

# An attempt to clarify phylogenetic affinities of erymid lobsters (Decapoda) using morphological characters

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**Abstract.** A morphological-based phylogenetic analysis of a total of 33 species: 27 fossil species from eight families recognized prior to this work (Chimaerastacidae, Clytiopsidae, Erymidae, Glypheidae, Litogastridae, Nephropidae, Pemphicidae, Uncinidae), and 6 extant species from four families recognized prior to this work (Astacidae, Enoplometopidae, Nephropidae, Stenopodidae) is proposed. The cladistic analysis demonstrates that the erymid lobsters should be included with the other clawed lobsters within the infraorder Astacidea. Among Astacidea, we observed the structure recalling the intercalated plate of erymids in the extant *Enoplometopus* reported by Schram & Dixon. In order to test Schram & Dixon's hypothesis, we considered this structure as homologous to the intercalated plate. Our results suggest that the sharing of this character does not indicate close relationships between *Enoplometopus* and erymids. The erymid lobsters form a monophyletic group of six genera (*Eryma*, *Enoploclytia*, *Palaeastacus*, *Pustulina*, *Stenodactylina*, *Tethysastacus*) included in the superfamily: Erymoidea. The inclusion of a character recently identified, a delimited post-orbital area, in the morphological dataset led to the split of Erymoidea into two clades. This topology justifies a systematic rearrangement of erymid genera within two families: Enoploclytiidae fam.n., lacking a delimited post-orbital area (*Enoploclytia*, *Pustulina*), and Erymidae, showing a delimited post-orbital area. The Erymidae are also separated in two sub-families: the simplicity of the carapace groove pattern of *Tethysastacus* justifies its placement within Tethysastacinae subfam.n., while *Eryma*, *Palaeastacus* and *Stenodactylina* form the Eryminae.

**Key words.** Astacidea, cladistics analysis, Crustacea, *Enoplometopus*, Erymidae, Glypheidea, phylogeny.

## 1. Introduction

Erymids (Malacostraca, Decapoda, Erymidae) are marine crustaceans with a subcylindrical carapace followed by an elongated pleon, the first three pairs of pereopods terminated by chelae, massive P1 chelae and characterized by the presence of a fusiform area located on the dorsal side of the cephalic region: the intercalated plate (VAN STRAELEN 1925; FÖRSTER 1966; GLAESSNER 1969; FELDMANN et al. 2012, 2015). These “lobsters” form an extinct group reported from the Late Permian (Changhsingian, 252–254 Ma; FÖRSTER 1966, 1967; DEVILLEZ & CHARBONNIER 2017) to the Paleocene (Selandian, 60 Ma; VEGA et al. 2007; MARTÍNEZ-DÍAZ et al. 2017). They are relatively abundant in the Mesozoic fossil record, especially during the Jurassic (OPPEL 1862; VAN STRAELEN 1925; FÖRSTER 1966; CHARBONNIER et al. 2012b) and had a worldwide distribution (Table 1).

### 1.1. High level classifications and systematic meandering

Most of the erymid genera were described during the 19th century: *Enoploclytia* M'Coy, 1849, *Eryma* Meyer, 1840a, *Klytia* Meyer, 1840b, *Palaeastacus* Bell, 1850, *Phlyctisoma* Bell, 1863, and *Pustulina* Quenstedt, 1857. Disregarding the successive systematic classifications applied to crustaceans, the idea that erymids were close relatives to extant clawed lobsters and crayfish was consensual throughout the literature of the 19th and 20th centuries. So, VAN STRAELEN (1925) established the family Erymidae as a part of the tribe Nephropsidea Ortmann, 1896 (Reptantia Boas, 1880: *Astacura Borradaile*, 1907). RATHBUN (1926a,b) and VAN STRAELEN (1928, 1936) maintained this classification, but BEURLIN (1927) included the erymids within the new family Paranephropsidae. He also hypothesized a link with Glypheidae Zittel, 1885 and suggested a direct ascendance of the Triassic lobster

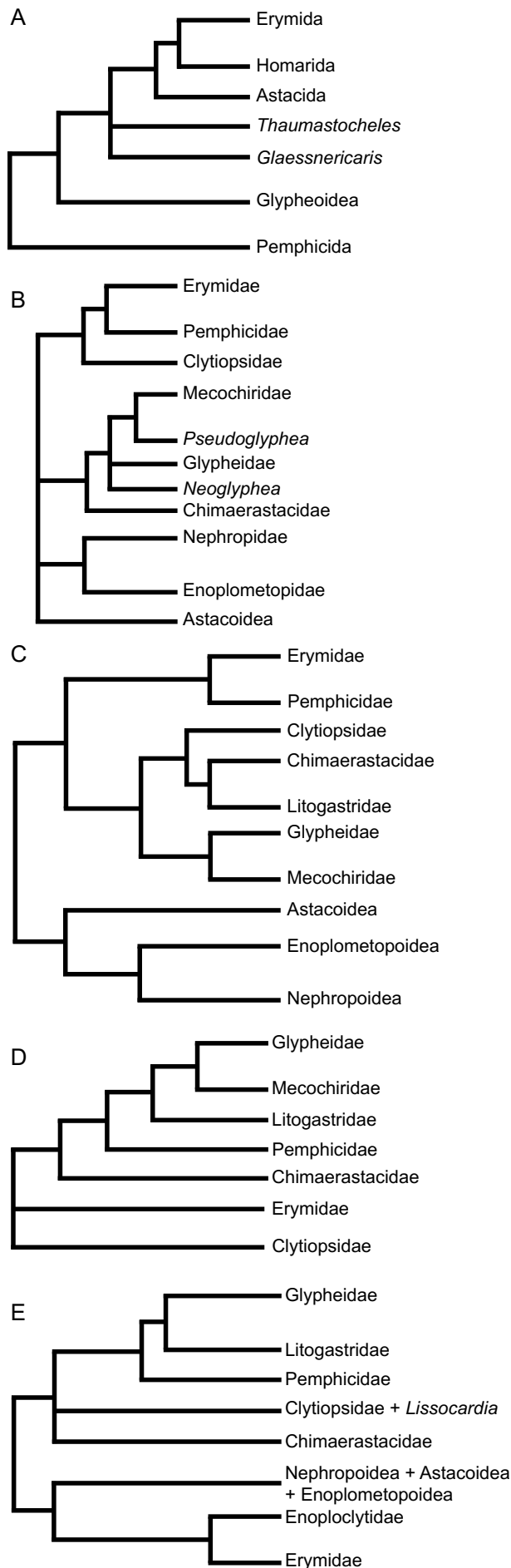
**Table 1.** Stratigraphic and geographic distribution of erymid lobsters with main references.

Age	Location	Taxa	Main References
<b>PERMIAN</b>	Asia	<i>Eryma</i>	FÖRSTER 1966, 1967; DEVILLEZ & CHARBONNIER 2017
<b>JURASSIC</b>	Africa	<i>Eryma</i> <i>Stenodactylina</i>	BEURLEN 1933; SECRÉTAN 1964; SECRÉTAN 1984; CHARBONNIER et al. 2012a
	America	<i>Eryma</i>	FELDMANN & TITUS 2006; FELDMANN & HAGGART 2007
	Asia	<i>Eryma</i>	FÖRSTER & SEYED-EMAMI 1982
	Europe	<i>Eryma</i> <i>Enoploclytia</i> <i>Palaeastacus</i> <i>Pustulina</i> <i>Stenodactylina</i>	OPPEL 1861, 1862; LAHUSEN 1894; VAN STRAELEN 1925; BEURLEN 1928; BACHMAYER 1959; FÖRSTER & RIEBER 1982; GARASSINO 1996; GARASSINO & KROBICKI 2002; BRAVI et al. 2014; DEVILLEZ & CHARBONNIER 2019
<b>CRETACEOUS</b>	Africa	<i>Enoploclytia</i> <i>Pustulina</i> <i>Stenodactylina</i>	JOLEAUD & HSU 1935; SECRÉTAN 1964; CHARBONNIER et al. 2012a
	America	<i>Enoploclytia</i> <i>Palaeastacus</i> <i>Pustulina</i>	RATHBUN 1923, 1926a,b; STENZEL 1945; FELDMANN & MCPHERSON 1980; AGUIRRE-URRETA & RAMOS 1981; AGUIRRE-URRETA 1982, 1989; SCHWEITZER & FELDMANN 2001; VEGA et al. 2007; MARTÍNEZ-DÍAZ et al. 2017
	Antarctica	<i>Palaeastacus</i>	TAYLOR 1979; FELDMANN 1984; AGUIRRE-URRETA 1989
	Asia	<i>Eryma</i> <i>Pustulina</i>	ROGER 1946; GARASSINO 1994; KARASAWA et al. 2008; KATO et al. 2010; CHARBONNIER et al. 2017
	Australia	<i>Palaeastacus</i>	WOODWARD 1877; ETHERIDGE JR. 1914; WOODS 1957
	Europe	<i>Eryma</i> <i>Enoploclytia</i> <i>Palaeastacus</i> <i>Pustulina</i> <i>Stenodactylina</i> <i>Tethysastacus</i>	MANTELL 1833; BELL 1850, 1863; REUSS 1854; VAN STRAELEN 1925; BEURLEN 1928; JAGT & FRAAIJE 2002; DEVILLEZ et al. 2016, 2017
<b>PALEOGENE</b>	America	<i>Enoploclytia</i>	VEGA et al. 2007; MARTÍNEZ-DÍAZ et al. 2017

*Clytiopsis* Bill, 1914. BEURLEN (1928) has then divided Paranephropsidae in two subfamilies, Eryminae and Clytiopsinae, in order to remove *Clytiopsis* and *Pseudopemphix* Wüst, 1903 from Glypheidae and to group them with other truly chelate Mesozoic lobsters. Later, BEURLEN & GLAESSNER (1930) attempted to establish a new classification for the “old” Reptantia, dividing them in new suborders: Trichelida and Heterochelida. Trichelida were based on the presence of chelae at the extremities of the first three pairs of pereopods. So, Trichelida included the penaeid and stenopodid shrimps (Nectochelida Beurlen & Glaessner, 1930) and the lobsters previously classified into Astacura (Proherpochelida Beurlen & Glaessner, 1930 and Herpochelida Beurlen & Glaessner, 1930). Erymidae (Eryminae + Clytiopsinae) were included within Proherpochelida, due to their carapace and pleonal features (e.g. presence of three main transversal grooves, first pleonal segment shorter than second one). This classification did not bring any consensus and was used only by KUHN (1961) and ORAVECZ (1962). MERTIN (1941) and FÖRSTER (1965, 1966) also kept Trichelida but used the same classification than Van Straelen and Rathbun at inferior ranks (i.e., Erymidae included within Nephropsidea). Instead of Kuhn, Oravec, Mertin and Förster, most of the authors who worked on erymids used BORRADAILE’S (1907) classification, with some variations under the “section” rank: the rank of Nephropsidea varied from tribe (WOODS 1930; WOODS 1957) to superfamily (STENZEL 1945); ROBERTS (1962) maintained erymid lob-

sters into Paranephropsidae and SECRÉTAN (1964) erected the tribe Homaridea to separate Erymidae and other clawed lobsters from Pemphicidae Van Straelen, 1928. The new classification proposed by GLAESSNER (1969) placed Erymidae together with other clawed lobsters into the infraorder Astacidea Latreille, 1802 (Decapoda, Pleocyemata Burkenroad, 1963). It was followed by many subsequent authors (TAYLOR 1979; BEIKIRCH & FELDMANN 1980; AGUIRRE-URRETA & RAMOS 1981; AGUIRRE-URRETA 1989; FOREST & SAINT LAURENT 1989; MARTILL 1991; WITTLER 1998; GARASSINO 1996; SCHWEIGERT et al. 2000; JAGT & FRAAIJE 2002; GARASSINO & KROBICKI 2002; CRÔNIER & COURVILLE 2004; ETTER 2004; GARASSINO & SCHWEIGERT 2006; SCHWEIGERT 2013; CHARBONNIER et al. 2013). Later, MARTIN & DAVIS (2001) introduced a superfamily rank to solve the nomenclatural problem resulting from the introduction of glypheid lobsters into Astacidea. Such organization at superfamily level, supported by the phylogeny of AMATI et al. (2004; Fig. 1B), was added to GLAESSNER’S (1969) classification and Erymidae became a part of Erymoidea Van Straelen, 1925 (FELDMANN & TITUS 2006; FELDMANN & HAGGART 2007; VEGA et al. 2007; KARASAWA et al. 2008; CHARBONNIER et al. 2017).

In the first decade of 21st century, some contributions led to reconsider the traditional position of Erymidae along with other clawed lobsters within the same infraorder: Astacidea. Indeed, AHYONG (2006), followed by DE GRAVE et al. (2009), included Erymoidea within the infraorder Glypheidea Zittel, 1885. This classifica-



tion, supported by the results of the phylogenetic analyses on extant and fossil lobsters of KARASAWA et al. (2013; Fig. 1C), was retained by some following authors (SCHWEITZER et al. 2010; CHARBONNIER & GARASSINO 2012; CHARBONNIER et al. 2012a,b; FELDMANN et al. 2012, 2015; MARTÍNEZ-DÍAZ et al. 2017). But the morphological phylogenetic analysis of CHARBONNIER et al. (2015) on glypheid lobsters, clearly excluded Erymidae (represented by *Enoploclytia collignoni* Secrétan, 1964, *Eryma ventrosus* (Meyer, 1835), *Pustulina spinulata* (Secrétan, 1964)) from Glypheoidea (Fig. 1D). As the phylogenetic position of Erymidae remains uncertain, some authors have then chosen to not list taxonomic rank beyond superfamily level (VEGA et al. 2013; BRAVI et al. 2014; CHARBONNIER et al. 2014; HYŽNÝ et al. 2015; DEVILLEZ et al. 2016, 2017, 2018; DEVILLEZ & CHARBONNIER 2017).

## 1.2. What is Erymidae?

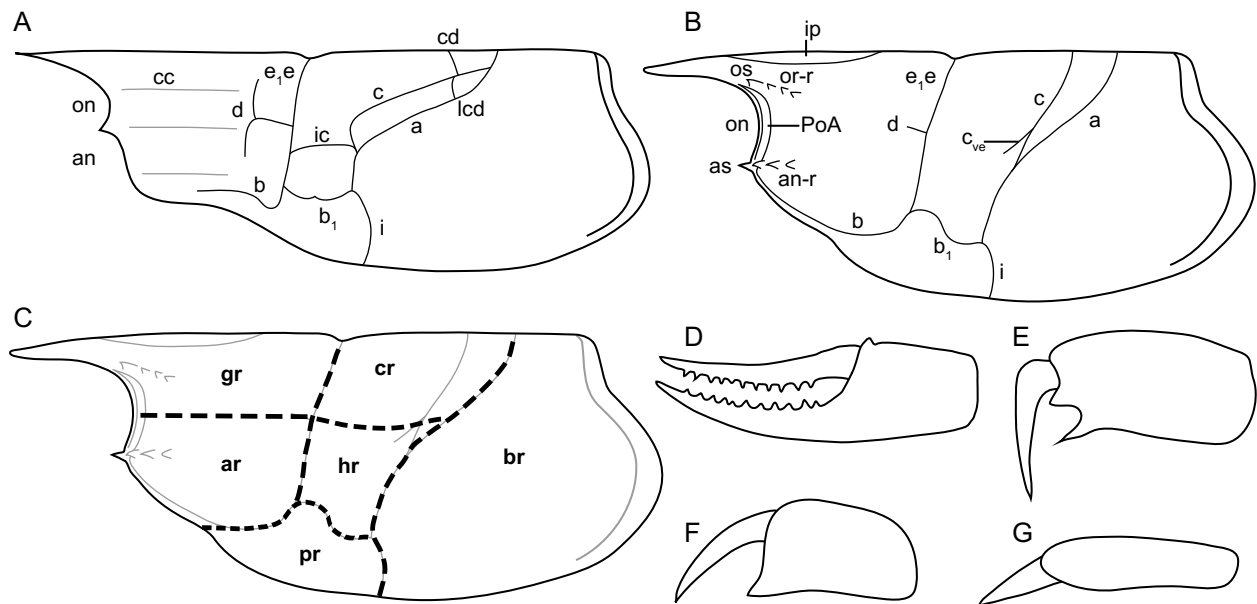
In addition to the unresolved phylogenetic affinities, the composition of Erymidae has been debated. Initially, VAN STRAELEN (1925) established the family to group *Eryma* and *Enoploclytia* (based on the presence of the intercalated plate), and also added (without real justification) *Olinaecaris* Van Straelen, 1925, *Palaeastacus* and *Pustulina*. Later, VAN STRAELEN (1928) added the Triassic genera *Aspidogaster* Assman, 1927, *Clytiopsis*, *Lissocardia* Meyer, 1851, *Piratella* Assman, 1927 and *Pseudopemphix*. While BEURLEN (1927) included *Clytia*, *Eryma*, *Erymastacus* Beurlen, 1928, *Enoploclytia* and *Stenodactylina* Beurlen, 1928 within Eryminae as a part of Paranephropsidae, GLAESSNER (1929) grouped all the previous genera (except *Olinaecaris*) and *Phlyctisoma* within Erymidae. BEURLEN & GLAESSNER (1930), FÖRSTER (1966), and GLAESSNER (1969) kept Beurlen's subfamilies with some rearrangements: (1) BEURLEN & GLAESSNER (1930) retired *Stenodactylina* from Eryminae; (2) FÖRSTER (1966) considered two genera within Clytiopsinae (*Clytiopsis*, *Paraclytiopsis* Oravec, 1962), and six genera within Eryminae (*Clytiella* Glaessner, 1931, *Enoploclytia*, *Eryma*, *Palaeastacus*, *Phlyctisoma* and *Protoclytiopsis* Birshtein, 1958); (3) GLAESSNER (1969) kept FÖRSTER's (1966) composition and reintegrated *Klytia* and *Stenodactylina* in Eryminae, while Clytiopsinae were extended with the reintroduction of *Lissocardia* and *Piratella*. After these works, the division of Erymidae in subfamilies was abandoned (e.g. FELDMANN & TITUS 2006; FELDMANN & HAGGART 2007), except by BEIKIRCH & FELDMANN (1980) and KLOMPMAKER & FRAAIJE (2011), who described and assigned *Oosterinkia* into Eryminae. DE GRAVE et al. (2009), followed by SCHWEITZER et al. (2010), kept almost the same genera as did GLAESSNER (1969) in Erymidae with consideration of more recent

**Fig. 1.** Cladistic relationships of erymid lobsters in different works. **A:** SCHRAM & DIXON (2004); **B:** AMATI et al. (2004); **C:** KARASAWA et al. (2013); **D:** CHARBONNIER et al. (2015); **E:** present work.

**Table 2.** List of the specimens used for coding. Species names in bold correspond to the type species of the genera.

Taxa	Stratigraphy	Specimens used to code the matrix	
		Type material	Additional specimens
<b><i>Chimaerastacus pacifluviatilis</i></b> (Amati et al., 2004)	Ladinian (Trias)	Holotype RTM 97.121.221; para-type RTM 97.121.15, 97.121.77, 97.121.435, 97.121.535	—
<b><i>Clytiopsis argentoratense</i></b> Bill, 1914	Carnian (Trias)	Type specimens lost	See BILL (1914) and GALL & FISCHER (1965)
<i>Dinochelus ausubeli</i> Ah Yong et al., 2010	Extant	Pictures of the holotype in original publication	—
<i>Enoploclytia collignoni</i> Secrétan, 1964	Campanian (Cretaceous)	Holotype MNHN.F.R03925; para-types MNHN.F.A33130, A33203	—
<b><i>Enoploclytia leachii</i></b> (Mantell, 1822)	Genomanian – Campanian (Cretaceous)	—	BMB 007766; NHMUK I.1977; NM 07125
<b><i>Enoplometopus pictus</i></b> A. Milne-Edwards, 1862	Extant	Holotype MNHN-IU-AS182	—
<i>Eryma compressum</i> Eudes-Deslongchamps, 1842	Toarcian – Bathonian (Jurassic)	Holotype NHMUK In.22917	GPIT/43/53 (Lectotype of <i>Eryma bedelium</i> ); NHMUK In.27131
<i>Eryma girodi</i> (Étallon, 1857)	Bathonian (Jurassic)	Syntype MNHN.F.A29783	MJSN Col. Del.475 (lectotype of <i>Eryma greppini</i> ); MJSN Col. Del.1 (paralectotype of <i>E. greppini</i> )
<b><i>Eryma modestiforme</i></b> (Schlotheim, 1822)	Kimmeridgian – Tithonian (Jurassic)	Holotype MFN 2236 P1383/2 MB.A.0252	MNHN.F.B13450
<i>Eryma sulcatum</i> Harbort, 1905	Hauterivian (Cretaceous)	Neotype SM B11437	—
<i>Eryma ventrosom</i> (Meyer, 1835)	Callovian – Kimmeridgian (Jurassic)	Cast of the holotype MNHN.F.B12484	MNHN.F.A29468
<b><i>Glyphea regleyana</i></b> (Desmarest, 1822)	Bathonian – Oxfordian (Jurassic)	Neotype MNHN.F.A29512	MNHN.F.A29516
<i>Glypheopsis robusta</i> (Feldmann & McPherson, 1980)	Bajocian (Jurassic)	Cast of the holotype MNHN.F.R62042	—
<b><i>Hoploparia longimana</i></b> (Sowerby, 1826)	Albian (Cretaceous)	—	MNHN.F.B14166, B14167
<b><i>Lissocardia silesiaca</i></b> Meyer, 1851	Anisian (Trias)	Lectotype MFN 2236 P1384/8 MB.A.0936	Paralectotypes BGR x268, 269; see GARASSINO et al. (2000)
<b><i>Litogaster obtusa</i></b> (Meyer, 1844)	Anisian (Trias)	Holotype SMNS 4401/653	—
<b><i>Nephrops norvegicus</i></b> (Linnaeus, 1758)	Extant	—	MNHN-IU-AS212
<i>Palaeastacus uranusienis</i> Devillez & Charbonnier, 2019	Barremian (Cretaceous)	Holotype BAS KG.50.4	—
<i>Palaeastacus fuciformis</i> (Schlotheim, 1822)	Tithonian (Jurassic)	Holotype MFN 2236 P1383/8 MB.A.0251	SMNS Inv.-Nr.64521
<b><i>Palaeastacus sussexiensis</i></b> (Mantell, 1824)	Aptian – Turonian (Cretaceous)	Lectotype NHMUK 5601	BMB 007750 (lectotype of <i>Palaeastacus dixonii</i> )
<b><i>Pemphix sueurii</i></b> (Desmarest, 1817)	Anisian – Ladinian (Trias)	Holotype lost	MNHN.F.A59975, A59979, A59980, B07888
<b><i>Pseudopemphix alberti</i></b> (Meyer, 1840)	Anisian (Trias)	Holotype SMNS 22109	—
<i>Pustulina minuta</i> (Schlotheim, 1822)	Tithonian (Jurassic)	Holotype MFN 2236 P1383/5 MB.A.0254	BSPG AS VIII 78; MFN 2236 P1383/5 MB.A.1119; MNHN.F.B13444
<i>Pustulina perroni</i> (Étallon, 1861)	Oxfordian – Kimmeridgian (Jurassic)	Syntype MNHN.F.B12485	—
<b><i>Pustulina suevica</i></b> Quenstedt, 1857	Kimmeridgian (Jurassic)	—	SMNS Inv.-Nr.3682/1 (holotype of <i>Eryma fraasi</i> )
<i>Pustulina tuberculata</i> (Bell, 1863)	Albian (Cretaceous)	Lectotype SM B22368; paralectotype SM B22369, B22370	—
<i>Stenodactylina australis</i> (Secrétan, 1964)	Tithonian (Jurassic)	Holotype MNHN.F.R03972	MNHN.F.A33228
<i>Stenodactylina lagardettei</i> (Hyžný et al., 2015)	Aalenian (Jurassic)	Holotype PF Aal 346	MNHL 20 103064
<i>Stenopus spinosus</i> Risso, 1826	Extant	—	MNHN-IU-Na3566, Na3567, Na3587, Na3588, Na10437
<b><i>Tethysastacus tithonius</i></b> (Van Straelen, 1936)	Valanginian (Cretaceous)	Holotype MNHN.F.J03351	—
<b><i>Uncina posidoniae</i></b> Quenstedt, 1851	Toarcian (Jurassic)	—	SMNS 23327, 29150





**Fig. 2.** Anatomical terminology. **A:** carapace grooves in glypheid lobster; **B:** carapace grooves in erymid lobster; **C:** delimitation of the carapace regions in lobsters; **D:** true chelate pereiopod extremity; **E–F:** pseudochelate pereiopod extremities: in glypheid lobster (**E**), and in enoplometopid lobster (**F**); **G:** achelate pereiopod extremity. — Line drawings: J. Devillez. — **Abbreviations:** a – branchiocardiac groove; an – antennal notch; an-r – antennal row; ar – antennal region; as – antennal spine; b – antennal groove; br – banchial region; b<sub>1</sub> – hepatic groove; c – postcervical groove; c<sub>ve</sub> – ventral extension of postcervical groove; cc – cephalic carina; cd – cardiac groove; cr – cardiac region; d – gastro-orbital groove; e<sub>1</sub>e – cervical groove; gr – gastric region; hr – hepatic region; i – inferior groove; ic – intercervical groove; ip – intercalated plate; lcd – laterocardiac groove; on – orbital notch; or-r – orbital row; os – orbital spine; PoA – post-orbital area; pr – pterygostomial region.

contributions: they added *Galicia* Garassino & Krobicki, 2002, they followed FÖRSTER'S (1967) opinion considering *Lissocardia* and *Piratella* to be synonyms, they considered *Erymastacus* and *Klytia* to be synonyms of *Eryma*, and, following SCHWEIGERT et al. (2000), they considered *Phlyctisoma* to be synonym of *Pustulina*. FELDMANN et al. (2012), based on the presence/absence of the intercalated plate, distinguished two families: Clytiopsidae, lacking in intercalated plate (*Clytiella*, *Clytiopsis*, *Galicia*, *Koryncheiros* Feldmann, Schweitzer, Hu, Zhang, Zhou, Xie, Huang & Wen, 2012, *Lissocardia*, *Paraclytiopsis*, *Protoclytiopsis*) and Erymidae, with an intercalated plate (*Enoplodytia*, *Eryma*, *Palaeastacus*, *Pustulina*, *Stenodactylina*). This separation was supported by the phylogenetic analyses of KARASAWA et al. (2013) and maintained by FELDMANN et al. (2015). However, Clytiopsidae were moved to Glypheoidea while Erymidae were maintained in Erymoidea and benefited from the reintegration of *Galicia*, *Olinaecaris* and *Oosterinkia*. Later, a review of Early Cretaceous erymid lobsters led DEVILLEZ et al. (2016) to erect *Tethysastacus*, and to include it in Erymidae based on the presence of an intercalated plate. Recently, DEVILLEZ & CHARBONNIER (2017) recognized *Galicia* and *Protoclytiopsis* to be junior synonyms of *Eryma*.

### 1.3. New hypothesis and aims of the study

Phylogenetic results of SCHRAM & DIXON (2004) suggested to reunite Erymidae and Enoplometopidae Saint

Laurent, 1988 into the same clade: Erymida (Fig. 1A). Indeed, they reported the presence of a structure interpreted as an intercalated plate on the extant *Enoplometopus* A. Milne-Edwards, 1862. This morphological feature is considered to be unique among Decapoda (FELDMANN et al. 2012) and could link these reef lobsters to erymids. If this link is verified, *Enoplometopus* would be a relict form of erymid and constitutes a new case of “living fossil”, like the the lobster *Neoglypheia* Forest & Saint Laurent, 1975.

Finally, considering the contribution of SCHRAM & DIXON (2004) and the recent phylogenetic analyses that questioned the relationships between Erymidae and other fossil and extant lobsters, the first purpose of this work is to clarify the systematic position of Erymidae and their possible links with supposed closely related taxa such as astacidean, enoplometopid, glypheidean and pemphicid lobsters. Additionally, as there is no clear consensus on the genera that should be considered as erymids, this work also aims to delimit Erymidae. Therefore this will allow to explore the internal relationships of the group.

## 2. Material and methods

The present phylogenetic analysis is based mostly on data derived from recent reviews on erymid lobsters of HYŽNÝ et al. (2015), DEVILLEZ et al. (2016), DEVILLEZ & CHARBONNIER (2017) and DEVILLEZ et al. (2017), which provided new synthesis with taxonomic treatment of

most of erymid genera *sensu* FELDMANN et al. (2015), and some of the species used in this work. The anatomical terminology used in this work is presented in Fig. 2.

## 2.1. Taxonomic sampling

The ingroup members are the erymid lobsters, which some authors suggested to have close relationships with glypheids while other considered them to be close to actual clawed lobsters. As a consequence, we include in our sampling taxa representing some of the families previously included within Glypheidea by CHARBONNIER et al. (2015), several fossil and extant clawed lobsters recognized to be Astacidea according to FELDMANN et al. (2015) and we also include fossil taxa of erratic systematic position, which have sometimes been considered as erymid lobsters (e.g., *Clytiopsis*, *Lissocardia*).

The outgroup consists of the stenopodid shrimp *Stenopus spinosus* Risso, 1826 because Stenopodidea Claus, 1872 are clearly outside the considered ingroup and phylogenetically distant from the considered sampling (SCHOLTZ & RICHTER 1995; DIXON et al. 2003; AHYONG & O'MEALLY 2004; SCHRAM & DIXON 2004; BRACKEN et al. 2009). This allows us to test the relations between erymid, glypheidean and astacidean lobsters at a large scale.

A total of 33 species are considered in this study (Table 2), encompassing 27 fossil species included within eight families recognized prior to this work (Chimaerastacidae, Clytiopsidae, Erymidae, Glypheidae, Litogastridae, Nephropidae, Pemphicidae, Uncinidae) and six extant species included within four families (Astacidae: *Astacus astacus* (Linnaeus, 1758); Enoplometopidae: *Enoplometopus pictus* A. Milne-Edwards, 1862; Nephropidae: *Dinochelus ausubeli* Ah Yong, Chan & Bouchet, 2010, *Homarus gammarus* (Linnaeus, 1758), *Nephrops norvegicus* (Linnaeus, 1758); Stenopodidae: *Stenopus spinosus*, the outgroup taxon).

As far as possible we have examined type specimens in order to ensure the accuracy of names applied to terminal taxa. Most of the genera are coded exclusively based upon their type species to ensure the stability of the inferred classification and to work with a representative sampling. As a consequence, all known genera of erymid lobsters were considered. The species *Clytiella spinifera* Glaessner, 1931, *Glaessnericaris macrochela* Garassino & Teruzzi, 1993 and *Paraclytiopsis hungaricus* Oravec, 1962 were excluded from the analysis because of the poor state of preservation of the carapace and/or the incompleteness of the type specimens, which does not allow a serious coding of the species. Similarly, Platychelidae was not considered herein due to the poor preservation of the carapace of the holotype of *Platychela trauthi* Glaessner, 1931. Furthermore, considering the broad triangular rostrum, the presence of oblique orbital carina, the carapace groove pattern (absence of intercalated plate, probable presence of gastro-orbital groove, deep cervical and branchiocardiac grooves, almost straight branchiocardiac

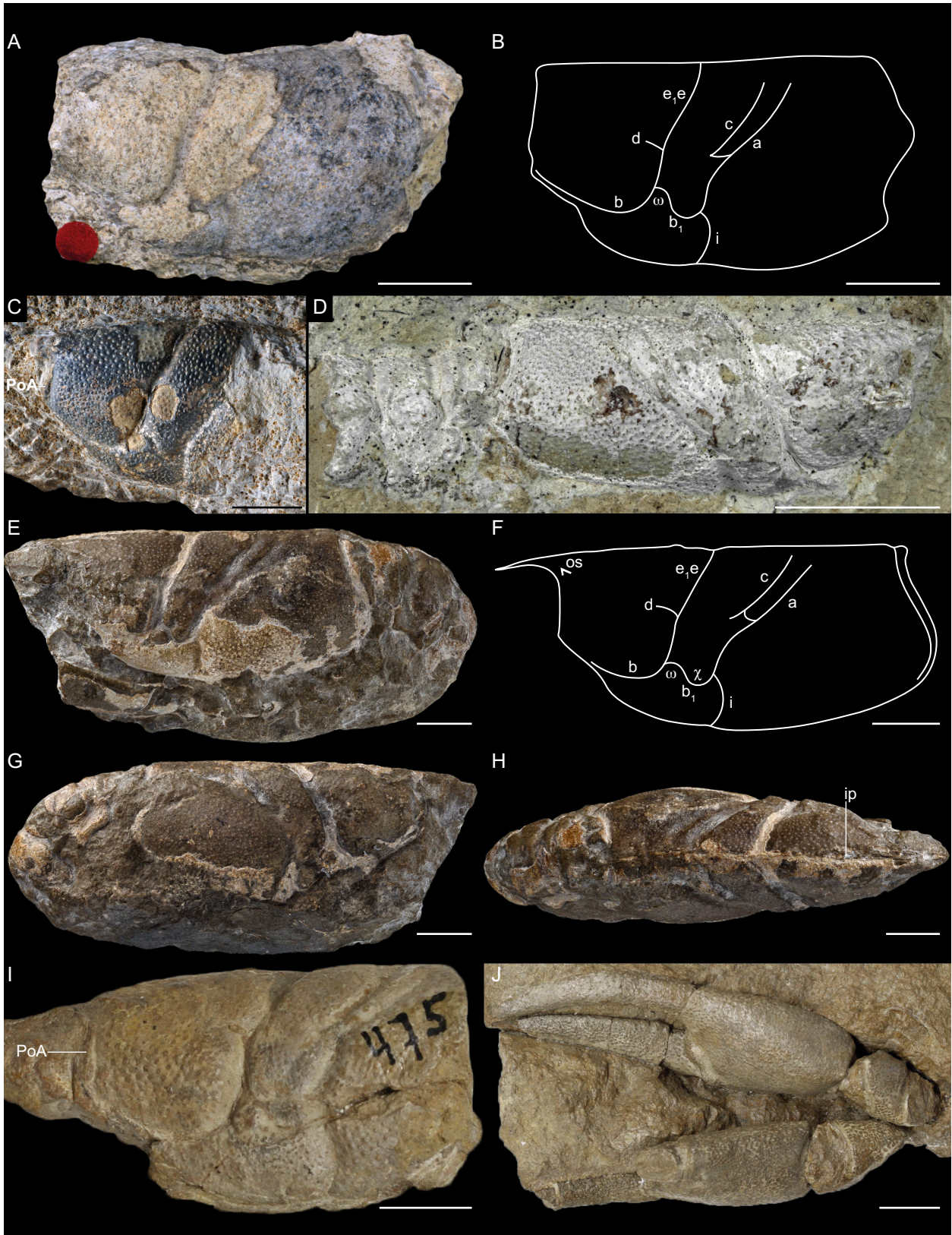
groove) and the shape of pleonal somites and pleura, we consider *Oosterinkia* as a probable synonym of *Clytiopsis*. *Oolinaecaris*, only known by a fragment of carapace, presents an elongated curved rostrum, a median carina above the cephalic region and no intercalated plate. We do not believe this genus to be an erymid lobster and follow SCHWEITZER et al. (2010) considering it as Incertae sedis, so it is not considered in this work.

We included some Jurassic erymid species that have not been reviewed recently. We propose a review for two of them: *Eryma bedeltum* (Quenstedt, 1857) and *E. greppini* (Opperl, 1861). Careful examination of the holotype of *E. compressum* Eudes-Deslongchamps, 1842 (Bathonian, France) and of the lectotype of *E. bedeltum* (Bajocian, Germany) revealed strong similarities (Fig. 3A–D). Both have: a wide, deep and slightly inclined cervical groove; a short and shallow gastro-orbital groove; a slightly curved postcervical groove; a shallow junction extending from the branchiocardiac groove to the ventral extremity of the postcervical groove at carapace mid-height; a deep and sinuous hepatic groove; a slightly inflated attachment site of mandibular muscle; a dense ornamentation, made of fine tubercles preceded by shallow crescent-shaped depressions. These two species share the same groove pattern and ornamentation. Considering these elements, we conclude that *E. bedeltum* is a junior synonym of *E. compressum*.

The Bathonian species *E. girodi* (Étallon, 1857) and *E. greppini* share strong affinities (Fig. 3E–J). Both have an inclined cervical groove delimiting a wide cephalic region. They also have wide and deep postcervical and branchiocardiac grooves, slightly curved and not joined to the dorsal midline. Moreover, the postcervical groove has a deep ventral extension. Their attachment sites of the mandibular muscle and of the adductor testis muscle are rounded and inflated. Both species have also the same ornamentation: small tubercles preceded by shallow depressions and a pair of dorsal domes in front of the junction between the cervical groove and the dorsal midline. These domes were highlighted and considered to be taxonomically significant by CHARBONNIER et al. (2014). Therefore, considering the previous arguments, we consider *E. greppini* to be a junior synonym of *E. girodi*.

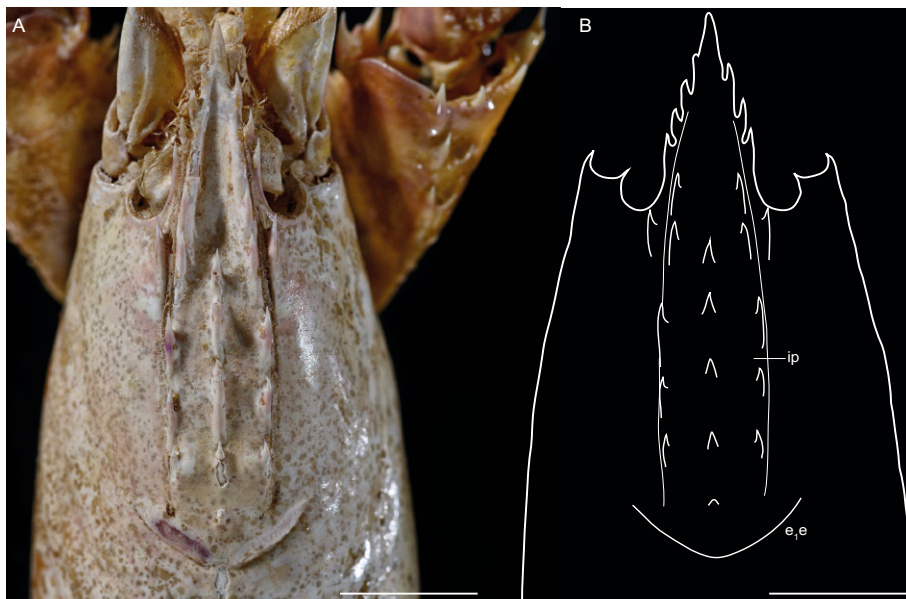
## 2.2. Morphological data

Morphological terms follow the descriptive terminology used in DEVILLEZ et al. (2016) (Fig. 2). For the fossil species, most of the diagnostic characters are mainly located on the carapace. The pereopods and the pleonal somites have important characters but usually are not sufficiently preserved to be used systematically. The cephalothoracic grooves and their mutual connections are the most appropriate source of characters with which to distinguish the erymid genera. So, most of the coded characters concern the carapace groove pattern. The carapace ornamentation appears to be important only at specific level.



**Fig. 3.** *Eryma compressum* Eudes-Deslongchamps, 1842 and *Eryma girodi* (Étallon, 1857). **A–D:** *Eryma compressum*: holotype NHMUK In.22917 (Jurassic, France): lateral view (A), and line drawing (B); lectotype GPIT/43/53–5 of *E. bedeltum* Quenstedt, 1857 (Jurassic, Germany) (C); specimen NHMUK In.27131 (Jurassic, United Kingdom) (D); **E–J:** *Eryma girodi*: syntype MNHN.F.A29783 (Jurassic, France): left lateral view (E), line drawing of the carapace (F), and dorsal view (H); lectotype MJSN Col.Del.475 of *Eryma greppini* Oppel, 1861 (Jurassic, France) (I), and paralectotype MJSN Col.Del.1 (J). — Photographs: J. Devillez (A, C, D), L. Cazes (E, G, H), D. Becker (I, J). Line drawings: J. Devillez. — Scale bars: 10 mm. — **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; ip – intercalated plate; os – orbital spine; PoA – post-orbital area; χ – attachment site of adductor testis muscle; ω – attachment site of mandibular muscle.





**Fig. 4.** *Enoplometopus pictus* A. Milne-Edwards, 1862 (holotype MNHN-IU-AS182; island of Réunion). **A:** dorsal view of the cephalic region; **B:** line drawing. — Photograph: L. Cazes. Line drawing: J. Devillez. — Scale bars: 10 mm. — **Abbreviations:** e<sub>1</sub>e – cervical groove; ip – intercalated plate.

Following SCHRAM & DIXON (2004), CHARBONNIER et al. (2013) and CHARBONNIER et al. (2015), we did not code characters that may correspond to intraspecific variations such as shape of P1 chelae. Due to the typically poor preservation of fossil crustaceans, delicate morphological features (e.g. antennae, gills, pleopods) were also excluded from the character list.

### 2.3. Phylogenetic analysis and character mapping

The data matrix comprises 35 characters and 33 taxa with *Stenopus spinosus* as outgroup. Wherever appropriate, we combined characters into multistate features to minimize dependence between characters such that 12 were multistate and 23 were binary. The multistate characters were analysed as unordered. We assigned equal weights for all characters. The morphological dataset was analysed using a parsimony method. Analyses were carried out with a heuristic search in PAUP\* 4.0b10 (SWOFFORD 2002) using random stepwise addition with the bisection reconnection (TBR) permutation algorithm and with 1000 replicates.

Trees were examined and characters optimized with Mesquite version 3.2 (MADDISON & MADDISON 2017). If inference for a character on the consensus tree provided several character distributions (resulting in an ambiguous state for some nodes), all optimizations were considered and one selected based upon biological constraints.

### 2.4. Depositories abbreviations

**BAS** – British Antarctic Survey, Cambridge (United Kingdom); **BGR** – Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin (Germany); **BM** – Booth Museum of Natural History, Brighton (United Kingdom); **BSPG** – Bayerische Staatssammlung für

Paläontologie und Geologie, München (Germany); **MFN** – Museum für Naturkunde, Berlin (Germany); **MHNL** – Musée des Confluences, Lyon (France); **MJSN** – Musée jurassien des sciences naturelles, Porrentruy (Switzerland); **MNHN** – Muséum national d’Histoire naturelle, Paris (France); **NHMUK** – Natural History Museum, London (United Kingdom); **NM** – Národní Muzeum, Prague (Czech Republic); **NMCR** – National Museum of the Philippines, Manila (Philippines); **PF** – Musée Pierres Folles, Saint-Jean-des-Vignes (France); **SM** – Sedgwick Museum of Earth Sciences, Cambridge (United Kingdom); **SMNS** – Staatliches Museum für Naturkunde, Stuttgart (Germany).

## 3. Results

### 3.1. List of characters

A total of 35 morphological characters were selected and deemed potentially phylogenetically informative and scorable amongst erymid, glypheidean and astacidean lobsters. Most characters are derived from grooves on the cephalothorax, which are surveyed in Fig. 2A–C. Characters and their states are given in the following list and the data matrix in Table 3.

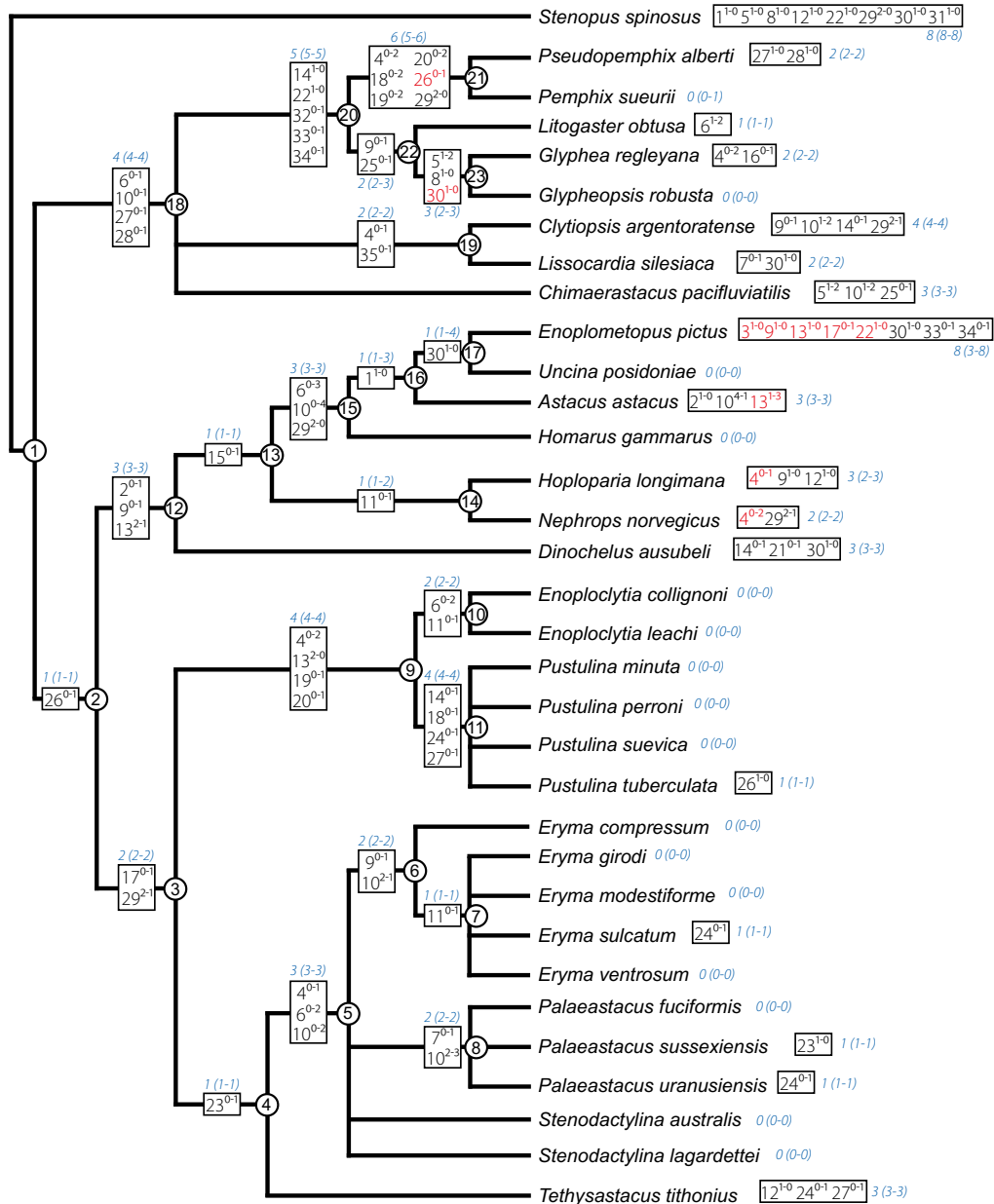
- 1 **Dorsal midline:** entire (0); sutured (1).
- 2 **Cervical groove (e<sub>1</sub>e), extension:** cross entirely the cephalic region (0); interrupted in gastric region (1).
- 3 **Cervical groove (e<sub>1</sub>e), interruption:** ventral, joined to dorsal midline and not to antennal groove (0); dorsal, joined to antennal groove and not to dorsal midline (1).
- 4 **Gastro-orbital groove (d):** absent (0); simple (1); bifurcated (2).
- 5 **Antennal groove (b):** absent (0); concave (1); sinuous (2).
- 6 **Hepatic groove (b<sub>1</sub>):** concave (0); biconcave (1); concavo-convex (2); absent (3).
- 7 **Postcervical groove (c), crossing hepatic region:** no (0); yes (1).

Table 3. Character matrix used in the analysis.

Character:	0 0 0 0 0 0 0 0 0 1	1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 3	3 3 3 3 3
Taxon:	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5
<i>Astacus astacus</i>	0 0 – 0 1 3 0 1 1 1	0 1 3 0 1 0 0 0 0 0	0 1 0 0 0 1 0 0 0 1	1 0 0 0 0
<i>Chimaerastacus pacifluviatilis</i>	1 0 – 0 2 1 0 1 0 2	0 1 2 0 0 0 0 0 0 0	0 1 0 0 0 1 ? 1 1 ? 1	1 0 0 0 0
<i>Clytiopsis argentoratense</i>	1 0 – 1 1 1 0 1 2 2	0 1 2 1 0 0 0 0 0 0	0 1 0 0 0 0 1 1 1 1	1 0 0 0 1
<i>Dinochelus ausubeli</i>	1 1 1 0 1 0 0 1 1 0	0 1 1 1 0 0 0 0 0 0	1 1 0 0 0 1 0 0 2 0	1 0 0 0 0
<i>Enoploclytia collignoni</i>	1 0 – 2 1 2 0 1 0 0	1 1 0 0 0 0 1 0 1 1	0 1 0 0 0 1 0 0 1 1	? 0 0 ? ?
<i>Enoploclytia leachii</i>	1 0 – 2 1 2 0 1 0 0	1 1 0 0 0 0 1 0 1 1	0 1 0 0 0 1 0 0 1 1	1 0 0 0 0
<i>Enoplometopus pictus</i>	0 1 0 0 1 3 0 1 0 4	0 1 0 0 1 0 1 0 0 0	0 1 0 0 0 1 0 0 0 0	1 0 1 1 0
<i>Eryma compressum</i>	1 0 – 1 1 2 0 1 1 1	0 1 2 0 0 0 1 0 0 0	0 0 1 0 0 1 0 0 1 1	1 0 0 0 ?
<i>Eryma girodi</i>	1 0 – 1 1 2 0 1 1 1	1 1 2 0 0 0 1 0 0 0	0 1 1 0 0 1 0 0 1 1	? 0 ? ? ?
<i>Eryma modestiforme</i>	1 0 – 1 1 2 0 1 1 1	1 1 2 0 0 0 1 0 0 0	0 1 1 0 0 1 0 0 1 1	1 0 0 0 0
<i>Eryma sulcatum</i>	1 0 – 1 1 2 0 1 1 1	1 1 2 0 0 0 1 0 0 0	0 1 1 1 0 1 0 0 1 1	? 0 ? ? ?
<i>Eryma ventrosum</i>	1 0 – 1 1 2 0 1 1 1	1 1 2 0 0 0 1 0 0 0	0 1 1 0 0 1 0 0 1 1	1 0 0 0 ?
<i>Glyphea regleyana</i>	1 0 – 2 2 1 0 0 3 1	0 1 2 1 0 1 0 0 0 0	0 0 0 0 1 0 1 1 2 0	1 1 1 1 0
<i>Glypheopsis robusta</i>	1 0 – 0 2 1 0 0 3 1	0 1 2 1 0 0 0 0 0 0	0 0 0 0 1 0 1 1 2 0	? 1 1 1 0
<i>Homarus gammarus</i>	1 1 1 0 1 3 0 1 1 4	0 1 1 0 1 0 0 0 0 0	0 1 0 0 0 1 0 0 0 1	1 0 0 0 0
<i>Hoploparia longimana</i>	1 1 1 1 1 0 0 1 – 0	1 0 – 0 1 0 0 0 0 0 0	0 1 0 0 0 1 0 0 2 1	1 0 ? ? ?
<i>Lissocardia silesiaca</i>	1 – – 1 1 1 1 1 1 1	0 1 2 0 0 0 0 0 0 0	0 1 0 0 0 0 1 1 2 0	1 0 0 0 1
<i>Litogaster obtusa</i>	1 – – 0 1 2 0 1 1 1	0 1 2 1 0 0 0 0 0 0	? ? 0 0 1 0 1 1 ? ?	? ? ? ? ?
<i>Nephrops norvegicus</i>	1 1 1 2 1 0 0 1 1 0	1 1 1 0 1 0 0 0 0 0	0 1 0 0 0 1 0 0 1 1	1 0 0 0 0
<i>Palaeastacus foersteri</i>	1 – – 1 1 2 1 1 0 3	– 1 2 0 0 0 1 0 0 0	0 1 1 1 0 1 ? 0 1 1	1 0 0 ? ?
<i>Palaeastacus fuciformis</i>	1 – – 1 1 2 1 1 0 3	– 1 2 0 0 0 1 ? ? ?	0 1 1 0 0 1 0 0 1 1	1 0 0 0 0
<i>Palaeastacus sussexiensis</i>	1 – – 1 1 2 1 1 0 3	– 1 2 0 0 0 1 0 0 0	0 1 0 0 0 1 0 0 1 1	1 0 0 0 ?
<i>Pemphix sueurii</i>	1 – – 2 1 1 0 1 1 1	0 1 2 1 0 0 0 2 2 2	0 0 0 0 0 1 1 1 0 1	1 1 1 1 1
<i>Pseudopemphix alberti</i>	1 – – 2 1 1 0 1 1 1	0 1 2 1 0 0 0 2 2 2	0 0 0 0 0 ? 0 0 0 1	1 1 1 1 1
<i>Pustulina minuta</i>	1 – – 2 1 0 0 1 0 0	0 1 0 1 0 0 1 ? ? 1	0 1 0 ? 0 ? 1 0 1 1	1 0 0 0 0
<i>Pustulina perroni</i>	1 – – 2 1 0 0 1 0 0	0 1 0 1 0 0 1 1 1 1	0 1 0 1 0 1 1 0 1 1	? 0 ? ? ?
<i>Pustulina suevica</i>	1 – – 2 1 0 0 1 0 0	0 ? ? ? 0 ? 1 ? ? ?	0 1 0 1 0 ? ? 0 ? ?	? 0 0 0 ?
<i>Pustulina tuberculata</i>	1 – – 2 1 0 0 1 0 0	0 1 0 1 0 0 1 1 1 1	0 1 0 1 0 0 1 0 1 1	? 0 ? ? ?
<i>Stenodactylina australis</i>	1 – – 1 1 2 0 1 0 2	– 1 2 0 0 0 1 0 0 0	0 1 1 0 0 0 0 0 1 1	? ? ? ? ?
<i>Stenodactylina lagardettei</i>	1 – – 1 1 2 0 1 0 2	– 1 2 0 0 0 1 0 0 0	0 1 ? 0 0 ? 0 0 ? ?	? 0 ? ? ?
<i>Stenopus spinosus</i>	0 – – 0 0 0 0 0 – 0	0 0 – 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0
<i>Tethysastacus tithonius</i>	1 – – 0 1 0 0 1 – 0	0 0 – 0 0 0 1 0 0 0	0 1 1 1 0 1 1 0 ? ?	? ? ? ? ?
<i>Uncina posidoniae</i>	? ? ? 0 ? ? 0 1 ? ?	? ? ? 0 1 0 ? ? ? ?	0 ? 0 0 0 1 ? 0 0 0	1 0 0 0 0

- 8 Intercervical groove (ic): present (0); absent (1).
- 9 Junction between postcervical (c) and branchiocardiac (a) grooves: absent (0); present (1).
- 10 Postcervical groove (c), ventral extremity: joined to posterior extremity of hepatic groove (0); joined to branchiocardiac groove (1); interrupted in hepatic region, not joined to any other groove (2); joined to the middle of hepatic groove (3); joined to antennal groove (4).
- 11 Postcervical groove (c<sub>ve</sub>), ventral extension: absent (0); present (1).
- 12 Branchiocardiac groove (a): absent (0); present (1).
- 13 Branchiocardiac groove (a), ventral extremity: interrupted in branchial region (0); joined to postcervical groove (1); joined to posterior extremity of hepatic groove (2); joined to cervical groove (3).
- 14 Cardiac groove (cd): absent (0); present (1).
- 15 Inferior groove (i): present (0); absent (1).
- 16 Laterocardiac groove (lcd): absent (0); present (1).

- 17 Intercalated plate (ip): absent (0); present (1). — Careful examination of the holotype of *Enoplometopus pictus* and specimens of *E. occidentalis* (Randall, 1840) led us to observe a fusiform area delimited by two narrow grooves along the dorsal rows of spines. This structure is the “median plate” which was considered homologous to the erymid intercalated plate by SCHRAM & DIXON (2004) (Fig. 4). We noticed that these grooves do not meet anteriorly or posteriorly, while the intercalated plate is fully circumscribed in erymids. So, the homology between the two structures is speculative but, in order to test SCHRAM & DIXON’s (2004) hypothesis, we have chosen to code the intercalated plate as “present” in *Enoplometopus pictus*.
- 18 Cardiac region (cr): not inflated (0); slightly inflated (1); strongly inflated (2).
- 19 Hepatic region (hr): not inflated (0); slightly inflated (1); strongly inflated (2).



**Fig. 5.** Strict consensus tree (101 steps) of 273 most-parsimonious trees (101 steps) recovered from analysis. Node numbers indicated in white circles. Box at roots indicates hypothesized character state at root (black when unambiguous, red when ambiguous). Boxes at each node list characters supporting the node (synapomorphies), with indication of the character state change in superscript. Accordingly, the number of changes after optimization (minimum and maximum in parentheses) at each node is indicated in blue.

**20 Branchial region (br):** not inflated (0); slightly inflated (1); strongly inflated (2).  
**21 Orbital notch (on):** present (0); absent (1).  
**22 Antennal notch (an):** present (0); absent (1).  
**23 Post-orbital area (PoA), delimitation:** absent (0); present (1). — The forward extension of the antennal groove that posteriorly bounds the post-orbital area (Fig. 2B) was firstly reported by TAYLOR (1979: 28) and FELDMANN & TITUS (2006: 64). Recently, the complex structure of the anterior termination of the cephalic region observed in some representatives of *Eryma*, *Palaeastacus*, *Stenodactylina* and *Tethysastacus* was formally described by DEVILLEZ et al. (2016: 516).

**24 Cephalic region with:** straight dorsal margin (0); down-curved dorsal margin (1).  
**25 Dorso-ventral compression of cephalic region:** absent (0); present (1).  
**26 Antennal spine (as):** absent (0); present (1).  
**27 Orbital spine (os):** present (0); absent (1).  
**28 Cephalic carina (cc):** absent (0); present (1).  
**29 Relief at the basis of pleura:** none (0); bulge (1); carina (2).  
**30 Pleura, shape:** rounded (0); triangular (1).  
**31 Diaeresis:** absent (0); present (1).  
**32 Pereiopod 1:** chelate (0); pseudo-chelate (1). — Following FELDMANN et al. (2012) and CHARBONNIER et al. (2015), we consider to be “chelate” pereiopods

in which index and dactylus are of equal or nearly equal length, “pseudochelate” pereopods in which the occlusal surface is formed by a propodus with or without a distal spine on the ventral margin, and we consider to be “achelate” pereopods in which the dactylus extends from the distal margin of the propodus without occlusal surface (Fig. 2D–G).

**33 Pereiopod 2:** chelate (0); pseudochelate (1).

**34 Pereiopod 3:** chelate (0); pseudochelate (1).

**35 Pereiopod 4:** achelate (0); pseudochelate (1).

### 3.2. Description of the trees

The cladistic analysis resulted in 273 most-parsimonious trees of 101 steps (consistency index CI = 0.4752, retention index RI = 0.7350). Character changes are studied on the strict consensus tree of 101 steps (CI = 0.4752, RI = 0.7350). Character states and character-state changes at each node are given on the strict consensus tree (Fig. 5). The boxes at each node list characters supporting the node (synapomorphies; black when unambiguous, red when ambiguous), with indication of the character-state change in superscript. Ambiguous character 26 have been optimized following an accelerated transformation parsimony model (ACCTRAN). Ambiguous characters 3, 4, 9, 13, 17, 22 and 30 have been optimized following a delayed transformation parsimony model (DELTRAN). After optimization, number of changes at each node is indicated in italics, with minimum and maximum of changes in parentheses. Nodes and taxonomic distribution among suprageneric groups are reported on Fig. 6.

**Node 1** connects all the ingroup taxa.

**Node 2** (Astacidea) is supported by one unambiguous synapomorphy: the presence of an antennal spine (26<sup>1</sup>). This node connects lobsters that belong to Astacidea with the erymid lobsters and support their close relationships. This result is in opposition with those of AMATI et al. (2004) and KARASAWA et al. (2013) which supported close relationships between erymid lobsters and Pemphicidae, within Glypheidea. However, the recent analysis of CHARBONNIER et al. (2015) led to a new definition of Glypheidea which excludes the erymid lobsters. Our results concur with those of CHARBONNIER et al. (2015) and suggest that erymid lobsters are closer to astacidean than glypheidean lobsters. In conclusion, we included erymid lobsters within Astacidea.

**Node 3** (Erymoidea). All the erymid lobsters are connected to this node. They constitute the clade Erymoidea, supported by two unambiguous synapomorphies: the presence of an intercalated plate (17<sup>1</sup>) and the presence of a bulge at the basis of the pleura (29<sup>1</sup>). This clade is different from the Erymoidea *sensu* AMATI et al. (2004) and KARASAWA et al. (2013) which included Erymidae and Pemphicidae. However, the analysis performed by CHARBONNIER et al. (2015) and the present work do not support such a relationship. Indeed, our analyses clearly separate Erymidae from Glypheidea while Pemphicidae belongs

to this infra-order (see below). So, the clade, Erymoidea, groups only taxa included within Erymidae according to the most recent works (*Enoploclytia*, *Eryma*, *Palaeastacus*, *Pustulina*, *Stenodactylina*, *Tethysastacus*; DEVILLEZ et al. 2016, 2017; DEVILLEZ & CHARBONNIER 2017). Our analyses allow us to explore the relationships within this clade. At this node the erymid are split in two groups, detailed through the explanations of the following nodes. **Node 4** (Erymidae) is supported by one unambiguous synapomorphy: the presence of a delimited post-orbital area (23<sup>1</sup>). *Eryma* (Figs. 3, 7A–G), *Tethysastacus* (Fig. 7H), *Palaeastacus* (Fig. 8) and *Stenodactylina* (Fig. 9) are connected to this node. Our observations during the acquisition of morphological data on each taxa we coded shows that only the four genera previously cited exhibit this recently described character (DEVILLEZ et al. 2016). This result leads us to modify the systematic definition of Erymidae: this family is now restricted to erymid genera exhibiting a post-orbital area. Moreover, *Tethysastacus* is sister group of the clade uniting three other genera. It is then possible to distinguish two groups morphologically distinct within Erymidae: Tethysastacinae subfam.n. lacking in branchiocardiac groove and orbital spine (12<sup>0</sup>; 27<sup>1</sup>) and with a down-curved dorsal margin in cephalic region (24<sup>1</sup>), including only *Tethysastacus*; and Eryminae, including *Eryma*, *Palaeastacus* and *Stenodactylina* (detailed explanations in the following node).

**Node 5** (Eryminae) is supported by three unambiguous synapomorphies: the gastro-orbital groove is simple (4<sup>1</sup>); the hepatic groove is concavo-convex (6<sup>2</sup>); the ventral extremity of the postcervical groove is interrupted in hepatic region (10<sup>2</sup>). This node connects the species of *Eryma*, *Palaeastacus* and *Stenodactylina*. Contrary to other genera, *Stenodactylina* appears paraphyletic in the strict consensus tree. This could be the result of the incompleteness of the coded species (only carapace and P1 chelae are preserved) and/or the too restricted number of considered species. Unfortunately, the fossils of the selected species are the most complete among the genus. Indeed, the other species assigned to *Stenodactylina* are only known by isolated, sometimes incomplete, P1 chelae or carapaces (DEVILLEZ et al. 2016).

**Node 6** (*Eryma*; Figs. 3, 7A–G) is supported by two unambiguous synapomorphies: there is a junction between postcervical and branchiocardiac grooves (9<sup>1</sup>) and the postcervical groove is joined ventrally to the branchiocardiac groove (10<sup>1</sup>).

**Node 7**, within *Eryma*, is supported by one unambiguous synapomorphy: a ventral extension of the postcervical groove is present (11<sup>1</sup>). This morphological feature is common among *Eryma* (DEVILLEZ et al. 2016), but some species do not have it. So, this node appears because of the absence of ventral extension of the postcervical groove in *E. compressum*.

**Node 8** (*Palaeastacus*; Fig. 8) is supported by two unambiguous synapomorphies: the hepatic region is crossed by the postcervical groove (7<sup>1</sup>); the ventral extremity of the postcervical groove is joined to the middle of the hepatic groove (10<sup>3</sup>).

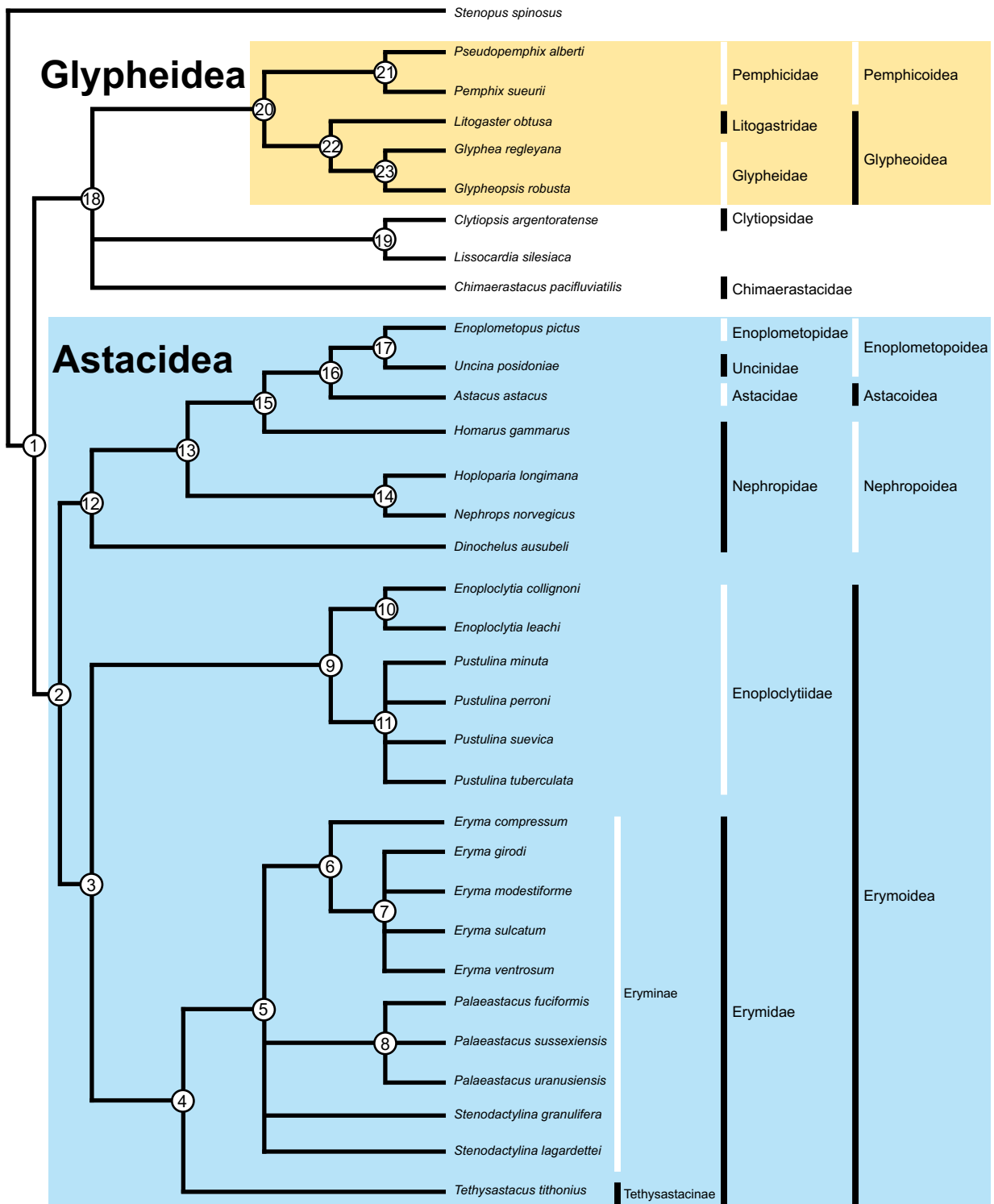


Fig. 6. Strict consensus tree with indication of node numbers (white circles) and subfamilies, families, superfamilies and infraorders.

**Node 9** (Enoploclytiidae) is supported by four unambiguous synapomorphies: a distal bifurcation of the gastro-orbital groove is present (4<sup>2</sup>); the ventral extremity of the branchiocardiac groove is interrupted in branchial region (13<sup>0</sup>); the hepatic and branchial regions are slightly inflated (19<sup>1</sup>; 20<sup>1</sup>). The clade is supported by a particular configuration of the grooves including a weakly developed branchiocardiac groove associated to a strong development of the gastro-orbital groove.

Moreover, these erymid lobsters do not have the post-orbital area. On this basis, this clade is erected as a new family, Enoploclytiidae fam.n., which includes two genera supported by nodes 9 and 10: *Enoploclytia* and *Pustulina*.

**Node 10** (*Enoploclytia*; Fig. 10) is supported by two unambiguous synapomorphies: the hepatic groove is concavo-convex (6<sup>2</sup>); a ventral extension of the postcervical groove is present (11<sup>1</sup>).



**Node 11** (*Pustulina*; Fig. 11) is supported by four unambiguous synapomorphies: the cardiac groove is present (14<sup>1</sup>); the cardiac region is slightly inflated (18<sup>1</sup>); the dorsal margin of the cephalic region is curved down (24<sup>1</sup>); the orbital spine is absent (27<sup>1</sup>).

**Node 12** (Nephropoidea + Astacoidea + Enoplometopoidea) is supported by three unambiguous synapomorphies: the cervical groove is interrupted in the gastric region (2<sup>1</sup>); there is a junction between postcervical and branchiocardiac grooves (9<sup>1</sup>); the ventral extremity of the branchiocardiac groove is joined to the postcervical groove (13<sup>1</sup>). This clade includes both extant lobsters (Fig. 12), freshwater crayfish and the fossil *Hoploparia longimana* Sowerby, 1826 (Fig. 13).

**Node 13** (Nephropidae + Astacidae + Uncinidae + Enoplometopidae) is supported by one unambiguous synapomorphy: the inferior groove is absent (15<sup>1</sup>). These taxa do not have inferior groove while it is well-marked in *Dinorchelus ausubeli* Ahyong, Chan & Bouchet, 2010 (Fig. 12A,B). In this lobster, the inferior groove extends almost to the ventral margin. So, the pterygostomial region is well circumscribed like in Erymoidea.

**Node 14** (*Nephrops* + *Hoploparia*) is supported by one unambiguous synapomorphy: a ventral extension of the postcervical groove is present (11<sup>1</sup>). *Nephrops norvegicus* and *Hoploparia longimana* are the only taxa with a ventral extension of their postcervical groove among the selected Astacoidea. However, the length of this extension differs between these species. That of *H. longimana* is strongly elongated while that of *N. norvegicus* is very short. We also noticed that the presence of such ventral extension is reported in most of the representatives of the erymid genus *Eryma* (see node 6). Moreover, the character 4 is ambiguous because of its different state in *Nephrops norvegicus* (gastro-orbital groove bifurcated: 4<sup>2</sup>) and *Hoploparia longimana* (gastro-orbital groove simple: 4<sup>1</sup>). ACCTRAN option implies to have the apparition of a simple gastro-orbital groove at node 14 (modification from 4<sup>0</sup> to 4<sup>1</sup>) and a modification of the gastro-orbital which is bifurcated in *N. norvegicus* (modification from 4<sup>1</sup> to 4<sup>2</sup>). DELTRAN option implies to report both modifications of character 4 to the terminal taxa *H. longimana* and *N. norvegicus* (modifications respectively from 4<sup>0</sup> to 4<sup>1</sup> and 4<sup>2</sup>). As the different states are reported on the two taxa, and in order to have clades supported by unambiguous synapomorphies as far as possible, we choose the DELTRAN option. In this analysis, *Hoploparia* and *Nephrops* are sister taxa. This is not exactly congruent with results of other morphology-based analyses including fossil and extant taxa that recognized *Hoploparia* to be sister taxon of *Homarus* among Nephropidae (TSHUDY & BABCOCK 1997; KARASAWA et al. 2013), or *Nephrops* to be sister taxon of *Homarus* (AMATI et al. 2004).

**Node 15** (*Homarus* + *Astacus* + Enoplometopoidea) is supported by three unambiguous synapomorphies: the hepatic groove is absent (6<sup>3</sup>); the ventral extremity of the postcervical groove is joined to the antennal groove (10<sup>4</sup>); there is no relief at the basis of pleura (29<sup>0</sup>). Our analysis results in the paraphyly of the family Nephropi-

dae, which includes *Homarus* but not *Astacus* (Astacidae), *Enoplometopus* (Enoplometopidae) and *Uncina* (Uncinidae). This does not correspond to results of most of recent works based on morphological or molecular characters. Indeed, studies of SCHRAM (2001), AMATI et al. (2004), PORTER et al. (2005), KARASAWA et al. (2013) and BRACKEN-GRISSOM et al. (2014) clearly demonstrated that *Astacus* and *Enoplometopus* belongs to two clades, each distinct from Nephropidae. The difference in our results is explained by the fact that our study is mainly focused on erymid lobsters. So, the characters we selected and their coding are mainly suitable to explore in detail the phylogenetic relationships of erymid lobsters and are not optimal for exploring the phylogeny of other lobster groups. Moreover, we have chosen to integrate only a few astacid, enoplometopid, nephropid and uncinid taxa.

**Node 16** (*Astacus* + Enoplometopoidea) is supported by one unambiguous synapomorphy: the dorsal midline is absent (1<sup>0</sup>). The superfamilies connected to this node are Astacoidea, including the freshwater crayfish, and Enoplometopoidea, including *Enoplometopus pictus* showing weakly marked carapace grooves and a structure recalling the intercalated plate of erymids (Fig. 4; SCHRAM & DIXON 2004). Our analysis clearly demonstrates that the presence of a potential intercalated plate in the enoplometopid lobsters is not sufficient to group them with the erymid lobsters in a same clade as suggested by SCHRAM & DIXON (2004), who included both of them in the clade Erymida. The character 13 (the connexion of the ventral extremity of the branchiocardiac groove) is ambiguous. It could be optimized on node 16 as a synapomorphy of Astacoidea + Enoplometopoidea from state 1 (branchiocardiac groove joined ventrally to the postcervical groove) to state 0 (branchiocardiac groove interrupted in branchial region), then another transformation of the character is applied from state 0 to state 3 (branchiocardiac groove joined ventrally to the cervical groove) in *Astacus astacus* (ACCTRAN option). The character 13 could also be optimized at the terminal taxa *Astacus astacus*, with a transformation from state 1 to state 3, and *E. pictus*, with a transformation from state 1 to state 0 (DELTRAN option). Because the state of this character has not been clearly observed in *Uncina posidoniae*, we choose DELTRAN option to report the transformation of this character to terminal taxa in which it has been observed.

**Node 17** (Enoplometopoidea) is supported by one unambiguous synapomorphy: the pleura are rounded (30<sup>0</sup>). Despite the several non-observed characters resulting in the bad preservation of the cephalothorax of the specimens of *Uncina posidoniae*, this taxon is sister to *Enoplometopus pictus* in our analyses. Considered for long as a unique family of the infraorder Uncinidea Beurlen, 1930 because it was thought to have massive pereopods 3 (BEURLEN 1930; BALSS 1957; GLAESSNER 1969; KARASAWA 2002). However, SCHWEIGERT et al. (2003) clearly established that it is the pereopod 1 which is massive instead of pereopod 3. So, the Uncinidae were moved to Astacoidea. AHYONG (2006) found the uncinids to be

closely related to the Enoplometopidae. The results of the recent phylogenetic analysis of KARASAWA et al. (2013) and of the present work support the clade including both enoplometopid and uncinid lobsters corresponding to Enoplometopidea. The characters 3 (transformation from state 1 to 0), 9 (transformation from state 1 to 0), 17 (transformation from state 0 to 1) and 22 (transformation from state 1 to 0) were optimized according to DELTRAN option to report these transformations in the terminal taxon *E. pictus* because they have been observed and coded only in this taxon. Indeed, the lack of preservation of the cephalothorax in *U. posidoniae* does not allow to clearly establish the state of these characters. ACCTRAN option implies an optimization of character 3 on node 16, and of characters 3, 17 and 22 on node 17.

**Node 18** (Glypheidea + *Clytiopsis* + *Lissocardia* + *Chimaerastacus*; Figs. 14, 15) is supported by four unambiguous synapomorphies: the hepatic groove is biconcave (6<sup>1</sup>); the ventral extremity of the postcervical groove being joined to the branchiocardiac groove (10<sup>1</sup>); the orbital spine is absent (27<sup>1</sup>); there are carina in cephalic region (28<sup>1</sup>). This node supporting *Clytiopsis*, *Lissocardia* and Chimaerastacidae (including only *Chimaerastacus pacifluviatilis* Amati, Feldmann & Zonneveld, 2004; Fig. 14D–F) suggests close relationships with Glypheidea, according to KARASAWA et al. (2013) and CHARBONNIER et al. (2015, only for *Chimaerastacus*). The position of *Clytiopsis* and *Lissocardia* will be discussed in description of the following node, so, we focus this discussion on *Chimaerastacus*. While KARASAWA et al. (2013) includes *Chimaerastacus* into Glypheidea, CHARBONNIER et al. (2015) excluded it, based on the chelate pereopods 1–3. In the analysis of CHARBONNIER et al. (2015) the absence of the antennal spine was also an unambiguous synapomorphy of the clade and the presence of cephalic carina was included within the synapomorphies, but was ambiguous. Our analysis supports the close relationship between Glypheidea and *Chimaerastacus* based on the shape of the hepatic groove (biconcave) characteristic of this clade. To conclude, we follow CHARBONNIER et al. (2015) to not extend Glypheidea to *Chimaerastacus* because of its chelate pereopods 1–3, absent in glypheidean lobsters.

**Node 19** (*Clytiopsis* + *Lissocardia*) is supported by two unambiguous synapomorphies: the simple gastro-orbital groove (4<sup>1</sup>); the pseudochelate pereopod 4 (35<sup>1</sup>). Sometimes considered as erymids in the literature (VAN STRAELLEN, 1928; FÖRSTER 1966, 1967; ETTER 2004; FELDMANN & HAGGART 2007; DE GRAVE et al. 2009; SCHWEITZER et al. 2010), the systematic positions of *Clytiopsis* and *Lissocardia* remain uncertain. In AMATI et al. (2004) *Clytiopsis* was sister to a clade including Erymidae and Pemphicidae. Such a relationship was not supported in analyses of KARASAWA et al. (2013) and CHARBONNIER et al. (2015). The first authors recognized *Clytiopsis* to be sister of a clade including *Chimaerastacus* and glypheid lobsters, so they moved this genus into Glypheidea. *Lissocardia* was also considered as member of Glypheidea by KARASAWA et al. (2013) and was assigned to a new family: Litogastridae Karasawa, Schweitzer & Feldmann, 2013, different

from Erymidae and Pemphicidae because of the presence of cephalic carinae. However, they recognized *Lissocardia* to be unusual because of its chelate pereopods 1–3. The work of CHARBONNIER et al. (2015) clearly rejects the assignment of *Clytiopsis* and *Lissocardia* to Glypheidea because they do not share any synapomorphies with the clade Glypheidea + *Chimaerastacus*. Our results indicate that *Clytiopsis* and *Lissocardia* are not erymid lobsters as suggested in some previous works. Indeed, they share three synapomorphies with *Chimaerastacus* and Glypheidea: a biconcave hepatic groove, the absence of an antennal spine and the presence of cephalic carina. Although *Clytiopsis* and *Lissocardia* are closely related to glypheid and pemphicid lobsters; we do not consider these taxa to be members of Glypheidea, for the same reason we exclude *Chimaerastacus*: the chelate pereopods 1–3.

The transformations in the following nodes will not be fully detailed and compared with previous works because they concern the relations among the infraorder Glypheidea, which are beyond the purposes of this work.

**Node 20** (Pemphicoidea + Glypheidea) is supported by five unambiguous synapomorphies also found in the study of CHARBONNIER et al. (2015): the absence of cardiac groove, the presence of antennal notch and the pseudochelate terminations of pereopods 1 to 3.

**Node 21** (Pemphicidae; Fig. 16), **node 22** (Glypheidea; Fig. 17), and **node 23** (Glypheidae; Fig. 17A–D) result in a topology of glypheid lobsters close to that of CHARBONNIER et al. (2015).

## 4. Discussion

Examination of the character transformations reveals the presence of 24 homoplasies on 20 characters. Most of them concern the carapace groove pattern (13 homoplasies on 10 characters) but they also concern the carapace ornamentation (3 homoplasies on 2 characters), the characteristics of the pleon (3 homoplasies on 2 characters) and the extremities of some pereopods (2 homoplasies on 2 characters). Moreover, 4 characters (characters 4, 9, 10, 29) have at least two homoplasious states: character state 4<sup>1</sup> at nodes 5, 19 and in *Hoploparia longimana*; character state 4<sup>2</sup> at nodes 9, 21 and in *Glypheia regleyana* and *Nephrops norvegicus*; character state 9<sup>0</sup> in *H. longimana* and *Enoplometopus pictus*; character state 9<sup>1</sup> at nodes 22, 26 and in *Clytiopsis argentoratense*; character state 10<sup>1</sup> at nodes 6, 18 and in *Astacus astacus*; character state 10<sup>2</sup> at node 5 and in *C. argentoratense* and *Chimaerastacus pacifluviatilis*; character state 29<sup>0</sup> at nodes 15 and 21; character state 29<sup>1</sup> at node 3 and in *C. argentoratense* and *N. norvegicus*. The presence of an intercalated plate is also homoplastic between the Erymoidea (node 2) and *E. pictus*. This point is discussed in a paragraph below. These numerous homoplasies make almost impossible to determine any evolutionary trend in the selected characters, especially about the carapace groove pattern. The bi-

ological significance of these grooves has not been clearly established yet. After SECRÉTAN (1973) and GLAESSNER (1960), the grooves could mark the boundaries of internal segmentation. ALBRECHT (1981) and TSHUDY & BABCOCK (1997), have concluded that the grooves are the external expression of sites of muscles attachments. But the work of TSHUDY & BABCOCK (1997) does not show that the idea of Secrétan and Glaessner was wrong. Considering the few works focused on this question, both hypotheses remain poorly tested. Anyway, this underlined the fact that the carapace grooves are fundamental morphological features that are more or less expressed in all decapods (SECRÉTAN 1964). So, the carapace grooves are considered phylogenetically significant.

This morphology-based phylogenetic analysis concurs with some of the results of CHARBONNIER et al. (2015). In both works the topologies of Glypheidea are very close and Pemphicidae are sister to Glypheidea. However, the position of *Clytiopsis* and *Lissocardia* as sister taxa of Glypheidea was not supported by CHARBONNIER et al. (2015), who consider these taxa to be external of the clade *Chimaerastacus* + Glypheidea while our study indicates they share some synapomorphies with this clade. Furthermore, the position of the Triassic *Clytiopsis*, *Lissocardia* and Pemphicidae demonstrates they are not related to erymid lobsters as previously suggested by VAN STRAELEN (1928), FÖRSTER (1966), FELDMANN & TITUS (2006), DE GRAVE et al. (2009), SCHWEITZER et al. (2010), or by the phylogenetic analyses of AMATI et al. (2004) and KARASAWA et al. (2013) (Fig. 1).

The exploration of the relations among astacid, enoplometopid, and nephropid lobsters is beyond the purposes of this work, and will not be discussed here. As for the glypheid lobsters, they are only used to determine the affinities of erymid lobsters with these groups.

Both representatives of erymids and Astacidea are connected to node 1 based on the presence of an antennal spine. Such topology leads us to place the erymid lobsters within this infra-order, as suggested by most of the authors of the 20th century. Our results show that erymid lobsters constitute the clade Erymoidea, clearly distinct from astacid, enoplometopid and nephropid lobsters among Astacidea. It is partially supported by the presence of the intercalated plate. This structure was considered to be unique among Decapoda but our observations confirmed SCHRAM & DIXON'S (2004) observation: two grooves delimit a fusiform area in *Enoplometopus*. The hypothetical case of the homology of this structure with the intercalated plate of the erymid tested in our analysis does not result in a clade including *Enoplometopus* and the erymids as it has been suggested. The intercalated plate of *Enoplometopus* has the particularity to not be delimited posteriorly (see Fig. 4B), contrary to that in Erymoidea (e.g., Fig. 10A). If these characters are homologous, the presence of this plate should be the consequence of a convergence but its delimitation (more or less complete) and relative size are different in erymids and enoplometopids. This absence of anterior and posterior boundaries in *Enoplometopus* could be linked to

the absence of dorsal suture in this genus. In addition, the fact that *Enoplometopus* remains very distant from the erymids despite it is scored as having an intercalated plate could also indicate that the structure seen in *Enoplometopus* and the intercalated plate of the erymids represent non-homologous characters. Consequently to this unresolved point we have emended the diagnoses of Enoplometopidae and Erymoidea by addition of details about, respectively, the two dorsal disjoined grooves in enoplometopid lobsters and the presence of an intercalated plate which is entirely delimited in erymid lobsters (see in 5. Systematic implications).

It is interesting to notice that, despite missing data on fifteen characters, *Uncina posidoniae* is sister to *Enoplometopus pictus*. It is congruent with the results of the phylogenetic studies of AHYONG (2006) and KARASAWA et al. (2013). If the clade Enoplometopoidea including both enoplometopid and enigmatic uncinid lobsters tends to get verified here, it is supported by only one unambiguous synapomorphy: the shape of pleura. This character supports also this clade in the analysis of KARASAWA et al. (2013).

Using the post-orbital area resulted in the constitution of two clades among Erymoidea: one including taxa without the post-orbital area, and one including taxa with the post-orbital area. Considering this result, this character is found of importance in erymid evolution and supports the systematic building of Erymoidea which now includes two families: Enoploclytiidae fam.n. (without post-orbital area) and Erymidae (with post-orbital area). This implies a definition of Erymidae more restrictive than that commonly accepted until now, because it now excludes *Enoploclytia* and *Pustulina*. The topology of the clade Erymidae shows *Tethysastacus* to be sister of the clade including *Eryma*, *Palaeastacus* and *Stenodactylina*. The careful observation of *Tethysastacus* shows the particular simplicity of its carapace groove pattern among Erymidae. Such differences led us to the placement of the previous genera within two subfamilies: Eryminae (including *Eryma*, *Palaeastacus*, *Stenodactylina*) and Tethysastacinae subfam.n. (including only *Tethysastacus*).

## 5. Systematic implications

### 5.1. Diagnoses

**Enoplometopidae Saint Laurent, 1988.** TYPE GENUS: *Enoplometopus* A. Milne-Edwards, 1862. — EMINDED DIAGNOSIS: Cephalothorax cylindrical; well-developed rostrum; cephalic ridges present; narrow, longitudinal grooves along gastric rows of spines, not joined anteriorly and posteriorly, partially delimiting a wide fusiform area; cervical groove weak; branchiocardiac groove indistinct; pleonal pleura rounded; pleon with small first and large second somite; pleura rounded and expanded anteriorly and posteriorly; sometimes with spines; well-calcified tailfan; telson rounded; with movable spines;

exopod of uropods with diaeresis; massive, chelate pereopods 1, pereopods 2–5 pseudochelate.

**Erymoidea Van Straelen, 1925.** INCLUDED FAMILIES: Erymidae Van Straelen, 1925; Enoploclytiidae fam.n. — EMENDED DIAGNOSIS: Subcylindrical carapace; narrow, fusiform intercalated plate, entirely delimited; deep cervical groove, crossing all cephalic region height, joined to dorsal margin and to antennal groove; postcervical groove well-developed; hepatic and inferior grooves present; exopodite of uropods with diaeresis; pereopods 1–3 chelate, massive pereopods 1; pereopods 4–5 achelate; pleon with triangular pleura; inflated base of pleura.

**Enoploclytiidae fam.n.** TYPE GENUS: *Enoploclytia* M’Coy, 1849. — DIAGNOSIS: Slightly inflated cardiac and branchial regions; gastro-orbital groove elongated, with two divergent branches; postcervical groove joined to posterior extremity of hepatic groove; branchiocardiac groove, subparallel to postcervical groove, interrupted in branchial region, not joined to postcervical groove.

**Erymidae Van Straelen, 1925.** TYPE GENUS: *Eryma* Meyer, 1840. — EMENDED DIAGNOSIS: Presence of a delimited post-orbital area, gastro-orbital groove short or absent.

**Eryminae Van Straelen, 1925.** EMENDED DIAGNOSIS: Short gastro-orbital groove; postcervical groove crossing at least half of the carapace height; branchiocardiac groove subparallel to postcervical groove, joined to posterior extremity of hepatic groove; hepatic groove concavo-convex.

**Tethysastacinae subfam.n.** TYPE GENUS: *Tethysastacus* Devillez, Charbonnier, Hyžný & Leroy, 2016. — DIAGNOSIS: Gastro-orbital groove absent; postcervical groove joined to posterior extremity of hepatic groove; branchiocardiac groove absent; hepatic groove concave.

## 5.2. Suggested classification of erymid lobsters

Infraorder ASTACIDEA Latreille, 1802

Superfamily Erymoidea Van Straelen, 1925

Family Enoploclytiidae fam.n.

*Enoploclytia* M’Coy, 1849

*Pustulina* Quenstedt, 1857

Family Erymidae Van Straelen, 1925

Subfamily Eryminae Van Straelen, 1925

*Eryma* Meyer, 1840

*Palaeastacus* Bell, 1850

*Stenodactylina* Beurlen, 1928

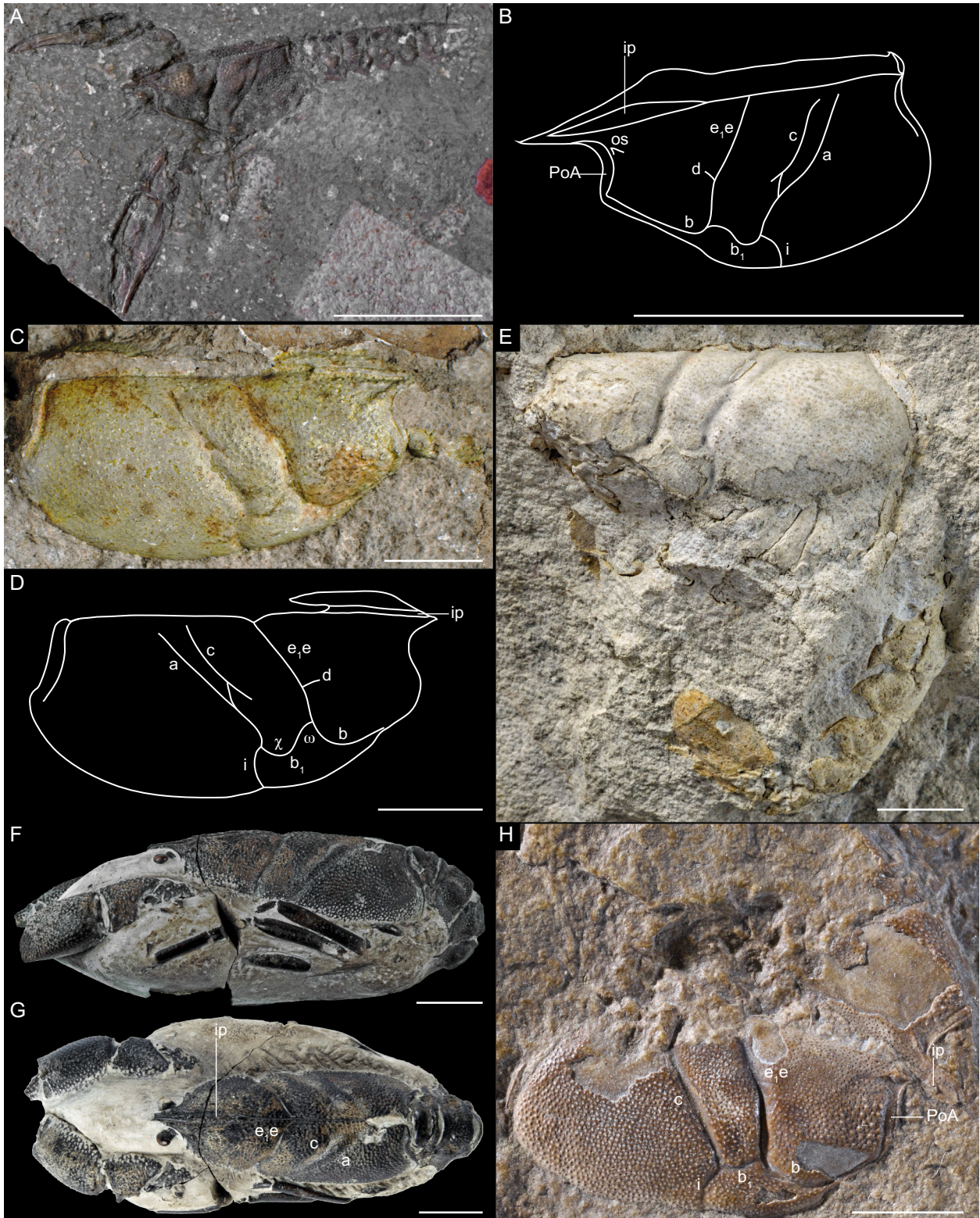
Subfamily Tethysastacinae subfam.n.

*Tethysastacus* Devillez, Charbonnier, Hyžný & Leroy, 2016

## 6. Conclusions

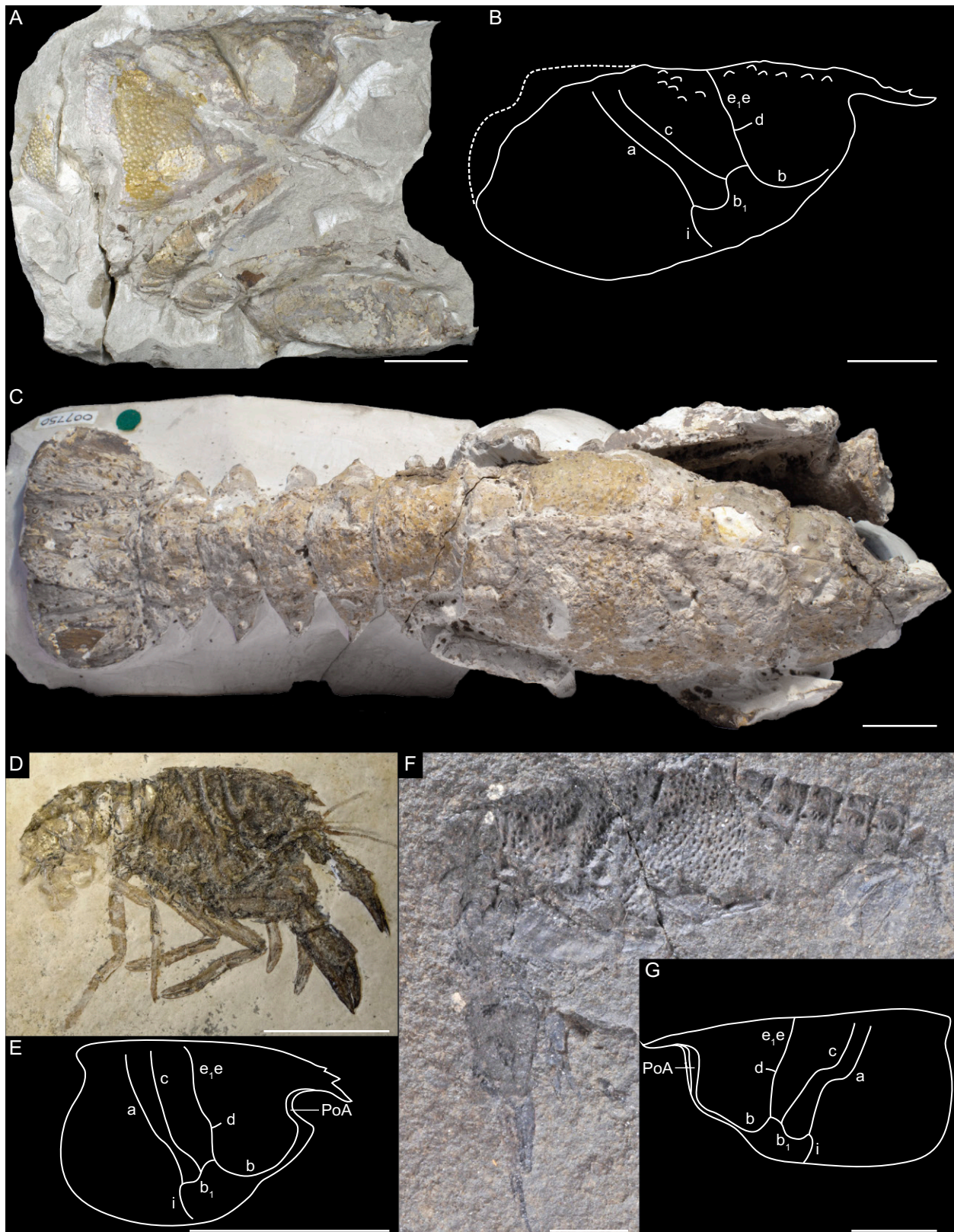
Our cladistic analysis demonstrates that taxa of uncertain affinities such as *Clytiopsis* and *Lissocardia* are clearly not erymids but are closely related to Glypheidea and *Chimaerastacus*. Furthermore, our results concur with those of CHARBONNIER et al. (2015) considering pemphicid lobsters, sometimes regarded as erymids, to be sister to Glypheoidea within the infra-order Glypheidea. This study was also the occasion to test SCHRAM & DIXON’s (2004) hypothesis, consisting in interpreting the presence of two gastric grooves partially delimiting a fusiform area in the extant *Enoplometopus* as a character homologous to the intercalated plate of the erymid lobsters. The fact that *Enoplometopus* remains distant from the erymids indicates that the homology between the two structures remains speculative and demonstrates that this genus does not represent an actual form of erymid. So, we consider only six genera, all fossil, to be erymid lobsters: *Eryma*, *Enoploclytia*, *Palaeastacus*, *Pustulina*, *Stenodactylina*, and *Tethysastacus*. The clade including all these genera, is sister to the clade including the taxa representatives of Astacidea. Our topology led us to assign the erymids to Astacidea, in opposition to recent works suggesting erymids to belong to Glypheidea. The topology of the clade including the erymids reflects relatively complex relationships between each genus and motivated us to propose a new systematic classification for this group. All erymid lobsters are assigned to the superfamily Erymoidea, which is subdivided in two families: Enoploclytiidae fam.n. (*Enoploclytia*, *Pustulina*) and Erymidae (*Eryma*, *Palaeastacus*, *Stenodactylina* and *Tethysastacus*). The presence of a delimited post-orbital area, a character recently described and used for the first time in a phylogenetic analysis, has proved to be of strong importance in order to distinct erymid families because it is the synapomorphy of Erymidae. This family has also been divided in two subfamilies based on the strong differences in the carapace groove pattern of assigned genera: Eryminae, including *Eryma*, *Palaeastacus* and *Stenodactylina*, and Tethysastacinae subfam.n., including only *Tethysastacus*. The study presented here is a first step to evaluate the position of the erymids among the lobsters. Further works should integrate the erymids with the purpose to precise the relationships of these extinct lobsters among Astacidea. Such study would benefit of an extended sample of astacidean taxa and of a more complete dataset to elaborate a matrix of characters that would fit all astacidean lobsters, including the Erymoidea.



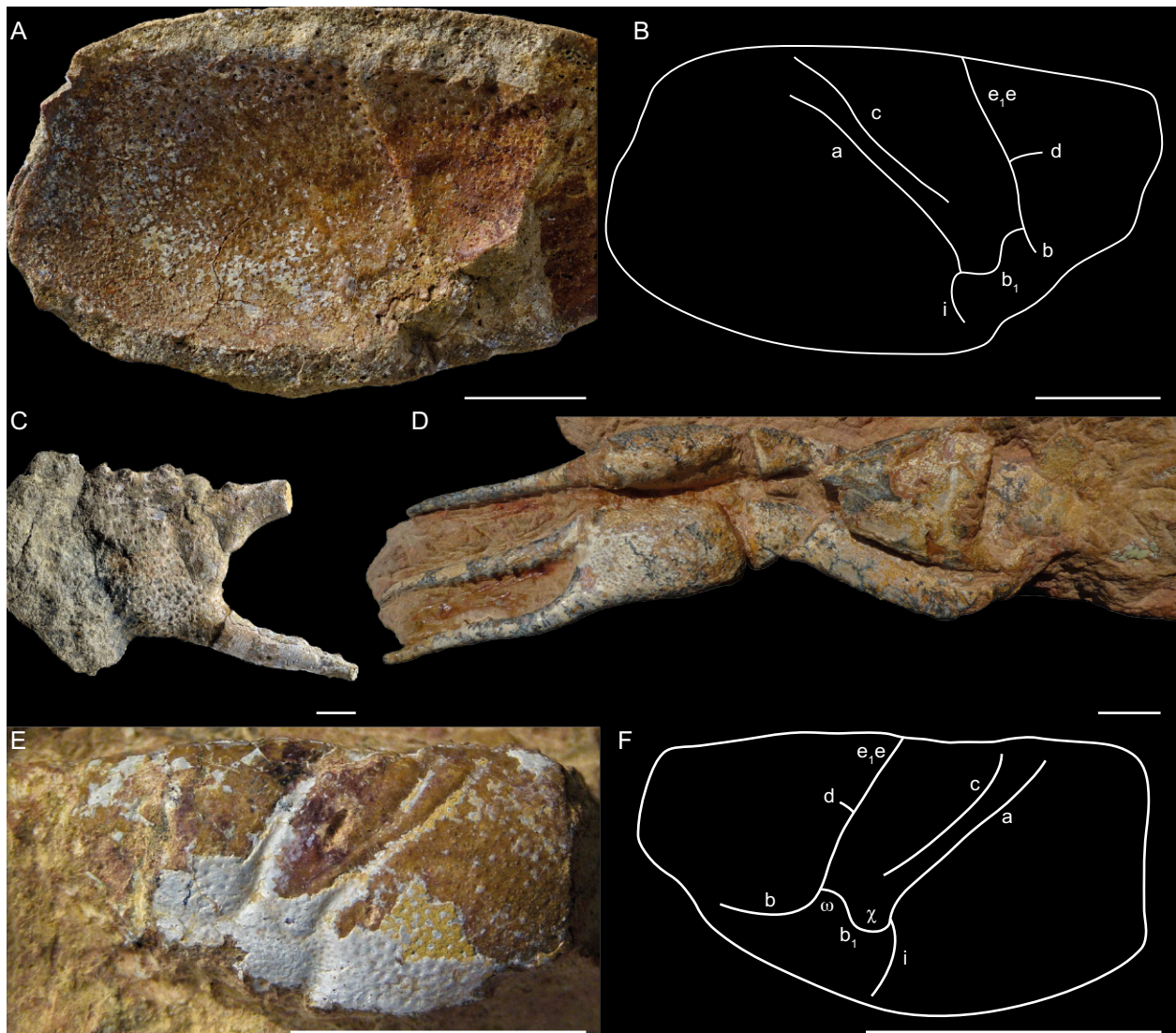


**Fig. 7.** *Eryma* Meyer, 1840 and *Tethysastacus* Devillez et al., 2016. **A–B:** holotype MFN 2236 P1383/2 MB.A.0252 of *Eryma modestiforme* (Schlotheim, 1822) (Jurassic, Germany): general view (A), and line drawing of the carapace (B); **C–E:** *Eryma ventrosus* (Meyer, 1835) (Jurassic, France): cast of the holotype MNHN.F.B12484 (C), line drawing (D), and specimen MNHN.F.A29468; **F–G:** neotype SM B11437 of *Eryma sulcatum* Harbort, 1905 (Cretaceous, United Kingdom): lateral (F), and dorsal view (G); **H:** holotype MNHN.F.J03351 of *Tethysastacus tithonius* (Van Straelen, 1936) (Cretaceous, France). — Photographs: L. Cazes (E, H), J. Devillez (A, F, G). Line drawings: J. Devillez. — Scale bars: 10 mm. — **Abbreviations:** a – branchiocardiac groove; b – antennal groove; b<sub>1</sub> – hepatic groove; c – post-cervical groove; d – gastro-orbital groove; e<sub>1</sub>e – cervical groove; i – inferior groove; ip – intercalated plate; os – orbital spine; PoA – post-orbital area;  $\chi$  – attachment site of adductor testis muscle;  $\omega$  – attachment site of mandibular muscle.



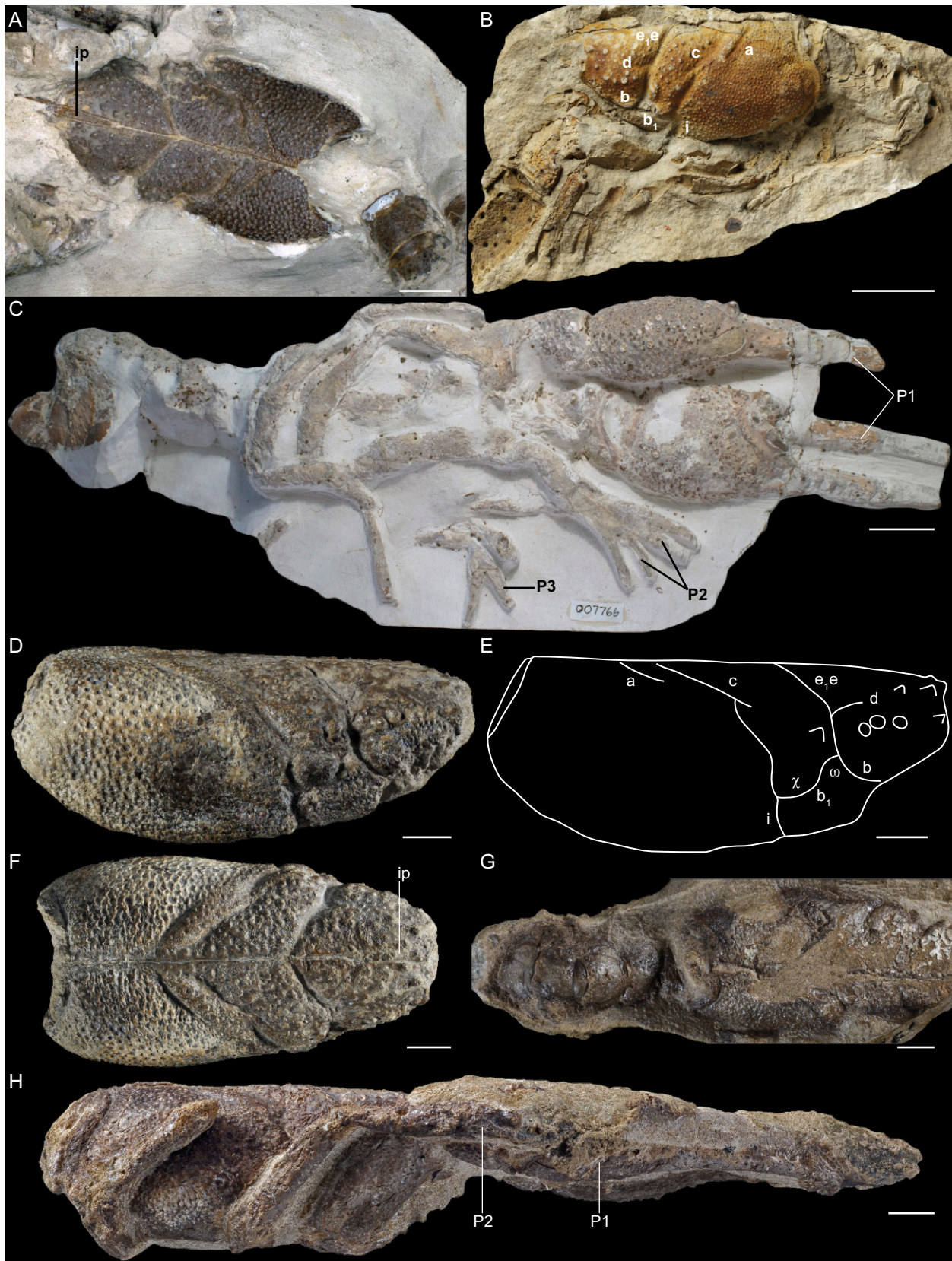


**Fig. 8.** *Palaeastacus* Bell, 1850. **A–C:** *Palaeastacus sussexiensis* (Mantell, 1824) (Cretaceous, United Kingdom): lectotype NHMUK 5601 (A), line drawing of the carapace (B), and specimen BMB 007750 (C); **D–E:** holotype MFN 2236 P1383/8 MB.A.0251 of *Palaeastacus fuciformis* (Schlotheim, 1822) (Jurassic, Germany): general view (D), and line drawing of the carapace (E); **F–G:** holotype BAS KG.50.4 of *Palaeastacus uranusienensis* Devillez & Charbonnier, 2019 (Cretaceous, Antarctica): general view (F), and line drawing of the carapace (G). — Photographs: J. Devillez (A, C, D), H. Blagbrough (F). Line drawings: J. Devillez. — Scale bars: 10 mm. — **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.



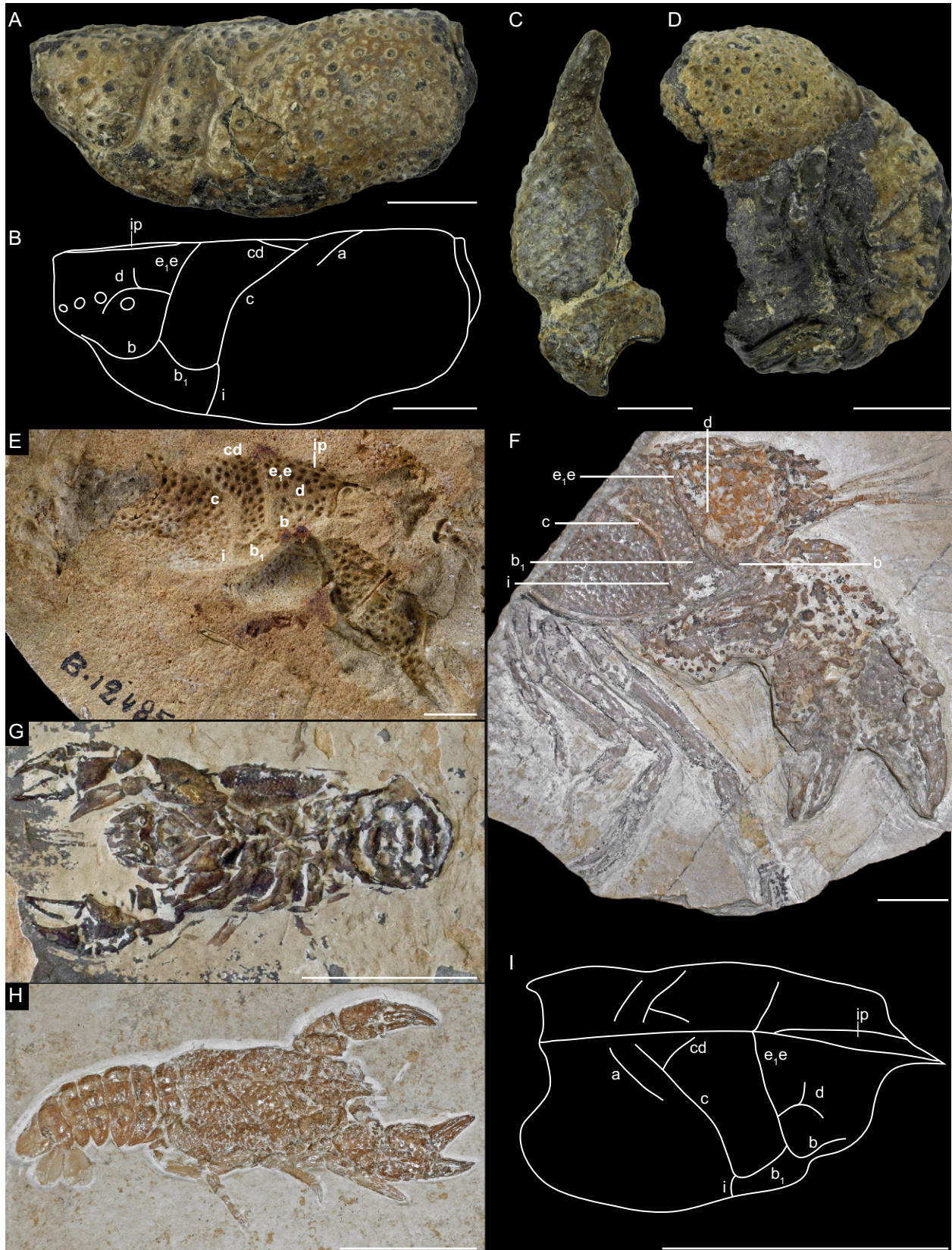
**Fig. 9.** *Stenodactylina* Beurlen, 1928. **A–C:** *Stenodactylina australis* (Secrétan, 1964) (Jurassic, Madagascar): specimen MNHN.F.33228 (C), line drawing of the carapace (B), and holotype MNHN.F.R03975 (C); **D–F:** *Stenodactylina lagardettei* (Hyžný et al., 2015) (Jurassic, France): holotype PF Aal 345 (D), specimen MHNL 20 103064 (E), and line drawing (F). — Photographs: L. Cazes (A), C. Lemzaouda (C), M. Hyžný (D, E). Line drawings: J. Devillez. — Scale bars: 10 mm. — **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; ip – intercalated plate; χ – attachment site of adductor testis muscle; ω – attachment site of mandibular muscle.





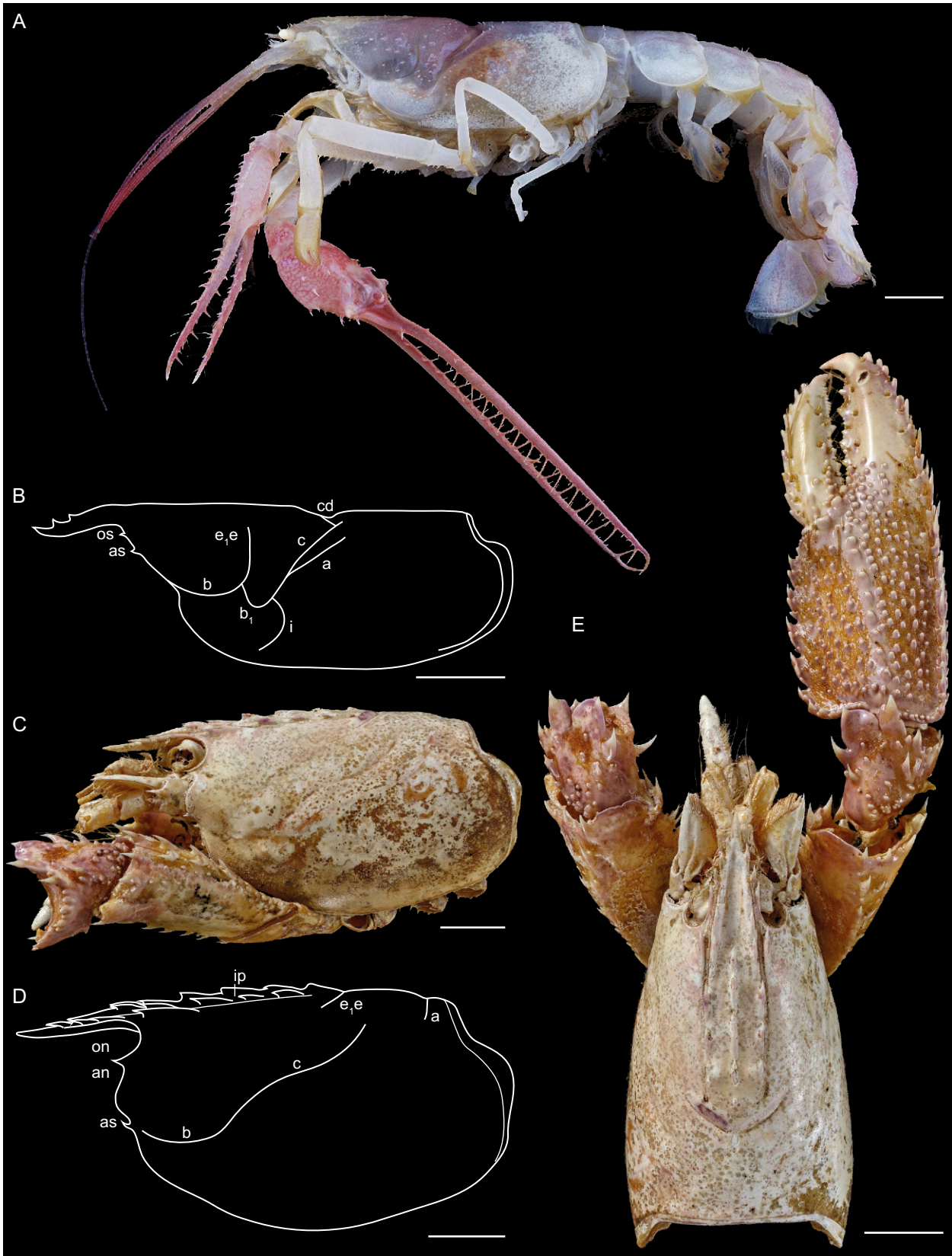
**Fig. 10.** *Enoploclytia* M’Coy, 1849. **A–C:** *Enoploclytia leachi* (Mantell, 1822) (Cretaceous): specimen NHMUK I.1977 (United Kingdom) (A), specimen NM O7125 (Czech Republic) (B), specimen BMB 007766 (United Kingdom) (C); **D–H:** *Enoploclytia collignoni* Secrétan, 1964 (Cretaceous, Madagascar): holotype MNHN.F.R03925 lateral (D), line drawing (E), and dorsal view (F), paratype MNHN.F.A33130 (G), and paratype MNHN.F.A33203 (H). — Preparation: C. Bouillet (G), Y. Despres (H). Photographs: L. Cazes (H), J. Devillez (A, C), M. Kocová Veselská (B), C. Lemzaouda (D, F), P. Loubry (G). Line drawing: J. Devillez. — Scale bars: 10 mm. — **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; ip – intercalated plate; P1–3 – pereopods 1 to 3; χ – attachment site of adductor testis muscle; ω – attachment site of mandibular muscle.





**Fig. 11.** *Pustulina* Quenstedt, 1857. **A–D:** *Pustulina tuberculata* (Bell, 1863) (Cretaceous, United Kingdom): lectotype SM B22368 (A), line drawing (B), paralectotype SM B22370 (C), and paralectotype SM B22369; **E:** syntype MNHN.F.B12485 of *Pustulina perroni* (Étallon, 1861) (Jurassic, France); **F:** specimen SMNS 3682/1 of *Pustulina suevica* Quenstedt, 1857 (Jurassic, Germany); **G–I:** specimens of *Pustulina minuta* (Schlotheim, 1822) (Jurassic, Germany): holotype MFN 2236 P1383/5 MB.A.0254 (G), specimen MFN 2236 P1383/5 MB.A.1119 (H), and line drawing of the carapace (I). — Photographs: J. Devillez (A, C, D, F–H), L. Cazes (E). Line drawings: J. Devillez. — Scale bars: 10 mm. — **Abbreviations:** a – branchiocardiac groove; b – antennal groove; b<sub>1</sub> – hepatic groove; c – postcervical groove; cd – cardiac groove; d – gastro-orbital groove; e,e – cervical groove; i – inferior groove; ip – intercalated plate.





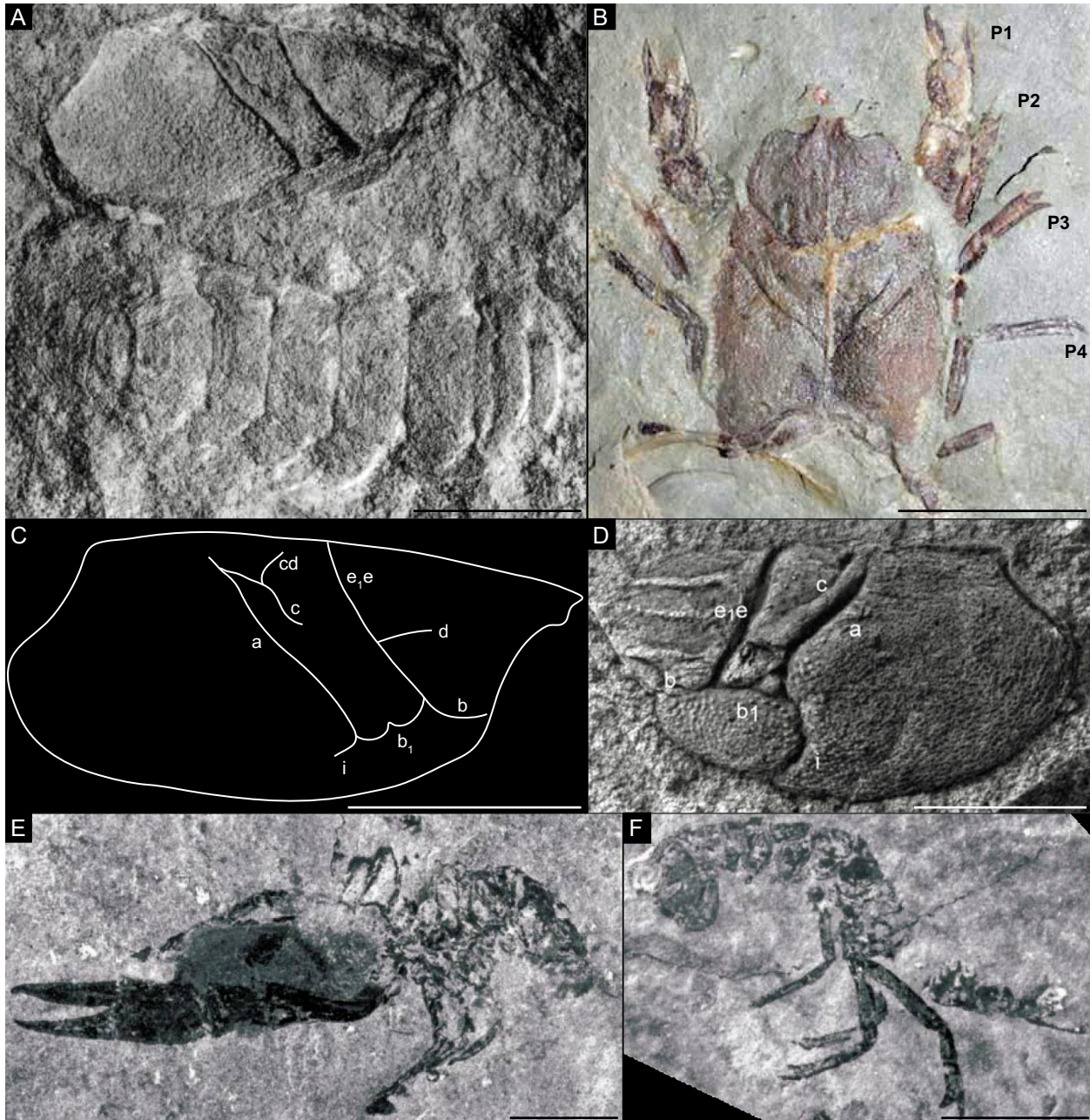
**Fig. 12.** Extant lobsters. **A–B:** holotype NMCR of *Dinochelus ausubeli* Ahyong et al., 2010 (Philippines): original figure of AHYONG et al. (2010: fig. 4A) of the holotype (A), and line drawing of the carapace; **C–E:** holotype MNHN-IU-AS182 of *Enoplometopus pictus* A. Milne-Edwards, 1862 (island of Réunion): left lateral view (C), line drawing of the carapace (D), and dorsal view (E). — Photographs: L. Cazes (C, E). Line drawings: J. Devillez. — Scale bars: 10 mm. — **Abbreviations:** a – branchiocardiac groove; an – antennal notch; as – antennal spine; b – antennal groove; b<sub>1</sub> – hepatic groove; c – postcervical groove; cd – cardiac groove; e,e – cervical groove; i – inferior groove; ip – intercalated plate; on – orbital notch; os – orbital spine.





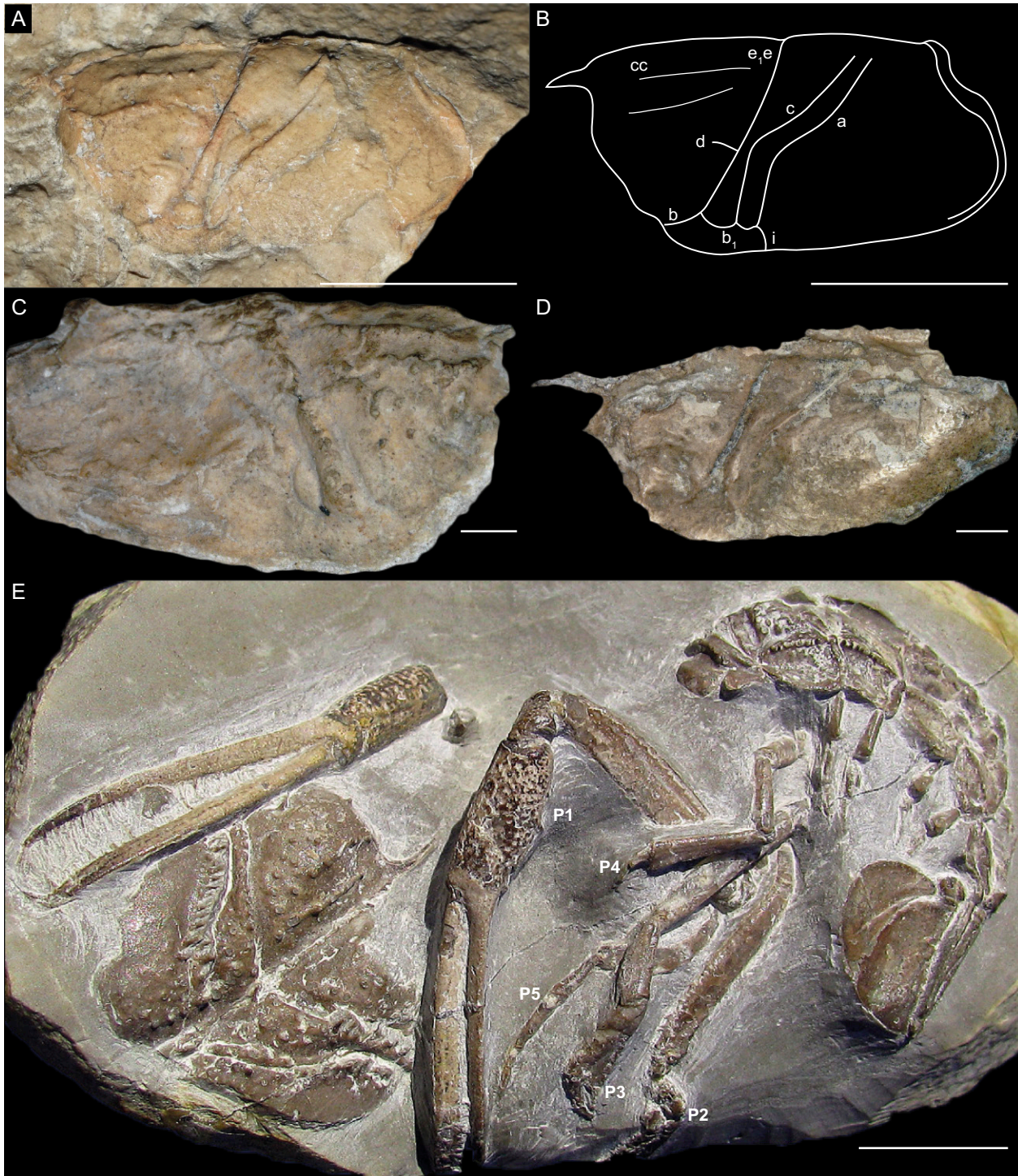
**Fig. 13.** *Hoploparia longimana* (Sowerby, 1826) (Cretaceous, United Kingdom). **A–B:** specimen MNHN.F.B14166 (**A**), and line drawing of the carapace (**B**); **C–D:** specimen MNHN.F.B14167. — Photographs: L. Cazes. Line drawing: J. Devillez. — Scale bars: 10 mm. — **Ab-** **bre** **viations:** b – antennal groove; b<sub>1</sub> – hepatic groove; c – postcervical groove; d – gastro-orbital groove; e, e<sub>1</sub> – cervical groove.





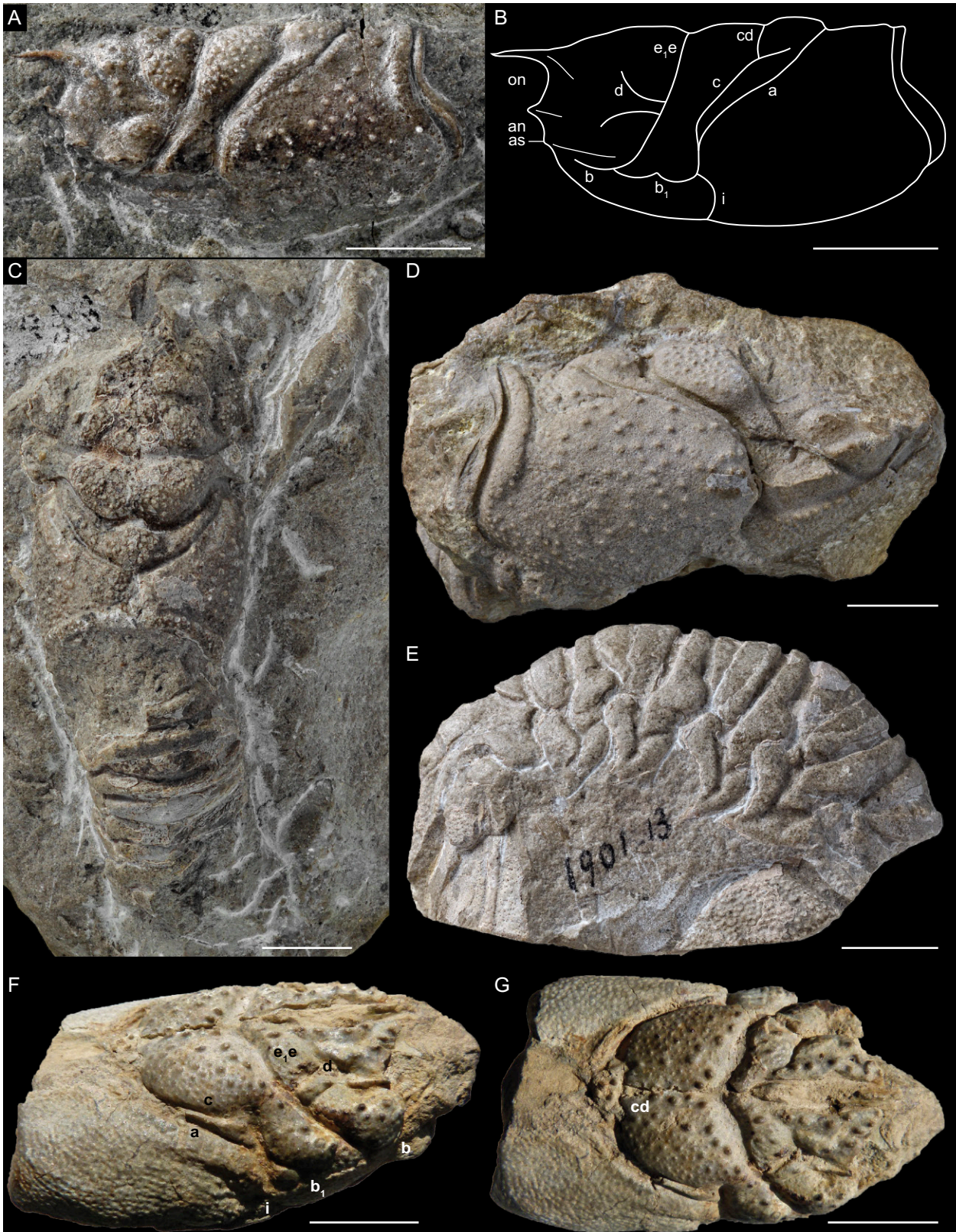
**Fig. 14.** *Clytiopsis argentoratense* Bill, 1914 and *Chimaerastacus pacifluviatilis* Amati et al., 2004. **A–C:** *Clytiopsis argentoratense* (Triassic, France): original figure of BILL (1914: pl. 10, fig. 2) (A), molted specimen (B), and line drawing of the carapace (C); **D–F:** *Chimaerastacus pacifluviatilis* (Triassic, Canada): original figures of AMATI et al. (2004: figs. 9.1, 9.7, 9.8) of the paratype RTM 97.121.15 (D), paratype RTM 97.121.77 (E), and paratype RTM 97.121.435 (F). — Line drawing: J. Devillez. — Scale bars: 10 mm. — **Abbreviations:** a – branchiocardiac groove; b – antennal groove; b<sub>1</sub> – hepatic groove; c – postcervical groove; cd – cardiac groove; d – gastro-orbital groove; e, e<sub>1</sub> – cervical groove; i – inferior groove; P1–4 – pereopods 1 to 4.





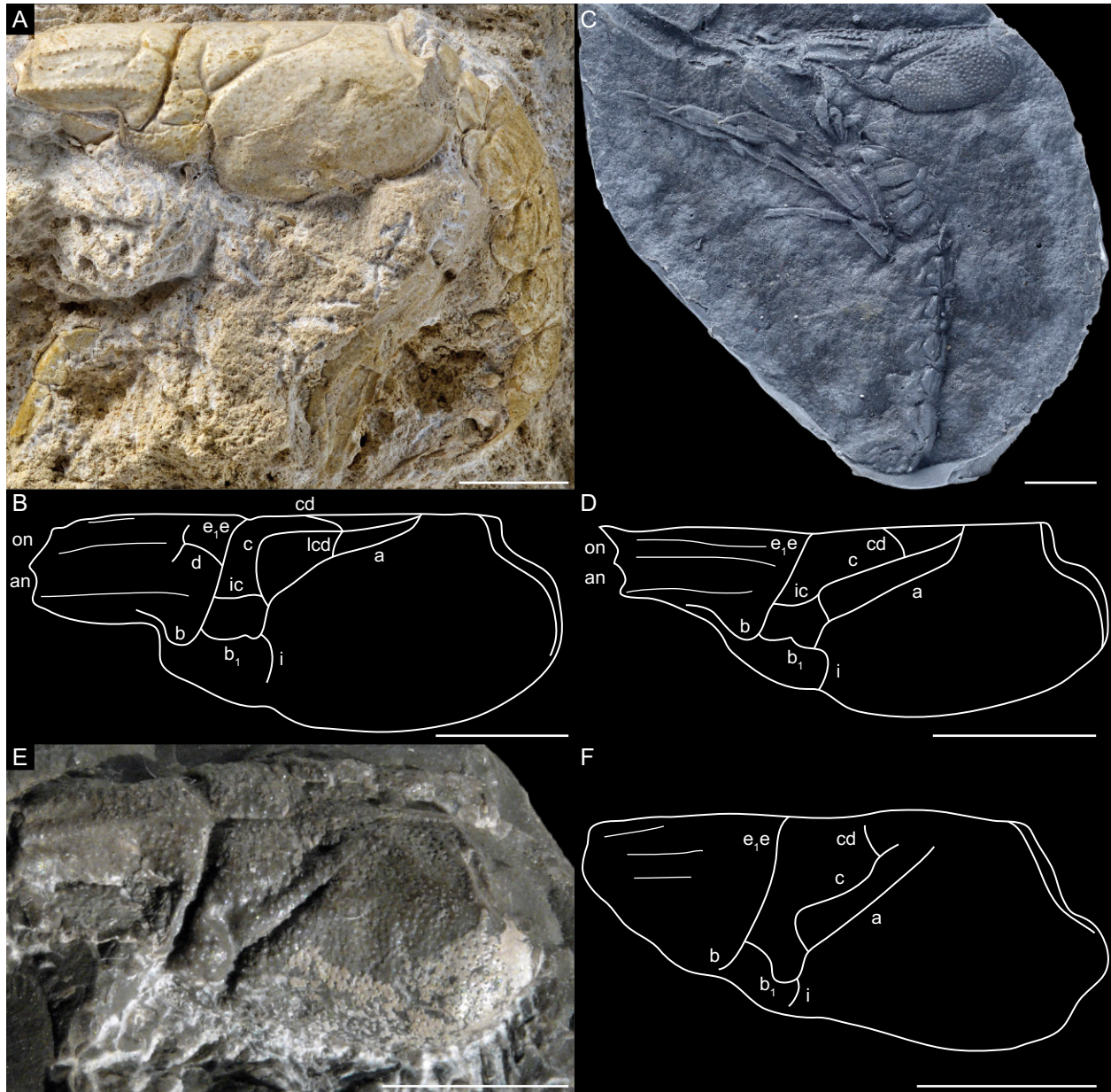
**Fig. 15.** *Lissocardia silesiaca* Meyer, 1851 (Triassic, Germany). **A–B:** lectotype MFN 2236 P1384/8 MB.A.0936: lateral view (A) and line drawing (B); **C:** syntype BGR x268; **D:** syntype BGR x269; **E:** molted specimen. — Photographs: J. Devillez (A), A. Ehling (C, D). Line drawing: J. Devillez. — Scale bars: 10 mm (A, B, E), 20 mm (C, D). — **Abbreviations:** a – branchiocardiac groove; b – antennal groove; b<sub>1</sub> – hepatic groove; c – postcervical groove; cc – cephalic carina; d – gastro-orbital groove; e,e – cervical groove; i – inferior groove; P1–5 – pereiopods 1 to 5.





**Fig. 16.** Pemphicid lobsters (Triassic, Germany). **A–E:** *Pemphix sueurii* (Desmarest, 1817): specimen MNHN.F.A59979 (A), line drawing of the carapace (B), specimen MNHN.F.A59975 (C), specimen MNHN.F.B07888 (D), and specimen MNHN.F.A59980 (E); **F–G:** *Pseudopemphix alberti* (Meyer, 1840): lateral view of the holotype SMNS 22109 (F), and dorsal view (G). — Preparation: Y. Despres (D). Photographs: L. Cazes (A, C, D, E), G. Schweigert (F, G). Line drawing: J. Devillez. — Scale bars: 10 mm. — **Abbreviations:** a – branchiocardiac groove; an – antennal notch; as – antennal spine; b – antennal groove; b<sub>1</sub> – hepatic groove; c – postcervical groove; cd – cardiac groove; d – gastro-orbital groove; e,e – cervical groove; i – inferior groove; on – orbital notch.





**Fig. 17.** Glypheid and litogastrid lobsters. **A–B:** *Glyphea regleyana* (Desmarest, 1822) (Jurassic, France): specimen MNHN.F.A29516 (A), and line drawing of the carapace (B); **C–D:** *Glypheopsis robusta* (Feldmann & McPherson, 1980) (Jurassic, Canada): cast of the holotype MNHN.F.R62042 (C), and line drawing of the carapace (D); **E–F:** *Litogaster obtusa* (Meyer, 1844) (Triassic, Germany): holotype SMNS 4401/653 (E), and line drawing of the carapace (F). — Scale bars: 10 mm. — **Abbreviations:** a – branchiocardiac groove; an – antennal notch; b – antennal groove; b<sub>1</sub> – hepatic groove; c – postcervical groove; cd – cardiac groove; d – gastro-orbital groove; e,e – cervical groove; i – inferior groove; ic – intercervical groove; lcd – laterocardiac groove; on – orbital notch.

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