on the carapace of these specimens and *E. mandelslohi* is covered by depressions (Devillez & Charbonnier 2019).

Beurlen (1933) identified as *Eryma* cf. *bedelta* a specimen found in Late Jurassic deposits of Tanzania (Fig. 5M). The careful examination of the specimen, stored in the collections of the MFN, reveals a carapace groove pattern and

an ornamentation very similar to those of *E. ventrosum*. So, we assigned this African specimen to this species. It is the most southern occurrence of *E. ventrosum*, the only one out of Europe.

Eryma ventrosum has very slightly curved postcervical and branchiocardiac grooves with non-convergent trajectories contrary to *E. georgeii*, *E. mandelslohi*, *E. modestiforme*, *E. quadriverrucatum*, and *E. westphali*. The ventral extension of the postcervical groove in *E. ventrosum* is absent in *E. lerasi* and *E. quadriverrucatum*. Then, the ornamentation of *E. ventrosum* is made of tubercles and depressions while that of *E. jungostrix*, *E. major*, *E. mandelslohi*, and *E. veltheimii* is only made of tubercles or depressions. Moreover, *E. ventrosum* has both antennal and orbital row of tubercles contrary to *E. jungostrix*, *E. lerasi*, *E. mandelslohi*, *E. modestiforme*, *E. quadriverrucatum*, *E. veltheimii*, and *E. westphali*.

Eryma lerasi (Étallon, 1861) (Fig. 6)

Macrourites lerasi Étallon, 1861: 170, pl. 1, fig. 6.

Eryma dutertrei Sauvage, 1891: 91, pl. 4, figs 7-12. — Van Straelen 1925: 270, fig. 126. — Moret 1946: 51, fig. 2. — Secrétan 1964: 69. — Förster 1966: 117, fig. 20, pl. 16, figs 6-7. — Carriol 1991: 223. — Feldmann & Titus 2006: 63. — Schweitzer *et al.* 2010: 23. **n. syn.**

Eryma gracilimana Lahusen, 1894: 320, pl. 1, fig. 9. — Van Straelen 1925: 272. — Glaessner 1929: 155. — Gerasimov 1955: 25, pl. 8, fig. 8. — Birshstein 1956: 75. — Förster 1966: 122. — Gerasimov *et al.* 1995: 10, 30. — Ilyin 2000: 152, 154, table 1. — Feldmann & Titus 2006: 63. **n. syn.**

Eryma portlandica Woods, 1930: 79, pl. 22, figs 2-4. — Secrétan 1964: 69. **n. syn.**

Eryma lerasi – Van Straelen 1925: 276. — Glaessner 1929: 155. — Schweitzer *et al.* 2010: 24.

Clytia dutertrei – Glaessner 1929: 115.

Eryma bedelta (pars.) – Förster 1966: 99.

Eryma gracilimanum – Schweitzer *et al.* 2010: 24.

TYPE MATERIAL. — Holotype lost (Förster 1966).

TYPE LOCALITY. — Haut-Rhin département, Alsace-Lorraine, France.

TYPE AGE. — Not precised in original publication. However, considering the specimens that could be assigned to *E. lerasi* (see discussion below), all from Late Jurassic deposits, and the absence of sediments corresponding to the end of the Kimmeridgian-Tithonian in Haut-Rhin department (Skrzypek *et al.* 2008), it is reasonable to consider that the lost holotype was probably found in Late Jurassic deposits (Oxfordian-Kimmeridgian).

DESCRIPTION

Carapace

Sub-cylindrical carapace; very narrow post-orbital area; deep and wide cervical groove, curved dorsally, subvertical ventrally, joined to dorsal margin and to antennal groove; deep antennal groove; short, deep gastro-orbital groove,

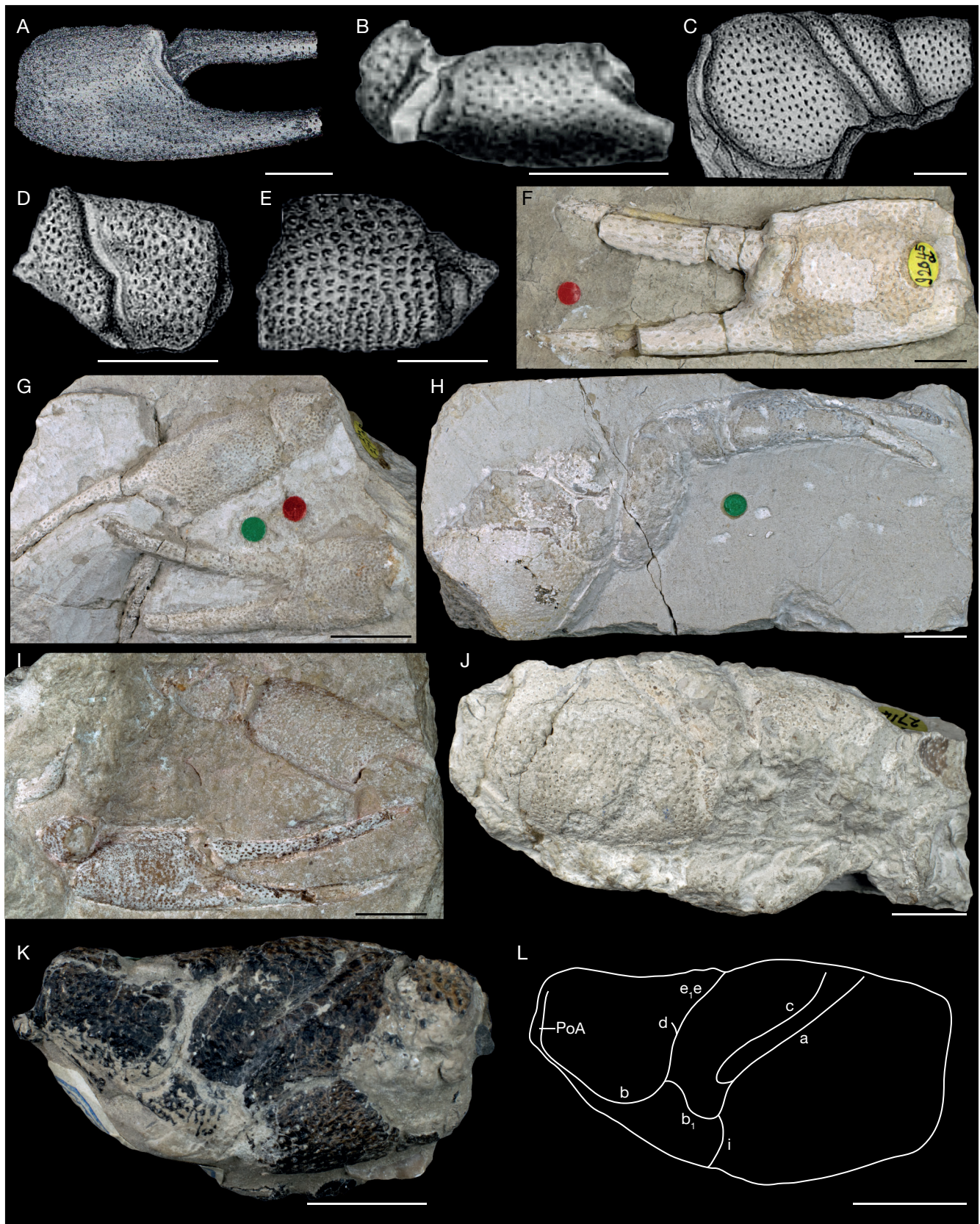


FIG. 6. — *Eryma lerasi* (Étallon, 1861): **A**, original figure of Étallon (1861: pl. 1, fig. 6) of the holotype (Haut-Rhin, France); **B**, original figure of Lahusen (1894: pl. 1, fig. 9) of the holotype of *Eryma gracilimanum* (Tithonian, Mnevnik, Russia); **C-E**, original figures of Sauvage (1891: pl. 4, figs 7-8, 10) of syntypes of *Eryma dutertrei* (Kimmeridgian, Boulogne-sur-Mer, France); **F**, specimen NHMUK 2045 (Kimmeridgian, Portland, United Kingdom); **G-J**, syntypes of *Eryma portlandica* Woods, 1930 (Tithonian, United Kingdom): NHMUK In.27136 from Weymouth (**G**), In.27141 from Portland (**H**), NHMUK I.2835 from Preston (**I**), NHMUK In.27140 from Portland (**J**); **K, L**, specimen NHMUK I.7494 (Kimmeridgian, Weymouth, United Kingdom). Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b₁**, hepatic groove; **c**, post-cervical groove; **d**, gastro-orbital groove; **e,e**, cervical groove; **i**, inferior groove; **PoA**, post-orbital area. Photographs and line drawing: J. Devillez. Scale bars: 1 cm.

originating as a median inflexion of cervical groove; deep postcervical groove, slightly curved, joined to dorsal margin and to branchiocardiac groove; deep and narrow branchiocardiac groove, subparallel to postcervical groove, inflected towards its junction to hepatic groove, strongly inclined, joined to dorsal margin and to hepatic groove; deep and narrow hepatic groove, concavo-convex, joined to cervical groove; flat ω and χ areas; deep and wide inferior groove.

Thoracic appendages

Chelate P1; P1 propodus subrectangular, wide, strongly compressed dorso-ventrally; narrow dactylar bulge, slightly inflated, posteriorly delimited by a groove; thin, elongated fingers, equal in length, almost straight or slightly curved inward; occlusal margins with short and widely spaced conical teeth; P1 carpus short, subtriangular; elongated P1 merus.

Ornamentation

Carapace with a heterogeneous ornamentation; carapace covered by small rounded tubercles preceded by crescent-shaped depressions, depressions wider and deeper in branchial region; P1 propodus, fingers and carpus densely covered by small tubercles preceded by shallow depressions.

DISCUSSION

Macrourites lerasi Étallon, 1861 was described on a P1 chela currently lost. It was assigned to *Eryma* by Van Straelen (1925). This assignation is supported by the subrectangular propodus, compressed dorso-ventrally, with elongated thin fingers curved inward, and a narrow dactylar bulge. Later, Förster (1966) integrated *Eryma lerasi* into the synonymy of *Eryma bedeltum* (Quenstedt, 1857). This synonymy is not maintained here because the P1 fingers of *E. lerasi* are thinner and its P1 propodus is clearly subrectangular and not trapezoidal.

The shape of the propodus, its fine and dense ornamentation, its thin fingers, their slight curvature and the narrow dactylar bulge are morphological features that *E. lerasi* shares with *Eryma portlandica* Woods, 1930 (Tithonian, United Kingdom; Fig. 6G-J). So, *E. portlandica* is here considered as a junior synonym of *E. lerasi*. The illustration of *Eryma gracilimanum* Lahusen, 1894 (Tithonian, Russia; Fig. 6B), an isolated P1 chela, exhibits the same morphological features. So, this species is also considered here as a junior synonym of *E. lerasi*. Contary to *E. lerasi* and *E. gracilimanum*, the type material of *E. portlandica* includes carapaces. *Eryma dutertrei* Sauvage, 1891 (Kimmeridgian, France; Fig. 6C-E) and the carapace identified as *Eryma* cf. *boloniensis* Sauvage, 1891 (Kimmeridgian, United Kingdom; Fig. 6K, L) by Förster (1966) share similar characteristics: the cervical groove is strongly inflected at carapace mid-height and curved dorsally, the junction between the postcervical and branchiocardiac grooves is low on the carapace, the ornamentation is dense, made of tubercles separated by well-marked depressions. So, we also add *E. dutertrei* and the specimen of *E. cf. boloniensis* of Förster (1966) within the synonymy of *E. lerasi*.

The carapace groove pattern of *E. lerasi* exhibits some characteristics distincts from other species of the genus. Indeed, the junction between the postcervical and branchiocardiac grooves is clearly lower than in *E. georgeii*, *E. jungostrix*, *E. mandelslohi*, *E. modestiforme*, *E. ventrosum*, and *E. westphali*. There is no ventral extension of the postcervical groove in *E. lerasi* contrary to *E. georgeii*, *E. jungostrix*, *E. mandelslohi*, *E. modestiforme*, *E. ventrosum*, and *E. westphali*. The morphology of the P1 chelae of *E. lerasi* are thinner than that of *E. georgeii*, *E. major*, *E. veltheimii*, and *E. westphali*. Finally, the ornamentation of *E. lerasi*, made of tubercles and depressions, differs from that of *E. jungostrix*, *E. major*, *E. mandelslohi*, and *E. veltheimii*, covered only by tubercles or depressions.

Eryma major Oppel, 1861 (Fig. 7A-C)

Eryma major Oppel, 1861: 358; 1862: 37, pl. 8, fig. 3. — Schweitzer *et al.* 2010: 24. — Devillez *et al.* 2016: 524.

Erymastacus major – Schweigert *et al.* 2000: 8, pl. 3, figs 4-5. — Dietl & Schweigert 2001: 54, fig. 88. — Schweigert & Garassino 2003: 178, fig. 2B. — Hyžný *et al.* 2015: 375, 376.

TYPE MATERIAL. — Holotype SMNS 3682.

TYPE LOCALITY. — Nusplingen, Baden-Württemberg, Germany.

TYPE AGE. — Kimmeridgian.

DESCRIPTION

Thoracic appendages

Chelate P1; elongated P1 propodus, subrectangular, dorso-ventrally compressed, with a longitudinal bulge on ventral surface; narrow dactylar bulge, slightly bulged, not posteriorly delimited by a groove; slender, elongated fingers, almost straight; occlusal margins with wide conical teeth, regularly spaced; P1 carpus short, subtriangular; elongated P1 merus.

Ornamentation

P1 propodus and fingers densely covered by fine tubercles.

DISCUSSION

This species is only known by some isolated P1, mainly from the lithographic limestones of southern Germany. The subrectangular, dorso-ventrally compressed propodus with long and narrowing fingers justifies the assignation to *Eryma*.

Eryma major is only known by some fragments of P1, so the comparisons are restricted to the species for which the P1 are also known (*E. georgeii*, *E. jungostrix*, *E. lerasi*, *E. mandelslohi*, *E. modestiforme*, *E. quadrierrucatum*, *E. veltheimii*, *E. ventrosum*, *E. westphali*). The straight fingers of *E. major* are clearly distinct from the curved ones of *E. georgeii*, *E. lerasi*, *E. mandelslohi*, *E. veltheimii*, *E. ventrosum*, and *E. westphali*. The propodus of *E. major* is also shorter than that of *E. veltheimii* and *E. westphali*. The propodus of *E. major* is covered by tubercles while that of *E. veltheimii* and *E. westphali* is smooth and that of *E. modestiforme* is covered by small depressions.

Eryma veltheimii (Münster, 1839)
(Fig. 7D-F)

Glypheia veltheimii Münster, 1839: 22, pl. 10, fig. 1. — Fraas 1855: 94. — Glaessner 1929: 159. — Woods 1930: 80, pl. 22, figs 5-6. — Van Straelen 1936: 9. — Förster 1966: 124, fig. 23, pl. 17, figs 2, 4. — Taylor 1979: 34. — Feldmann & Titus 2006: 64. — Karasawa *et al.* 2013: table 1.

Eryma veltheimii — Bronn 1849: 579. — Oppel 1861: 358; 1862: 36, pl. 7, fig. 5. — Beurlen 1928: 156. — Schweigert *et al.* 2000: 7, fig. 1c, pl. 4, figs 1-3. — Garassino & Schweigert 2006: 8, fig. 8, pl. 1, fig. 2, pl. 11, figs 3-4. — Feldmann & Titus 2006: 64. — Fürsich *et al.* 2007a: table 2. — Odin *et al.* 2019: 652.

Clytia veltheimii — Beurlen 1928: 170.

Galicia veltheimii — Schweitzer *et al.* 2010: 25. — Charbonnier & Garassino 2012: 864. — Audo *et al.* 2014: 462. — Schweigert 2015: fig. 544.

TYPE MATERIAL. — Holotype BSPG AS VII 186.

TYPE LOCALITY. — Kapfelberg quarry near Kelheim, Bavaria, Germany.

TYPE AGE. — Kimmeridgian.

DESCRIPTION

Carapace

Short, spiny rostrum; fusiform intercalated plate; elongated cephalic region, representing almost half of the length of the carapace; wide, deep cervical groove, strongly inclined, joined to dorsal margin; deep gastro-orbital groove, elongated and oblique; postcervical groove not identified; wide, deep branchiocardiac groove, strongly inclined.

Pleon and uropods

Somites with subtriangular pleurites; telson with a median line and two longitudinal crests along its lateral margins, crests ended by a small spine; uropods as long as telson, with a small spine on the external margin; uropodal endopods with a longitudinal carina; uropodal exopods with a diaeresis, and a longitudinal carina.

Thoracic appendages

Chelate P1; P1 propodus subrectangular, strongly elongated, dorso-ventrally compressed; presence of a strong spine at the inner distal extremity of the propodus, above the dactylus; slender fingers, progressively narrowing to their distal extremity, slightly curved inward; occlusal margin without teeth; P1 carpus short, subtriangular; thin P2-P5.

Ornamentation

Carapace covered by small tubercles; intercalated plate covered by small tubercles; oblique orbital row of tubercles in cephalic region; presence of a strong antennal spine; smooth P1 propodus and fingers.

DISCUSSION

This species is known by some specimens, mainly from the Kimmeridgian plattenkalks of Wattendorf (Audo *et al.* 2014). Because of the compression of the holotype, it is difficult to

clearly identify the grooves of the carapace. Indeed, only the cervical, gastro-orbital and branchiocardiac grooves are well-marked. However, the assignation to *Eryma* is supported by the gastro-orbital groove which is not divided in two branches and by the shape of the P1 chelae (elongated subrectangular propodus; elongated fingers, curved inward and narrowing to their distal extremity).

The difficulty to identify the carapace grooves does not allow the comparison with that of other species. The presence of a spine at the distal extremity of the inner margin of the propodus (Fig. 7D) is characteristic of this species. Moreover, the lack of ornamentation on the P1 chelae is a characteristic only found in *E. veltheimii* and *E. westphali*. A spiny rostrum like in *E. veltheimii* is not found in *E. mandelslohi*, *E. modestiforme*, and *E. ventrosum*. Garassino & Schweigert (2006) pointed out the absence of spines on the margin of the telson, contrary to *E. modestiforme*. However, the careful examination of the type specimen shows that two marginal spines are present (Fig. 7F). Finally, the carapace of *E. veltheimii* is only covered by tubercles, contrary to *E. georgeii*, *E. mandelslohi*, *E. quadriverrucatum*, *E. ventrosum*, and *E. westphali*.

Eryma westphali Schweigert, Dietl & Röper, 2000
(Fig. 7G-J)

Eryma westphali Schweigert, Dietl & Röper, 2000: 6, pl. 3, figs 1-3. — Dietl & Schweigert 2001: 53, 110, fig. 85. — Garassino & Schweigert 2006: 8. — Feldmann & Titus 2006: 64.

Galicia westphali — Schweitzer *et al.* 2010: 25. — Hyžný *et al.* 2015: 375.

TYPE MATERIAL. — Holotype SMNS 24227.

TYPE LOCALITY. — Nusplingen, Baden-Württemberg, Germany.

TYPE AGE. — Kimmeridgian.

DESCRIPTION

Carapace

Short, spiny rostrum; fusiform intercalated plate; deep, wide cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove; short, sub-horizontal gastro-orbital groove; postcervical groove slightly curved forward, not joined to dorsal margin, joined to branchiocardiac groove at carapace mid-height, with a short ventral extension; branchiocardiac groove dorsally deep, narrowing in its ventral part, not joined to dorsal margin, joined to hepatic groove; hepatic groove concavo-convex.

Pleon and uropods

Somites with subtriangular pleurites, with a bulge on their basis; wide rounded uropods; uropodal endopods with a longitudinal carina; uropodal exopods with a small spine on external margin.

Thoracic appendages

Chelate P1; P1 propodus subrectangular, narrow and strongly elongated; P1 fingers shorter than propodus, slender, almost

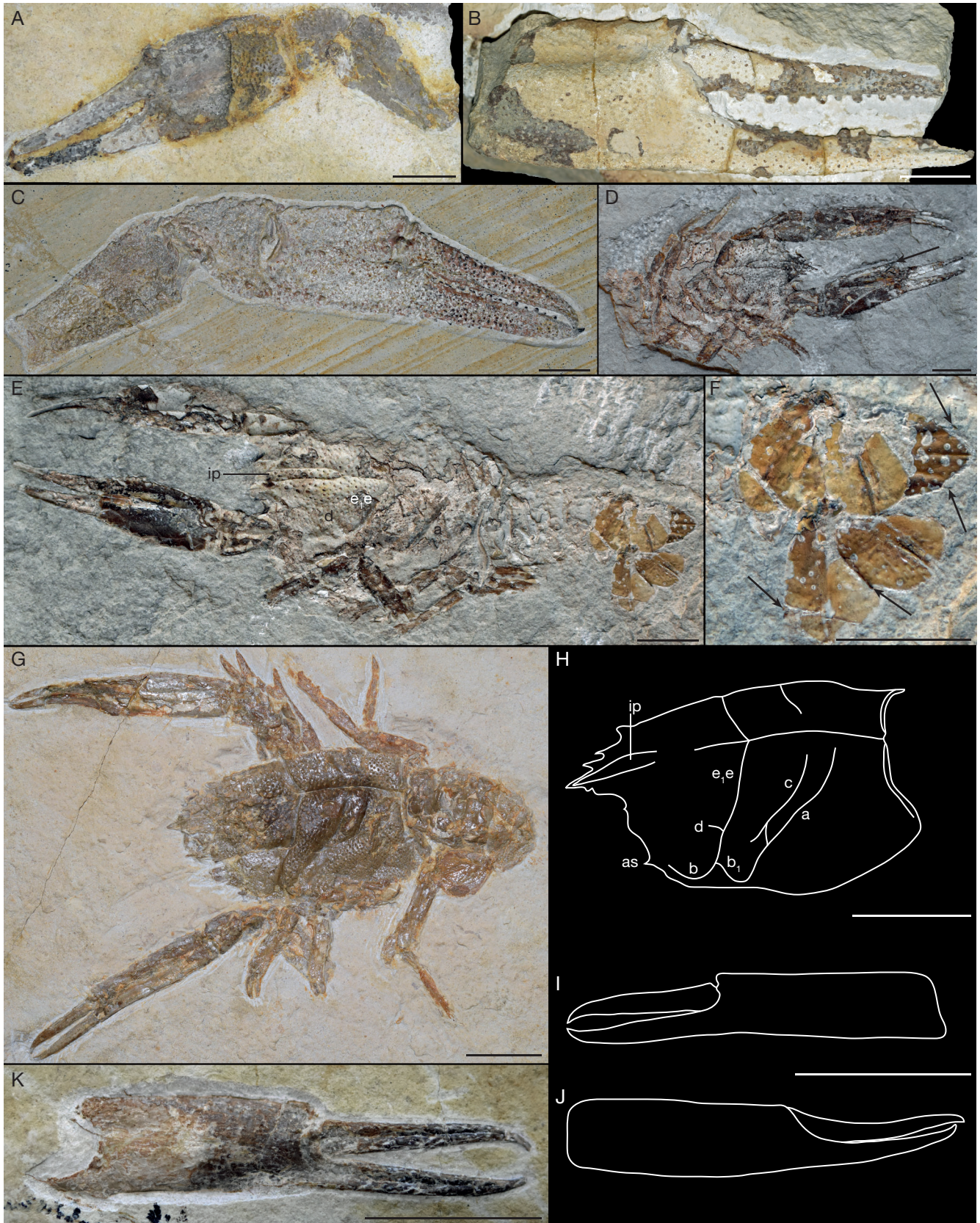


FIG. 7. — *Eryma major* Oppel, 1861, *Eryma veltheimii* (Münster, 1839) and *Eryma westphali* Schweigert, Dietl & Röper, 2000 from the Kimmeridgian of Germany: **A**, holotype SMNS 3682 of *E. major* from Egesheimer; **B**, specimen SMNS 67655 of *E. major* from Gerhausen; **C**, specimen SMNS 64371 of *E. major* from Nusplingen; **D-F**, holotype BSPG AS VII 186 of *E. veltheimii* from Kehlheim: part (**D**), counter-part (**E**), details of telson and uropods (**F**); **G-J**, holotype SMNS 24227 of *E. westphali* from Nusplingen: general view (**G**), schema of the carapace (**H**), schema of left chela (**I**), schema of right chela (**J**); **K**, specimen SMNS 63733 from Nusplingen. Abbreviations: **a**, branchiocardiac; **as**, antennal spine; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical; **d**, gastro-orbital groove; **e₁e**, cervical groove; **ip**, intercalated plate. Black arrows show the spines. Photographs and line drawings: J. Devillez. Scale bars: 1 cm.

straight or slightly curved inward, with a terminal hook; occlusal margin without teeth; P1 carpus short, subtriangular; thin P2-P5; P2-P3 chelate.

Ornamentation

Carapace with a dense, heterogeneous ornamentation; gastric and cardiac regions covered by tubercles; antennal, hepatic, and branchial regions covered by small rounded depressions; presence of an orbital spine; tergites and pleurites densely covered by small rounded depressions; presence of a strong antennal spine; smooth P1-P5.

DISCUSSION

This species is only known by three specimens. It is assigned to *Eryma* because of its typical carapace groove pattern (short gastro-orbital groove, postcervical and branchiocardiac grooves joined at carapace mid-height, hepatic groove concavo-convex) and the shape of the P1 chelae (elongated propodus, subrectangular, with slender fingers progressively narrowing to their distal extremity).

Among the erymid lobsters, *Eryma westphali* is the only species with heterochelous P1 chelae on a same specimen. Left propodus is more elongated and narrower than the right one, and the left fingers are straight and short while the right ones are curved and slightly longer (Fig. 7I, J). The strongly elongated and narrow P1 propodus with relatively short fingers of *E. westphali* is characteristic of the species. Only *Eryma veltheimii* (Münster, 1839) have P1 with a very long propodus, but it is clearly wider.

In *E. westphali* the branchial region is dorsally shorter than in *E. georgeii*, *E. jungostrix*, *E. lerasi*, *E. modestiforme*, and *E. ventrosum*. Contrary to *E. lerasi* and *E. quadriverrucatum*, *E. westphali* exhibits a ventral extension of the postcervical groove. Moreover, the dichotomy of the ornamentation of the carapace between the gastric and cardiac regions, covered by tubercles, and the remaining regions of *E. westphali*, covered by small depressions, is unique among the genus.

Eryma modestiforme (Schlotheim, 1822) (Figs 8; 9)

Macrourites modestiformis Schlotheim, 1822: 29, pl. 2, fig. 3.

Astacus leptodactylus Germar, 1827: 100, pl. 1, fig. 4.

Glyphea crassula Münster, 1839: 17, pl. 8, fig. 5.

Glyphea elongata Münster, 1839: 18, pl. 8, fig. 8, 11-12.

Glyphea laevigata Münster, 1839: 20, pl. 9, figs 5-7.

Palaeastacus poeschli Schweigert & Röper, 2001: 5, figs 3-4. — Garassino & Schweigert 2006: 11. — Schweitzer *et al.* 2010: 25. **n. syn.**

Glyphea modestiformis – Münster 1839: 17, pl. 8, fig. 9, pl. 9, figs 1-3.

Eryma modestiformis – Bronn 1849: 579. — Oppel 1861: 358; 1862: 33, pl. 6, figs 5-8. — Van Straelen 1925: 271. — Beurlen 1928: 156, 157, 163, 164. — Glaessner 1929: 156. — Roger 1946: 42. — Kuhn 1961: 22. — Secrétan 1964: 69. — Förster 1965: 138, fig. 1, pl. 2, fig. 5. — Förster 1966: 118, fig. 21, pl. 16, figs 7-8 (non 9), pl. 17, fig. 1. — Schweigert & Garassino 2003: 178. — Fürsich *et al.* 2007b: 57. — De Grave *et al.* 2009: fig. 1B. — Feldmann & Schweitzer 2017: fig. 1c. — Odin *et al.* 2019: 652, fig. 6, ap. 1.

Astacus modestiformis – Quenstedt 1852: 268; 1867: 320; 1885: 409. — Fraas 1855: 94.

Eryma leptodactylina – Oppel 1861: 358; 1862: 35, pl. 7, figs 1-4. — Zittel 1885: fig. 873. — Secrétan 1964: 69. — Garassino & Schweigert 2006: 8.

Eryma leptodactylus – Van Straelen 1925: 273.

Clytia leptodactylina – Beurlen 1928: 170. — Vialle 1948: 65.

Clytia leptodactylus – Glaessner 1929: 116. — Kuhn 1961: 22.

Eryma elongata – Frickhinger 1994: 118, figs 201-202.

Eryma modestiforme – Schweigert *et al.* 2000: 4, fig. 1a, pl. 1, figs 1-5. — Dietl & Schweigert 2001: 53, 110, fig. 86. — Schweigert & Röper 2001: 2, 7. — Garassino & Schweigert 2006: 6, fig. 8, pl. 1, fig. 1, pl. 11, figs 1-2. — Schweitzer *et al.* 2010: 24. — Charbonnier & Garassino 2012: 864, fig. 3B-C. — Karasawa *et al.* 2013: table 1, fig. 9A. — Hyžný *et al.* 2015: 375, fig. 3A. — Schweigert 2015: fig. 541. — Devillez *et al.* 2016: 518, 524. — Devillez & Charbonnier 2017: table 1, fig. 2a.

TYPE MATERIAL. — Holotype MFN 2236 P1383/2 MB.A.0252.

TYPE LOCALITY. — Eichstätt, Bavaria, Germany.

TYPE AGE. — Kimmeridgian-Tithonian.

DESCRIPTION

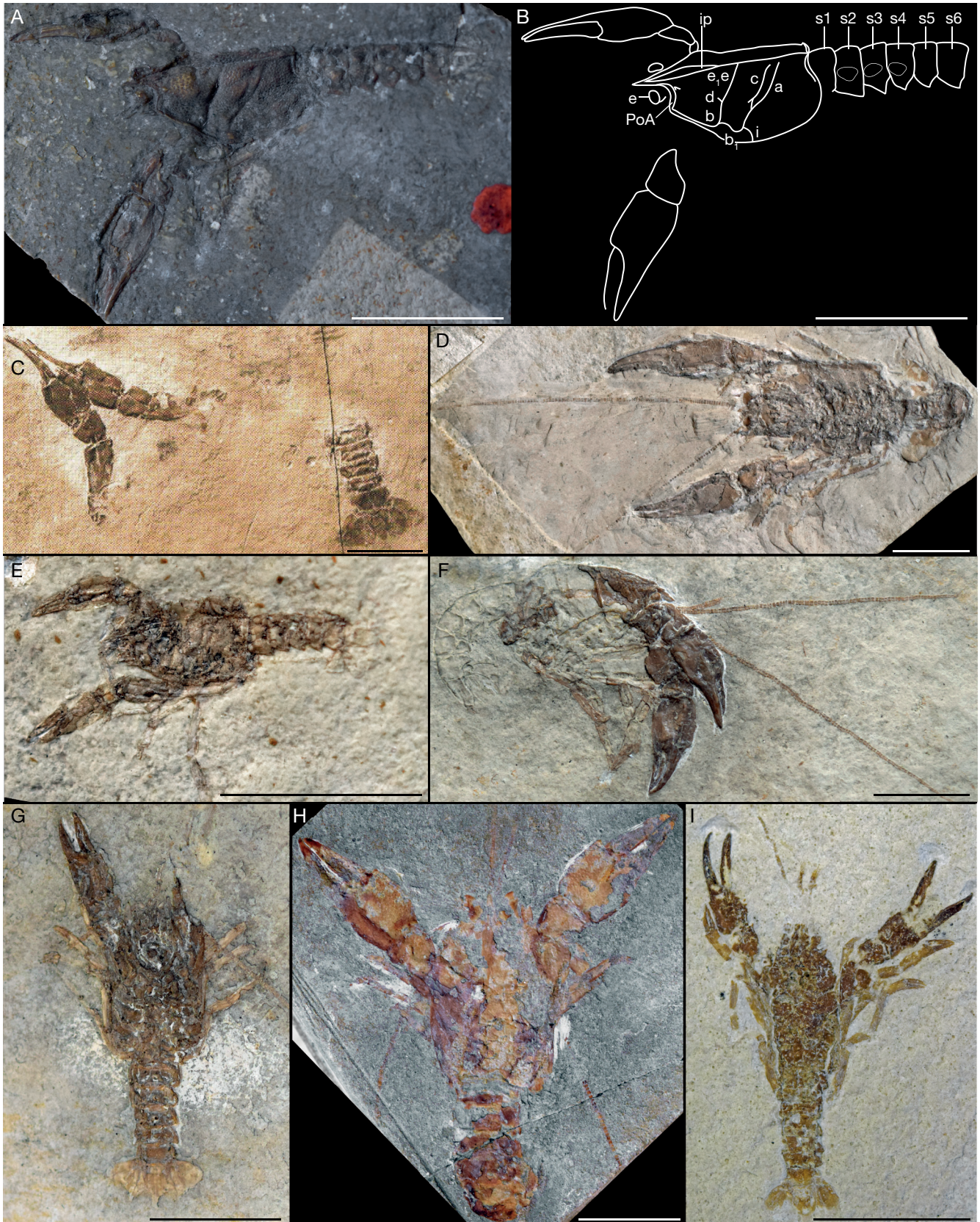
Carapace

Sub-cylindrical carapace; slightly elongated, spineless rostrum; fusiform intercalated plate; orbital notch widely curved; narrow post-orbital area; elongated cephalic region, representing almost half of the length of the carapace; deep and wide cervical groove, almost straight dorsally, strongly inflected at carapace mid-height, joined to dorsal margin and to antennal groove; deep antennal groove; short, narrow gastro-orbital groove, oblique, originating as median inflexion of cervical groove; postcervical and branchiocardiac grooves subparallel, slightly curved, slightly inclined, not joined to dorsal margin; shallow postcervical groove, joined to branchiocardiac groove, with a short ventral extension; narrow, shallow branchiocardiac groove, joined to the posterior extremity of hepatic groove; hepatic groove concavo-convex, joined to cervical groove; inferior groove joined to hepatic groove.

Pleon and uropods

Somites with wide, short subtriangular pleurites, with a bulge on their basis; s2 pleurites wider than others; telson with a longitudinal median groove and two longitudinal crests along

FIG. 8. — *Eryma modestiforme* (Schlotheim, 1822) and its synonyms from the Kimmeridgian – Tithonian of Germany: **A, B**, holotype MFN 2236 P1383/2 MB.A.0252 from Eichstätt: general view (**A**), schema (**B**); **C**, original figure of Garassino & Schweigert (2006: pl. 11, fig. 2) of the holotype of *Astacus leptodactylus* Germar, 1827 from Solnhofen; **D**, syntype BSPG AS VI 188 of *Glyphea elongata* Münster, 1839 from Solnhofen; **E, F**, syntypes of *Glyphea laevigata* Münster, 1839 from



Solnhofen: specimen BSPG AS VII 198 (C), AS VII 194 (D), AS VII 197 (E); **G**, holotype BSPG AS VII 193 of *Glyphea crassula* Münster, 1839 from Solnhofen; **H**, holotype SMNS 64520 of *Palaeastacus poeschli* Schweigert & Röper, 2001 from Mülheim. Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **e**, eye; **e_e**, cervical groove; **i**, inferior groove; **ip**, intercalated plate; **PoA**, postorbital area; **s1-s6**, pleonal somites. Photographs and line drawing: J. Devillez. Scale bars: 1 cm.

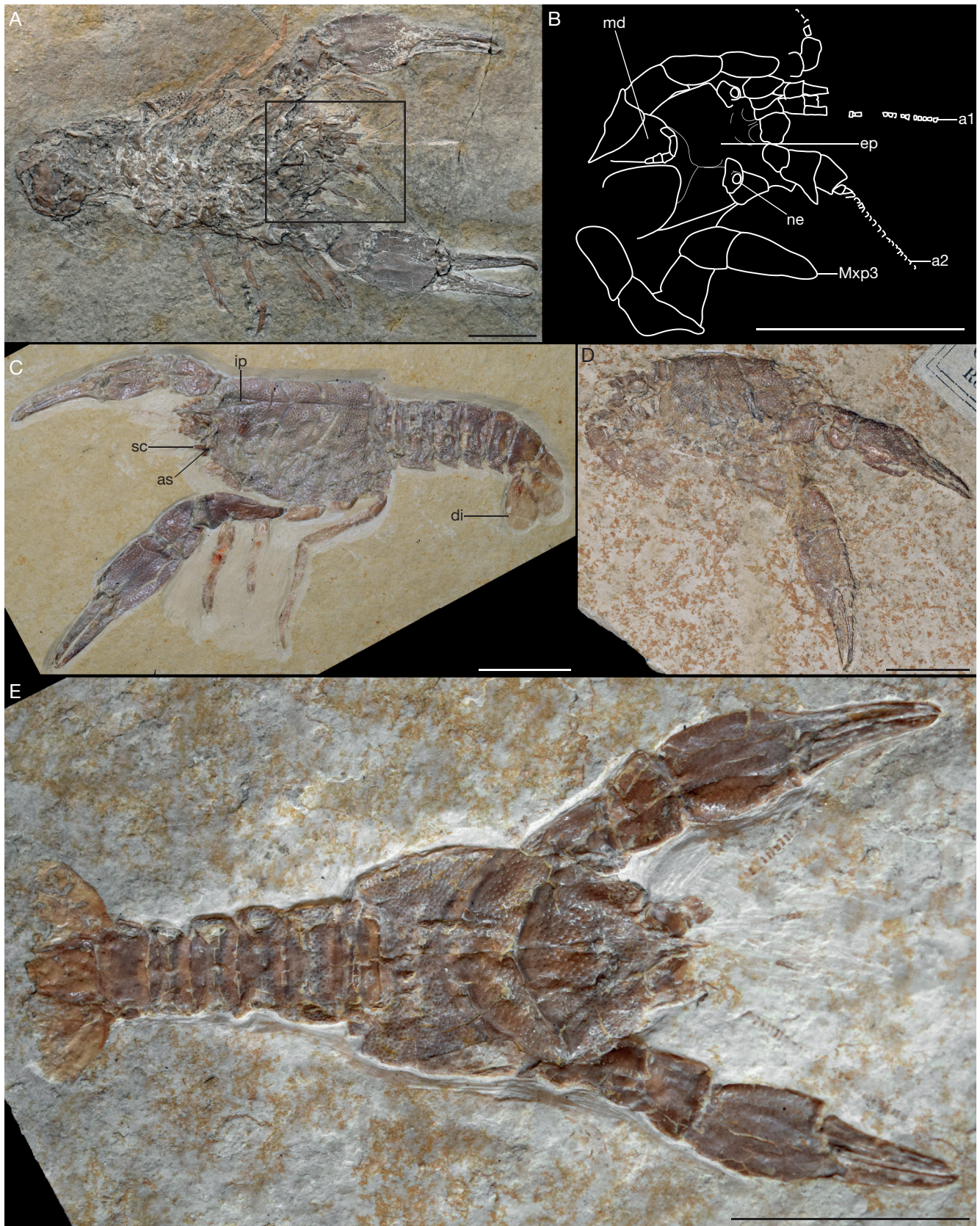


FIG. 9. — Additional specimens of *Eryma modestiforme* (Schlotheim, 1822) from the Kimmeridgian–Tithonian of Germany: **A, B**, specimen BSPG AS VI 15 from Eichstätt: general view (**A**), schema of ventral side of cephalic region (**B**); **C**, specimen SMNS 64260 from Solnhofen; **D**, specimen MB.A2880 from Solnhofen; **E**, specimen BSPG AS VIII 79 from Eichstätt. Abbreviations: **a1**, antennulae; **a2**, antenna; **as**, antennal spine; **di**, diaeresis; **ep**, epistom; **ip**, intercalated plate; **md**, mandible; **Mxp3**, third maxilliped; **ne**, nephridiopore; **sc**, scaphocerite. Photographs and line drawing: J. Devillez. Scale bars: 1 cm.

lateral margins; uropods as long as telson; uropodal endopods with a longitudinal carina; uropodal exopods with a diaeresis, and a longitudinal carina.

Cephalic appendages

Last segment of antennular peduncles (basipodite) articulated with two flagella, flagella made of numerous and short cylindrical articles; antennae made of numerous and short cylindrical articles; short, triangular scaphocerite; wide epistome, with a linear contact with the carapace; wide, subrectangular mandibles (Fig. 9A-C).

Thoracic appendages

Elongated Mxp3; chelate P1; P1 propodus subrectangular; slender, straight P1 fingers, longer than propodus, equal in length, sometimes with a small distal hook; occlusal margin without teeth; P1 carpus short, subtriangular; elongated P1 merus; P2-P3 chelate.

Ornamentation

Carapace with a homogeneous ornamentation; carapace densely covered by small tubercles and depressions; gastric region with an orbital spine; antennal region with an antennal spine; pleonal tergites and pleurites densely covered by small rounded depressions; telson covered by small depressions; P1 covered by small depressions; smooth P2-P5.

DISCUSSION

Eryma modestiforme is known by numerous specimens, almost complete. This is the most common erymoid of the lithographic limestones of southern Germany.

The type materials of *Astacus leptodactylus* Germar, 1827 (Fig. 8C), *Glypheia crassula* Münster, 1839 (Fig. 8H), *Glypheia elongata* Münster, 1839 (Fig. 8D), *Glypheia laevigata* Münster, 1839 (Fig. 8E-G) and *Palaeastacus poeschli* Schweigert & Röper, 2001 (Fig. 8I), from the same formations than *E. modestiforme*, share the same characteristics: a subrectangular propodus bearing longer fingers, these fingers are slender and straight, without teeth on their occlusal margins, the carapace ornamentation is dense, made of small tubercles and depressions. These characteristics support the integration of *A. leptodactylus*, *G. crassula*, *G. elongata*, *G. laevigata* and *P. poeschli* into the synonymy of *E. modestiforme*.

The ventral extension of the cervical groove seen on *E. modestiforme* is absent in *E. lerasi* and *E. quadriverrucatum*. The morphology of the P1 is also distinct from some other representatives of the genus. Indeed, the propodus is rectangular in *E. modestiforme* while it is trapezoidal in *E. georgeii* and *E. mandelslohi*. It is also relatively narrower than the propodus of *E. georgeii*, *E. mandelslohi* and *E. quadriverrucatum*. The almost straight P1 fingers of *E. modestiforme* contrast with the curved ones of *E. georgeii*, *E. lerasi*, *E. veltheimii*, *E. ventrosum*, and *E. westphali*. Finally, the fine ornamentation of *E. modestiforme*, made of tubercles and depressions, is clearly distinct from the ornamentation of *E. georgeii*, *E. jungostrix*, *E. mandelslohi*, *E. veltheimii*, and *E. westphali*.

Eryma punctatum Oppel, 1861

(Fig. 10)

Eryma punctata Oppel, 1861: 359; 1862: 38, pl. 8, fig. 4. — Van Straelen 1925: 275. — Beurlen 1928: 165. — Glaessner 1929: 158. — Schweigert *et al.* 2000: 5, fig. 1b, pl. 2, figs 1-5. — Feldmann & Titus 2006: 64.

Eryma punctatum — Dietl & Schweigert 2001: 110, fig. 141. — Schweitzer *et al.* 2010: 24. — Schweigert 2015: fig. 542. — Devillez *et al.* 2016: 518, 524.

TYPE MATERIAL. — Holotype SMNS 3682.

TYPE LOCALITY. — Nusplingen, Baden-Württemberg, Germany.

TYPE AGE. — Kimmeridgian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; short, spineless rostrum; fusiform intercalated plate; deep and wide cervical groove, curved dorsally, subvertical and almost straight ventrally, strongly inflected at carapace mid-height, joined to dorsal margin and to antennal groove; deep antennal groove; short, shallow gastro-orbital groove originating as strong median inflexion of cervical groove; postcervical and branchiocardiac grooves convergent, sinuous, slightly inclined, not joined to dorsal margin; deep postcervical groove, more strongly sinuous than branchiocardiac groove, joined to branchiocardiac groove under the level of the gastro-orbital groove; deep branchiocardiac groove, joined to the posterior extremity of hepatic groove; hepatic groove concavo-convex; inferior groove joined to hepatic groove.

Pleon and uropods

Somites with wide subtriangular pleurites, directed backward, with a bulge at their basis; s2 with elongated pleurites, subrectangular anteriorly and subtriangular posteriorly; s5-6 pleurites shorter; telson with a median longitudinal crest; uropods as long as telson; uropodal endopods with a longitudinal carina; uropodal exopods with a diaeresis, and a longitudinal carina.

Cephalic appendages

Last segment of antennular peduncles (basipodite) articulated with two flagella, flagella made of numerous and short cylindrical articles; antennae made of numerous and short cylindrical articles; short, triangular scaphocerite.

Thoracic appendages

Elongated Mxp3, with small spines on the ventral margin of each article excepted the two distal ones; chelate P1; P1 propodus short, subrectangular; narrow, inflated dactylar bulge; P1 fingers usually slightly longer than propodus, straight dorsally, equal in length, with a distal hook; occlusal margin with small teeth and a strong one on index proximal third; P1 carpus short, subtriangular; elongated P1 merus, with a short process at outer side of its ventral extremity; P2-P3 chelate.

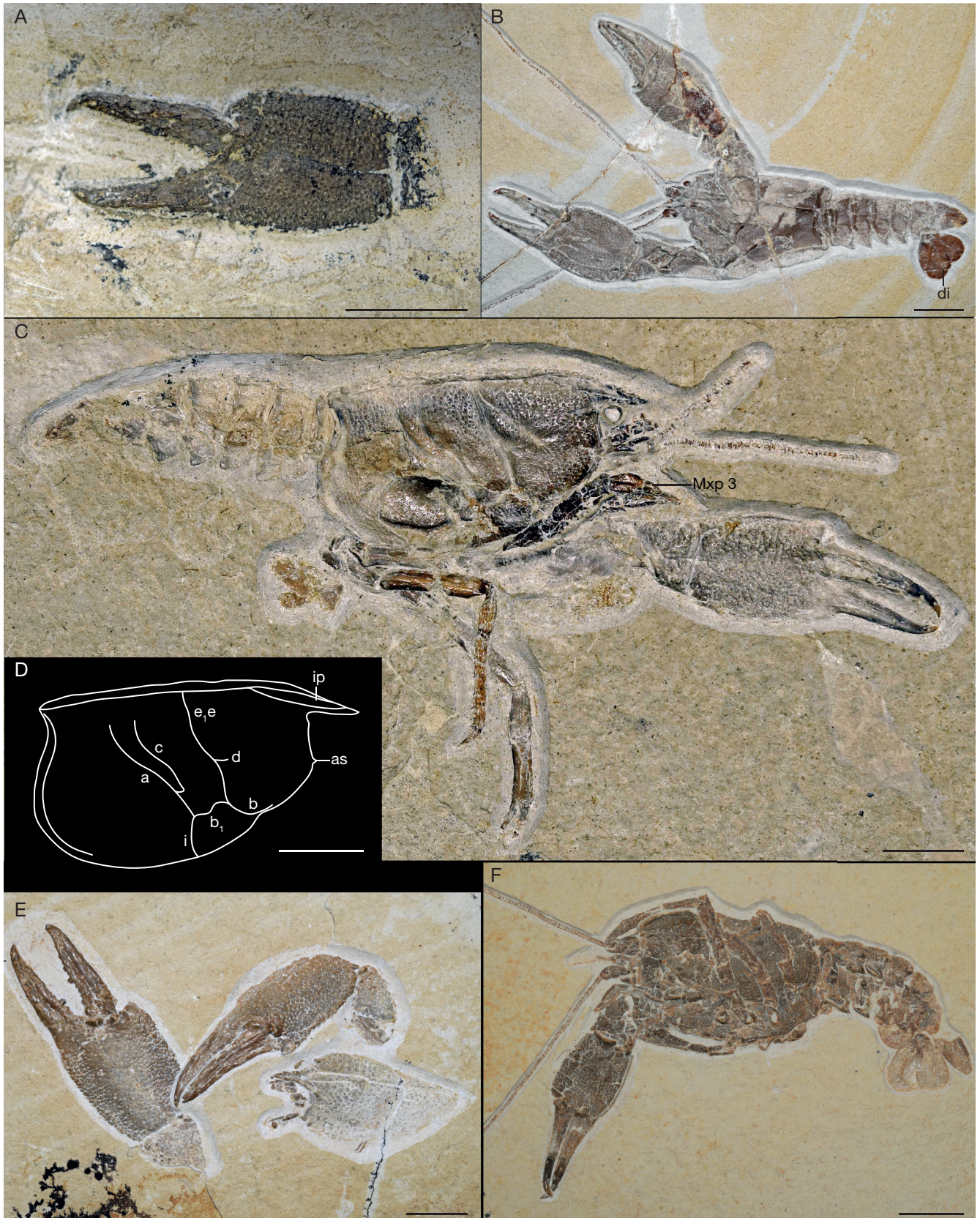


FIG. 10. — *Eryma punctatum* Oppel, 1861 from the Kimmeridgian of Nusplingen (Germany): **A**, holotype SMNS 3682; **B**, specimen SMNS 66128; **C**, **D**, specimen SMNS 63849: general view (**C**), schema (**D**); **E**, specimen SMNS 63688; **F**, specimen SMNS 64960. Abbreviations: **a**, branchiocardiac groove; **as**, antennal spine; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **di**, diaeresis; **e₁e**, cervical groove; **i**, inferior groove; **ip**, intercalated plate; **Mxp3**, third maxilliped. Photographs and line drawing: J. Devillez. Scale bars: 1 cm.

Ornamentation

Carapace densely covered by rounded depressions; gastric region with an orbital spine; antennal region with an antennal spine; tergites and pleurites of pleonal somites densely covered by rounded depressions; uropodal exopods with a spine on external margin, anterior to the diaeresis; P1 propodus densely covered by small tubercles preceded by crescent-shaped depressions; P1 carpus densely covered by small tubercles, coarse tubercles along the distal extremity; P1 merus covered by small tubercles and strong spines directed forward along ventral margins; P2-3 and P5 with small and widely spaced depressions; P4 propodus with posterior spines.

DISCUSSION

This species is currently known by some specimens, but it has been firstly described by Oppel (1861) from an isolated P1 chela and assigned to *Eryma*. On the specimens recently found and preserved with the carapace we can observe the carapace groove pattern (Fig. 10C). The postcervical and branchiocardiac grooves are joined and the postcervical groove is not connected ventrally to hepatic groove. This pattern is characteristic of *Eryma*. Most of the specimens of *E. punctatum* exhibit short P1 fingers in comparison to their P1 propodus, which is unusual for the genus.

The ornamentation of the carapace of *E. punctatum*, only made of closely spaced depressions, is only shared with *E. mandelslohi* among *Eryma*, so its identification is easy. It is also the only *Eryma* with a dactylus clearly inserted under the level of inner margin, which is strongly prominent above the basis of the dactylus. The low position of the junction between postcervical and branchiocardiac grooves and the absence of ventral extension of the postcervical groove beyond this junction are two characteristics which distinguished *E. punctatum* from *E. georgeii*, *E. jungostrix*, *E. mandelslohi*, *E. modestiforme*, *E. ventrosum*, and *E. westphali*. Moreover, the P1 fingers of *E. punctatum* are straight, contrary to *E. georgeii* and *E. ventrosum*. They are also usually shorter than P1 fingers of *E. georgeii*, *E. lerasi*, *E. major*, and *E. ventrosum*.

Eryma quadriverrucatum Trautschold, 1866 (Fig. 11)

Eryma quadriverrucata Trautschold, 1866: 20, pl. 3, fig. 5. — Quenstedt 1885: 410. — Lahusen 1894: 313, 316, 318, pl. 1, figs 2-5. — Van Straelen 1925: 274, fig. 127. — Glaessner 1929: 158. — Gerasimov 1955: 24, pl. 8, figs 1-3. — Birshtein 1956: 74, 75. — Secrétan 1964: 70. — Förster 1966: 121. — Gerasimov *et al.* 1996: 9, 30, pl. 6, figs 1-3. — Ilyin 2000: 151. — Feldmann & Titus 2006: 64.

Eryma mosquensis Lahusen, 1894: 318, pl. 1, figs 6-8. — Van Straelen 1925: 244, 276. — Glaessner 1929: 157. — Gerasimov 1955: 25, pl. 8, figs 5-7. — Birshtein 1956: 75. — Secrétan 1964: 70, 74. — Förster 1966: 122. — Gerasimov *et al.* 1995: 9, 30, pl. 4, figs 8-10. — Ilyin 2000: 152, 154, table 1. — Feldmann & Titus 2006: 64. — Schweitzer *et al.* 2010: 24. n. syn.

Eryma mosquensis pustulifera — Glaessner 1929: 157.

Eryma aff. *quadriverrucata* — Gerasimov 1955: 64, pl. 8, fig. 9.

Eryma quadriverrucata — Ilyin 2000: 151, table 1.

Eryma quadriverrucatum — Schweitzer *et al.* 2010: 24.

TYPE MATERIAL. — Holotype stored in the Museum of Paleontology and Stratigraphy of the University of Saint Petersburg (not examined).

TYPE LOCALITY. — Choroshovo, Podmoskovié, Russia.

TYPE AGE. — Tithonian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; fusiform intercalated plate; narrow post-orbital area; deep and wide cervical groove, strongly inclined and curved dorsally, subvertical ventrally, joined to dorsal margin and to antennal groove; deep and narrow antennal groove; short, deep gastro-orbital groove, originating as a median inflexion of cervical groove; deep postcervical groove, curved, not joined to dorsal margin, joined to branchiocardiac groove under the level of the gastro-orbital groove, without ventral extension; deep branchiocardiac groove, strongly inclined, strongly curved, with a strong inflexion towards its junction to hepatic groove, not joined to dorsal margin, joined to hepatic groove; shallow and narrow hepatic groove, concavo-convex, joined to cervical groove; inflated ω and χ areas; deep and wide inferior groove, joined to hepatic groove.

Pleon and uropods

Somites with subrectangular tergites; somites with subtriangular pleurites, directed backward, with a rounded bulge on their basis.

Thoracic appendages

Chelate P1; P1 propodus trapezoidal, compressed dorso-ventrally, with a ventral surface inflated medially, median bulge bordered by a depression parallel to inner margin; narrow dactylar bulge, posteriorly delimited by a shallow and narrow groove; wide basis of the index; elongated P1 merus; thin P2-P5.

Ornamentation

Carapace densely covered by small tubercles surrounded by irregular depressions; intercalated plate with a row of small tubercles; cephalic region with an oblique orbital row of tubercles; cephalic region with an oblique orbital row of tubercles; antennal region with an antennal spine; pleonal tergites and pleurites covered by small depressions; P1 propodus densely covered by small tubercles; smooth P1 merus; smooth P2-P5.

DISCUSSION

Trautschold's (1866) description of *Eryma quadriverrucatum* is supported by an isolated carapace from the Tithonian of Russia. He assigned it to *Eryma* because of the short gastro-orbital groove, the junction between the postcervical and branchiocardiac grooves and the sinuosity of the hepatic groove typical of the genus.

Eryma mosquensis Lahusen, 1894 (Tithonian, Russia; Fig. 10E-F) was described on a fragment of P1 chela showing



FIG. 11. — *Eryma quadriverrucatum* Trautschold, 1866 and its synonyms from the Tithonian of Russia: **A, B**, original figures of Trautschold (1866: pl. 3, fig. 5) of the holotype from Choroshovo: lateral view (**A**), dorsal view (**B**); **C**, original figure of Gerasimov (1955: pl. 8, fig. 3) from Ryazan; **D**, original figure of Gerasimov (1955: pl. 8, fig. 1) from Ryazan; **E, F**, original figures of Lahusen (1894: pl. 1, fig. 6) of one of the syntypes of *Eryma mosquensis* from Mneviki: dorsal view (**E**), ventral view (**F**); **G**, original figure of Gerasimov *et al.* (1995: pl. 4, fig. 9) from Moscow; **H**, original figure of Gerasimov *et al.* (1995: pl. 4, fig. 8) from Moscow; **I**, original figure of Gerasimov *et al.* (1995: pl. 4, fig. 10) from Moscow. Scale bars: 1 cm.

a subrectangular propodus, compressed dorso-ventrally and bearing thin, elongated fingers characteristics of *Eryma*. Gerasimov *et al.* (1995) later assigned to this species a carapace with convergent postcervical and branchiocardiac grooves, joined in the inferior half of the carapace, and with a fine ornamentation that gives a granular aspect to the carapace. *E. quadriverrucatum* exhibits very similar features. So, we consider *E. mosquensis* as a junior synonym of *E. quadriverrucatum*.

The junction of the postcervical and branchiocardiac grooves of *Eryma quadriverrucatum* is located very low on the carapace. It is very uncommon in *Eryma*, this junction is usually located at carapace mid-height, more or less at the level of the gastro-orbital groove, like in *E. georgeii*, *E. jungostrix*, *E. mandelslohi*, *E. modestiforme*, *E. ventrosum*, and *E. westphali*. Moreover, contrary to *E. georgeii*, *E. jungostrix*, *E. mandelslohi*, *E. modestiforme*, *E. ventrosum*, and *E. westphali*, the postcervical groove of *E. quadriverrucatum* does not have a ventral extension under its junction with the branchiocardiac groove. Both ω and χ areas are inflated in *E. quadriverrucatum*, while only one or none of them is inflated in *E. georgeii*, *E. jungostrix*, *E. lerasi*, *E. mandelslohi*, and *E. ventrosum*. The P1 propodus of *E. quadriverrucatum* is wider than that of *E. jungostrix*, *E. lerasi*, *E. major*, *E. mandelslohi*, *E. modestiforme*, *E. veltheimii*, *E. ventrosum*, and *E. westphali*. It is also subrectangular while that of *E. georgeii*, and *E. mandelslohi* is trapezoidal.

FRAGMENTS ATTRIBUTED TO *ERYMA*

REMARKS

In the literature, many fragments of *Eryma* were reported without identification at specific level. Krause (1891) righteously assigned to *Eryma* sp. a carapace from the Oxfordian of Listring (Germany). The description mentions explicitly the junction between the postcervical and branchiocardiac grooves at carapace mid-height.

Förster (1966) assigned to *Eryma stricklandi* (Phillips, 1871) a carapace and some fragments of P1 propodi from the Oxfordian of Blauen and Chatillon (Switzerland), stored in the collections of the NMB (NMB 253, 93). These fossils exhibit the characteristics of *Eryma*, but are too incomplete to be identified at the specific level. Indeed, the carapace is strongly deformed and damaged in its dorsal part and the propodus does not have particular features, so we consider these fragments as *Eryma* sp.

Carpentier *et al.* (2006) identified as *Eryma* sp. a fragment of P1 chela found in the Kimmeridgian of Bure (France). Only the distal part of the propodus and the proximal part of the fingers are preserved. These elongated fingers and the ornamentation made of small tubercles, and the presence of other fossils of *Eryma* in the same locality, suggest that this fragment belongs to the same genus.

In Fukushima prefecture (Japan), Kato *et al.* (2010: 764, fig. 3) reported a fragment of a P1 chela from the

Kimmeridgian-Tithonian boundary. Its subrectangular propodus, elongated, dorso-ventrally compressed, with an inflated dactylar bulge and a long and thin index justify the identification as *Eryma* sp.

Gerasimov *et al.* (1995: pl. 4, figs 14, 18) assigned to *Glypheopsis vosinskyi* (Lahusen, 1894) and figured two fragments of P1 chelae from the Tithonian of Moscow (Russia). The propodi are subrectangular, elongated, dorso-ventrally compressed, with an inflated dactylar bulge and a thin index curved inward. These P1 chelae are typical of *Eryma*.

Genus *Palaeastacus* Bell, 1850

(Fig. 1F-G)

Palaeastacus Bell, 1850: 344. — Zittel 1885: 695. — Beurlen 1928: 180. — Förster 1966: 126. — Glaessner 1969: 626. — Aguirre-Urreta & Ramos 1981: 606. — Aguirre-Urreta 1989: 509. — Schweitzer & Feldmann 2001: 174. — Feldmann *et al.* 2015: 3. — Hyžný *et al.* 2015: 375. — Devillez *et al.* 2016: 525, fig. 1G-H. — Devillez *et al.* 2017: 782.

Enoploclytia Palaeastacus – Martin 1941: 161. — Glaessner 1969: 455.

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

DIAGNOSIS BY Devillez & Charbonnier (2019). — 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 the cervical groove; postcervical and branchiocardiac grooves subparallel, joined to hepatic groove; hepatic groove concavo-convex, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove; chelate P1; P1 propodus short, thick, slightly globose, with a narrow dactylar bulge; P1 fingers usually wide, slightly longer than propodus, progressively narrowing to their distal extremity, occlusal margin curved at the basis of the index.

Palaeastacus rothgaengeriae Schweigert & Röper, 2001

(Fig. 12A, B)

Palaeastacus rothgaengeriae Schweigert & Röper, 2001: 4, fig. 2. — Garassino & Schweigert 2006: 11. — Schweitzer *et al.* 2010: 25.

TYPE MATERIAL. — Holotype BSPG 1993 XVIII-200.

TYPE LOCALITY. — Quarry near Brunn, Bavaria, Germany.

TYPE AGE. — Kimmeridgian.

DESCRIPTION

Thoracic appendages

Chelate P1; P1 propodus subrectangular; wide P1 fingers, straight, equal in length, as long as propodus; P1 carpus short, subtriangular; P1 merus short, subrectangular.

Ornamentation

P1 propodus covered by small tubercles; inner margin with a row of strong spines directed forward; fingers without ornamentation; P1 carpus covered by small tubercles and with strong spines directed forward on inner margin; P1 merus with strong spines directed forward on dorsal margin.

DISCUSSION

Palaeastacus rothgaengeriae is known by a very few isolated P1 with chelae characteristic of *Palaeastacus*: short and subrectangular propodus, short and wide fingers, and strongly spiny ornamentation.

P. rothgaengeriae is clearly distinct among the other species of *Palaeastacus* by the particular shape of P1 fingers, which gives its characteristic appearance to the chelae. Indeed, the fingers are very wide with strongly rounded inner margin of dactylus and outer margin of index.

Palaeastacus fuciformis (Schlotheim, 1822) (Fig. 12)

Macrourites fuciformis Schlotheim, 1822: 30, pl. 2, fig. 2.

Glyphea fuciformis – Münster 1839: 16, pl. 8, figs 1-2.

Glyphea intermedia – Münster 1839: 17, pl. 8, fig. 6-7.

Glyphea crassula – Münster 1839: 17, pl. 8, fig. 4 (non 5).

Glyphea elongata – Münster 1839: 18, pl. 8, fig. 11-12 (non figs 8-10).

Eryma fuciformis – Bronn 1849: 579. — Oppel 1861: 359. — Oppel 1862: 41, pl. 9, figs 2-6. — Beurlen 1928: 164. — Glaessner 1929: 154. — Vialle 1948: 61. — Kuhn 1961: 22. — Secrétan 1964: 68.

Astacus fuciformis – Quenstedt 1852: 268, pl. 20, fig. 14. — Quenstedt 1867: 320, pl. 25, fig. 14. — Quenstedt 1885: 409, pl. 32, fig. 7.

Eryma elongata – Oppel 1861: 358. — Oppel 1862: 37, pl. 8, figs 1-2.

Enoploclytia fuciformis – Van Straelen 1925: 285.

Clytia elongata – Beurlen 1928: 170.

Palaeastacus fuciformis – Förster 1966: 130, fig. 25. — Förster & Rieber 1982: 774, 777. — Frickhinger 1994: 122, figs 218-219. — Schweigert *et al.* 2000: 5. — Schweitzer & Feldmann 2001: 174. — Schweigert & Röper 2001: 8, fig. 5. — Garassino & Schweigert 2006: 9, fig. 8, pl. 1, fig. 3, pl. 11, fig. 5. — Schweitzer *et al.* 2010: 25. — Charbonnier & Garassino 2012: 859, 864, fig. 3d. — Karasawa *et al.* 2013: 102, table 1. — Audo *et al.* 2014: 463. — Odin *et al.* 2019: 654, fig. 7A-C, ap. 1.

TYPE MATERIAL. — Holotype MFN 2236 P1383/8 MB.A.0251.

TYPE LOCALITY. — Solnhofen area, Bavaria, Germany.

TYPE AGE. — Tithonian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; short, spiny rostrum; fusiform intercalated plate; orbital notch widely curved; narrow post-orbital area; elongated cephalic region; wide deep cervical groove, slightly sinuous, joined to dorsal margin and to antennal groove; deep antennal groove; short, shallow gastro-orbital groove, joined to cervical groove at carapace mid-height; postcervical and branchiocardiac grooves subparallel, then converging under the level of the gastro-orbital groove and diverging before their junction

with hepatic groove, slightly inclined, not joined to dorsal margin; wide, deep postcervical groove, joined to hepatic groove; shallow branchiocardiac groove, joined to the posterior extremity of hepatic groove; hepatic groove concavo-convex, joined to cervical groove; deep inferior groove, joined to hepatic groove.

Pleon and uropods

Somites with wide subtriangular pleurites, with a bulge on their basis; telson with two longitudinal crests along the lateral margin; uropods as long as telson; uropodal endopods with a longitudinal carina; uropodal exopods with a diaeresis, and with a longitudinal carina.

Cephalic appendages

Last segment of antennular peduncles (basipodite) articulated with two flagella, flagella made of numerous and short cylindrical articles; antennae made of numerous and short cylindrical articles; short, triangular scaphocerite.

Thoracic appendages

Elongated Mxp3, with small spines on the ventral margin of each article excepted the two distal ones; chelate P1; P1 propodus short, subrectangular; wide P1 fingers, as long as propodus, straight dorsally, slightly curved downward, equal in length, with a distal hook; occlusal margin with very small teeth, closely spaced; P1 carpus short, subtriangular; elongated P1 merus; P2-P3 chelate.

Ornamentation

Carapace with a heterogeneous ornamentation; branchial, hepatic and pterygostomial regions densely covered by small tubercles, cardiac region covered by small tubercles and some spiny tubercles directed forward, cephalic region with strong and widely spaced spines directed forward and small tubercles; intercalated plate covered by a row of tubercles; presence of an antennal spine; tergites and pleurites of pleonal somites covered by small depressions; telson with two small spines on external margin; uropodal endopods with two small spines on external margin; uropodal exopods with a spine on external margin anterior to the diaeresis; P1 propodus covered by longitudinal rows of strong spines directed forward; inner margin with a row of strong spines directed forward; P1 carpus covered by rows of strong spines directed forward; P1 merus covered by small tubercles and strong spines directed forward along dorsal and ventral margins; P2-P3 and P5 with small and widely spaced depressions; P4 propodus with posterior spines.

DISCUSSION

Palaeastacus fuciformis is known by many subcomplete specimens. Its assignation to *Palaeastacus* is based on its typical carapace groove pattern and shape of P1 chelae: short gastro-orbital groove, both postcervical and branchiocardiac grooves joined to the sinuous hepatic groove, short and subrectangular P1 propodus, wide, short and straight fingers.

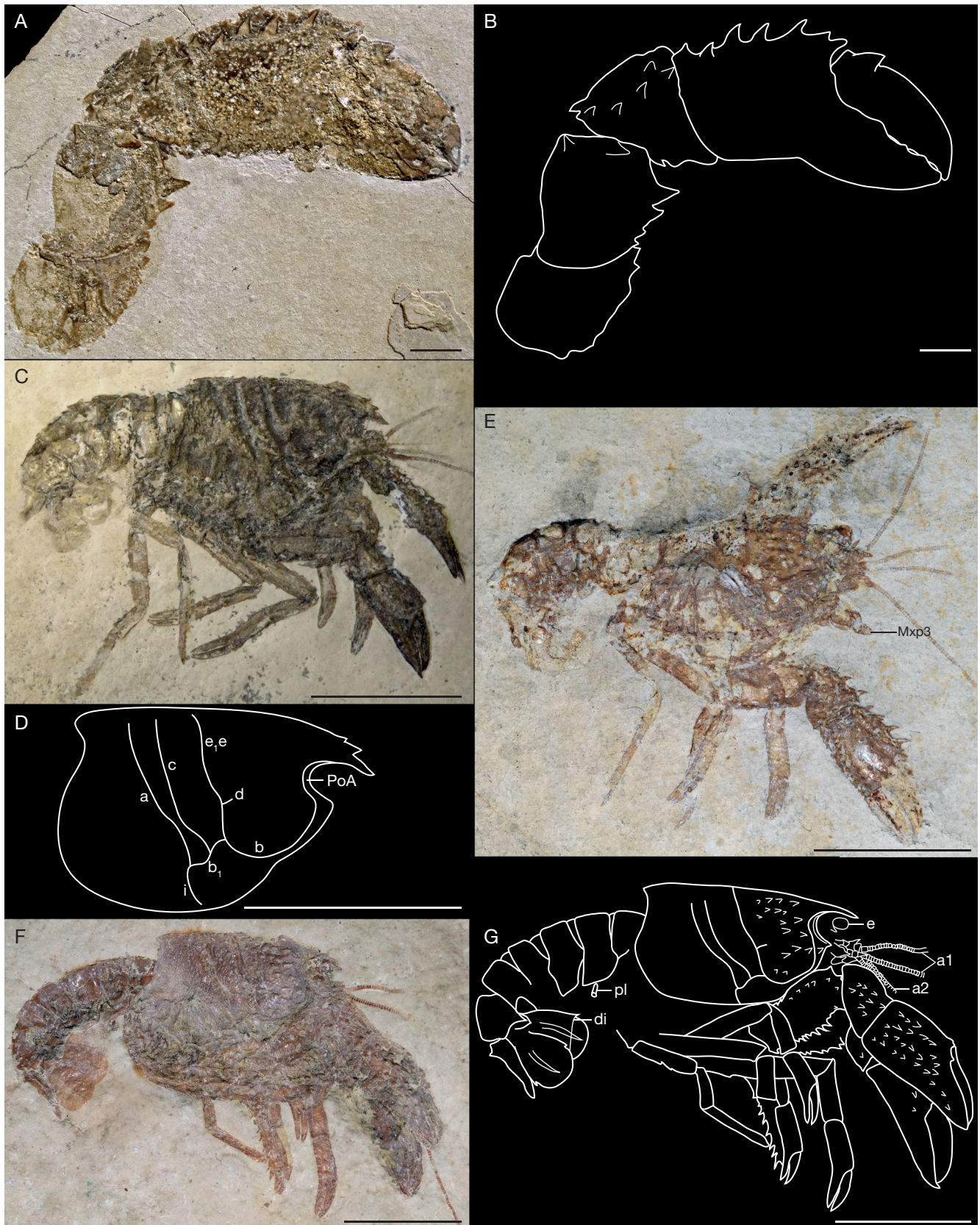


FIG. 12. —*Palaeastacus rothgaengerae* Schweigert & Röper, 2001 and *Palaeastacus fuciformis* (Schlotheim, 1822) from Germany: **A, B**, holotype BSPG 1993 XXVIII 200 of *P. rothgaengerae* from the Kimmeridgian of Brunn quarry: general view (**A**), schema (**B**); **C, D**, holotype MFN 2236 P1383/8 MB.A.0251 of *P. fuciformis* from the Tithonian of Solnhofen: general view (**C**), schema of the carapace (**D**); **E**, specimen MFN 2236 P1383/7 MB.A.2985 from the Tithonian of Eichstätt; **F–G**, specimen MFN 2236 P1383/7 MB.A.2992 from the Tithonian of Solnhofen: general view (**F**), schema (**G**). Abbreviations: **a**, branchiocardiac groove; **a1**, antennulae; **a2**, antenna; **b**, antennal groove; **b1**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **di**, diaeresis; **e**, eye; **e1e**, cervical groove; **i**, inferior groove; **ip**, intercalated plate; **Mxp3**, third maxilliped; **pl**, pleopod; **PoA**, postorbital area. Photographs: C, E, F, J. Devillez; A, G. Schweigert. Line drawings: J. Devillez. Scale bars: 1 cm.

Except *Palaeastacus argoviensis* Förster & Rieber, 1982 from the Aalenian, *Palaeastacus fuciformis* is the only species of the genus to have a sinuous cervical groove. The trajectories of the postcervical and branchiocardiac grooves are also particular: they are convergent under the level of the gastro-orbital groove and become divergent above their junctions to the hepatic groove. Similar trajectories of these grooves are only found in *Palaeastacus terraereginae* from the Barremian. Another characteristic is the presence of strong spines in the cephalic region while the remaining parts of its carapace are covered by small tubercles. None of other representatives of *Palaeastacus* exhibits such ornamentation. That of *Palaeastacus sussexiensis* (Mantell, 1824) from the Cretaceous is very close but *P. fuciformis* does not have oblique rows of strong spines in its cardiac region (Devillez *et al.* 2016, 2017). The P1 propodus of *P. fuciformis* is ornamented by longitudinal rows of spines contrary to most of the other species for which the P1 chelae are known.

Genus *Pustulina* Quenstedt, 1857 (Fig. 1H-I)

Pustulina Quenstedt, 1857: 807. — Glaessner 1969: 481. — Feldmann *et al.* 2015: 3. — Devillez *et al.* 2016: 531, fig. 1K-L. — Devillez *et al.* 2017: 792.

Phlyctisoma Bell, 1863: 34. — Zittel 1885: 695. — Glaessner 1929: 314. — Secrétan 1964: 74. — Förster 1966: 135. — Glaessner 1969: 626.

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

EMENDED DIAGNOSIS BY Devillez *et al.* (2016). — 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 the cervical groove, with two divergent, curved 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.

Pustulina suevica Quenstedt, 1857 (Figs 13; 14)

Pustulina suevica Quenstedt, 1857: 807, pl. 99, fig. 30. — Van Straelen 1925: 289. — Beurlen 1928: 200, fig. 24a (non 24b). — Schweigert *et al.* 2000: 9, pl. 5, figs 1-3. — Dietl & Schweigert 2001: 53, 54, fig. 87. — Schweitzer *et al.* 2010: 26.

Eryma fraasi Oppel, 1861: 359; 1862: 39, pl. 9, fig. 1.

Enoploclytia perroni Étallon, 1861: 161, pl. 9, fig. 1. — Van Straelen 1925: 279. — Glaessner 1929: 148. — Secrétan 1964: 70. **n. syn.**

Palaeastacus solitarius Oppel, 1862: 46, pl. 11, fig. 1. — Schweitzer *et al.* 2010: 25.

Eryma pseudobabeau Dollfus, 1863: 36, pl. 1, figs 1-2. — Sauvage 1891: 94, pl. 4, fig. 5 (non 4). — Glaessner 1929: 158. — Carriol 1991: 225. **n. syn.**

Enoploclytia edwardsi Sauvage, 1891: 87, pl. 3, figs 1-4. — Van Straelen 1925: 282. — Glaessner 1929: 146. — Schweitzer *et al.* 2010: 22. **n. syn.**

Enoploclytia dorsetensis Woods, 1930: 81, pl. 23, figs 1-3. **n. syn.**

Eryma perroni — Oppel 1861: 358; 1862: 33. — Woodward 1900: 9. — Whiteaves 1903: 322. — Beurlen 1928: 157, 164, 278. — Mertin 1941: 160. — Charbonnier *et al.* 2012b: 558, fig. 18E-F.

Eryma suevica — Oppel 1861: 359; 1862: 38, pl. 8, fig. 9.

Enoploclytia pseudo-babeau — Van Straelen 1925: 280.

Phlyctisoma perroni — Förster 1965: 140; 1966: 141, pl. 18, fig. 6. — Taylor 1979: 24.

Phlyctisoma pseudobabeau — Förster 1966: 141, pl. 18, fig. 6.

Phlyctisoma sp. — Förster 1966: 142, pl. 18, fig. 7.

Pustulina edwardsi — Carriol 1991: 224.

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

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

TYPE MATERIAL. — Holotype GPIT without number.

TYPE LOCALITY. — Nusplingen, Baden-Württemberg, Germany.

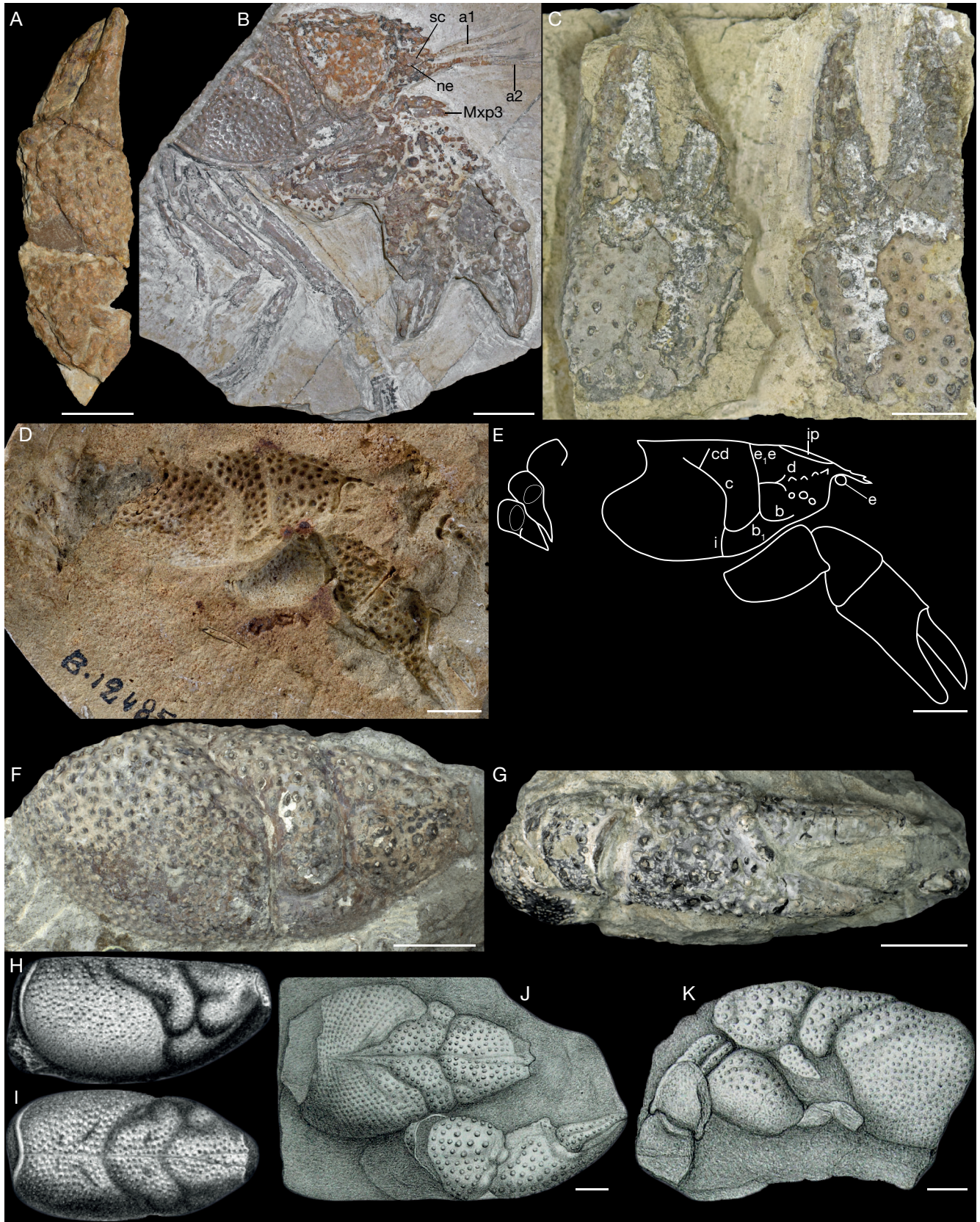
TYPE AGE. — Kimmeridgian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; short, spiny rostrum; dorsal margin of cephalic region curved downward; fusiform intercalated plate; orbital notch slightly curved; inflated cardiac, hepatic and branchial regions; deep cervical groove, almost straight and sub-vertical, joined to dorsal margin and to antennal groove; deep, wide antennal groove; elongated gastro-orbital groove, joined to cervical groove at carapace mid-height, with two divergent branches delimiting two gastro-orbital lobes; deep postcervical groove, inflected at carapace mid-height, strongly inclined dorsally, not joined to dorsal margin; shallow branchiocardiac groove, almost straight, not joined to dorsal margin and interrupted in branchial region; shallow cardiac groove, straight, slightly inclined forward, joined to the postcervical groove and to dorsal margin.

FIG. 13. — *Pustulina suevica* Quenstedt, 1857 and its synonyms. **A**, holotype GPIT without number (Kimmeridgian, Nusplingen, Germany); **B**, holotype SMNS 3682-1 of *Eryma fraasi* Oppel, 1862 (Kimmeridgian, Nusplingen, Germany); **C**, holotype SMNS 3682-4 of *Palaeastacus solitarius* Oppel, 1862 (Kimmeridgian, Nusplingen, Germany); **D**, syntype MNHN.F.B12485 of *Enoploclytia perroni* (Oxfordian, Frasné, France): general view (**C**), line drawing (**D**); **F**, **G**, type material of *Enoploclytia dorsetensis* Woods, 1930 (Oxfordian, Weymouth, United Kingdom): holotype NHMUK In.27137 (**F**), paratype NHMUK 33414 (**G**); **H-I**, holotype of



Eryma pseudobabeau Dollfus, 1863 (Kimmeridgian, Le Havre, France): original figures of Dollfus (1863: pl. 1, figs 1-2); **J-K**, syntypes of *Enoploclytia edwardsi* Sauvage, 1891 (Kimmeridgian, Boulogne-sur-Mer, France): original figures of Sauvage (1891: pl. 3, figs 1-2). Abbreviations: **a1**, antennulae; **a2**, antenna; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **cd**, cardiac groove; **d**, gastro-orbital groove; **e**, eye; **e₁e**, cervical groove; **i**, inferior groove; **ip**, intercalated plate; **Mxp3**, third maxilliped; **ne**, nephridiopore; **sc**, scaphocerite. Photographs and line drawing: J. Devillez. Scale bars: 1 cm.

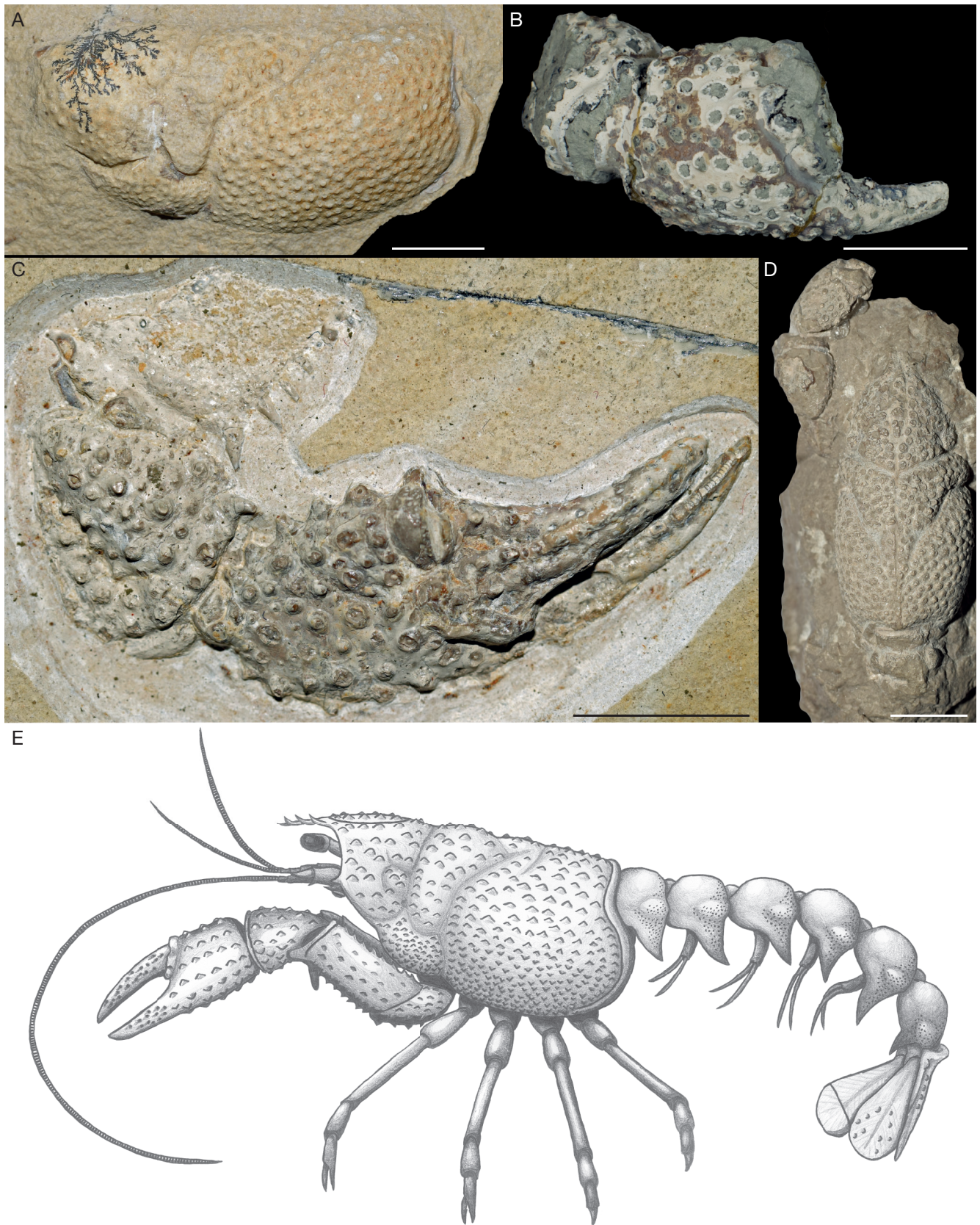


FIG. 14. — Additional specimens of *Pustulina suevica* Quenstedt, 1857 and reconstruction: **A**, specimen SMNS 60159 (Kimmeridgian, Bisingen-Ochsenwang); **B**, specimen NHMUK In.61550 (United Kingdom); **C**, specimen SMNS 70489 (Kimmeridgian, Nusplingen, Germany); **D**, specimen MFN 2236 P1383/5 MB.A.1538 (Oxfordian, Dollnstein, Germany); **E**, reconstruction of *P. suevica*. Photographs and drawing: J. Devillez. Scale bars: 1 cm.

Pleon and uropods

Somites with narrow subtriangular pleurites, with a rounded bulge on their basis.

Cephalic appendages

Last segment of antennular peduncles (basipodite) articulated with two flagella, flagella made of numerous and short cylindrical articles; antennae made of numerous and short cylindrical articles.

Thoracic appendages

Elongated Mxp3, made of cylindrical spineless segments; chelate P1; P1 propodus short, as long as wide; narrow, inflated dactylar bulge; short, wide P1 fingers, straight dorsally, slightly curved downward, equal in length; occlusal margin without teeth; P1 carpus short, subtriangular; elongated P1 merus, with a short process at outer side of its ventral extremity; P2-P3 chelate.

Ornamentation

Carapace densely covered by rounded tubercles, smaller in ventral part of branchial region and in pterygostomial region; intercalated plate covered by tubercles; row of tubercles parallel to the intercalated plate in gastric region; oblique row of tubercles ended by an orbital spine in gastric region; antennal row of coarse tubercles; tergites of pleonal somites covered by small rounded depressions, mainly on their posterior part; pleurites of pleonal somites covered by small depressions; P1 propodus densely covered by coarse tubercles organised in longitudinal rows on both ventral and dorsal surfaces; P1 fingers covered by rounded depressions; P1 carpus covered by coarse tubercles; P1 merus covered by small tubercles on dorsal margin, and with a row of spines along the extern ventral margin; smooth P2-P5.

DISCUSSION

Because the species was described from a single isolated P1 chela from the Kimmeridgian of Nusplingen (Germany), *Pustulina suevica* was recognized as an erymoid lobster only recently. Indeed, Schweigert *et al.* (2000) pointed out the strong similarities between the holotype of *P. suevica* and the P1 chelae of the holotypes of *Eryma fraasi* Oppel, 1861 (Fig. 13B) and *Palaeastacus solitarius* Oppel, 1862 (Fig. 13C), from the same locality. These species share a subrectangular P1 propodus bearing wide and short fingers, ornamented by longitudinal rows of coarse tubercles. Considering these elements, Schweigert *et al.* (2000) concluded that *E. fraasi* and *P. solitarius* are junior synonyms of *P. suevica*. Moreover, the carapace of *E. fraasi* is mostly preserved. This allowed Schweigert *et al.* (2000) to point out the similarities of the carapace groove pattern of *Pustulina* and *Phlyctisoma* Bell, 1863. So, *Phlyctisoma* became a junior synonym of *Pustulina*, and we concur with the conclusions of Schweigert *et al.* (2000).

Étallon (1861) described *Enoploclytia perroni* from the Oxfordian of Frasné (France; Fig. 13D-E). In the literature, this species was assigned to *Eryma* (Oppel 1861,

1862; Woodward 1900; Whiteaves 1903; Beurlen 1928; Mertin 1941; Charbonnier *et al.* 2012b), *Phlyctisoma* (Förster 1965; Förster 1966; Taylor 1979) or *Pustulina* (Schweitzer *et al.* 2010). Examination of the syntype of *E. perroni* shows a carapace groove pattern and P1 chela typical of *Pustulina*: the elongated gastro-orbital groove with two divergent branches, the concave hepatic groove, the inflected postcervical groove joined to the posterior extremity of the hepatic groove, the presence of the cardiac groove, the short and subrectangular propodus with its short and wide fingers. The ornamentation of *E. perroni* made of coarse rounded tubercles, becoming smaller ventrally, is also identical to that of *P. suevica*. So, we consider *E. perroni* as another junior synonym of *P. suevica*. For the same reasons than *E. perroni*, *Eryma pseudobabeau* Dollfus, 1863 (Kimmeridgian, Le Havre, France; Fig. 13H, I), *Enoploclytia edwardsi*, Sauvage, 1891 (Kimmeridgian, Boulogne-sur-Mer, France; Fig. 13J, K) and *Enoploclytia dorsetensis* Woods, 1930 (Oxfordian, Weymouth, United Kingdom; Fig. 13F, G) are considered as junior synonyms of *P. suevica*. We noticed that *E. edwardsi* has already been considered as a synonym of *Phlyctisoma pseudobabeau* and *E. dorsetensis* as a synonym of *P. perroni* by Förster (1966).

Among the crustacean faunas of the Oxfordian-Kimmeridgian, *Pustulina suevica* is a typical species with a wide distribution in Western Europe. Fossils of this species are reported from many localities in France, Germany and United Kingdom. Moreover, it is the only erymoid species from the lithographic limestones of southern Germany to have been reported out of this country.

P. suevica is distinct from some other species of the genus by its ornamentation. Indeed, there are no depressions as in *P. calloviensis* (Förster, 1966) and *P. elegans* (Förster, 1966), the tubercles of *P. suevica* are coarser than those of *P. trisulcata* (Schweitzer & Feldmann, 2001), there are no small tubercles between the coarse ones as in *P. tuberculata* (Bell, 1863), and there is a strong antennal row in *P. suevica* contrary to *P. calloviensis*, *P. cretacea* (Roger, 1946), *P. elegans*, *P. minuta*, and *Pustulina victori* Devillez, Charbonnier, Hyžný & Leroy, 2016. *Pustulina suevica* is also the only species with *P. elegans* to have an oblique orbital row. Like *P. minuta*, the cervical groove of *P. suevica* is almost straight contrary to *P. calloviensis*, *P. collosa* Devillez, Charbonnier, Hyžný & Leroy, 2016, *P. elegans*, and *P. occitana* Devillez, Charbonnier, Hyžný & Leroy, 2016. The gastro-orbital groove is also sub-horizontal while that of *P. calloviensis*, *P. collosa*, *P. elegans*, *P. occitana*, *P. spinulata* (Secrétan, 1964), and *P. tuberculata* is oblique. Moreover, the P1 fingers of *P. suevica* are sometimes ended by a hook contrary to *P. minuta* and *P. tuberculata*. Finally, the pleurites of the pleon are narrower than that of *P. minuta* and *P. trisulcata*.

Pustulina minuta (Schlotheim, 1822)
(Fig. 15)

Macrourites minutus Schlotheim, 1822: 28, pl. 3, fig. 3.

Glyphea verrucosa Münster, 1839: 21, pl. 9, fig. 11 (non 12). — Fraas 1855: 94.

Astacus minutus – Germar 1827: 102.

Glyphea minuta – Münster 1839: 20, pl. 9, figs 8-10.

Eryma minuta – Bronn 1849: 579. — Oppel 1861: 356; 1862: 39, pl. 8, figs 6-8. — Beurlen 1928: 164. — Vialle 1948: 61. — Secrétan 1964: 68.

Enoploclytia minuta – Van Straelen 1925: 284. — Glaessner 1929: 154 (pars.).

Enoploclytia fuciformis – Van Straelen 1925: 285 (pars.). — Glaessner 1929: 156 (pars.).

Phlyctisoma minuta – Förster 1965: 140; 1966: 142, pl. 18, fig. 9. — Frickhinger 1994: 126, fig. 224.

Pustulina minuta – Feldmann & Titus 2006: 64. — Garassino & Schweigert 2006: 11, 36, fig. 8, pl. 2, fig. 1, pl. 11, fig. 6, pl. 12, figs 1-2. — Schweitzer *et al.* 2010: 26. — Charbonnier & Garassino 2012: 864, 865, fig. 3E. — Schweigert 2015: fig. 545. — Odin *et al.* 2019: 654, fig. 7D, ap. 1.

Eryma verrucosa – Oppel 1861: 359; 1862: 38, pl. 8, fig. 5. — Feldmann & Titus 2006: 64. — Schweitzer *et al.* 2010: 26.

TYPE MATERIAL. — Holotype MFN 2236 P1383/5 MB.A.0254.

TYPE LOCALITY. — Eichstätt, Bavaria, Germany.

TYPE AGE. — Tithonian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; short, spiny rostrum; fusiform intercalated plate; orbital notch slightly curved; deep cervical groove, almost straight and sub-vertical, joined to dorsal margin and to antennal groove; deep antennal groove; elongated gastro-orbital groove, joined to cervical groove at carapace mid-height, with two divergent branches delimiting two gastro-orbital lobes; deep postcervical groove, inflected at carapace mid-height, inclined dorsally, not joined to dorsal margin; shallow branchiocardiac groove, not joined to dorsal margin and interrupted in branchial region; narrow and shallow cardiac groove, straight, strongly inclined forward, joined to the postcervical groove and to dorsal margin.

Pleon and uropods

Somites with wide subtriangular pleurites, becoming shorter from s4 to s6, with a slightly rounded posterior margin, with a strongly inflated and rounded bulge on their basis; telson with a median groove and two longitudinal crests; uropods as long as telson; uropodal endopods with a longitudinal carina; uropodal exopods with a diaeresis.

Cephalic appendages

Last segment of antennular peduncles (basipodite) articulated with two flagella, flagella made of numerous and short cylindrical articles; antennae made of numerous and short cylindrical articles; short, triangular scaphocerite.

Thoracic appendages

Elongated Mxp3, with two cylindrical distal segments lacking of spines; chelate P1; P1 propodus short, as long as wide; narrow, slightly inflated dactylar bulge; short, wide P1 fingers, straight dorsally, slightly curved downward, equal in length; occlusal margin without teeth; P1 carpus short, subtriangular; elongated P1 merus; P2-P3 chelate.

Ornamentation

Carapace densely covered by rounded tubercles, smaller and closer in branchial region; intercalated plate covered by tubercles; tergites and pleurites of pleonal somites covered by small depressions; longitudinal crest of the telson bearing a row of tubercles; telson covered by thin tubercles and with two small spines on its external margin; uropodal endopods covered by thin tubercles; P1 propodus densely covered by coarse tubercles; P1 fingers with irregular carina and rounded depressions; P1 carpus densely covered by coarse tubercles; P1 merus with coarse tubercles in its distal part; smooth P2-P3 and P5; P4 propodus with posterior spines.

DISCUSSION

The assignation to *Pustulina* is based on the typical groove pattern: the wide and long gastro-orbital groove with two divergent branches, the inflected postcervical groove, joined to the posterior extremity of the hepatic groove, the concave hepatic groove, and the presence of a cardiac groove.

After the original description by Schlotheim (1822), Münster (1839) described *Glyphea verrucosa* based on an isolated P1 chela from the same locality. Later, Glaessner (1929), followed by Förster (1966) and Garassino & Schweigert (2006), established the synonymy between *M. minutus* and *G. verrucosa*, while Schweitzer *et al.* (2010) reported *Eryma verrucosa* as Incertae sedis in Erymidae section. The lectotype of *G. verrucosa* is a true chelae, so it cannot be maintained within *Glyphea* Meyer, 1835, because glypheid lobsters have subchelate P1-P3. Moreover, comparisons with the specimens of *Pustulina minuta* show strong similarities in both forms: rectangular propodus with short and wide fingers typical of *Pustulina*; a propodus densely and irregularly covered by coarse rounded tubercles and fingers with depressions and irregular carina. These similarities support the synonymy between *P. minuta* and *G. verrucosa* previously established by Glaessner (1929).

The compression of the specimens of *Pustulina minuta* makes difficult comparisons with other species. The cervical groove is almost straight while that of *P. calloviensis*, *P. colossea*, and *P. elegans* is clearly curved or sinuous. Moreover, contrary to *P. colossea*, *P. occitana*, *P. spinulata*, *P. suevica*, and *P. tuberculata*, there is no well-marked antennal row in *P. minuta*. There is also no row in the gastric region contrary to *P. trisulcata* and no depressions contrary to *P. calloviensis* and *P. elegans*. Finally, the P1 fingers of *P. minuta* do not have a terminal hook contrary to *P. cretacea* and some specimens of *P. suevica*.

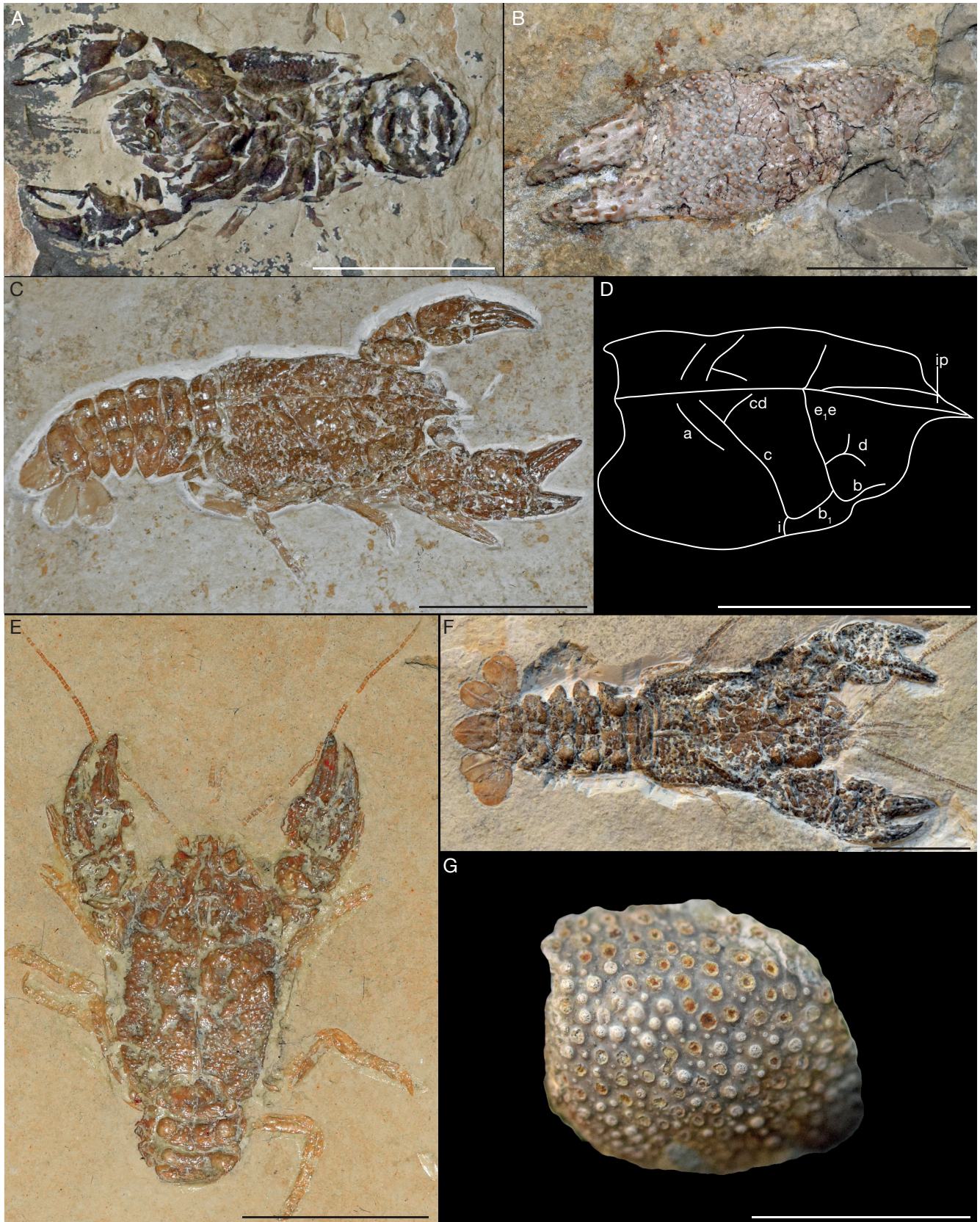


FIG. 15. — *Pustulina minuta* (Schlotheim, 1857) from the Tithonian of Germany and *Pustulina* sp.: **A**, holotype MFN 2236 P1383/5 MB.A.0254 of *P. minuta* from Eichstätt; **B**, lectotype BSPG AS VII 182 of *Glypheo verrucosa* Münster, 1839 from Eichstätt; **C**, **D**, specimen MFN 2236 P1383/5 MB.A.1119 of *P. minuta* from Solnhofen; general view (**C**), schema of the carapace (**D**); **E**, specimen 2236 P1383/5 MB.A.2863 of *P. minuta* from Solnhofen; **F**, specimen BSPG AS VIII 78 of *P. minuta* from Solnhofen; **G**, specimen BSPG 1952 XV 570 of *P. sp.* (Kimmeridgian, Nagelsberg near Heubach, Germany). Abbreviations: *a*, branchiocardiac groove; *b*, antennal groove; *b₁*, hepatic groove; *c*, postcervical groove; *cd*, cardiac groove; *d*, gastro-orbital groove; *e₁e*, cervical groove; *i*, inferior groove; *ip*, intercalated plate. Photographs and line drawing: J. Devillez. Scale bars: 1 cm.

FRAGMENTS ATTRIBUTED TO *PUSTULINA*

REMARKS

Förster (1965) reported a P1 chela from the Tithonian of Unterhausen near Neuburg a. d. Donau (Germany). It exhibits a shape of propodus and fingers and a coarse ornamentation close to that of *P. minuta* and *P. suevica*.

Another P1 propodus from the Kimmeridgian of Nögelsberg near Heubach (Germany) is stored in the collections of the BSPG (Fig. 15G). It is subrectangular, short with a well-marked coarse ornamentation typical of *Pustulina*.

Genus *Stenodactylina* Beurlen, 1928 (Fig. 1J-L)

Stenodactylina Beurlen, 1928: 175. — Glaessner 1969: 456. — Schweigert 2013: 411. — Devillez *et al.* 2016: 522, figs 1D-F.

Erymastacus Beurlen, 1928: 171 (pars.). — Secrétan 1964: 71. — Glaessner 1969: 456 (pars.). — Hyžný *et al.* 2015: 375.

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

DIAGNOSIS BY Devillez & Charbonnier (2019). — Fusiform intercalated plate; narrow post-orbital area; deep, very wide 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; hepatic groove concavo-convex, joined to cervical groove; inferior groove convex posteriorly, joined to hepatic groove; chelate P1; P1 propodus rectangular or trapezoidal, with inner margin more compressed than outer margin, with a wide dactylar bulge; P1 with extremely long and slender fingers, equal in length; P1 chela (form I; Fig. 1K) with strong, rectangular or trapezoidal propodus, bearing straight or sinuous fingers, strongly narrowing immediately after their basis; outer margin convex at the basis of the index; P1 chela (form II; Fig. 1L) with trapezoidal propodus, outer margin straight or convex, straight fingers, narrowing gradually to their distal extremity.

Stenodactylina insignis (Oppel, 1862) (Fig. 16A-C)

Eryma insignis Oppel, 1862: 33, pl. 10, fig. 1. — Van Straelen 1925: 264. — Förster 1966: 110.

Eryma anisodactylus Krause, 1891: 207, pl. 13, fig. 4. — Van Straelen 1925: 270. — Förster 1966: 116.

Eryma ornata – Étallon 1861: 166, pl. 8, fig. 2.

Erymastacus insignis – Beurlen 1928: 175. — Glaessner 1929: 162. — Secrétan 1964: 74. — Hyžný *et al.* 2015: 376.

Erymastacus anisodactylus – Beurlen 1928: 175. — Glaessner 1929: 162.

Eryma anisodactylum – Schweitzer *et al.* 2010: 23.

Erymastacus anisodactylina – Hyžný *et al.* 2015: 376.

Stenodactylina insignis – Devillez *et al.* 2016: 524, table 1.

TYPE MATERIAL. — Cast of the holotype MNHN.FA24613.

TYPE LOCALITY. — Unknown locality, Haute-Saône département, Bourgogne, France.

TYPE AGE. — Oxfordian.

DESCRIPTION

Thoracic appendages

Chelate P1; elongated P1 propodus, trapezoidal, slightly globose medially; inflated dactylar bulge; elongated P1 fingers; dactylus progressively narrowing in its proximal half, inflected at mid-length, slender in its distal half, with a terminal hook; index with a wide basis, progressively narrowing in its proximal third, strongly inflected at its proximal third, slender and sinuous distally; occlusal margin with short conical teeth.

Ornamentation

Propodus and fingers covered by small tubercles.

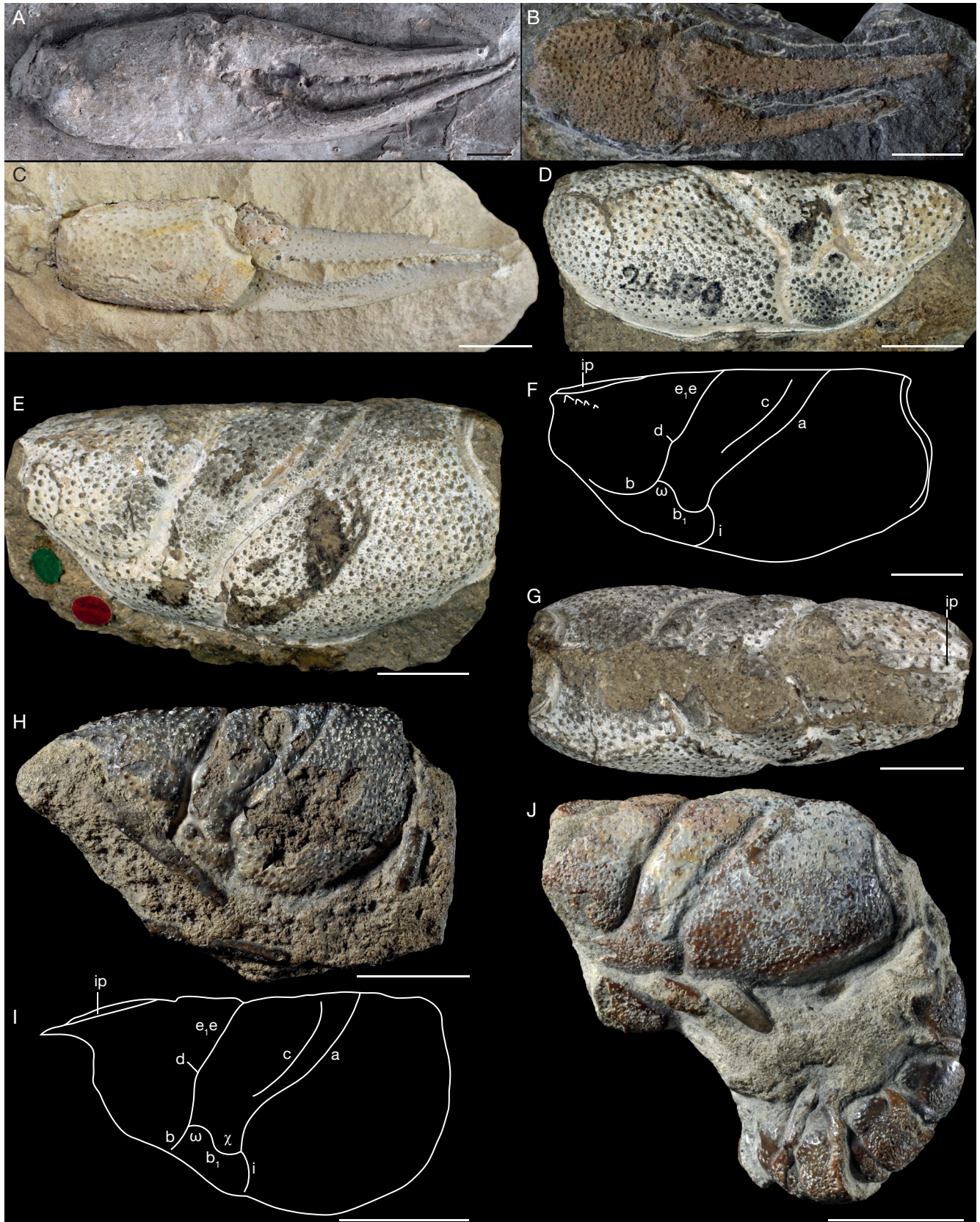
DISCUSSION

The holotype of *Eryma insignis* is a P1 chela currently lost, but a cast is stored in the MNHN collections. In the literature, some authors assigned this species to *Eryma* (Van Straelen 1925; Förster 1966), while others assigned it to *Erymastacus* (Beurlen 1928; Glaessner 1929; Secrétan 1964; Hyžný *et al.* 2015), which was established to group erymid chelae showing particularly elongated fingers. Later, Devillez *et al.* (2016) considering the elongated propodus with the long, slender, inflected and sinuous fingers, integrated *E. insignis* into *Stenodactylina*.

Like *E. insignis*, *Eryma anisodactylus* Krause, 1891 (Fig. 16B) has a complex history. Sometimes regarded as a species of *Eryma* (Van Straelen 1925; Förster 1966; Schweitzer *et al.* 2010) or *Erymastacus* (Beurlen 1928; Glaessner 1929; Secrétan 1964; Hyžný *et al.* 2015), Devillez *et al.* (2016) finally pointed out the similarities between these two species. Indeed, they are synonyms because of the shape of the P1 propodus and the length and shape of the fingers.

Stenodactylina insignis is only known by isolated P1 chelae, so comparisons to other species are limited. The wide basis of the index and its inflexion are diagnostic of the species. Moreover, the ornamentation lacking of coarse tubercles and spines on the propodus is distinct from *S. armata* (Secrétan, 1964), *S. australis* (Secrétan, 1964), *S. falsani* (Dumortier, 1867), *S. lagardettei* (Hyžný, Schlögl, Charbonnier, Schweigert, Rulleau & Gouttenoire, 2015), *S. liasina* Beurlen, 1928, *S. rogerfurzei* Schweigert, 2013, *S. spinosa* (Étallon, 1861), *S. strambergensis* (Bachmayer, 1959), and *S. triglypta* (Stenzel, 1945).

FIG. 16. — *Stenodactylina insignis* (Oppel, 1862), *Stenodactylina shotoveriganti* n. sp. and *Stenodactylina granulifera* (Secrétan, 1964): **A**, holotype of *S. insignis* (Oxfordian, Haute-Saône, France); **B**, holotype MFN 2236 P1383/2 MB.A.1536 of *Eryma anisodactylus* Krause, 1891 (Kimmeridgian, Holzen, Germany); **C**, specimen IRSNB without number of *S. insignis* (Kimmeridgian, La Rochelle, France); **D-G**, holotype NHMUK 24559 of *S. shotoveriganti* n. sp. (Oxfordian, Shotover,



United Kingdom): right lateral view (D), left lateral view (E), schema (F), dorsal view (G); H-J, holotype MNHN.F.R03975 of *S. granulifera* (Kimmeridgian, Antsalova, Madagascar): lateral view (H), schema (J); C, D, holotype MNHN.F.R03974 of *Eryma madagascariensis* Secrétan, 1964 (Kimmeridgian, Antsalova, Madagascar). Abbreviations: a, branchiocardiac groove; b, antennal groove; b₁, hepatic groove; c, postcervical groove; d, gastro-orbital groove; e, e, cervical groove; i, inferior groove; ip, intercalated plate; χ, attachment site of adductor testis muscle; ω, attachment site of mandibular muscle. Photographs: A, L. Cazes; B-E, G, J. Devillez; H, J, C. Lemzaouda. Line drawings: J. Devillez. Scale bars: 1 cm.

Stenodactylina shotoverigiganti n. sp.
(Fig. 16D-G)

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Eryma cf. *bedelta* – Woods 1930: pl. 21, fig. 2.

TYPE MATERIAL. — Holotype NHMUK 24559.

ETYMOLOGY. — The specific epithet comes from the Latin “*gigantes*”, meaning giant, associated to the name of the type locality, Shotover. It refers to the giant of Shotover, a geoglyph, mentioned during the 17th century by Jean Aubrey, that has disappeared now.

TYPE LOCALITY. — Shotover, Oxfordshire, United Kingdom.

TYPE AGE. — Oxfordian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; fusiform intercalated plate; elongated cardiac region; deep and wide cervical groove, becoming wider ventrally, slightly sinuous at its median inflexion, joined to dorsal margin and to antennal groove; deep and very wide antennal groove; short, shallow gastro-orbital groove, oblique, originating as a slight median inflexion of cervical groove; subparallel postcervical and branchiocardiac grooves, slightly curved; deep and wide postcervical groove, not joined to dorsal margin and interrupted in hepatic region; deep and wide branchiocardiac groove, becoming wider towards its junction to the hepatic groove, joined to dorsal margin, joined to the posterior extremity of the hepatic groove; wide hepatic groove, concavo-convex, joined to the cervical groove; slightly inflated ω area, ventrally delimited by a shallow depression extending between cervical and hepatic grooves; flat χ area; deep and wide inferior groove, joined to hepatic groove.

Ornamentation

Carapace covered by rounded tubercles; intercalated plate with small tubercles irregularly spaced; gastric region with an oblique row of tubercles ended by an orbital spine.

DISCUSSION

Stenodactylina shotoverigiganti n. sp. is known by a unique carapace previously mentioned and figured by Woods (1930) as *Eryma* cf. *bedelta*. Careful examination of the specimen shows the absence of junction between postcervical and branchiocardiac grooves, and the interruption of the postcervical groove in hepatic region while the branchiocardiac groove is joined to the hepatic groove. This groove pattern is diagnostic of *Stenodactylina*. Moreover, some morphological features allow the distinction of this specimen from all other representatives of the genus for which the carapace is known. Indeed, the postcervical groove is shorter than that of *S. australis*, *S. delphinensis* (Moret, 1946), *S. deslongchampsii* (Van Straelen, 1925), *S. granulifera*, *S. lagardettei*, *S. pseudoventrosa*, and *S. walkerae* (Feldmann & Haggart, 2007). It is also slightly curved contrary to *S. burgundiaca* (Crônier & Courville, 2004), *S. delphinensis*, *S. granulifera*,

S. triglypta, and *S. walkerae*. Only the ω area is inflated while it is flat in some species (*S. australis*, *S. delphinensis*, *S. deslongchampsii*) or both ω and χ areas are inflated in some others (*S. burgundiaca*, *S. granulifera*, *S. guisei* (Wright, 1881), *S. lagardettei*). The ornamentation of the specimen is thin and only made of tubercles contrary to *S. australis*, *S. burgundiaca*, *S. delphinensis*, *S. granulifera*, *S. guisei*, *S. lagardettei*, and *S. pseudoventrosa*. Finally, there is an orbital row, which is absent in *S. australis*, *S. burgundiaca*, *S. delphinensis*, *S. deslongchampsii*, *S. guisei*, and *S. triglypta*. Considering all these elements, we consider this specimen as a representative of a new species of erymid lobsters: *Stenodactylina shotoverigiganti* n. sp.

Stenodactylina granulifera (Secrétan, 1964)
(Fig. 16H-J)

Eryma granulifera Secrétan, 1964: 64, pl. 1, fig. 1, pl. 3, fig. 1. — Förster 1966: 125. — Garassino & Schweigert 2006: 8. — Feldmann & Titus 2006: 64. — Schweitzer *et al.* 2010: 24.

Eryma madagascariensis Secrétan, 1964: 61, pl. 3, figs 2-3. — Förster 1966: 116, 125, 162. — Taylor 1979: 36. — Förster & Seyed-Ema-mi 1982: 44. — Garassino & Schweigert 2006: 8. — Feldmann & Titus 2006: 64. — Schweitzer *et al.* 2010: 24.

Eryma cf. *bedelta* – Beurlen 1933: 89, fig. 1.

Stenodactylina granulifera – Devillez *et al.* 2016: 524, table 1.

TYPE MATERIAL. — Holotype MNHN.F.R03975.

TYPE LOCALITY. — East of Antsalova, Maintirano region, Tuléar province, Madagascar.

TYPE AGE. — Kimmeridgian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; fusiform intercalated plate; narrow post-orbital area; wide cephalic region; deep and wide cervical groove, strongly inclined, joined to dorsal margin and to antennal groove; deep and narrow antennal groove; short, shallow gastro-orbital groove, oblique, originating as a slight median inflexion of cervical groove; inferior gastro-orbital lobe slightly inflated; postcervical and branchiocardiac grooves subparallel; deep postcervical groove, strongly inclined and curved forward, joined to dorsal margin and interrupted in hepatic region; deep branchiocardiac groove, slightly curved forward, joined to dorsal margin and to hepatic groove; hepatic groove concavo-convex, joined to cervical groove; ω and χ areas slightly inflated; deep, wide inferior groove, joined to hepatic groove.

Pleon and uropods

Somites with subtriangular pleurites, with a longitudinal bulge on their basis.

Thoracic appendages

Elongated P2-P5 merus.

Ornamentation

Carapace densely covered by small tubercles preceded by depressions, the tubercles are coarser along the intercalated plate; pleonal somites densely covered by small rounded depressions; P2-P5 merus covered by small rounded and widely spaced depressions.

DISCUSSION

This species was described from a carapace firstly assigned to *Eryma* (Secrétan 1964). A second species, *E. madagascariensis* Secrétan, 1964, based on a carapace connected to a fragment of pleon was also described (Fig. 16J). The review of the decapod crustaceans of Madagascar by Charbonnier *et al.* (2012a) concluded to the synonymy between *Eryma granuliferum* and *E. madagascariensis* because of their very close carapace groove pattern. Later, Devillez *et al.* (2016) assigned *E. granuliferum* to *Stenodactylina* because of the absence of junction between the postcervical and branchiocardiac grooves and the interruption of the postcervical groove in hepatic region. In addition to the carapace groove pattern, the slight inflation of ω and χ areas, and the ornamentation made of small tubercles preceded by depressions support the synonymy between *S. granulifera* and *E. madagascariensis*.

Both ω and χ areas are inflated in *Stenodactylina granulifera*, contrary to *S. australis*, *S. delphinensis*, *S. deslongchampsii*, *S. shotoveriganti* n. sp., *S. triglypta*, and *S. walkerae*. *S. granulifera* is one of the species within the genus, with *S. walkerae*, to exhibit an inflated gastro-orbital lobe. Its thin ornamentation is also distinct from that of *S. australis*, *S. granulifera*, *S. lagardettei*, *S. pseudoventrosa*, *S. shotoveriganti* n. sp., *S. triglypta*, and *S. walkerae*.

Stenodactylina pseudoventrosa (Beurlen, 1928) n. comb. (Fig. 17A, B)

Eryma pseudoventrosa Beurlen, 1928: 158; 1933: 90. — Schweitzer *et al.* 2010: 24.

Eryma modestiformis (pars.) – Förster 1966: 118.

TYPE MATERIAL. — Holotype GPIT Ar/294/3.

TYPE LOCALITY. — Hülben, Baden-Württemberg, Germany.

TYPE AGE. — Kimmeridgian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; spiny rostrum; fusiform intercalated plate; narrow post-orbital area; deep and wide cervical groove, strongly inclined dorsally, inflected at carapace mid-height, joined to dorsal margin and to antennal groove; deep and wide antennal groove; short, wide gastro-orbital groove, deep and oblique, originating as a median inflexion of cervical groove; postcervical and branchiocardiac grooves subparallel, slightly curved, very close; deep postcervical groove, not joined to dorsal margin and interrupted in hepatic region; deep branchiocardiac groove, strongly inclined, not joined to dorsal margin.

Ornamentation

Carapace covered by small tubercles preceded by crescent-shaped depressions; cephalic region with an oblique orbital row of tubercles.

DISCUSSION

Known by a single cast of carapace, this species was originally assigned to *Eryma* (Beurlen 1928), and then regarded as a synonym of *Eryma modestiforme* (see Förster 1966). Careful examination of the holotype clearly shows the absence of junction between postcervical and branchiocardiac grooves and the interruption of the postcervical in the hepatic region. This groove pattern is diagnostic of *Stenodactylina*. So, the new combination *Stenodactylina pseudoventrosa*, n. comb. is here proposed.

The strong proximity of the postcervical and branchiocardiac grooves allows the distinction of *S. pseudoventrosa*, n. comb. from *S. burgundiaca* and *S. delphinensis*. Moreover, the ventral extremity of the postcervical groove of *S. pseudoventrosa*, n. comb. is lower than in *S. burgundiaca*, *S. guisei*, *S. shotoveriganti* n. sp., *S. triglypta*, and *S. walkerae*. Contrary to *S. australis*, *S. burgundiaca*, *S. delphinensis*, *S. deslongchampsii*, *S. granulifera*, *S. guisei*, and *S. triglypta*, an orbital row is present in *S. pseudoventrosa*. There are also depressions and no coarse elements in its ornamentation contrary to *S. australis*, *S. deslongchampsii*, *S. lagardettei*, *S. shotoveriganti* n. sp., *S. triglypta*, and *S. walkerae*.

Stenodactylina australis (Secrétan, 1964) (Fig. 17C-F)

Erymastacus australis Secrétan, 1964: 72, pl. 1, figs 2-6, pl. 2, figs 1-5. — Förster 1966: 135. — Taylor 1979: 36. — Schweitzer *et al.* 2010: 23. — Hyžný *et al.* 2015: 376.

Palaeastacus australis – Förster & Rieber 1982: 377.

Eryma australe – Charbonnier *et al.* 2012a: 327, fig. 11.

Stenodactylina australis – Devillez *et al.* 2016: 524, table 1.

TYPE MATERIAL. — Holotype MNHN.F.R03972; three paratypes MNHN.F.A31660, A33207, R03971.

TYPE LOCALITY. — Nord of Analavelona Massif, Sikily region, Tuléar province, Madagascar.

TYPE AGE. — Tithonian.

DESCRIPTION

Carapace

Sub-cylindrical carapace; elongated cardiac region; deep cervical groove, strongly inclined, joined to dorsal margin and to antennal groove; shallow and narrow antennal groove; short, shallow gastro-orbital groove, oblique, originating as a slight median inflexion of cervical groove; postcervical and branchiocardiac grooves subparallel; postcervical groove deep and wide dorsally, narrowing and shallowing ventrally, strongly inclined and inflected forward, joined to dorsal margin and interrupted in hepatic region; shallow and narrow branchio-

cardiac groove, not joined to dorsal margin, joined to hepatic groove; shallow and narrow hepatic groove, concavo-convex, joined to cervical groove; flat ω and χ areas; narrow inferior groove, joined to hepatic groove.

Thoracic appendages

Chelate P1; P1 propodus elongated, subrectangular, slightly globose; inner margin more compressed than outer margin; deviation of outer margin at the basis of the index; wide, inflated dactylar bulge; slender, elongated P1 fingers; curved downward; occlusal margin with short conical teeth regularly spaced.

Ornamentation

Carapace densely covered by tubercles preceded by depressions, the tubercles are coarser and the depressions are wider and deeper in the dorsal third of the carapace; P1 propodus covered by rounded tubercles; inner margin with an irregular row of strong subspiny tubercles, directed forward; basis of inner margin of the dactylus with two strong spines.

DISCUSSION

Secrétan (1964) assigned this species, described from fragments of P1, to *Erymastacus* Beurlen, 1928. Later, Devillez *et al.* (2016) assigned this species to *Stenodactylina* because of its subrectangular P1 propodus, the inflated dactylar bulge, the deviation of the outer margin at the basis of the index and the slender fingers. A cast of a carapace has been recently found in the MNHN collections. It comes from the same stage than the type material of *Stenodactylina australis* and from a locality where one paratype was found. This carapace exhibits the typical groove pattern of *Stenodactylina*: short gastro-orbital groove, sinuous hepatic groove, postcervical and branchiocardiac grooves not joined, postcervical groove interrupted in hepatic region, and branchiocardiac groove joined to posterior extremity of hepatic groove. The correlation of the groove pattern and the shape of P1 chelae, characteristics of *Stenodactylina*, and the stratigraphic and geographic arguments lead us to consider the cast of the carapace as a specimen of *S. australis*.

Stenodactylina australis is one of the rare species of the genus, with *S. burgundiaca*, *S. deslongchampsii*, *S. lagardettei*, and *S. triglypta*, for which both carapace and P1 chelae are known. The carapace of *S. australis* is distinct from all other species by its shallow postcervical and branchiocardiac grooves. These grooves are also clearly more inclined than those of *S. burgundiaca*, *S. pseudoventrosa*, *S. triglypta*, and *S. walkerae*. The flat ω area of *S. australis* is also distinct from *S. burgundiaca*, *S. granulifera*, *S. guisei*, *S. lagardettei*, *S. shotoverigiganti* n. sp., *S. triglypta*, and *S. walkerae*. Moreover, *S. australis* is the only species, with *S. triglypta*, to have a coarser ornamentation on the dorsal part of the carapace. There is also no antennal row, contrary to *S. lagardettei*,

S. pseudoventrosa, *S. shotoverigiganti* n. sp., and *S. walkerae*. The P1 chelae of *S. australis* are clearly distinct from those of *S. armata*, *S. falsani*, *S. lagardettei*, *S. liasina*, *S. rogerfurzei*, *S. spinosa*, *S. strambergensis*, and *S. triglypta* because of their finer ornamentation without rows of coarse tubercles on dorsal and ventral surfaces. The P1 propodus of *S. australis* has a row of spines on its inner margin, this row is absent in *S. australis*, *S. burgundiaca*, *S. deslongchampsii*, *S. falsani*, and *S. insignis*.

Stenodactylina strambergensis (Bachmayer, 1959) (Fig. 17G-I)

Erymastacus strambergensis Bachmayer, 1959: 940, pl. 2, fig. 2.

Phlyctisoma strambergensis – Förster 1966: 144, pl. 18, fig. 8.

Eryma strambergensis – Schweitzer *et al.* 2010: 24.

Stenodactylina strambergensis – Devillez *et al.* 2016: 524.

TYPE MATERIAL. — Holotype NMW 344/1959.

TYPE LOCALITY. — Stramberg, Moravian-Silesian, Czech Republic.

TYPE AGE. — Tithonian.

DESCRIPTION

Thoracic appendages

Chelate P1; P1 propodus sub-rectangular, slightly globose dorso-ventrally; inner margin strongly compressed; rounded outer margin with a slight deviation at the basis of the index; slender index; wide and inflated dactylar bulge.

Ornamentation

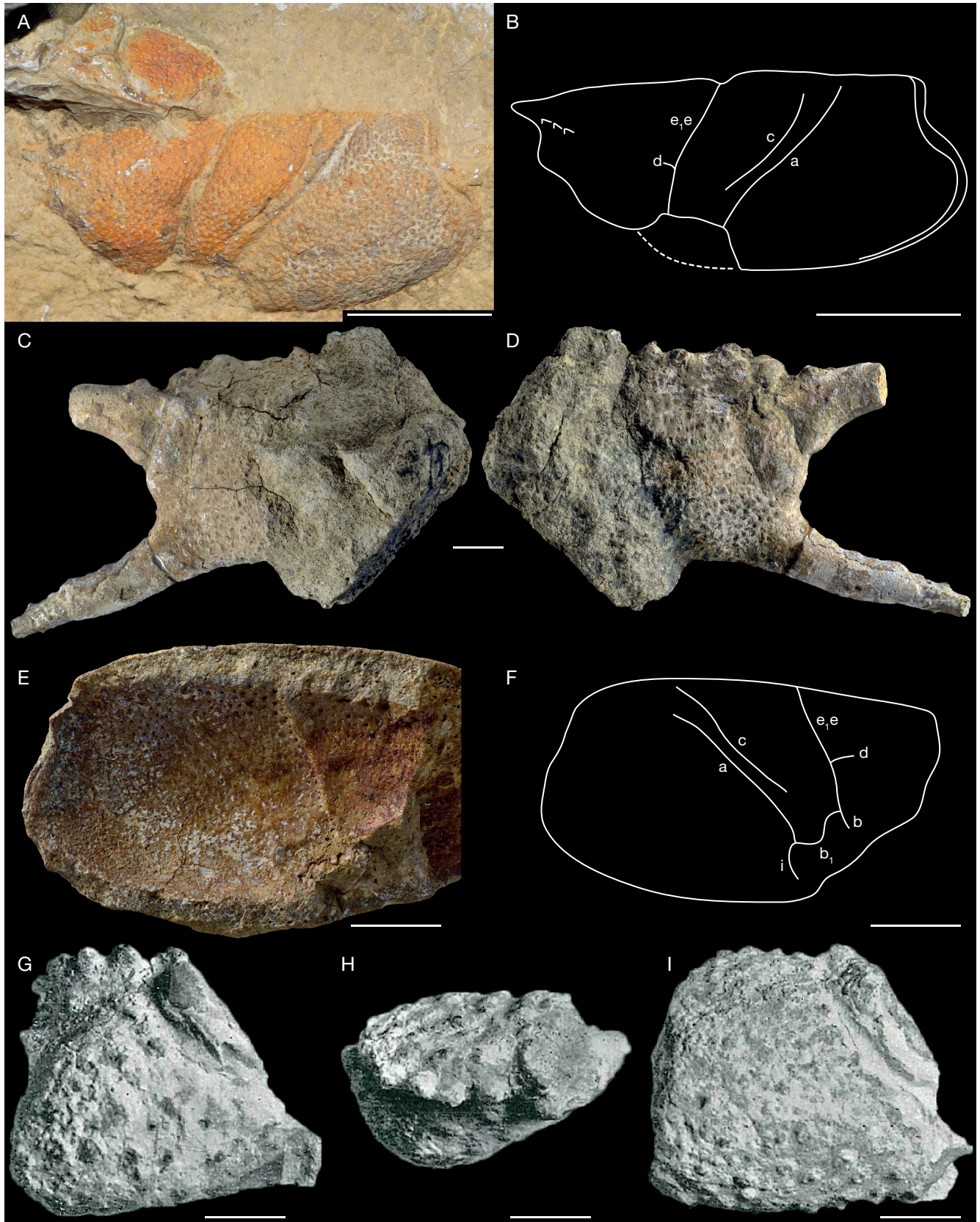
P1 propodus covered by rounded, coarse and widely spaced tubercles; inner margin with a row of spines.

DISCUSSION

This species is known by some P1 propodi. Initially included within *Erymastacus*, then moved into *Phlyctisoma* (see Förster 1966) and *Eryma* (see Schweitzer *et al.* 2010), and finally to *Stenodactylina* by Devillez *et al.* (2016). This assignment is supported by the stronger compression of the inner margin than that of outer margin, the presence of a row of coarse tubercles on inner margin (present in most of the species of the genus), the strongly inflated dactylar bulge, and the fine basis of the index.

Because only the P1 propodus of this species is known, the comparisons with other species of *Stenodactylina* are limited. *Stenodactylina strambergensis* has the particularity to have a relatively short propodus. Moreover, the ornamentation of *S. strambergensis* is homogeneous – only made of coarse tubercles – contrary to other species, except *S. armata* and *S. triglypta*.

FIG. 17. — *Stenodactylina pseudoventrosa* (Beurlen, 1928) n. comb., *Stenodactylina australis* (Secrétan, 1964) and *Stenodactylina strambergensis* (Bachmayer, 1959): **A, B**, holotype GPIT Ar/294/3 of *S. pseudoventrosa*, n. comb. (Kimmeridgian, Hülben, Germany): general view (**A**), schema (**B**); **C, D**, holotype MNHN.F.R03972 of *S. australis* (Tithonian, north of Analavelona Massif, Madagascar): ventral view (**C**), dorsal view (**D**); **E, F**, specimen MNHN.F.A33228 of *S. australis* (Tithonian,



Marolalitra, Madagascar: general view (**E**), schema (**F**); **G**, **H**, original figures of Bachmayer (1959: pl. 2, fig. 2b, c) of the holotype of *S. strambergensis* (Tithonian, Stramberg, Czech Republic); **I**, original figure of Bachmayer (1959: pl. 2, fig. 2a) of the paratype of *S. strambergensis* (Tithonian, Stramberg, Czech Republic). Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **e, e**, cervical groove; **i**, inferior groove. Photographs: A, J. Devillez; C, D, C. Lemzaouda; E, L. Cazes. Line drawings: J. Devillez. Scale bars: 1 cm.

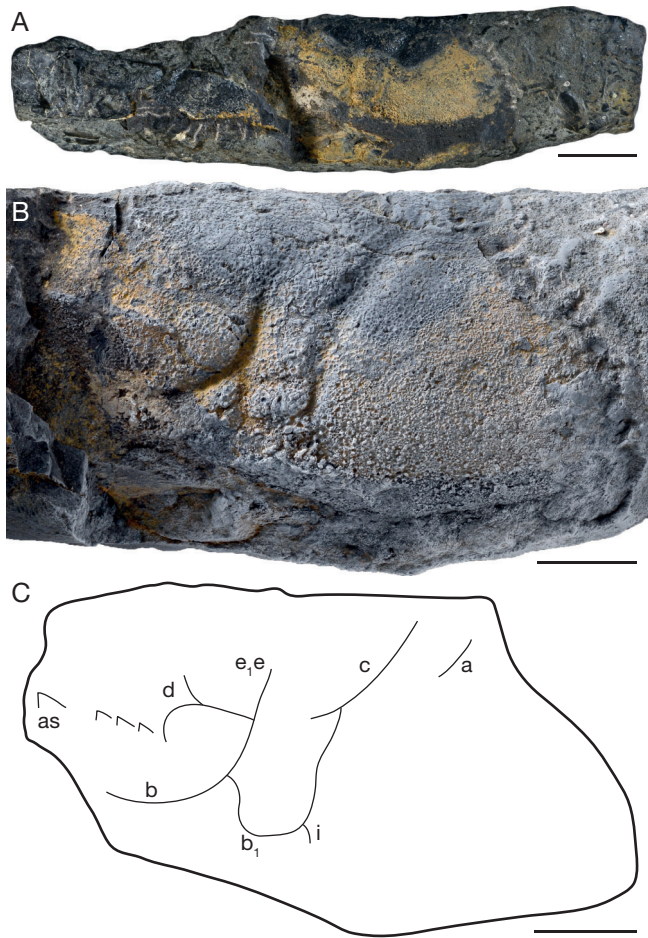


FIG. 18. — *Enoploclytia* sp. from the Oxfordian of Cricqueboeuf (France): **A**, specimen MNHN.F.A66892; **B**, detail of the carapace whitened with ammonium chloride; **C**, schema of the carapace. Abbreviations: **a**, branchiocardiac groove; **as**, antennal spine; **b**, antennal groove; **b₁**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **e,e**, cervical groove; **i**, inferior groove. Photographs: A, P. Loubry; B, L. Cazes. Line drawing: J. Devillez. Scale bars: 1 cm.

OTHER SPECIES OF *STENODACTYLINA* RECENTLY DESCRIBED

REMARKS

Recently, Schweigert & Härer (2020) have described two species from the Solnhofen-type lithographic limestones based on isolated P1 chelae. The holotype of *Stenodactylina devillezi* Schweigert & Härer, 2020 from the Kimmeridgian of Nusplingen was previously figured as *Erymastacus* sp. by Schweigert & Garassino (2003: fig. 2B). The second species, *Stenodactylina geigeriae* Schweigert & Härer, 2020, was found in the lower Tithonian of Marxheim.

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

Enoploclytia M'Coy, 1849: 330; 1854: 137. — Zittel 1885: 694. — Fritsch & Kafka 1887: 27. — Van Straelen 1925: 278. — Beurlen 1928: 164. — Rathbun 1926: 128. — Secrétan 1964: 81. — Förster

1966: 146. — Taylor 1979: 25. — Aguirre-Urreta 1989: 514. — Feldmann *et al.* 2015: 3. — Devillez *et al.* 2016: 530, fig. 11-J; 2017: 786, fig. 4A-B; 2018: 144, fig. 2A-B.

Enoploclytia Enoploclytia – Martin 1941: 160. — Glaessner 1969: 455.

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

DIAGNOSIS BY Devillez *et al.* (2018). — Fusiform intercalated plate; wide, deep cervical groove, joined to dorsal margin and to antennal groove; long, wide gastro-orbital groove originating as a median inflexion of cervical groove, delimiting two gastro-orbital lobes; sinuous postcervical groove, joined to dorsal margin and to hepatic groove, with ventral extension at carapace mid-height; short branchio-cardiac groove, interrupted in upper part of carapace, joined to dorsal margin, not joined to postcervical groove; concavo-convex hepatic groove, joined to cervical groove; prominent 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; P1 merus with strong, prominent distal process at extern side of its ventral extremity.

DISCUSSION

Recently, Devillez *et al.* (2018) reported a specimen identified as *Enoploclytia* sp. from the Oxfordian of France (Fig. 18). Despite its poor preservation, this fossil exhibits the typical carapace groove pattern of the genus: elongated gastro-orbital groove, with two divergent distal branches, a sinuous postcervical groove joined to the posterior extremity of the hepatic groove and not joined to the branchiocardiac groove, which is short and interrupted in the branchial region (Fig. 18C). This specimen is the oldest occurrence of *Enoploclytia*, and the only known in the Jurassic. Indeed, *Enoploclytia* is more typical of the Cretaceous.

CONCLUSIONS

After this study of the the Late Jurassic erymoid lobsters, 23 species within four of the six erymoid genera (*Eryma*, *Palaeastacus*, *Pustulina*, *Stenodactylina*) are identified. *Enoploclytia* is also present with its oldest representative. Excepting *Eryma mandelslohi*, which is present in Late Jurassic but with a type age in Middle Jurassic (recent description in Devillez & Charbonnier 2019) and the recently described *Stenodactylina devillezi* and *S. geigeriae*, all the Late Jurassic species are described here.

With 11 species, *Eryma* is the most diversified genus in the Late Jurassic and, considering the numerous specimens of *E. ventrosum* and *E. modestiforme*, it is also the most common genus. Moreover, due to its abundance and to its stratigraphic extension running from Bathonian to Kimmeridgian, *E. ventrosum* can be considered as an emblematic lobster of the Middle-Late Jurassic of Western Europe. Moreover, the only Late Jurassic erymoid occurrence of North America belongs to *Eryma*: *E. jungostrix* Feldmann & Titus, 2006 (Oxfordian). Then, no erymoids are reported

there until the Albian (Devillez *et al.* 2017). Other genera are less common than *Eryma*, and *Palaeastacus* is only known in the Lithographic limestones of Germany. In this Lagerstätte, *P. fuciformis* is the most abundant erymoid after *E. modestiforme*.

This review also points out the spectacular richness of the erymoid fauna of the German lithographic limestones in which four genera (*Eryma*, *Palaeastacus*, *Pustulina*, *Stenodactylina*) and 11 species are reported.

Finally, with the example of a specimen of *E. ventrosum*, this study also illustrates the strong effect of decortication on the erymoids ornamentation. Considering the importance of this feature, the differences between the internal mould and the remaining cuticle can lead to taxonomic complications. So, the state of decortication of these lobsters should be carefully examined in any taxonomic study.

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APPENDIX 1. — List of the examined material.

Taxa	Examined material	Ages	Localities
<i>Eryma</i> Meyer, 1840			
<i>Eryma georgeii</i> Carter, 1886	holotype SM J 3247; paratype SM J 3248 NMB F501	Oxfordian	United Kingdom Switzerland
<i>Eryma jungostricta</i> Feldmann & Titus, 2006	holotype USNM 530027	Oxfordian	United States
<i>Eryma mandelslohi</i> (Meyer, 1840)	MNHN.F.A29726; NMB 3525	Oxfordian	France, Switzerland
<i>Eryma ventrosum</i> (Meyer, 1835)	cast of holotype MNHN.F.B12484	Oxfordian	France
	syntypes MNHN.F.A29484, A29584, B12479 of <i>Bolina ventrosa major</i> Étallon, 1861		
	holotype BSPG 1961 VIII 114 of <i>Eryma radiatum</i> Oppel, 1861		Germany
	syntypes MNHN.F.A29727, A29728 of <i>Eryma affinis</i> Ferry, 1865	Bathonian	France
	syntype MNHN.F.A29783 of <i>Bolina girodi</i> Étallon, 1857		
	lectotype MJSN Col.Del.475 of <i>Eryma greppini</i> Oppel, 1861;		Switzerland
	paralectotype MJSN Col.Del.1		
	holotype of <i>Eryma cumonti</i> Van Straelen, 1921 stored at the IRNSB without number	Callovian	France
	cast of holotype MNHN.F.B13231 of <i>Eryma babeau</i> Étallon, 1861	Kimmeridgian	
	syntype MNHN.F.A29782 of <i>Bolina thirriae</i> Étallon, 1859		
	BSPG 1961 VIII 148; 5 specimens stored at the GPIT without number; IRSNB IST AIE 211 IG 9229, IG 9271, IG 10591, drawer without number with specimen IG 18657; 3 specimens stored at the MAN without number; MC-P E v 7, Fo Ev 13, Fr Ev 16, Vi Ecfv 4; MHNLM 2008.12.613.8, 2008.12.613.16, 2008.12.613.17, 2008.12.613.18; MFN 2236 P1383/2 MB.A.1537;	Bathonian - Kimmeridgian	France, Germany, Switzerland, Tanzania, United Kingdom
	MNHN.F.A29459, A29461, A29462, A29463, A29464, A29465, A29466, A29467, A29468, A29469, A29470, A29471, A29472, A29473, A29474, A29475, A29476, A29477, A29478, A29479, A29480, A29482, A29483, A29485, A29486, A29487, A29528, A29549, A29554, A29560, A30217, A30218, A30221, A30222, A30232, A32390, A32391, A32392, A32394, A59527, A70299, B12473, B12480, B12481, B14259, S05376, 21 specimens stored at the MNHN without number; NHMUK In.27134, In.27135, In.27146; NMB 96, F484, F505, F511; OSUG UJF-ID 1797, 11543, 11544, 11895, 11906, 1 specimen stored at the OSUG without number; PVM 1842-B0, 2013.1.26, 2013.1.164, 2013.1.186, 2013.1.288 (52 specimens), V1-R (2 specimens), V1a-R, V1b-R, V234-R, 6 specimens stored at the PVM without number; FSL 170529, 170597, 170752, 170757, 170758, 170764, 170765, 170770, 170778, 170780, 170779, 501719, 2 specimens stored at the FSL without number; UR 7 spécimens non numérotés; 11 specimens from private collections.		
<i>Eryma lerasi</i> (Étallon, 1861)	syntypes NHMUK 2835, In.27136, In.27140, In.27141 of <i>Eryma portlandica</i> Woods, 1930	Tithonian	United Kingdom
	NHMUK 2045, I.7494	Kimmeridgian	France, United Kingdom
<i>Palaeastacus punctatus</i> Oppel, 1861	holotype SMNS 3682	Kimmeridgian	Germany
	GPIT 1866; SMNS 63688, 63727, 63849, 64376, 64681, 64960, 66128, 4 specimens stored at the SMNS without number; NHMUK I.3480		
<i>Eryma veltheimii</i> (Münster, 1839)	holotype BSPG AS VII 186	Kimmeridgian	Germany
<i>Eryma westphali</i> Schweigert, Dietl & Röper, 2000	holotype SMNS 24227	Kimmeridgian	Germany
<i>Eryma major</i> Oppel, 1861	SMNS 63733, 63743 holotype SMNS 3682 SMNS 62865, 64371, 64403, 67655	Kimmeridgian	Germany

APPENDIX 1. — Continuation.

Taxa	Examined material	Ages	Localities
<i>Eryma modestiforme</i> (Schlotheim, 1822)	holotype MFN 2236 P1383/2 MB.A.0252 syntypes BSPG AS VII 188, 191 of <i>Glypheea elongata</i> Münster, 1839 holotype BSPG AS VII 193 of <i>Glypheea crassula</i> Münster, 1839 syntypes BSPG AS VII 194, 197, 198 of <i>Glypheea laevigata</i> Münster, 1839 holotype SMNS 64520 of <i>Palaeastacus poeschli</i> Schweigert & Röper, 2001 BSPG 1957 VI 1244, 1245, 1246, AS VI 15, 16, 17, AS VII 187, 189, 195, 196, AS VIII 79, 81, 82; 6 specimens stored at the GPIT without number; IRSNB IST AIE 211 IG 9694; MAN 142.A.1; MFN 2236 P1383/2 MB.A.0405, 2236 P1383/2 MB.A.0406, 2236 P1383/2 MB.A.0408, 2236 P1383/2 MB.A.1121, 2236 P1383/2 MB.A.2859, 2236 P1383/2 MB.A.2860, 2236 P1383/2 MB.A.2861, 2236 P1383/2 MB.A.2862, 2236 P1383/2 MB.A.2879, 2236 P1383/2 MB.A.2880, 2236 P1383/2 MB.A.2881, 2236 P1383/2 MB.A.2882, 2236 P1383/2 MB.A.2884, 2236 P1383/2 MB.A.2885, 2236 P1383/3 MB.A.0810, 2236 P1383/3 MB.A.1120, 2236 P1383/3 MB.A.2886, 2236 P1383/3 MB.A.2887, 2236 P1383/3 MB.A.2888, 2236 P1383/3 MB.A.2889, 2236 P1383/3 MB.A.2890, 2236 P1383/3 MB.A.2892, 2236 P1383/3 MB.A.2893, 2236 P1383/3 MB.A.2894, 2236 P1383/3 MB.A.2895, 2236 P1383/3 MB.A.2896, 2236 P1383/3 MB.A.2897, 2236 P1383/3 MB.A.2898, 2236 P1383/3 MB.A.2900, 2236 P1383/3 MB.A.2901, 2236 P1383/3 MB.A.2902, 2236 P1383/3 MB.A.2903, 2236 P1383/3 MB.A.2904, 2236 P1383/3 MB.A.2905, 2236 P1383/3 MB.A.2906, 2236 P1383/3 MB.A.2907, 2236 P1383/3 MB.A.2908, 2236 P1383/3 MB.A.2909, 2236 P1383/3 MB.A.2910, 2236 P1383/3 MB.A.2911, 2236 P1383/3 MB.A.2912, 2236 P1383/3 MB.A.2913, 2236 P1383/3 MB.A.2914, 2236 P1383/3 MB.A.2915, 2236 P1383/3 MB.I.054.24, 2236 P1383/3 MB.I.054.24, 2236 P1383/4 MB.A.2916, 2236 P1383/4 MB.A.2917, 2236 P1383/4 MB.A.2918, 2236 P1383/4 MB.A.2919, 2236 P1383/4 MB.A.2920, 2236 P1383/4 MB.A.2921, 2236 P1383/4 MB.A.2924, 2236 P1383/4 MB.A.2925, 2236 P1383/4 MB.A.2926, 2236 P1383/4 MB.A.2927, 2236 P1383/4 MB.A.2928, 2236 P1383/4 MB.A.2929, 2236 P1383/4 MB.A.2930, 2236 P1383/4 MB.A.2931, 2236 P1383/4 MB.A.2932, 2236 P1383/4 MB.A.2933, 2236 P1383/4 MB.A.2934, 2236 P1383/4 MB.A.2935, 2236 P1383/4 MB.A.2937, 2236 P1383/4 MB.A.2938, 2236 P1383/4 MB.A.2965, 2236 P1383/8 MB.A.2883; MNHN.F.A32408, A33507, B13446, B13450, B13452, B13463; NHMUK 44777, I.3480; NMB F1088, F1094, F1108, R455; SMNS 62575, 62932, 63689, 63747, 64260, 64380, 1 specimen stored at the SMNS without number; FSL 170771	Kimmeridgian - Tithonian Tithonian Kimmeridgian - Tithonian	Germany
<i>Eryma</i> sp.	NMB 93, 253	Oxfordian	Switzerland

APPENDIX 1. — Continuation.

Taxa	Examined material	Ages	Localities
<i>Palaeastacus</i> Bell, 1850			
<i>Palaeastacus rothgaengeriae</i> Schweigert & Röper, 2001	holotype BSPG 1993 XVIII-200	Kimmeridgian	Germany
<i>Palaeastacus fuciformis</i> (Schlotheim, 1822)	2 additional specimens from private collections holotype MFN 2236 P1383/8 MB.A.0251	Tithonian	Germany
	BSPG AS VI 11, AS VI 12, AS VI 13, AS VI 18, AS VII 183, AS VII 184, AS VII 185, AS VII 192, AS VIII 83; GPIT T32 F7; IRSNB IST AIE 211 IG 9664; MFN 2236 P1383/7 MB.A.0409, 2236 P1383/7 MB.A.0410, 2236 P1383/7 MB.A.0411, 2236 P1383/7 MB.A.0428, 2236 P1383/7 MB.A.0429, 2236 P1383/7 MB.A.0430, 2236 P1383/7 MB.A.0432, 2236 P1383/7 MB.A.0433, 2236 P1383/7 MB.A.0434, 2236 P1383/7 MB.A.0435, 2236 P1383/7 MB.A.2984, 2236 P1383/7 MB.A.2985, 2236 P1383/7 MB.A.2986, 2236 P1383/7 MB.A.2987, 2236 P1383/7 MB.A.2988, 2236 P1383/7 MB.A.2990, 2236 P1383/7 MB.A.2991, 2236 P1383/7 MB.A.2992, 2236 P1383/7 MB.A.2993, 2236 P1383/7 MB.A.2994, 2236 P1383/7 MB.A.2995, 2236 P1383/7 MB.A.2996, 2236 P1383/7 MB.A.2997, 2236 P1383/7 MB.A.2998, 2236 P1383/7 MB.A.2999, 2236 P1383/8 MB.A.2973, 2236 P1383/8 MB.A.3002, 2236 P1383/8 MB.A.3003, 2236 P1383/8 MB.A.3004, 2236 P1383/8 MB.A.3005, 2236 P1383/8 MB.A.3006, 2236 P1383/8 MB.A.3007, 2236 P1383/8 MB.A.3008, 2236 P1383/8 MB.A.3009, 2236 P1383/8 MB.A.3010, 2236 P1383/8 MB.A.3011, 2236 P1383/8 MB.A.3012, 2236 P1383/8 MB.A.3013, 2236 P1383/8 MB.A.3014, 2236 P1383/8 MB.A.3015, 2236 P1383/8 MB.A.3016, 2236 P1383/8 MB.A.3017, 2236 P1383/8 MB.A.3018, 2236 P1383/8 MB.A.3019, 2236 P1383/8 MB.A.3020, 2236 P1383/8 MB.A.3021, 2236 P1383/8 MB.A.3022, 2236 P1383/8 MB.A.3023, 2236 P1383/8 MB.A.3024, 2236 P1383/8 MB.A.3025, 2236 P1383/8 MB.A.3026, 2236 P1383/8 MB.A.3027, 2236 P1383/8 MB.A.3028; SMNS 3694, 64521; MNHN.F.B13449, MNHN.GG.2004/8245; FSL 170765, 170769		
<i>Pustulina</i> Quenstedt, 1857			
<i>Pustulina suevica</i> Quenstedt, 1857	holotype stored at the GPIT without number	Kimmeridgian	Germany
	holotype NHMUK In.27137 and paratypes NHMUK 33414 and NHMUK In.27138 of <i>Enoploclytia dorsetensis</i> Woods, 1930 syntype MNHN.F.B12485 of <i>Enoploclytia perroni</i> Étallon, 1861	Oxfordian	United Kingdom
	holotype SMNS 3682-1 of <i>Eryma fraasi</i> Oppel, 1861	Kimmeridgian	France Germany
	holotype SMNS 3682-4 of <i>Palaeastacus solitarius</i> Oppel, 1862		
	IRSNB IST AIE 235 IG 9227; MAN 144.A.6; MFN 2236 P1383/5 MB.A.1538; NHMUK 25976, In.61550; SMNS 60159, 64369, 70032, 1 specimen stored at the SMNS without number	Oxfordian, Kimmeridgian	France, Germany
<i>Pustulina minuta</i> (Schlotheim, 1822)	holotype MFN 2236 P1383/5 MB.A.0254	Tithonian	Germany
	holotype BSPG AS VII 182 of <i>Glyphea verrucosa</i> Münster, 1839		
	BSPG AS I 619, AS VII 180, AS VII 181, AS VIII 78; 1 specimen stored at the GPIT without number; MFN 2236 P1383/5 MB.A.1119, 2236 P1383/5 MB.A.2863, 2236 P1383/5 MB.A.2864, 2236 P1383/5 MB.A.2866, 2236 P1383/5 MB.A.2867, 2236 P1383/5 MB.A.2868, 2236 P1383/5 MB.A.2869, 2236 P1383/5 MB.A.2870, 2236 P1383/5 MB.A.2871, 2236 P1383/5 MB.A.2872, 2236 P1383/5 MB.A.2873, 2236 P1383/5 MB.A.2874, 2236 P1383/5 MB.A.2875, 2236 P1383/5 MB.A.2876, 2236 P1383/5 MB.A.2877, 2236 P1383/5 MB.A.2878; MNHN.F.B13444, B13445		
<i>Pustulina</i> sp.	BSPG 1952 XV 570	Kimmeridgian	Germany

APPENDIX 1. — Continuation.

Taxa	Examined material	Ages	Localities
<i>Stenodactylina</i> Beurlen, 1928			
<i>Stenodactylina insignis</i> (Oppel, 1862)	cast of the holotype MNHN.F.A24613	Oxfordian	France
	holotype MFN 2236 P1283/2 MB.A.1536	Kimmeridgian	Germany
	GPIT 10646, 1 specimen stored in the GPIT without number; 1 specimen stored in the IRSNB without number; NMB F730	Oxfordian- Kimmeridgian	France, Germany, Switzerland
<i>Stenodactylina shotoverigiganti</i> n. sp.	holotype NHMUK 24559	Oxfordian	United Kingdom
<i>Stenodactylina granulifera</i> (Secrétan, 1964)	holotype MNHN.F.R03975	Kimmeridgian	Madagascar
	holotype MNHN.F.R03913 of <i>Eryma madagascariensis</i> Secrétan, 1964		
<i>Stenodactylina pseudoventrosa</i> (Beurlen, 1928) n. comb.	holotype GPIT Ar/294/3	Kimmeridgian	Germany
<i>Stenodactylina australis</i> (Secrétan, 1964)	holotype MNHN.F.R03972; 3 paratypes MNHN.F.A31660, A33207, R03971 MNHN.F.A33228	Tithonian	Madagascar
<i>Enoploclytia</i> M'Coy, 1849			
<i>Enoploclytia</i> sp.	MNHN.F.A66892	Oxfordian	France