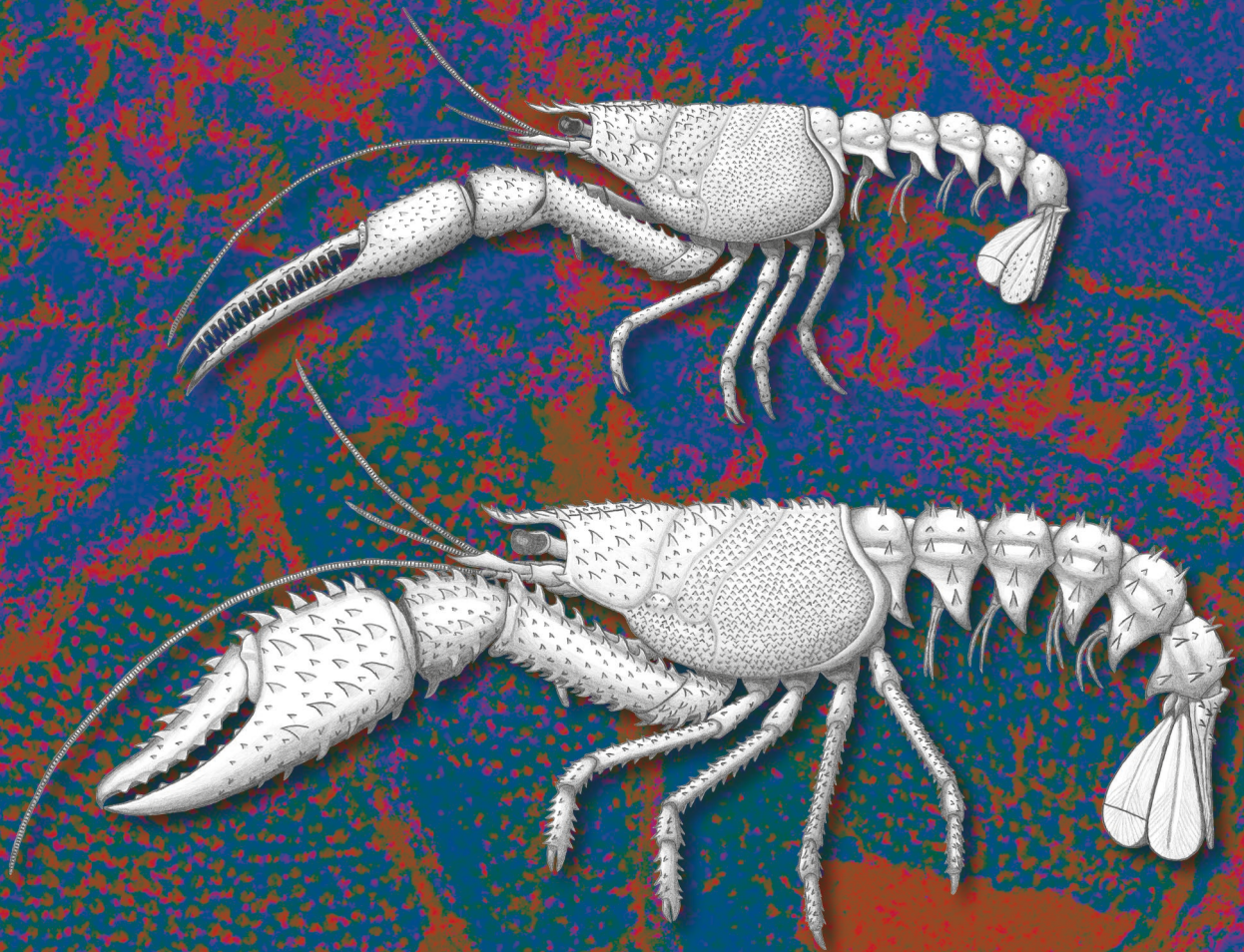


## A synthesis of the evolutionary history of erymoid lobsters (Crustacea, Decapoda, Erymoidea)

Julien DEVILLEZ & Sylvain CHARBONNIER





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# A synthesis of the evolutionary history of erymoid lobsters (Crustacea, Decapoda, Erymoidea)

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## ABSTRACT

A synthesis of our current knowledge of erymoid lobsters is presented. The superfamily Erymoidea includes two families, Erymidae Van Straelen, 1925 and Enoploclytiidae Devillez, Charbonnier & Barriel, 2019, together encompassing 81 species within six genera. Our examination of the palaeobiodiversity of this group and its evolution has revealed some variations through the Mesozoic with three important peaks, at the boundaries of: 1) Lower-Middle Jurassic; 2) Middle-Upper Jurassic; and 3) Lower-Upper Cretaceous. Whereas the origin of the first peak remains poorly known, the two others coincide with major modifications of the environment: the development of the European Jurassic carbonate platforms and the development of the European Chalk Sea and the partial flooding of North America during the mid- and Late Cretaceous. In addition to a notable peak of diversity, the Cretaceous is an important time interval in the evolutionary history of erymoids because the Early Cretaceous represented a long period of relatively low diversity and during the Late Cretaceous a strong decline of erymoid faunas is observed in Europe. However, the erymoids had already attained a worldwide distribution during the Early Cretaceous with occurrences in all oceans of the time. The analysis of the palaeobiogeographic distribution of these lobsters suggests the presence of important migratory paths, which probably favoured their spread and faunal exchanges between different areas across the globe.

## KEY WORDS

Mesozoic,  
Jurassic,  
Cretaceous,  
crustaceans,  
Lagerstätten,  
migration.

## RÉSUMÉ

*Une synthèse de l'histoire évolutive des homards érymoïdes (Crustacea, Decapoda, Erymoidea).*

Une synthèse des connaissances sur les érymoïdes est ici présentée. La super-famille Erymoidea inclut deux familles, Erymidae Van Straelen, 1925 et Enoploclytiidae Devillez, Charbonnier & Barriol, 2019, comprenant 81 espèces réparties dans six genres. L'examen de la paléobiodiversité de ce groupe et de son évolution révèle des variations au cours du Mésozoïque avec trois pics importants, aux limites: 1) du Jurassique inférieur et moyen; 2) du Jurassique moyen et supérieur; et 3) du Crétacé inférieur et supérieur. Si l'origine du premier pic demeure peu connue, les deux autres coïncident avec des modifications environnementales majeures: le développement des plateformes carbonatées européennes au Jurassique et le développement de la mer de la craie en Europe ainsi que l'ennoiement partiel de l'Amérique du Nord au Crétacé. En plus d'un important pic de diversité, le Crétacé est important dans l'histoire évolutive des érymoïdes, car le Crétacé inférieur est une longue période de diversité relativement faible, tout comme le Crétacé supérieur, pendant lequel un fort déclin des faunes d'érymoïdes est observé en Europe. Cependant, les érymoïdes avaient déjà atteint leur distribution mondiale au Crétacé inférieur, avec des occurrences dans tous les océans. L'analyse de la distribution paléobiogéographique de ces homards suggère la présence d'importantes voies migratoires qui ont probablement favorisé leur dispersion et les échanges faunistiques entre les différentes régions du monde.

## MOTS CLÉS

Crétacé,  
crustacés,  
Jurassique,  
Lagerstätten,  
Mésozoïque,  
migration.

## INTRODUCTION

Erymoid lobsters are extinct decapod crustaceans that are considered to have been an important component of Mesozoic faunal assemblages because of their relative abundance and worldwide distribution (e.g. Reuss 1854; Beurlen 1933; Joleaud & Hsu 1935; Stenzel 1945; Roger 1946; Woods 1957; Bachmayer 1959; Aguirre-Urreta 1982, 1989; Garassino 1994; Schweitzer & Feldmann 2001; Garassino & Schweigert 2006; Feldmann & Haggart 2008; Karasawa *et al.* 2008; Charbonnier *et al.* 2012a, 2017; Vega *et al.* 2013).

These lobsters have been studied since the early nineteenth century. Indeed, the first descriptions of fossils, now considered to be erymoids, were produced by Mantell (1822, 1824, 1833), who studied the fauna found in the chalk formations of southern England, as well as by Desmarest (1817, 1822), Schlotheim (1822) and Münster (1839), who recorded material from the Solnhofen Lithographic Limestones in southern Germany. Those authors described *Astacus leachii* Mantell, 1822 (type species of *Enoploclytia* M'Coy, 1849), *Astacus sussexiensis* Mantell, 1824 (type species of *Palaeastacus* Bell, 1850), and *Macrourites modestiformis* Schlotheim, 1822 (type species of *Eryma* Meyer, 1840). The palaeontological studies of Meyer (1840a, b), Quenstedt (1854) and Bell (1850) constituted a second wave, during which several erymoid species were erected, including *Eryma ventrosum* (Meyer, 1840b), which is typical of the Middle - Late Jurassic of western Europe. Later, at the beginning of the second half of the nineteenth century numerous extinct species of decapod crustaceans, including several erymoids, have been recorded on the basis of material from France, Germany and England, by Bell (1857, 1863), Étallon (1857, 1859, 1861) and Opperl (1861, 1862). With the exception of the description of a small number of species by Trautschold (1866), Schlüter (1879) and Wright (1881),

knowledge of erymoid faunas did not increase during the following twenty years. Important, yet mostly descriptive, contributions by Morière (1888), Sauvage (1891) and Lahunsen (1894) appeared in print at the end of the nineteenth century. Following a study by Méchin (1901) on some crustacean fauna from the Lorraine region (eastern France), almost no work was done on erymoid lobsters at the start of the twentieth century. During the 1920s and early 1930s, our knowledge of European erymoid lobsters benefitted from important contributions by Van Straelen (1921, 1922, 1923, 1925), Beurlen (1928) and Woods (1930). Indeed, Van Straelen (1925) clearly recognised the intercalated plate as a diagnostic morphological feature of erymoids. Hence, he established the new family Erymidae to accommodate all lobsters that were characterised by the presence of such a plate. This family was accepted among subsequent workers, but its composition was strongly debated, as outlined in Devillez *et al.* (2019). The first important studies on extra-European crustacean faunas that included erymoid lobsters were those by Rathbun (1923, 1926a, b, 1935) for North America and by Secrétan (1964) for Madagascar. Soon after, a major contribution by Förster (1966) came out; this was an extensive study that included a taxonomic review, phylogenetic considerations and a palaeobiological synthesis as well as observations on allometric growth and palaeoenvironmental considerations. Since then, a limited number of papers have appeared during the 1970s to 1990s (e.g. Feldmann 1979; Taylor 1979; Feldmann & McPherson 1980; Förster & Seyed-Emami 1982; Secrétan 1984; Garassino 1996).

Since the beginning of the twenty-first century, research on ancient crustacean faunas has been flourishing anew. Indeed, many contributions on erymoid lobsters appeared in print during the past twenty years (Schweigert *et al.* 2000; Schweigert & Röper 2001; Garassino & Krobicki



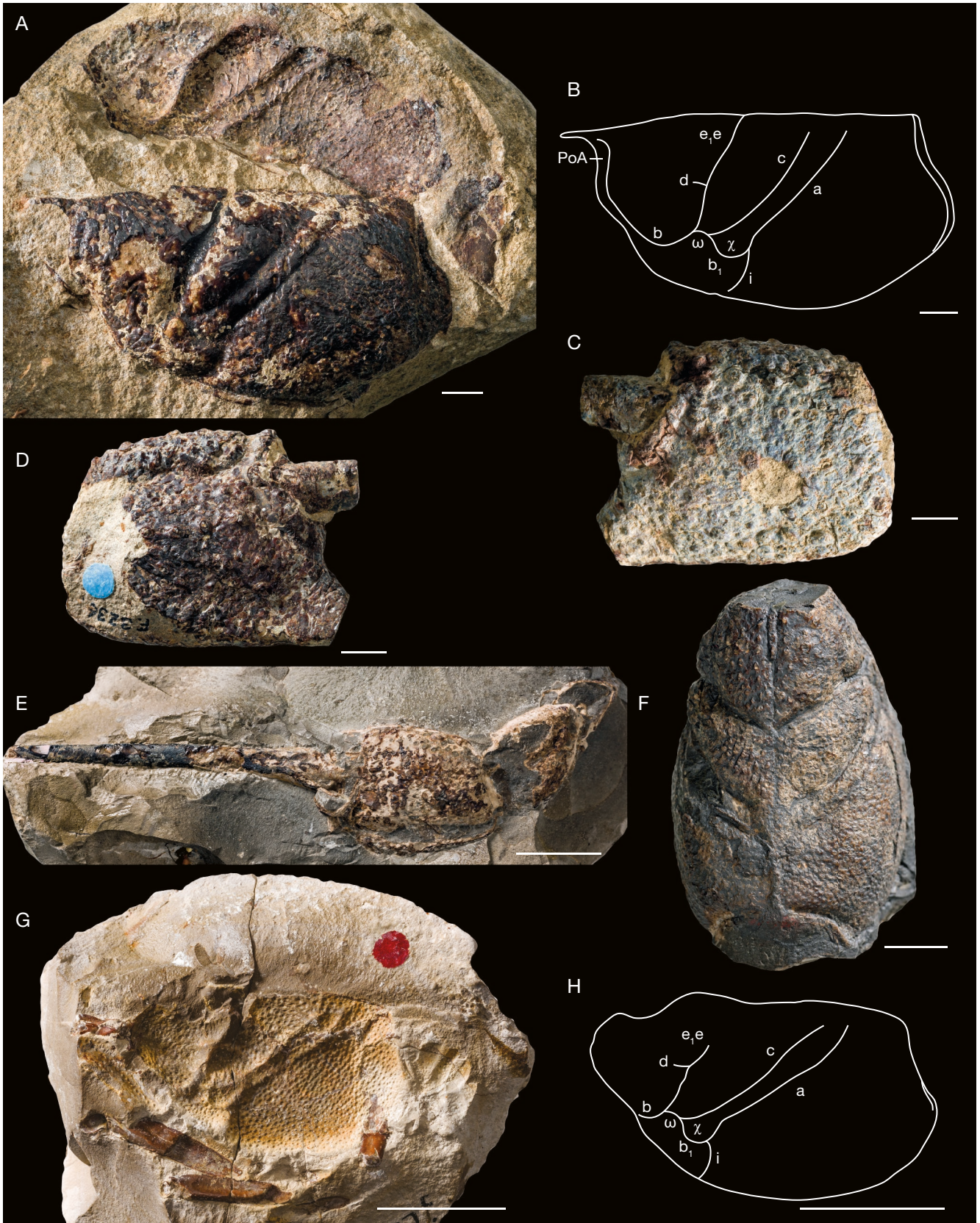


FIG. 1. — *Palaeastacus terraereginae* (Etheridge Jr, 1914) from Australia: **A, B**, holotype QM 3234 from the Barremian of the Barcoo river: general view (**A**), schema (**B**); **C, D**, specimen QM F3236: dorsal view (**C**), ventral view (**D**); **E, F**, holotype UQ F13410 of *Enoplodytia tenuidigitata* Woods, 1957 from the Aptian of Boomers: P1 chela (**E**), dorsal view of the carapace (**F**); **G, H**, specimen UQ F13417 from the Aptian of Boomer: carapace (**G**), schema (**H**). Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b<sub>1</sub>**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **e, e**, cervical groove; **i**, inferior groove; **POA**, post-orbital area; **χ**, attachment site of adductor testis muscle; **ω**, attachment site of mandibular muscle. Scale bars: 1 cm. Photographs: P. Waddington. Line drawings: J. Devillez.



2002; Jagt & Fraaije 2002; Schweigert & Garassino 2003; Amati *et al.* 2004; Crônier & Courville 2004; Etter 2004; Carpentier *et al.* 2006; Feldmann & Titus 2006; Vega *et al.* 2007; Charbonnier 2009; Garassino *et al.* 2009; Schweitzer *et al.* 2009; Charbonnier & Garassino 2012; Charbonnier *et al.* 2012b; Karasawa *et al.* 2013; Klomp maker *et al.* 2013; Schweigert 2013; Bravi *et al.* 2014; Charbonnier *et al.* 2014, 2015; Hyžný *et al.* 2015; Jagt *et al.* 2015; Devillez *et al.* 2016, 2017, 2019; Devillez & Charbonnier 2017, 2019; Fanțescu *et al.* 2018; Jagt *et al.* 2018; Feldmann *et al.* 2020; Schweigert & Härer 2020; Garassino *et al.* 2021; Metodiev *et al.* 2021). On the basis of these new studies, it is now possible to produce a meaningful synthesis of erymoid lobsters, which is the aim of the present paper.

## MATERIAL AND METHODS

The overview of the palaeobiodiversity and palaeobiogeography presented here strongly relies on the most recent papers on erymoid lobsters. Indeed, Devillez *et al.* (2016, 2017, 2018) and Devillez & Charbonnier (2017, 2019, 2020) proposed an extensive review of these lobsters including novel descriptions of genera and most of the species, supported by an unambiguous use of characteristics of carapace groove pattern, the shape of P1 chelae, and the ornamentation of both carapace and P1 chelae. These studies were motivated by numerous uncertainties over the systematic and taxonomy of erymoid lobsters. For example, at the species level, Charbonnier *et al.* (2014) looked at the case of *Eryma greppini* Opper, 1861, which was synonymised with *Eryma bedeltum* (Quenstedt, 1857) following Förster's (1966) review. They identified a pair of dorsal domes in the former species that are missing in *E. bedeltum* and, on that evidence, concluded that *E. greppini* was a distinct species and questioned the validity of the synonymies established within the Erymidae by previous workers. Confusions also ruled at the genus level. Indeed, this persisted for a long time between *Enoploclytia* M'Coy, 1849 and *Palaeastacus* Bell, 1850. In this case, the confusion probably was the result of a combination of facts, revealed by the study of old literature sources. Originally, Mantell (1822) described *Astacus leachii* on the basis of heterogeneous material: P1 chelae with a globose propodus and long, slender fingers and other P1 chelae with short, wide fingers and adorned with strong spines. Considering these features, Mantell (1824) subdivided *A. leachii* in order to distinguish *Astacus sussexiensis*. M'Coy (1849) later established the genus *Enoploclytia*, and designated *A. leachii* as type species. However, the illustration supplied for the genus shows a carapace groove pattern, a morphology of the P1 chelae and an ornamentation that all correspond to that of *A. sussexiensis*. Moreover, *A. sussexiensis* was later designated type species of *Palaeastacus* by Glaessner (1929). Thus, the combination of these elements probably explains the confusion between these two genera, well illustrated in Glaessner (1969), who treated *Palaeastacus* as a subgenus of *Enoploclytia*, despite the strong differences between their carapace groove patterns.

We also note here that most of the erymoid records are from Europe, which means that this synthesis also reflects a strong bias in collection and literature records.

Finally, the present work uses the systematic framework recently proposed by Devillez *et al.* (2019) for erymoid lobsters, as follows:

- MALACOSTRACA Latreille, 1802;
- DECAPODA Latreille, 1802;
- ASTACIDEA Latreille, 1802;
- ERYMOIDEA Van Straelen, 1925;
- ENOPLOCLYTIIDAE Devillez, Charbonnier & Barri-  
riel, 2019;
- Enoploclytia* M'Coy, 1849;
- Pustulina* Quenstedt, 1857;
- ERYMIDAE Van Straelen, 1925;
- ERYMINAE Van Straelen, 1925;
- Eryma* Meyer, 1835;
- Palaeastacus* Bell, 1850;
- Stenodactylina* Beurlen, 1928;
- TETHYSASTACINAE Devillez, Charbonnier & Bar-  
riel, 2019;
- Tethysastacus* Devillez, Charbonnier, Hyžný &  
Leroy, 2016.

## INSTITUTIONAL ABBREVIATIONS

- AMNH American Museum of Natural History, New York;
- BAS British Antarctic Survey, Cambridge;
- BM Booth Museum of Natural History, Brighton;
- BSPG Bayerische Staatssammlung für Paläontologie und  
Geologie, Munich.
- CPC Museo del Desierto, Saltillo;
- FSL Université Claude Bernard Lyon 1, Lyon;
- GPIT Palaeontological Collection, Eberhard-Karls-Universität,  
Tübingen;
- GSC Geological Survey of Canada, Ottawa;
- IGM Instituto de Geología, Universidad Nacional de Pale-  
ontología, Mexico;
- MAN Musée-aquarium, Nancy;
- MFN Museum für Naturkunde, Berlin;
- MNHN Muséum national d'Histoire naturelle, Paris;
- MSNM Museo di Storia Naturale di Milano, Milan;
- MUZ Museo de Múzquiz, Coahuila;
- NHMUK Natural History Museum, London;
- NPL Non-Vertebrate Paleontology Laboratory, Jackson  
School of Geosciences, University of Texas, Austin;
- OSUG Observatoire des Sciences de l'Univers, Grenoble;
- PIN Palaeontological Institute, Moscow;
- QM Queensland Museum, Brisbane;
- SMNS Staatliches Museum für Naturkunde, Stuttgart;
- UQ University of Queensland, Brisbane;
- USNM United States National Museum of Natural History,  
Smithsonian Institution, Washington DC;
- WMNH-GE Wakayama Prefectural Museum of Natural History,  
Wakayama.

## PALAEODIVERSITY

### HISTORICAL STUDIES AND STATE OF THE ART

Our review of the literature has revealed that, to date, 174 described species have been assigned to an erymoid gen-



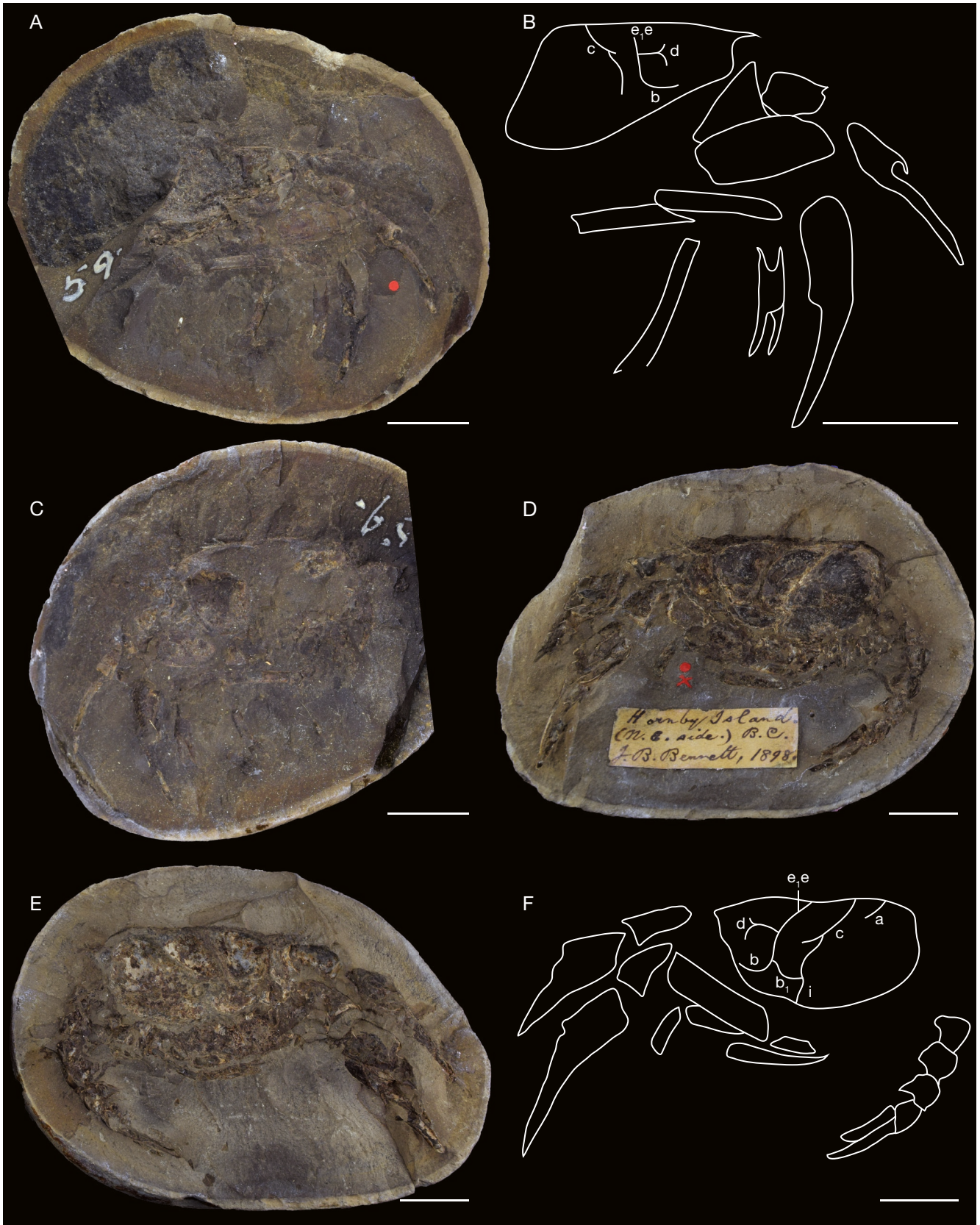


FIG. 2. — *Enoploclytia minor* Woodward, 1900 from the Upper Cretaceous of Hornby Island (Canada): **A–C**, holotype GSC 5971: general view of the specimen (**A**), line drawing (**B**), counterpart (**C**); **D, E**, holotype of *Eryma dawsoni* GSC 5969: general view of the specimen (**D**), counterpart (**E**), line drawing (**F**). Abbreviations: **a**, branchiocardiac groove; **b**, antennal groove; **b<sub>1</sub>**, hepatic groove; **c**, postcervical groove; **d**, gastro-orbital groove; **e<sub>1</sub>e**, cervical groove; **i**, inferior groove. Scale bars: 1 cm. Photographs: M. Coyne. Line drawings: J. Devillez.

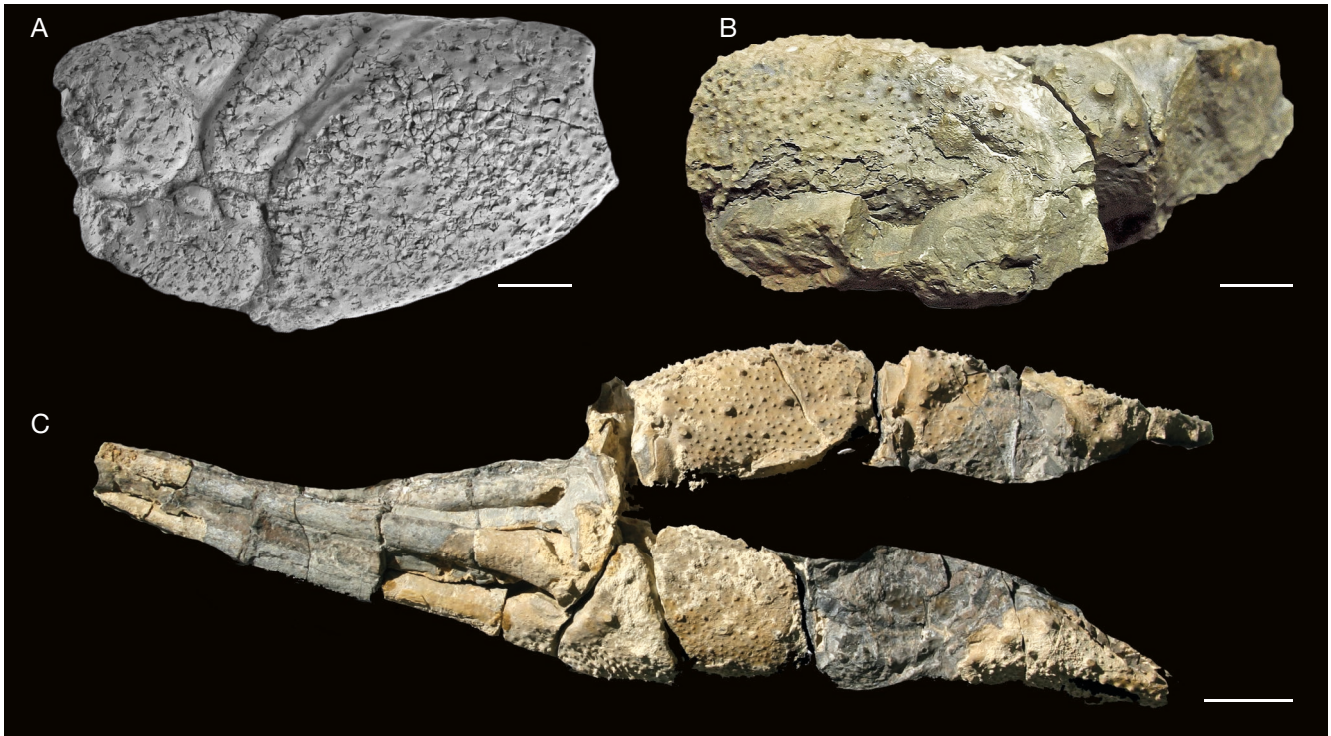


FIG. 3. — Erymoid lobsters from the Palaeozoic and the Paleogene: **A**, holotype PIN 1453 of *Eryma antiquum* (Birshtein, 1958) from the Changhsingian of Ust-Jenisseisk (Russia); **B, C**, *Enoploclytia gardnerae* (Rathbun, 1935) from the Selandian of Coahuila (Mexico): specimen CPC 1982 (**B**), specimen IGM-9095 (**C**). Scale bars: 1 cm. Photographs: F. Schram (A), F. Vega (B, C).

TABLE 1. — Numbers of valid species of the six genera here recognised to be erymoid lobsters in the present study.

Genera	Förster's (1966) review	Schweitzer <i>et al.</i> 's (2010) list	After reviews by Devillez <i>et al.</i> (2016, 2017), and Devillez & Charbonnier (2017, 2019, 2020)
<i>Enoploclytia</i> M'Coy, 1849	9	19	10
<i>Eryma</i> Meyer, 1840	36	60	24
<i>Galicía</i> Garassino & Krobicki, 2002	–	3	(synonymised with <i>Eryma</i> )
<i>Protoclytiopsis</i> Birshtein, 1958	1	1	(synonymised with <i>Eryma</i> )
<i>Palaeastacus</i> Bell, 1850	13	24	14
<i>Pustulina</i> Quenstedt, 1857	8	12	11
<i>Stenodactylina</i> Beurlen, 1928	–	1	21
<i>Tethysastacus</i> Devillez, Charbonnier, Hyžný & Leroy, 2016	–	–	1
Total	67	120	81

era since the nineteenth century. However, the number of valid species has varied widely in subsequent studies. In the review proposed by Förster (1966), of the 139 species already described, less than 50% (i.e., 67 species) have been considered valid ones (Table 1). Indeed, some of the described species were wrongly assigned to erymoid genera or synonymized with other species. In the synthetic list of Schweitzer *et al.* (2010), which is not a taxonomic review, the number of species rose to 120, if only genera recognised to belong to the superfamily Erymoidea (see the systematics above), and their synonyms (*Galicía* Garassino & Krobicki, 2002, *Protoclytiopsis* Birshtein, 1958), as based on the most recent papers (Feldmann *et al.* 2015; Devillez *et al.* 2016, 2017, 2018, 2019; Devillez & Charbonnier 2017, 2019, 2020) are considered. We have noted that some of the species men-

tioned, but not discussed in detail by Devillez *et al.* (2016) and Devillez *et al.* (2017) deserved careful re-examination. Devillez *et al.* (2016: 530) transferred *Enoploclytia tenuidigitata* Woods, 1957 (Aptian, Australia) to *Palaeastacus* on account of the typical groove pattern of carapaces assigned to that taxon. Further comparisons with the type material of *Palaeastacus terraereginae* (Etheridge Jr, 1914) (Barremian, Antarctica, Australia) have documented strong similarities between the two species. Indeed, both exhibit: 1) a closely similar groove pattern, with postcervical and branchiocardiac grooves becoming divergent towards their ventral termination; 2) a homogeneous ornamentation consisting of tubercles preceded by depressions; 3) both inflated  $\omega$  and  $\chi$  areas; and 4) P1 chelae with a short, rectangular and slightly globose propodus bearing straight and unusually fine fingers



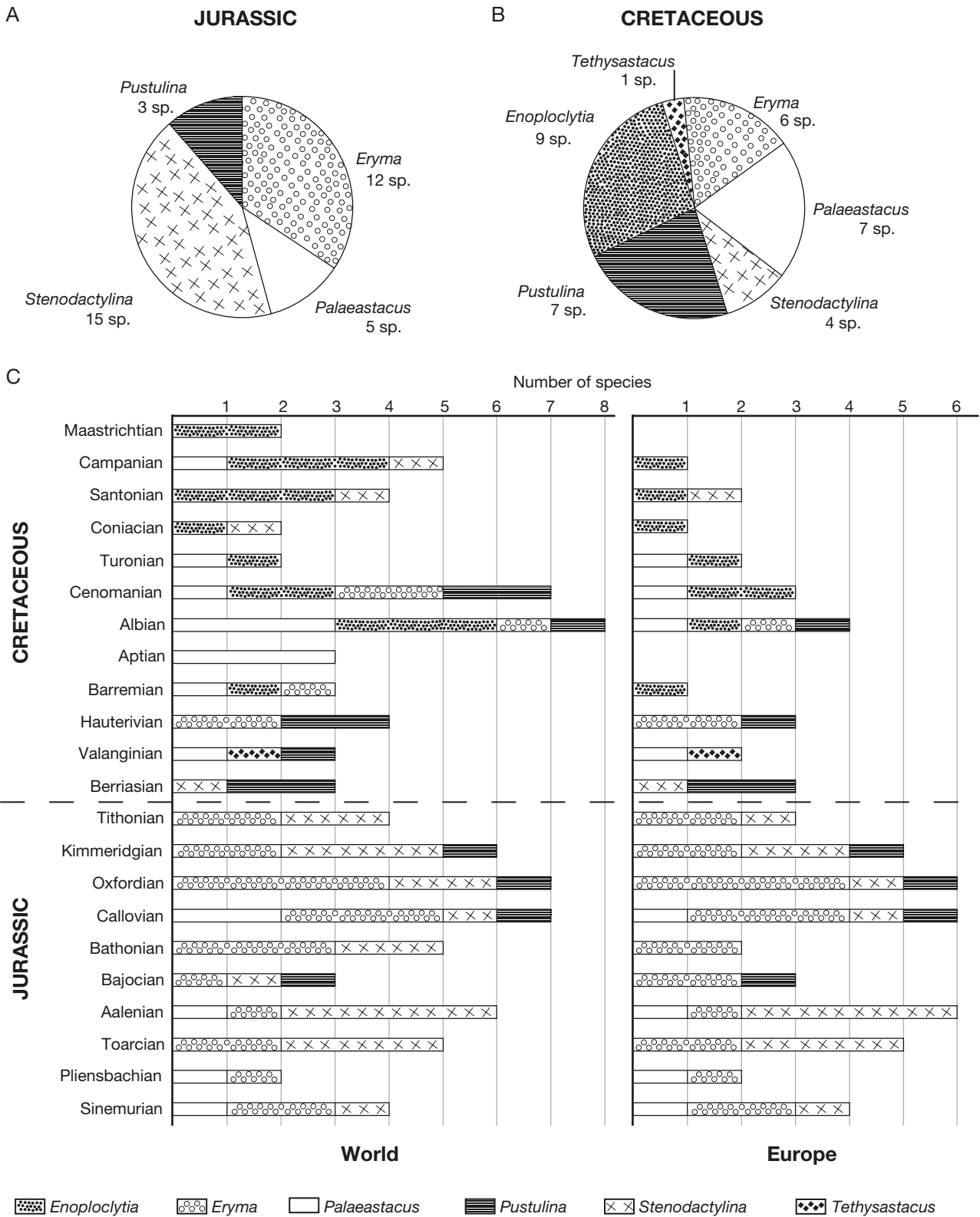


FIG. 4. — Erymoid lobster palaeobiodiversity: **A**, specific diversity for each genus during the Jurassic; **B**, specific diversity for each genus during the Cretaceous; **C**, evolution of the specific diversity during the Mesozoic for each genus across the globe (**left**) and in Europe (**right**). These graphs do not include those species that are exclusively found in the Solnhofen Lagerstätten.

for the genus (Fig. 1). On evidence of these morphological similarities, we here consider *E. tenuidigitata* to be a junior synonym of *P. terraereginae*.

Devillez *et al.* (2017) maintained *Enoploclytia minor* Woodward, 1900 (Maastrichtian, Hornby Island, Canada) in *Enoploclytia* because the only known specimen has a subrectangular



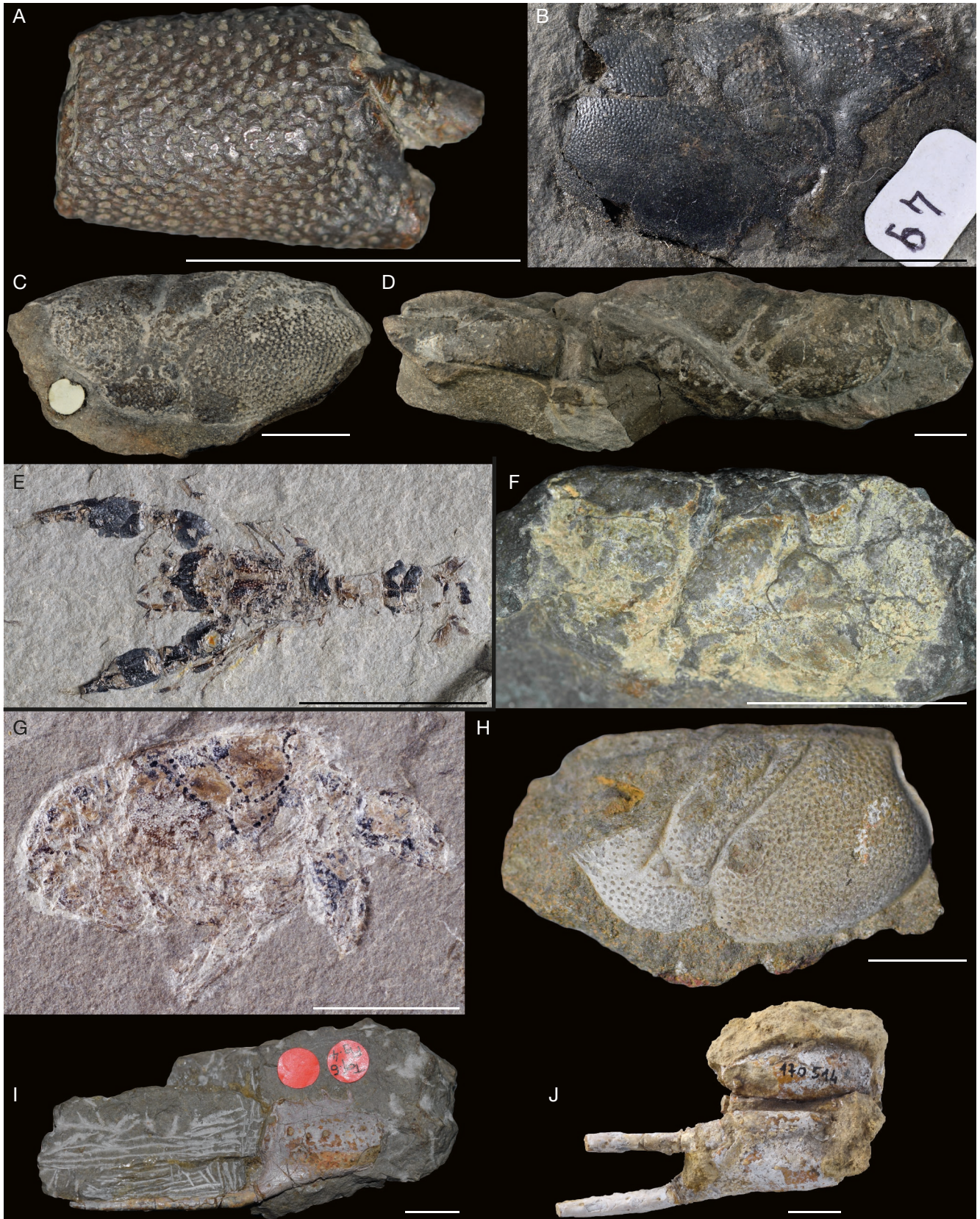


FIG. 5. — Early Jurassic erymid lobsters: **A, B**, *Eryma amalthei* (Quenstedt, 1854) from the Pliensbachian, lectotype GPIT/43/24/57 from Holzmaden (Germany) (**A**), specimen MAN unregistered from Nancy (France) (**B**); **C, D**, *Eryma birdi* Woods, 1930, from the Toarcian of Peak (United Kingdom): holotype NHMUK In.27125 (**C**), paratype NHMUK In.27123 (**D**); **E**, paratype MSNM i0450 of *Eryma sinemurianum* (Garassino, 1996), from the Sinemurian of Osteno (Italy); **F**, specimen GPIT unregistered of *Eryma* sp. from the Sinemurian of Ofterdingen (Germany); **G**, holotype MSNM i7606 of *Palaeastacus meyeri* (Garassino, 1996), from the Sinemurian of Osteno (Italy); **H**, specimen MAN 2015.0.227 of *Stenodactylina guisei* (Wright, 1881) (holotype of *Eryma lemairei*



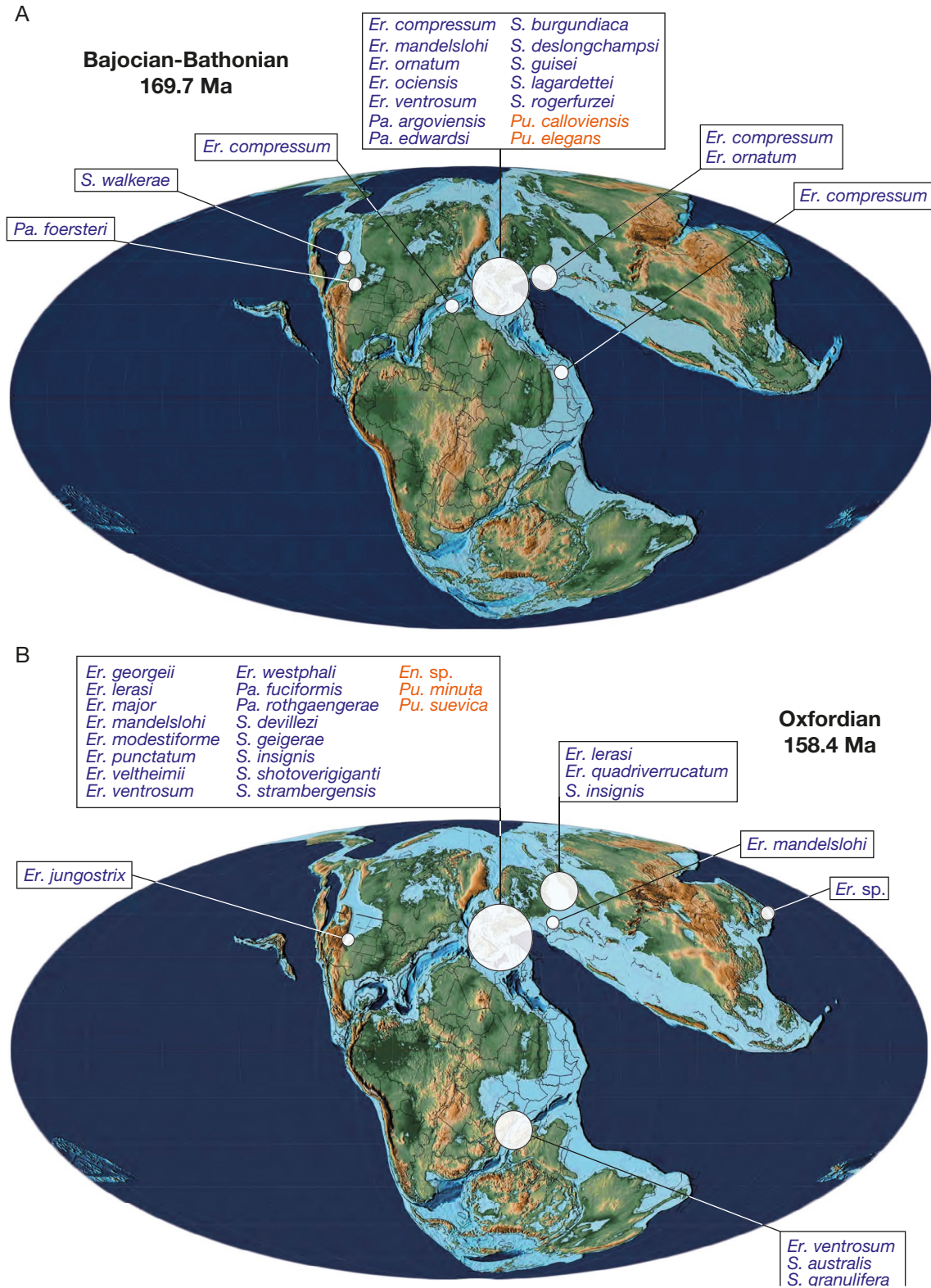
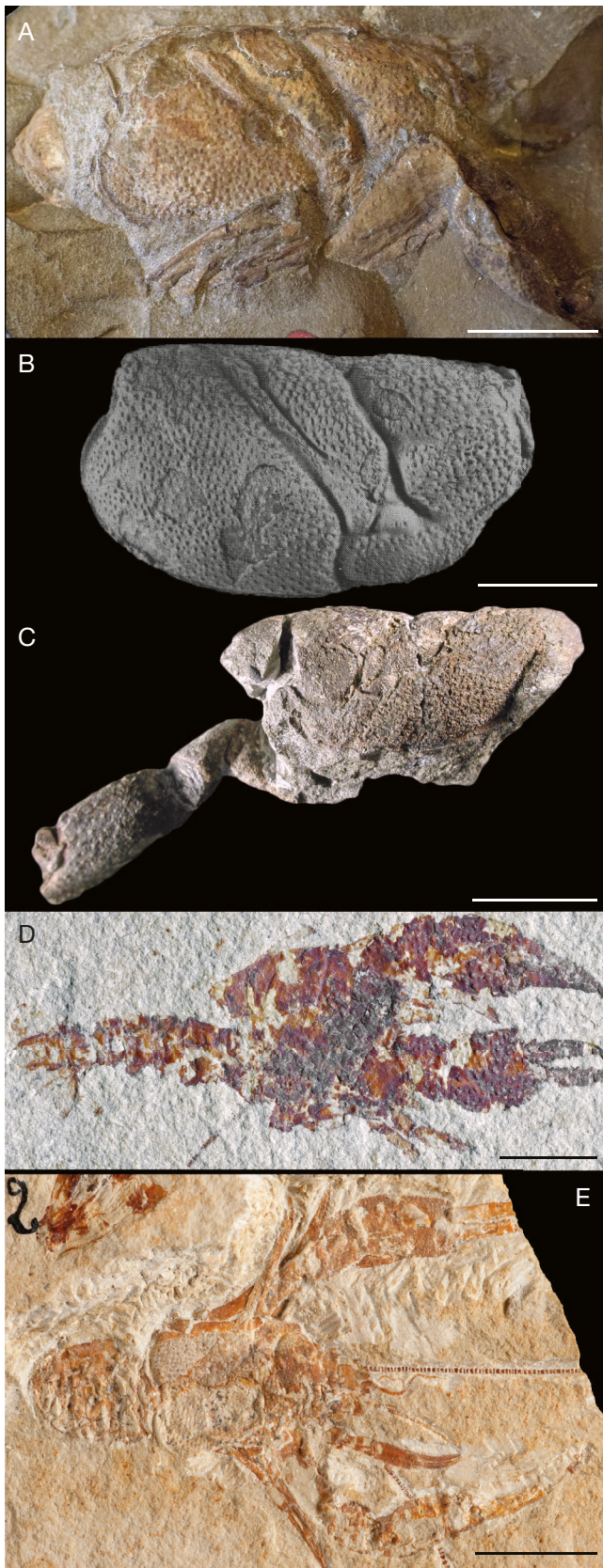


FIG. 6. — Distribution of Erymoidea during the Jurassic: **A**, palaeobiogeography of Middle Jurassic; **B**, palaeobiogeography of Late Jurassic. Colors: **blue**, Erymidae; **orange**, Enoplocyrtidae. Abbreviations: **En.**, *Enoplocyrtia*; **Er.**, *Eryma*; **Pal.**, *Palaeastacus*; **Pu.**, *Pustulina*; **S.**, *Stenodactylina*. Source of maps: Scotese 2014c.

Méchin, 1901) from the Toarcian of Chavigny (France); **I**, holotype SMNS 7785 of *Stenodactylina liasina* Beurlen, 1928 from the Toarcian of Holzmaden (Germany); **J**, holotype FSL 170514 of *Stenodactylina falsani* (Dumortier, 1867). Scale bars: 1 cm. Photographs: L. Cazes (**J**), J. Devillez (**A**, **C**, **D**, **F**, **H**, **I**), A. Garassino (**E**, **G**), P. Loubry (**B**).



FIG. 7. — African, Middle East and Far East erymoid lobsters, excepting *E. moriedaorum*: **A**, specimen MFN 2236 P1383/2 MB.A.1537 of *Eryma ventrosom* (Meyer, 1835), from the Upper Jurassic of Tanzania; **B**, original figure of Förster & Seyed-Emami (1982: fig. 3) of the specimen of *Eryma compressum* Eudes-Deslongchamps, 1842, from the Aalenian of the Imamzadeh Hashim Pass northeast of Teheran (Iran); **C**, holotype WMNH-Ge-1140320056 of *Eryma nippon* Karasawa, Ohara & Kato, 2008 from the Barremian of Sahara (Japan); **D**, specimen MSNM i12292 of *Pustulina cretacea* (Roger, 1946), from the Cenomanian of Hakel (Lebanon); **E**, holotype MNHN.F.B18902 of *Eryma oscari* Charbonnier, Audo, Garassino & Hyžný, 2017, from the Cenomanian of Hadjoula (Lebanon). Scale bars: 1 cm. Photographs: J. Devillez (A), H. Karasawa (C), G. Teruzzi (D), D. Audo (E).

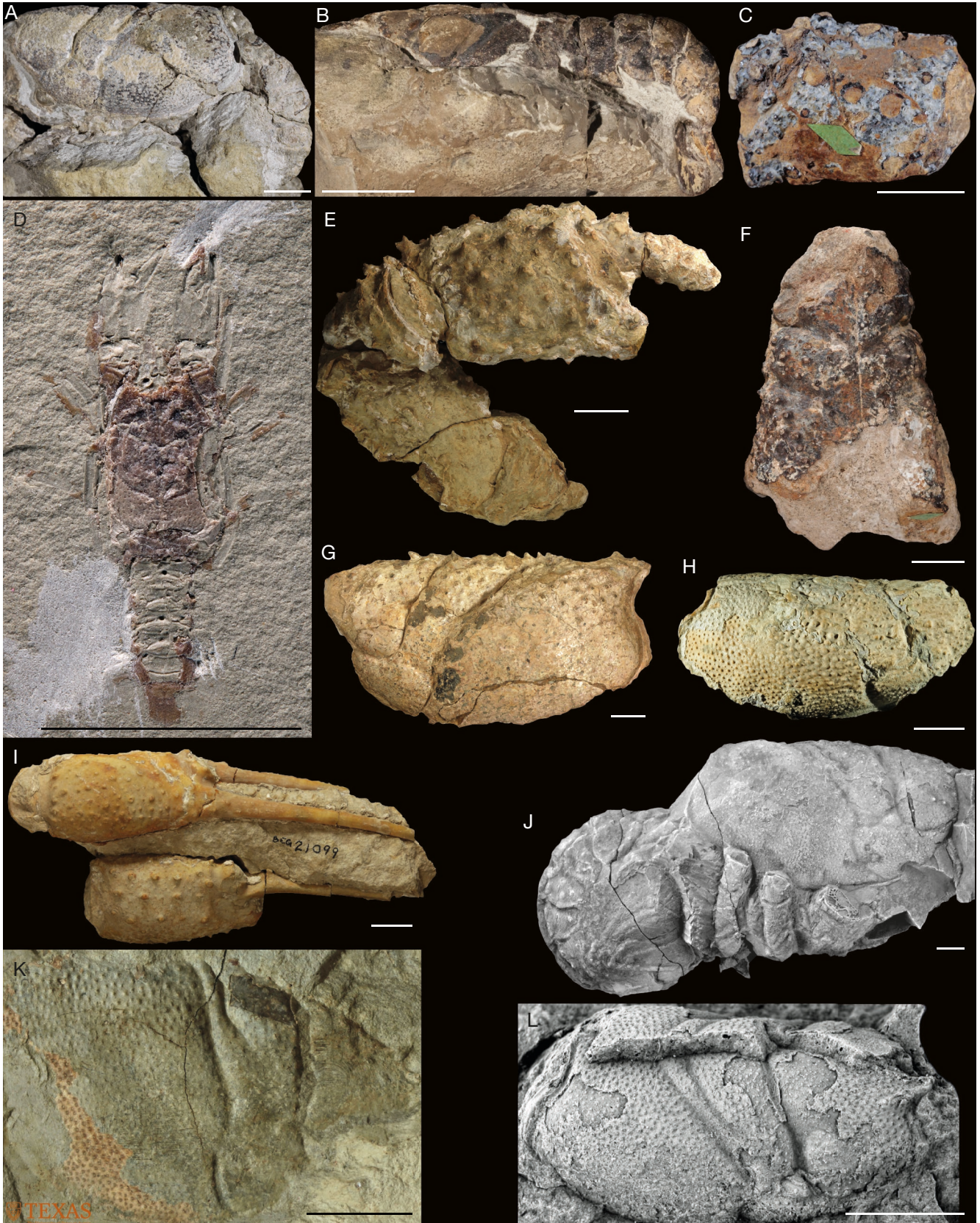


and globose P1 propodus with long and slender fingers. They also maintained *Pustulina dawsoni* (Woodward, 1900) (upper Campanian - lower Maastrichtian, Hornby Island, Canada) in *Pustulina*, however, but failed to mention any anatomical arguments in support of such an assignment. A careful examination of high-resolution pictures of the type specimens stored in the collections of the Geological Survey of Canada has now allowed their carapace groove pattern to be observed (Fig. 2); that of the holotype of *E. minor* is not preserved in its entirety: it has an elongated and bifurcated gastro-orbital groove, joined at mid-length of the cervical groove, and a sinuous postcervical groove with a short extension at carapace mid-height (Fig. 2B). The carapace groove pattern of *P. dawsoni* is almost complete. An elongated and bifurcated gastro-orbital groove is joined posteriorly at the mid-length of the cervical groove; the cervical groove is joined ventrally to a curved antennal groove; the postcervical groove is sinuous, with an extension at the level of carapace mid-height, and joined ventrally to a sinuous hepatic groove, joined anteriorly to the cervical groove; a short and isolated branchiocardiac groove is interrupted in the branchial region; a curved inferior groove is also joined to the posterior extremity of the hepatic groove. This specimen also has a rectangular P1 propodus bearing long fingers (Fig. 2F). This groove pattern and the morphology of P1 chelae of *P. dawsoni* are typical of *Enoploclytia*. Moreover, the type specimens of both *E. minor* and *P. dawsoni* have a very similar tuberculated ornamentation. These specimens also from localities on Hornby Island that are close in geography and stratigraphy. In conclusion, the morphological similarities as well as the geographic and stratigraphic arguments lead us to interpret *P. dawsoni* as a junior synonym of *E. minor*.

Considering the recent revisions of erymoid lobsters proposed by Devillez *et al.* (2016, 2017) and Devillez & Charbonnier (2017, 2019, 2020), the previous remarks made above and novel contributions by Schweigert & Härer (2020), Feldmann *et al.* (2020), Ando *et al.* (2020) and Garassino *et al.* (2021),

FIG. 8. — Jurassic and Cretaceous erymoid lobsters from North America, excepting *E. minor* and *P. haidaensis*: **A**, holotype USNM PAL 530027 of *Eryma jungostrix* Feldmann & Titus, 2006, from the Oxfordian of Utah (United States); **B**, holotype USNM PAL 512150 of *Pustulina trisulcata* (Schweitzer & Feldmann, 2001), from the Cenomanian of Sites (California, United States); **C**, paratype USNM PAL 335146 of *Palaeastacus kimzeyi* Rathbun, 1935, from the Campanian of Farmersville (Texas, United States); **D**, holotype AMNH FI 35862 of *Palaeastacus foersteri* (Feldmann, 1979), from the Callovian of Bush Canyon (Wyoming, United States); **E**, specimen NPL TMM-BEG 21123 of *Palaeastacus walkeri* (Whitfield, 1883), from the Albian of Fort Worth (Texas, United States); **F**, holotype USNM PAL 73799 of *Enoploclytia tumimana* Rathbun, 1935, from the Maastrichtian of Allenton (Alabama, United States); **G**, holotype NPL TMM-BEG 21126 of *Enoploclytia gigantea* Devillez, Charbonnier, Hyžný & Leroy, 2016, from the Albian of Fort Worth (Texas, United States); **H**, holotype MUZ-824 of *Enoploclytia tepeyacensis* Vega, Nyborg, Fraaije & Espinosa, 2013, from the Campanian of Jiménez (Mexico); **I**, holotype NPL TMM-BEG 21099 of *Enoploclytia*





*wintoni* Stenzel, 1945, from the Albian of Crowley (Louisiana, United States); **J**, original figure of Feldmann *et al.* (2020: fig. 1A) of the holotype of *Stenodactylina beardi* Feldmann, Schweitzer & Haggart, 2020, from the upper Santonian - lower Campanian of Vancouver Island (Canada); **K**, lectotype NPL TMM-BEG 21127 of *Stenodactylina triglypta* (Texas, United States); **L**, original figure of Feldmann & Haggart (2008: fig. 2) of the holotype of *Stenodactylina walkerae* (Feldmann & Haggart, 2008), from the Middle Jurassic of McDonnell Lake (Canada). Scale bars: 1 cm. Photographs: T. Jorstad (F), Non-vertebrate Paleontology Laboratory, Jackson School of Geosciences, The University of Texas at Austin (E, G, I, K), L. O'Reilly (A-C), S. Thurston (D), F. Vega (H).



81 valid species are recognised here (Table 1), meaning a reduction of at least one third when compared to the list of Schweitzer *et al.* (2010).

According to the present review, the number of valid species of *Pustulina* (11 species, rather than 12) remains stable, while that of *Enoploclytia* and *Palaeastacus* has almost been halved (10 species [versus 19] and 14 [versus 24]; Table 1). *Eryma* shows the strongest reduction in number of species that are considered valid by us. This number was divided by almost three between the listing by Schweitzer *et al.* (2010) and the most recent review (i.e., 24 versus 60 species). This reduction is due to: 1) the numerous species now identified as synonyms of others (e.g., *Eryma ventrosum* is an extreme case with 23 synonymised names recognised; Devillez & Charbonnier 2020); and 2) the species that have been reassigned to other genera, (e.g., *Eryma foersteri* Feldmann, 1979 is now regarded as a representative of *Palaeastacus*; Devillez & Charbonnier 2019). *Stenodactylina* is the sole genus to show an increase in the number of constituent species. This is due to reassignment of species earlier referred to *Enoploclytia*, *Palaeastacus* and, mainly, from *Eryma*. These changes result from a more detailed characterization of the genus that followed upon the publication of specimens with carapaces preserved in association with P1 chelae by Hyžný *et al.* (2015). Indeed, prior to that study, the genus *Stenodactylina* was known exclusively from a couple of isolated P1 chelae (Beurlen 1928; Schweigert 2013), so the carapace and its groove pattern remained unknown until 2015. All in all, *Stenodactylina* remains an uncommon genus, and Devillez *et al.* (2018) pointed out an important gap of almost 50 myr between the two Cretaceous occurrences of *S. delphinensis* (Moret, 1946) (Berriasian) and *S. triglypta* (Stenzel, 1945) (Coniacian).

#### EVOLUTION OF PALAEOBIODIVERSITY

The palaeobiodiversity of the Erymoidea can be analysed at different temporal (systems, series and stages) and taxonomic (family, genus and species) levels. In view of the fact that there is only a single species each on record from the Late Permian (Changhsingian; Fig. 3A) and the Paleocene (Fig. 3B, C), and because there are no records of Triassic erymoid lobsters, our discussion of erymoid palaeobiodiversity is restricted to Jurassic and Cretaceous occurrences. Moreover, in consideration of the relatively low number of known species and biases in collection and literature records, the elements given in our analysis proposed here should be only regarded merely as general trends.

More erymoid species have been recorded from the Jurassic strata (45 species) than from Cretaceous deposits (34 species). However, of those 45, ten species occur exclusively in Lagerstätten of Late Jurassic (Kimmeridgian-Tithonian). By removing the Lagerstätten effect, as discussed by Klompmaker *et al.* (2013), the Jurassic yields 35 species, a specific diversity that is very close to that of the Cretaceous (Fig. 4A, B). However, we have noted a marked change in the importance of the families Erymidae and Enoploclytiidae between the Jurassic and the Cretaceous. Indeed, the later family comprises fewer species during the entire Jurassic and an increase to almost half of the diversity of all Erymoidea during the Cretaceous.

At the generic level, *Eryma* (17 species) and *Stenodactylina* (17 species) are the most speciose during the Jurassic: they include 80% of the species known for this system. For the Cretaceous, *Enoploclytia* is the genus which comprises most species (nine), while the number of species of *Palaeastacus* remains stable (seven species in Jurassic and Cretaceous), and *Pustulina* is the sole genus to have an increased specific diversity compared to that of the Jurassic (four Jurassic species, seven Cretaceous ones). The number of species for other genera already recorded from the Jurassic is less important during the Cretaceous: 17 Jurassic species of *Eryma* and six for the Cretaceous, 17 Jurassic species of *Stenodactylina* and four for the Cretaceous.

Considering the stage-by-stage-evolution of erymid palaeobiodiversity, leaving out the taxa from Lagerstätten, three major peaks in specific diversity can be noted (Fig. 4C).

The first peak is seen at the boundary between the Lower and Middle Jurassic (Toarcian-Aalenian). This is strongly supported by the specific diversity of the genus *Stenodactylina*, which attains the highest number of species. This peak is followed by a reduction of 50% in species during the Bajocian. Subsequently, the specific diversity increases from the Bathonian to reach a second peak at the limit between Middle and Upper Jurassic (Callovian-Oxfordian). This coincides with the development of carbonate platforms across Europe, when *Eryma* reaches its maximum diversity. The Bathonian is also characterised by the rise of *Eryma ventrosum*, a common species in the Middle and Late Jurassic of western Europe, while there are no records anymore *Eryma compressum* (Eudes-Deslongchamps, 1842), which had been common since the Toarcian. A progressive reduction in the number of species starts during the Kimmeridgian-Tithonian. Indeed, from seven erymoid species on record from Oxfordian strata, the uppermost Jurassic has yielded only three reported species to date. This low specific diversity continues into the earliest of the Cretaceous, with only three reported species during the Berriasian, and characterises almost the entire Lower Cretaceous until the third peak at the boundary between the Lower and Upper Cretaceous (Albian-Cenomanian) is reached. However, contrary to the general trend, with five reported species, *Pustulina* reaches a higher specific diversity during the Early Cretaceous. The third peak coincides with the interval that witnesses the last occurrences of *Eryma* and *Pustulina*, while *Enoploclytia*, already present during the Oxfordian (Devillez *et al.* 2018) and Barremian (Devillez *et al.* 2016), flourishes and becomes the most diverse erymoid genus of all the Late Cretaceous. The Albian-Cenomanian boundary also corresponds to the development of the Chalk Sea in western Europe and of the Western Interior Seaway of North America (United States and Canada) that provided new environments for erymoid lobsters. Subsequent to the Cenomanian, erymoid diversity decreases progressively in Europe up to the last occurrences, that have been assigned to *Enoploclytia leachii* (Mantell, 1822) in the Campanian of Belgium and Germany. Following the Campanian, the erymoid lobsters seem to have disappeared except for North America, along both Pacific and Atlantic coasts during the Maastrichtian and only on the Atlantic side (Gulf of Mexico) during the Paleocene.



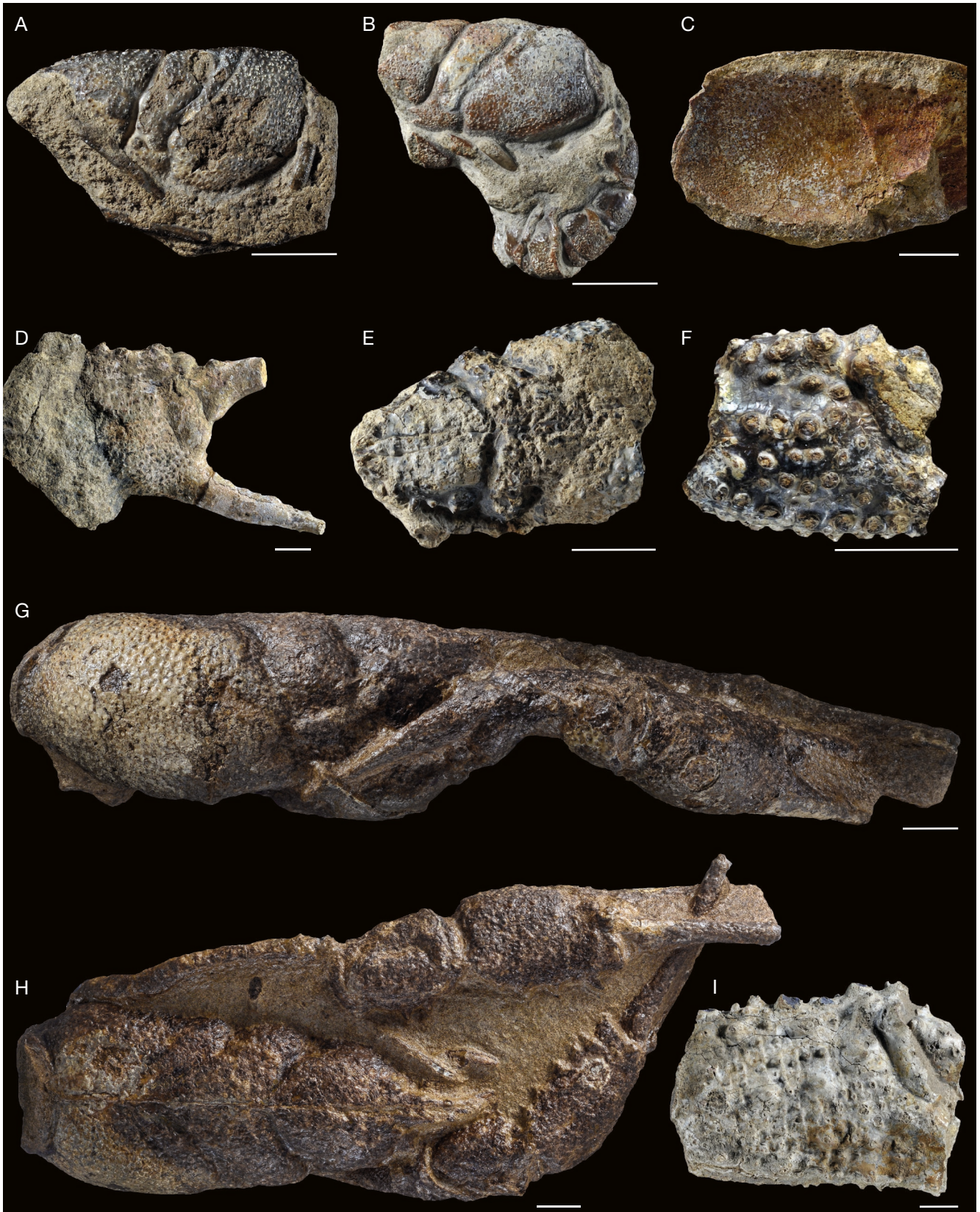


FIG. 9. — Erymoid fauna from Madagascar: **A, B**, *Stenodactylina granulifera* (Secrétan, 1964) from the Kimmeridgian of Antsalova: holotype MNHN.F.R03975 (**A**), specimen MNHN.F.R.03974, holotype of *Eryma madagascariensis* Secrétan, 1964 (**B**); **C, D**, *Stenodactylina australis* (Secrétan, 1964), from the Tithonian: specimen MNHN.F.A33228 from Marolalitra (**C**), holotype MNHN.F.R03972 from Analavelona Massif (**D**); **E, F**, *Pustulina spinulata* (Secrétan, 1964), from the Valanginian-Hauterivian of Soromaraina, holotype MNHN.F.R03961 (**E**), paratype MNHN.F.A33189 (**F**); **G, H**, paratype MNHN.F.A33132 of *Enoploclytia collignoni* Secrétan, 1964, from the Campanian of Bevahio; **I**, holotype MNHN.F.R03913 of *Stenodactylina armata* (Secrétan, 1964), from the Campanian of Belo-sur-Tsiribihina. Scale bars: 1 cm. Preparation: C. Bouillet (G-H). Photographs: L. Cazes (C, G, H), C. Lemzaouda (A, B, D, E, I).



## PALAEOBIOGEOGRAPHY

### PALAEOZOIC AND TRIASSIC

There is only a single representative of the Erymoidea on record from the end of the uppermost Permian (Changhsingian), namely *Eryma antiquum* (Birshtein, 1958). Hitij *et al.* (2019: 32) have recently recorded the presence of erymoid lobsters in Triassic (Carnian) strata of the Julian Alps of Slovenia. However, the general shapes of the specimen illustrated, and the wide and rounded extremities of the pleonal pleurites in particular, are close to *Clytiopsis* Bill, 1914, a genus already well known from the Triassic of Western Europe. *Clytiopsis* is not an erymoid lobsters (Devillez *et al.* 2019). In consequence, there are no representatives of this group on record to date from the Triassic; it is therefore impossible to extract any palaeobiogeographic data.

### JURASSIC

For the Lower Jurassic, Erymoidea are exclusively known in western Europe. Only the erymid genera *Eryma*, *Palaeastacus* and *Stenodactylina* have been recorded from the Sinemurian in France, Germany, Italy, and the United Kingdom (Devillez & Charbonnier 2019; Fig. 5). Moreover, an unidentified species of *Pustulina*, originally referred to as *Eryma* sp. by Woods (1930), has also been noted from the uppermost Lower Jurassic of the United Kingdom (Förster 1966; Devillez & Charbonnier 2019). Considering the sheer number of palaeontological studies carried out across Europe since the nineteenth century, the bias in collection may be considered to be weak for this continent. It is then strongly speculative to assume that western Europe was a central spot from where erymoid lobsters spread out across the globe, since it is the only area from which the oldest Mesozoic representatives of the group have been reported.

All Erymoidea recorded from the Middle Jurassic strata were found in the Northern Hemisphere, in Europe, northwestern North America and in northwestern and northeastern Africa (Fig. 6A). The only two enoploclytiids, *Pustulina calloviensis* (Förster, 1966) and *Pustulina elegans* (Förster, 1966), are known from western Europe, while erymids are widely distributed. Of *Eryma compressum*, in particular, the commonest species in Europe during the Middle Jurassic, there two southerly occurrences, in present-day Iran (Förster & Seyed-Emami 1982; Fig. 7B) and Morocco (Secréta 1984). This suggests that this species spread to nearly the entire European part of the Tethys Ocean, the Central Atlantic margin (occurrence in the Bajocian), which had started to open up the onset of the Middle Jurassic (Scotese 2014c), and the North African margin in the southern Tethys Ocean (occurrence in the Aalenian). A recently reported specimen of *E. compressum* and *Eryma ornatum* (Fig. 6A), another well-known western European species, extends the geographical distribution of the genus to eastern Europe (Fanțescu *et al.* 2018, Metodiev *et al.* 2021).

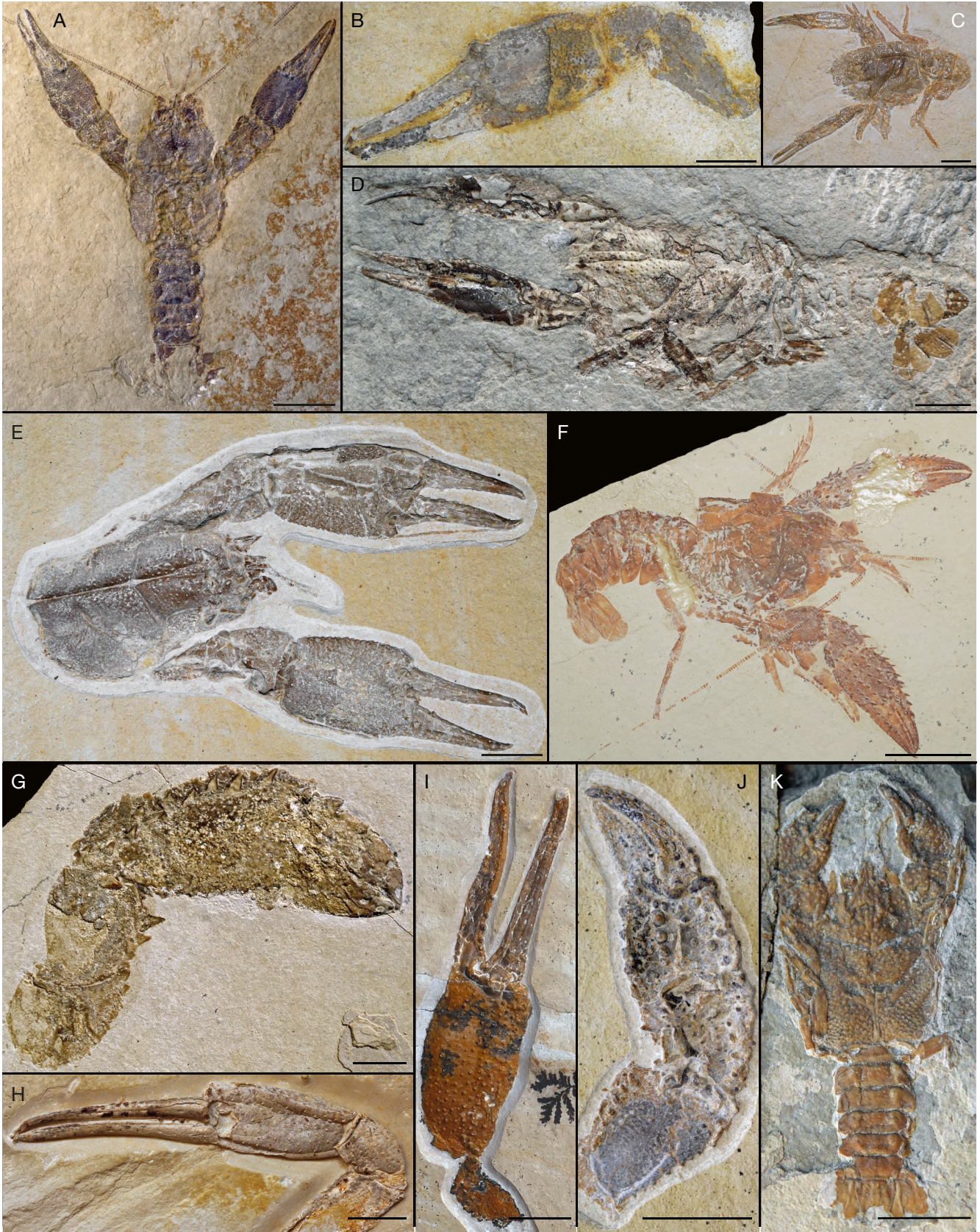
Some erymids have also been reported from northwestern North America, which was flooded during the Middle Jurassic: *Stenodactylina walkerae* (Feldmann & Haggart, 2008) (Fig. 8L) and *Palaeastacus foersteri* (Feldmann, 1979) (Fig. 8D). Their presence could have resulted from migrations of European populations. Indeed, both *Stenodactylina* and *Palaeastacus* had been present in western Europe since the Early Jurassic. Western Europe was also the closest region from where the northwest of North America via the Boreal Ocean could have been reached.

The geographic distribution of erymoid lobsters looks to have been wider during the Late than during the Middle Jurassic. The few reported enoploclytiids on record – *Enoploclytia* sp. (Devillez *et al.* 2018), *Pustulina minuta* (Schlotheim, 1822) and *Pustulina suevica* Quenstedt, 1857 – are still in western Europe, but erymids are distributed in both hemispheres: Asia, Europe, North America, and southeastern Africa (Madagascar, Tanzania; Fig. 6B and Fig. 9A, D). Representatives of *Eryma* are still very well represented in Europe. On other continents, *Eryma jungostrix* Feldmann & Titus, 2006 (Fig. 8A) documents the continued presence of the genus in North America after the Middle Jurassic, while an incomplete P1 chela indicates the presence of *Eryma* in the Far-East (Japan; Kato *et al.* 2010) and a specimen recently assigned to *Eryma ventrosum* has been described from Tanzania (Beurlen 1933: as “*Eryma cf. bedelta*”; Devillez & Charbonnier 2020; Fig. 7A). This species, already known in western Europe during the Bathonian (Devillez & Charbonnier 2020), extends the distribution of *Eryma* further to the south than *E. compressum* seems to have done during the Middle Jurassic. The presence of *E. ventrosum* so far south during the Late Jurassic strongly suggests the existence of migrations of erymoid populations from western Europe to the Southern Hemisphere. Moreover, the presence of *Stenodactylina* in Madagascar during the Kimmeridgian-Tithonian could be a result of such migrations. This genus already occurred in western Europe and North America during the Middle Jurassic. However, the North American inlet was only connected to the Boreal Ocean only far in the north during the Middle Jurassic and only to the Pacific Ocean in the west during the Late Jurassic, so it was closed to the south.

In western Europe, the Solnhofen-type Kimmeridgian-Tithonian lithographic limestones of southern Germany have yielded an exceptionally diverse erymoid fauna with eleven species in four genera: *Eryma modestiforme* (Schlotheim, 1822), *E. major* Oppel, 1861, *E. punctatum* Oppel, 1861, *E. veltheimii* (Münster, 1839), *E. westphali* Schweigert, Dietl & Röper, 2000, *Palaeastacus fuciformis* (Schlotheim, 1822), *P. rothgaengeriae* Schweigert & Röper, 2001, *Pustulina minuta*, *P. suevica*, *Stenodactylina devillezi* Schweigert & Härer, 2020, and *S. geigeriae* Schweigert & Härer, 2020 (Fig. 10).

Fig. 10. — Erymoid fauna from the Kimmeridgian-Tithonian “Plattenkalk” of Bavaria (Germany): **A**, specimen MFN 2236 P1383/3 MB.A.2891 of *Eryma modestiforme* (Schlotheim, 1822) from Solnhofen; **B**, holotype SMNS 3682 of *Eryma major* Oppel, 1861, from Nusplingen; **C**, holotype SMNS 24227 of *Eryma westphali* Schweigert, Dietl & Röper, 2000, from Nusplingen; **D**, holotype BSPG AS VII 186 of *Eryma veltheimii* (Münster, 1839), from Kehlheim; **E**, specimen SMNS 64681 of *Eryma punctatum* Oppel, 1861, from Nusplingen; **F**, specimen SMNS 64521 of *Palaeastacus fuciformis* (Schlotheim, 1822), from Zandt; **G**, holotype BSPG





1993 XXVIII 200 of *Palaeastacus rothgaengeriae* Schweigert & Röper, 2001, from Brunn; **H**, holotype SMNS 70507 of *Stenodactylina geigerae* Schweigert & Härer, 2020, from Marxheim; **I**, holotype SMNS 64872 of *Stenodactylina devillezi* Schweigert & Härer, 2020, from Nusplingen; **J**, specimen SMNS 64319 of *Pustulina suevica* Quenstedt, 1857, from Nusplingen; **K**, specimen BSPG AS I 619 of *Pustulina minuta* (Schlotheim, 1822), from Solnhofen. Scale bars: 1 cm. Photographs: J. Devillez (A-F, J-K), G. Schweigert (G-I).



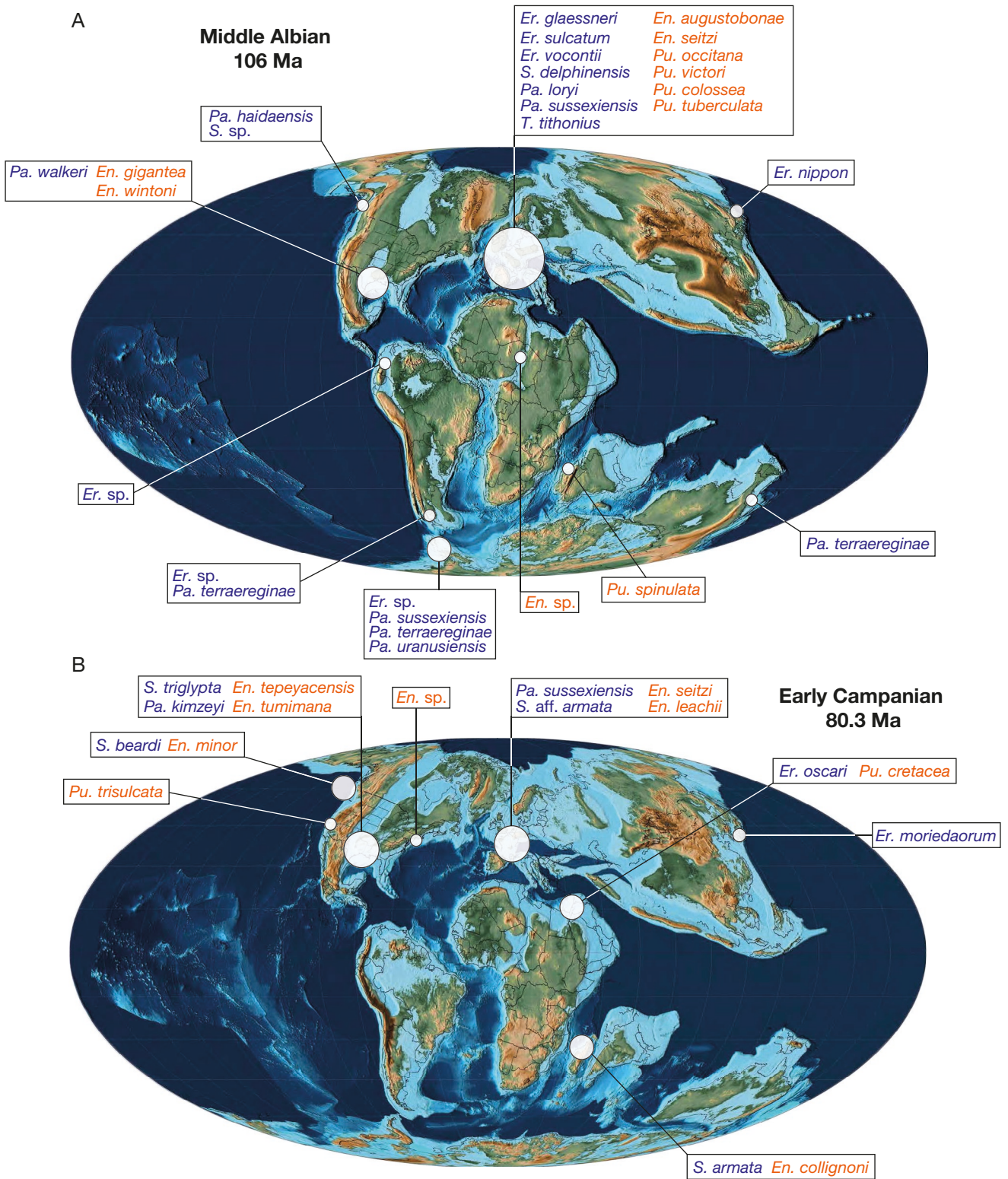


FIG. 11. — Distribution of Erymoidea during the Cretaceous: **A**, palaeobiogeography of the Early Cretaceous; **B**, palaeobiogeography of the Late Cretaceous. Colors: **blue**, Erymidae; **orange**, Enoploclytiidae. Abbreviations: **En.**, *Enoploclytia*; **Er.**, *Eryma*; **Pal.**, *Palaeastacus*; **Pu.**, *Pustulina*; **S.**, *Stenodactylina*; **T.**, *Tethysastacus*. Source of maps: Scotese 2014a, b.

However, in contrast to *E. modestiforme* and *P. fuciformis*, the other species are far less common: indeed, except for *P. minuta*, of the other species only a very low number of

specimens are available. Thus, in spite of the paucity of most of the reported species, these “Plattenkalks” have yielded the most diverse erymoid fauna of all times.



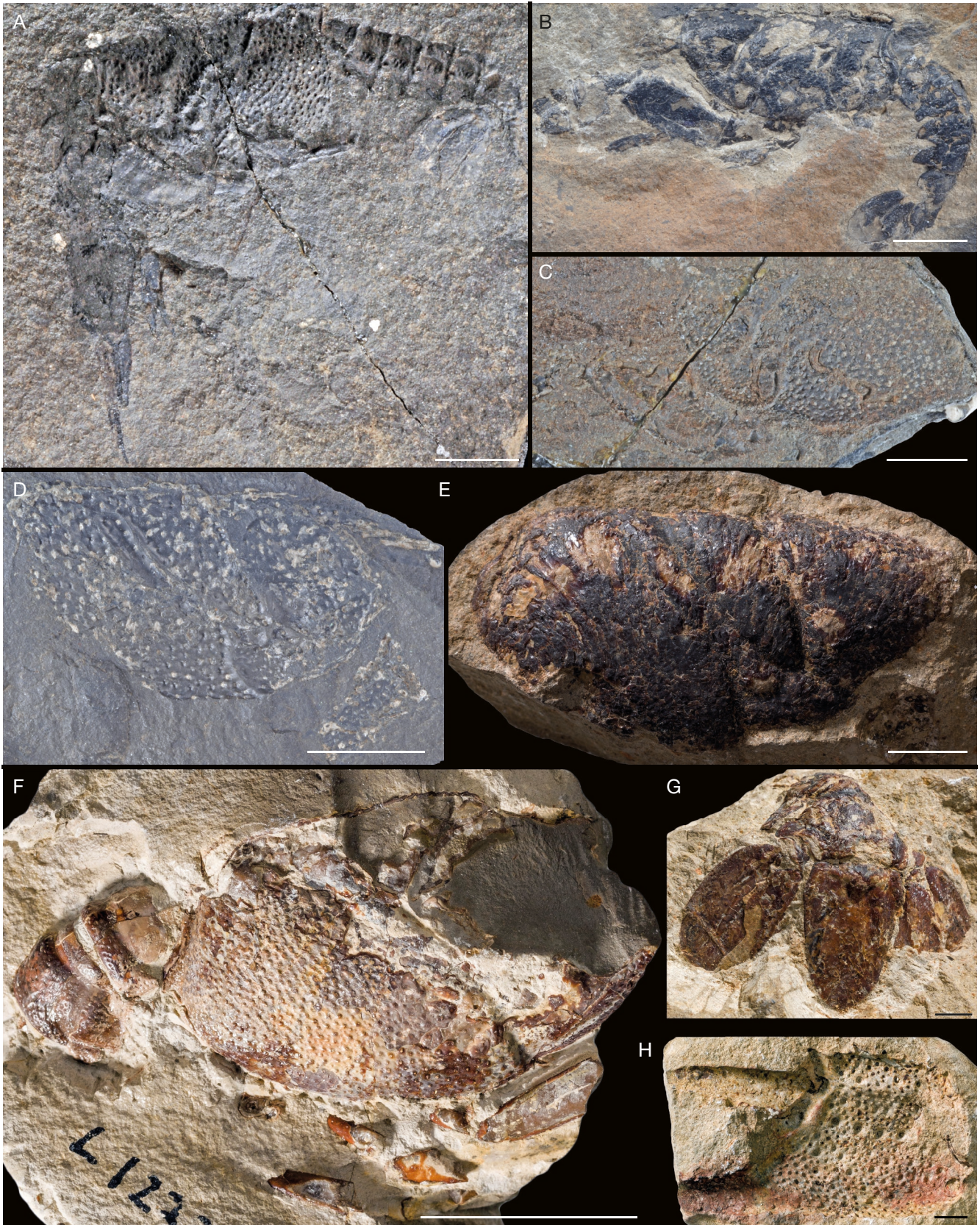


FIG. 12. — Early Cretaceous erymoid fauna from the extreme south: **A**, holotype BAS KG.50.4 of *Palaeastacus uranusiensis* Devillez & Charbonnier, 2019, from the Aptian of Alexander Island (Antarctica); **B**, Specimen BAS KG.103.134 of *Palaeastacus sussexiensis* (Mantell, 1824), from the Aptian of Alexander Island (Antarctica); **C**, specimen BAS KG.11.4 of *Palaeastacus terraereginae* (Etheridge Jr, 1914), from the Barremian of Antarctica; **D**, specimens BAS KG-2-214 of *Eryma* sp. from the Aptian of Alexander Island (Antarctica); **E-H**, Australian specimens of *P. terraereginae*: specimen QM F3235, from the Barremian of Currane (**E**), specimen UQ F13417 from the Aptian of Boomers (**F**), specimen QM F3235 from the Barremian of Currane (**G**), specimen QM F3236 from the Barremian of Currane (**H**). Scale bars: 1 cm. Photographs: H. Blagbrough (A-D), P. Waddington (E-H).



CRETACEOUS

With occurrences in Antarctica, Australia, Europe, Japan, Madagascar and North and South America, the erymoids seem to have extended their geographical distribution into the Southern Hemisphere. However, most specimens and species on record still originate from the Northern Hemisphere.

In Lower Cretaceous strata, thirteen (out of 21) species were found in western Europe (Fig. 11A). The main difference with the Late Jurassic is that the number of enoploclytiids has strongly increased. Indeed, in Europe and North America there is almost the same number of species assigned to this family than that assigned to the Erymidae.

The presence of *Eryma nippon* Karasawa, Ohara & Kato, 2008 (Barremian, Japan; Fig. 7C) and *Eryma moriedaorum* Ando, Hirose, Ugai & Shimada, 2020 (Cenomanian, Japan) suggests the persistence of an erymoid fauna in the Far-East since at least the Kimmeridgian-Tithonian (Kato *et al.* 2010). In addition, important during the Early Cretaceous is the presence of erymoid faunas at the extreme south of the globe (Antarctica, Australia, Patagonia [Argentina]). The erymoids recorded from there exclusively belong to the Erymidae and constitute the first occurrences of these lobsters in Antarctica (Taylor 1979; Aguirre-Urreta 1989; Devillez *et al.* 2017), in Australia (Etheridge Jr 1914; Woods 1957; Förster 1966; Devillez *et al.* 2017) and in Patagonia (Aguirre-Urreta & Ramos 1981; Aguirre-Urreta 1982, 1989). These occurrences concern mainly the genus *Palaeastacus* (Fig. 12). Some specimens from the Aptian of Patagonia were assigned to *Palaeastacus sussexiensis* (Mantell, 1824) by Aguirre-Urreta (1989: fig. 8). This assignment was accepted by Devillez *et al.* (2016, 2017). However, these specimens exhibit some differences with *P. sussexiensis*: the P1 propodus is rounded in shape, the basis of the dactylus is relatively thin, the carapace ornamentation is fine and lacks strong spines in the cephalic and cardiac regions, and there are no rows of strong spines on the dorsal surface of P1 propodus. The shape of the P1 chelae and the dense, fine ornamentation of the carapace and P1 chelae of the Patagonian specimens are closely similar to those of *Palaeastacus terraereginae* (Etheridge Jr, 1914), a species recorded from the Barremian of Antarctica, Australia and Patagonia and from the Aptian of Queensland (Australia). Therefore, the Patagonian specimens recorded by Aguirre-Urreta (1989) are here considered to be conspecific with *P. terraereginae*. Thus, among the erymoids of the extreme south of the globe, *P. terraereginae* was widespread in this area of the world during the late Early Cretaceous.

Devillez *et al.* (2016) described an exceptional fauna from southeastern France. During the Early Cretaceous, this north-east oriented area of almost 350 × 300 km provided eight species assigned to five (out of six) erymoid genera currently known: *Eryma vocontii* Devillez, Charbonnier, Hyžný & Leroy, 2016, *Eryma glaessneri* (Van Straelen, 1936), *Palaeastacus loryi* (Van Straelen, 1923), *Pustulina colossea* Devillez, Charbonnier,

Hyžný & Leroy, 2016, *Pustulina occitana* Devillez, Charbonnier, Hyžný & Leroy, 2016, *Pustulina victori* Devillez, Charbonnier, Hyžný & Leroy, 2016, *Stenodactylina delphinensis* (Moret, 1946), and *Tethysastacus tithonius* Devillez, Charbonnier, Hyžný & Leroy, 2016 (Fig. 13). With eight species (of 21) on record, this area of limited extent is known to have yielded: 1) the most diverse erymoid fauna of the Lower Cretaceous; 2) the most diverse *Pustulina* assemblage; and 3) the two sole fossils of *Tethysastacus* currently known (holotype MNHN.F.J03351 of *T. tithonius* and cast MNHN.F.A70286 of another specimen from an unknown locality).

The only erymoid fauna known from the Southern Hemisphere during the Late Cretaceous (Fig. 11B) has been described from the Campanian of Madagascar (Secrétan 1964; Charbonnier *et al.* 2012a; Devillez *et al.* 2017; Fig. 9). Secrétan (1964) noted the affinities between erymoid faunas from Madagascar and Australia (Figs 1; 12), Europe and North America (Fig. 8) and deduced from this the existence of migratory paths that allowed exchanges between Madagascar and other continents. An isolated P1 chela from the Santonian of France assigned to *Stenodactylina cf. armata* (see Devillez *et al.* 2017; Fig. 14K) confirms the probable exchange of faunas between Europe and Madagascar.

In the south of the Northern Hemisphere, in present-day Lebanon, it is interesting to point out the presence of representatives of both enoploclytiids and erymids: *Pustulina cretacea* (Roger, 1946) (Fig. 7D) and *Eryma oscari* Charbonnier, Audo, Garassino & Hyžný, 2017 (Fig. 7E).

We have noted a spectacular change in erymoid distribution in the Upper Cretaceous. A shift of the pole of diversity from Europe to North America with the addition of an apparent reduction of specific diversity (21 species in the Lower Cretaceous, 15 in Upper Cretaceous). The flooding of the southern USA and northeastern Mexico since the Early Cretaceous (Scotese 2014a, b) could have provided new environments favourable for the settlement and diversification of an erymoid fauna. In contrast, the development and relative stability of the western European Chalk Sea possibly did not provide enough changes in environmental conditions to enable a strong diversification and modification of the erymoid fauna (Fig. 14). Indeed, this stability could have allowed the persistence of well-adapted species – in this case, *Enoploclytia leachii* and *Palaeastacus sussexiensis* – without competitive pressure of too many immigrant forms.

Devillez *et al.* (2017) discussed in detail the absence of erymoids in North America between the Oxfordian and the Albian. They proposed two hypotheses to explain this 50 myr hiatus: 1) a bias in collection or literature records; or 2) a genuine absence of erymoid lobsters in North America. As to the second hypothesis, the authors emphasised that the Cretaceous fauna in the Gulf of Mexico could have resulted from immigrations of populations from Eurasia. Indeed, the proximity of this continent at the end of the Early Creta-

Fig. 13. — Early Cretaceous erymoid fauna from the South-East Basin (France): **A**, cast MNHN.F.R10204 of the holotype of *Eryma glaessneri* (Van Straelen, 1936), from the Hauterivian of Escoragnolles; **B, C**, specimens of *Eryma vocontii* Devillez, Charbonnier, Hyžný & Leroy, 2016 from the Albian of Rosans: holotype MNHN.F.A57457 (**B**), paratype MNHN.F.A57458 (**C**); **D**, original figure of Van Straelen (1923: fig. 10) of the holotype of *Palaeastacus loryi* (Van Straelen, 1923) from the Valanginian of Malleval; **E**, original figure of Van Straelen (1936: pl. 2, fig. 3) of the holotype of *Pustulina victori* Devillez, Charbonnier, Hyžný & Leroy,





2016, from the Berriasian of Leyssse; **F**, holotype MNHN.F.A57459 of *Pustulina colossea* Devillez, Charbonnier, Hyžný & Leroy, 2016, from the Hauterivian of Castellane; **G**, holotype MNHN.F.A57460 of *Pustulina occitana* Devillez, Charbonnier, Hyžný & Leroy, 2016, from the Berriasian of Laciterne-Boisset; **H**, holotype OSUG.UJF-ID 11152 of *Stenodactylina delphinensis* (Moret, 1946), from the Berriasian of Noyarey; **I**, holotype MNHN.F.J03351 of *Tethysastacus tithonius* (Van Straelen, 1936), from the Valanginian of Laciterne-Boisset. Scale bars: 1 cm. Photographs: L. Cazes.



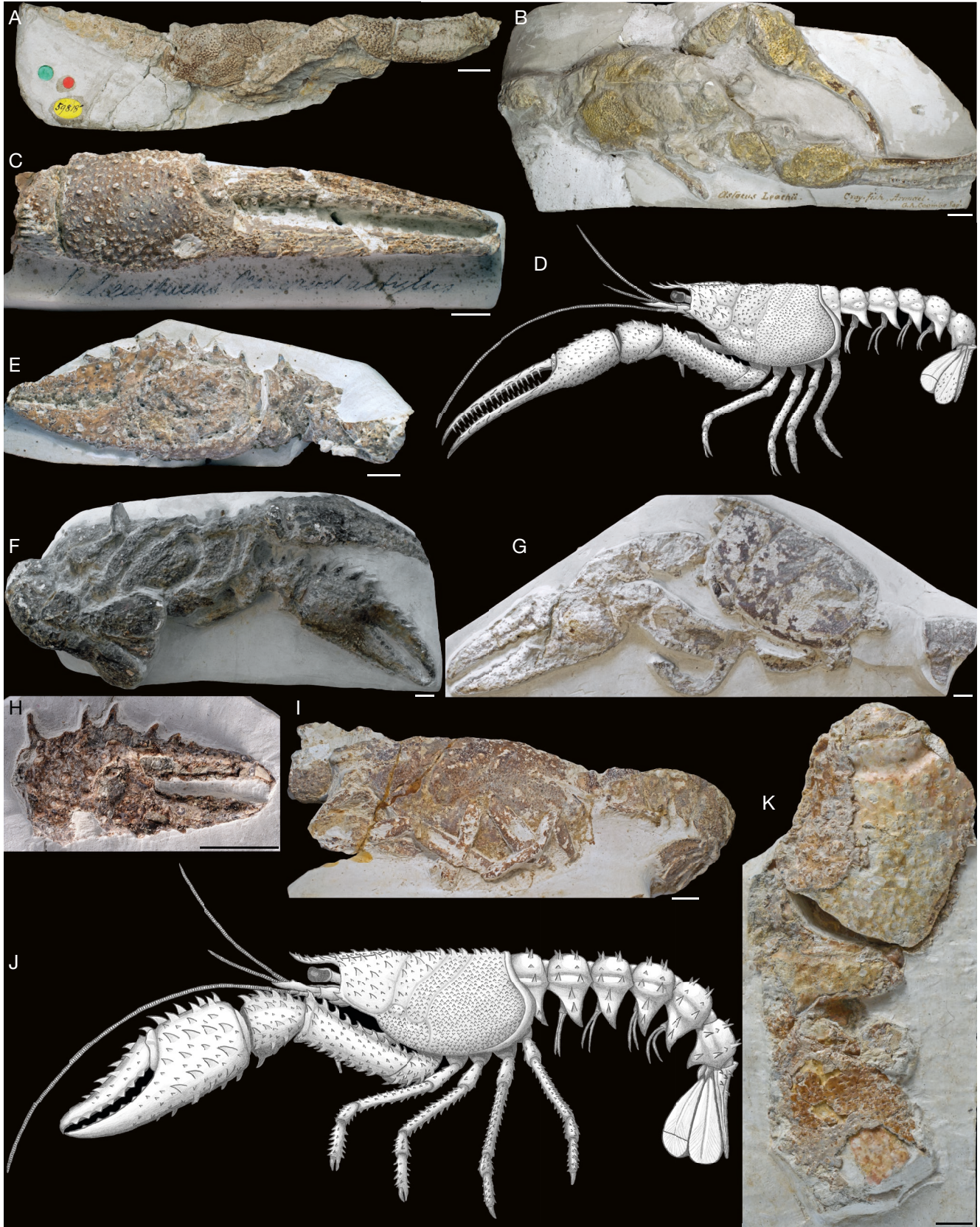


FIG. 14. — Erymoid fauna from the Chalk Sea (Late Cretaceous): **A**, specimen NHMUK 5918 of *Enoploclytia seitzii* Glaessner, 1932, from the Cenomanian of Dover (United Kingdom); **B-D**, *Enoploclytia leachii* (Mantell, 1822), from United Kingdom: specimen NHMUK 34404 from Arundel (**B**), specimen BM 016987 (**C**), reconstruction (**D**); **E-J**, *Palaeastacus sussexiensis* (Mantell, 1824): specimen BM 007757, from Glynde (United Kingdom) (**E**), specimen NHMUK unregistered, from Maidstone (United Kingdom) (**F**), specimen NHMUK 59824, from Lewes (United Kingdom) (**G**), specimen MNHN.F.S07674, from Couvrot (France) (**H**), specimen BM 016988, from United Kingdom (**I**), reconstruction (**J**); **K**, specimen MNHN.F.A66891 of *Stenodactylina* cf. *armata*, from the Santonian of Cognac (France). Scale bars: 1 cm. Preparation: Y. Despres (H, K). Photographs: L. Cazes (H), J. Devillez (A-C, E-G, I), P. Loubry (K). Drawings: J. Devillez.



ceous, the potential access in the North through the Boreal Sea and the presence of all genera recorded from the Lower Cretaceous (i.e., *Enoploclytia*, *Palaeastacus* and *Stenodactylina*) provide strong support for this scenario.

They also pointed out the absence of occurrences of erymoid lobsters in the Western Interior Seaway (WIS), which connected the Boreal Ocean in the north with the Atlantic Ocean in the south during almost the entire Late Cretaceous (Gill & Cobban 1966, 1973; Molenaar & Rice 1988; Eicher & Diner 1989; Scotese 2014a, b). Five erymoid species were recorded from Texas, at the southern extremity of the WIS. In view of the fact that the connection between the WIS and the Atlantic had no clear geographical boundary and remained relatively stable, Devillez *et al.* (2017) suggested that the apparent absence of erymoids in the WIS could have resulted from a bias in collection or literature records.

#### PALEOGENE

*Enoploclytia gardnerae* (Rathbun, 1935), the sole erymoid species to have been recorded from the Cenozoic, is from the Paleocene of Alabama (southern United States; Rathbun 1935) and northern Mexico (Vega *et al.* 2007; Martínez-Díaz *et al.* 2017; Fig. 3B, C). Thus, as far as we are aware, the last known erymoid populations lived in the Gulf of Mexico.

#### CONCLUSIONS

The present synthesis supplies a general overview of current knowledge of erymoid lobsters, for which 81 valid species within six genera are currently known. During their almost 190 myr-long evolutionary history, their palaeobiodiversity fluctuated with three periods of higher specific diversity at the boundaries of the: 1) Lower-Middle Jurassic; 2) Middle-Upper Jurassic; and 3) Lower-Upper Cretaceous. The second and third peaks could have been linked to important palaeoenvironmental changes: the development of carbonate platforms across Europe and the development of the European Chalk Sea in addition to the flooding of vast North American territories, respectively.

During their long history, erymoids colonised the shelves around each continent. Such a colonisation may have been possible through some migratory paths, which seem to have had a Eurasian origin. However, in consideration of the smaller number of data for the Southern Hemisphere, this interpretation could reflect a collection/recording bias. Nevertheless, the fossil record does indicate that erymoid lobsters have already attained their worldwide distribution by the Early Cretaceous.

Despite the survival of these crustaceans through the three last “biological crises”, the reasons that led to the extinction of the erymoid lobsters during the Paleogene cannot be identified as yet. Our study of erymoid palaeobiodiversity points out a decline of the group since the beginning of the Late Cretaceous, especially in Europe. New data on the relationships between erymoid lobsters and other groups of decapod crustaceans, such as the nephropid lobsters, for which the diversity seems to increase during the Cretaceous, may yield additional data allowing us to explain the demise of erymoids.

The clear definition of erymoid genera and the consistent application of the taxonomic criteria, as provided in the most recent papers, have brought to light numerous cases of synonymy and erroneous assignments. In short, the case of the erymoid lobsters is a very good example of the great importance of taxonomic reviews in order to provide useful data in the studies of past biodiversity study and of evolution at different systematic and geographic scales.

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