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Astacus multicavatus Bell, 1863 is a marine lobster (Decapoda: Erymoidea: Erymidae), not a freshwater crayfish

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ABSTRACT

Crayfishes comprise a large and diverse group of freshwater lobster-like crustaceans. Despite being abundant in the recent, they are extremely rare in the fossil record. We revise a putative occurrence of *Astacus multicavatus* Bell, 1863 from the marine Hauterivian of Speeton Clay (Speeton, United Kingdom), which was used a few years ago as a calibration fossil representing *Astacus* Fabricius, 1775 for divergence time analyses. This species is actually a senior synonym to *Eryma sulcatum* Harbort, 1905. It so appears that *Eryma multicavatum* (Bell, 1863) comb. nov. is not a freshwater crayfish but a marine representative of Erymidae. Two co-occurring isolated chelae, also from the Speeton Clay, may correspond to larger, older specimens of *E. multicavatum* comb. nov.

Key Words: Astacoidea, Cretaceous, fossil crayfishes, Speeton Clay

INTRODUCTION

Crayfishes (Decapoda, Astacidea), comprising Astacoidea Latreille, 1802 and Parastacoidea Huxley, 1879, form a diverse group of freshwater lobster-like decapod crustaceans with ~669 modern species (several additional freshwater crayfishes have been described every year, for several years, so this figure is probably an underestimate) and 13 extinct fossil species (Feldmann *et al.*, 2011; Crandall & De Grave, 2017). The ancestor of freshwater crayfishes derived from marine lobsters that were initially thought to have lived during the Permian or Triassic, both from palaeontological evidence (Amati *et al*. 2004; Schram & Dixon, 2003; Porter *et al*., 2005) and molecular analyses (Crandall & Buhay 2008; Toon *et al*., 2010; Bracken-Grissom *et al.*, 2014). The discovery of Late Permian burrows (Hasiotis, 1993) confirms this origin is at least Permian, and one recent molecular analysis (Wolfe *et al.*, 2019) points to an even older origin. This evidence provides an evolutionary scenario for dispersal distribution of freshwater crayfishes (Ďuriš & Petrusek, 2015). A single marine ancestor species of the freshwater crayfishes invaded freshwater during the Permian or earlier; at that time our current five continents were aggregated as the supercontinent Pangea (Dercourt *et al*., 1993). Despite this long history, freshwater crayfishes are extremely rare in the fossil record (Feldmann *et al.*, 2011). The number of extinct fossil species is less than 2% that of extant species (Crandall & De Grave, 2017). This is particularly unfortunate since the distribution of modern crayfishes is considered as a textbook example of vicariance, diversification events linked to the apparition of barriers to dispersal (Ďuriš & Petrusek, 2015; Pârvulescu *et al.*, 2019; Scholtz, 1999).

With such a scarce fossil record, and the stakes to interpret correctly the rare occurrences that are known, it is important to examine correctly what is already known. We review *Astacus multicavatus* Bell, 1863 from the Hauterivian of Speeton Clay. This putative

crayfish occurrence (Feldmann *et al.*, 2011) had drawn our attention for several reasons: first, it is assigned to *Astacus* Fabricius, 1775, a genus that initially embraced the majority of European species before many of these were moved to other genera (i.e. the earliest subdivision of *Astacus* by Huxley, 1879, leading to the recognition of *Parastacus* Huxley, 1879, or more recently Bott, 1950 who recognized subgenera within *Astacus* leading to the erection of *Pacifastacus* Bott, 1950) including fossil species (O'Flynn *et al.*, 2021); and also because this species was described from the Speeton Clay, a marine formation (Lott *et al.*, 1986). This species is important because it was used as a calibration fossil to represent *Astacus* in a divergence time analysis (Bracken-Grissom, 2014). Our observations show that this species is not a freshwater crayfish, but belongs to Erymidae, an extinct group of marine lobster-like crustaceans (Devillez *et al.*, 2019).

MATERIAL AND METHODS

Sampling

Our study is based upon 14 specimens, including the syntypes of *Astacus multicavatus* Bell, 1863 and *Eryma sulcatum* Harbort, 1905, the neotype, casts of the lectotype and paralectotypes, and additional specimens. The specimens are housed in Museum für Naturkunde, Berlin, Germany (MFN), Natural History Museum, London, UK (NHMUK), and Sedgwick Museum of Earth Sciences, Cambridge, UK (SM) (see Table 1).All photographs were taken in natural light, without cross-polarisation. The systematics follows that proposed by Devillez *et al.* (2019).

RESULTS

Systematic palaeontology

Malacostraca Latreille, 1802

Decapoda Latreille, 1802

Pleocyemata Burkenroad, 1963

Reptantia Bouvier, 1917

Astacidea Latreille, 1802

Erymoidea Van Straelen, 1925

Erymidae Van Straelen, 1925

Eryminae Van Straelen, 1925

Eryma Meyer, 1840

Eryma multicavatum (Bell, 1863) comb. nov.

(Figs. 1–3)

Astacus multicavatus Bell, 1863, 31, pl. 9 figs. 7, 8. — Glaessner, 1929: 61. — Schweitzer *et al.*, 2010: 32. — Feldmann *et al.*, 2011: table 1. — Bracken-Grisson, 2014: 465. — Crandall & De Grave, 2017: 621.

Astacus? *multicavatus* – Woodward, 1877: 9.

Eryma sulcata Harbort, 1905 nov. syn.: 15, pl. 1, fig. 11, pl. 11, fig. 4. — Glaessner, 1929: 159. — Woods, 1930: 80, pl. 22, figs. 5–7. — Van Straelen, 1936: 9. — Förster, 1966: 124, fig. 23, pl. 17 figs. 2, 4. — Taylor, 1979: 34. — Feldmann & Titus, 2006: 64.

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

Eryma sulcatum – Schweitzer *et al.*, 2010: 25. — Karasawa *et al.*, 2013: 102 — Devillez *et al.*, 2016 : 521, figs. 4I–4L; 2017: 793; 2019: 368, fig. 7F, G. — Devillez & Charbonnier, 2017: 3, figs. 3I–L.

Astacodes falcifer (pro parte) – Bell, 1863: pl. 9, figs. 7, 8.

*Lectotype***:** NHMUK.In.61411 (Figs. 1A–D), selected herein from the two syntypes.

*Paralectotype***:** NHMUK.In.61410 (Figs. 1E–H).

Type material of Eryma sulcatum**:** neotype SM.B11437; casts of lost original material lectotype NHMUK.In.27305 and paralectotypes NHMUK.In.27307, NHMUK.In.27308, NHMUK.In.27309, NHMUK.In.27310.

*Examined material***:** see full list in Table 1.

Type locality and formation: Speeton, North Yorkshire, England, UK: Hauterivian of the Speeton Clay Formation.

*Occurrence***:** Hauterivian of Speeton and Hilston (England, UK) and Stadthagen (Lower Saxony, Germany).

*Diagnosis***:** fFusiform intercalated plate delimited by grooves; deep cervical groove, intercepting dorsal margin at ca 66° angle; short gastro-orbital groove originating as slight median inflexion of cervical groove; deep branchiocardiac groove, strongly inclined, subparallel to postcervical groove; massive P1 propodus, relatively thick, with rounded inner and outer margins; narrow dactylar bulge; fingers, almost straight, with short teeth on occlusal margin; branchial region with fine tubercles (heterogeneous ornamentation); tuberculate intercalated plate.

Emended description:*Cephalothorax:* Subcylindrical carapace (cephalothoracic shield); dorsal margin of cephalic region slightly down-curved; short rostrum with small lateral spines; fusiform intercalated plate delimited by grooves; post-orbital area narrowing dorsally; deep cervical groove, intercepting dorsal margin at ca 66° angle, joined to antennal groove; short gastro-orbital groove originating as slight median inflexion of cervical groove; postcervical groove slightly convex forward, not joined to dorsal margin, joined medially to branchiocardiac groove; deep branchiocardiac groove, strongly inclined, subparallel to postcervical groove, not joined to dorsal margin, joined to hepatic groove; concavo-convex hepatic groove; slightly inflated ω bulge, delimited ventrally by narrow, shallow depression extending between antennal and hepatic grooves; slightly inflated χ bulge; inferior groove curved backward.

Pleon and telson: Pleonal somites with subrectangular dorsal part of terga and sub-triangular tergopleura; longitudinal bulge above tergopleura basis; tergopleura with post tergopleural spine; ventral margin of tergopleura pointing backward; subrectangular telson with longitudinal carina.

Eyes and cephalic appendages: Small stalked eyes with numerous small ommatidia.

Thoracic appendages: Chelate P1 (thoracopod 4); massive P1 propodus, relatively thick with rounded inner and outer margins, longer than wide, inner and outer margins slightly curved in outline; inflated, narrow dactylar bulge; thin fingers, almost straight, of almost same width, with short teeth on occlusal margin; dactylus with longitudinal carina; short, rounded P1 carpus; P1 merus with a strong process on distal extremity of external margin; slender P2-P5 (thoracopods 5-8).

Pleonal appendages: Wide, rounded uropods with median longitudinal carina.

Ornamentation: Carapace and pleonal somites densely covered by small tubercles, pits with irregular outline; branchial region with finer tubercles; tuberculate intercalated plate; post-orbital area slightly granular; cephalic region with oblique orbital row of tubercles ending by strong orbital spine (antennal row absent); telson and uropods ornamented with small rounded punctuations (cupula); P1 palm densely covered by small prominent tubercles preceded by pits; dactylar bulge with 2 spines, pointed forward; fingers covered by large rounded pits; P1 carpus with same ornamentation than propodus, with strong spine at distal extremity of external margin; P1 merus with same ornamentation of P1 carpus, spines on dorsal margin; P2-P5 with small punctation.

Remarks: Astacus multicavatus Bell, 1863 is described based upon two syntypes, NHMUK.In.61410 and NHMUK.In.61411. We herein designate NHMUK.In.61411 as the lectotype of *A. multicavatus* since it preserves more diagnostic characters. Consequently, the second syntype NHMUK.In.61410 is herein considered the paralectotype.

Eryma sulcatum (Bell, 1863) is assigned to *Eryma* Meyer, 1840 based upon its fusiform intercalated plate (notably lacking in crayfishes), deep cervical groove joined to median line, short gastro-orbital groove, postcervical and branchiocardiac grooves subparallel (branchiocardiac diverging from postcervical in crayfishes), the sinuous (also termed concavo-convex) hepatic groove joined to inferior groove and inflated ω area, orbital row of tubercles with a large distal spine, large antennal spine, compressed P1 (thoracopod 4) propodus with narrow inner and outer margins, narrow P1 dactylar bulge; P1 fingers (dactylus and index) longer than the palm (propodus not including the index) and index wider than dactylus (diagnostic characters of *Eryma* following Devillez *et al.* (2016, 2017).

Eryma sulcatum Harbort, 1905 is considered herein as synonymous with *Astacus multicavatus* Bell, 1863 due to the absence of observable differences between the two species, and common origin and age of their type material, namely the lectotype and paralectotype of *A. multicavatus* and the neotype of *E. sulcatum* (designated by Devillez *et al.*, 2016 due to the loss of the original syntypes). It is noteworthy that Devillez *et al.* (2016) had already considered the two syntypes (lectotype and paralectotype herein) of *A. multicavatus* as specimens of *E. sulcatum* without realizing their status. In application to the principle of priority (ICZN, 1999: article 23), the name *A. multicavatum* Bell, 1863 has the priority over *E. sulcata* Harbort, 1905.

DISCUSSION

Because of the preservation of eyes, carapace (shield), pleon, telson, pereiopods (thoracopods 4–8), and uropods, *Eryma multicavatum* comb. nov. is the most complete species of *Eryma* from Lower Cretaceous deposits. It is also one of the most complete erymoids, together with *Enoploclytia seitzi* Glaessner, 1932 (carapace, pleon and first pereiopod) and *Palaeastacus uranusiensis* Devillez & Charbonnier, 2019 (carapace, pleon, telson, first and second pereiopods and uropods).

Together with other specimens of *Eryma multicavatum* comb. nov. from England, two isolated P1 chelae were collected at Speeton in the Speeton Clay Formation (NHMUK.52081; Fig. 4). These chelae have a compressed and a slightly trapezoidal propodus, bearing long fingers progressively narrowing to their distal extremity. These features are diagnostic of *Eryma*. The propodus with slightly curved margins and the ornamentation made of numerous small tubercles and small depressions, are characteristics shared with *E. multicavatum*. The shape of the fingers, however, is different. In the two specimens, the index is strongly curved

and wider than the straight one of *E. multicavatum*. These two P1 chelae are around twice as large as those of the type material of *E. multicavatum*. As such, these isolated chelae could be from older, more mature specimens of *E. multicavatum*, and the morphological differences could be the result of an allometric growth that modified their general shape. The isolated P1 chela from Hilston (MFN.MB.A.2853; Fig. 3D) is otherwise closer to the size of the unidentified chelae (NHMUK.52081; Fig. 4). The morphology of this specimen does not resemble closely to that of the unidentified P1 chelae, but it exhibits a morphology very similar to the type material of *E. multicavatum*. In conclusion, considering our previous remarks, and because no other species of *Eryma* has been reported in the same formation, we consider that these two isolated P1 chelae have affinities with *E. multicavatum* but cannot be related to this species. We therefore identify them as *Eryma* aff. *E. multicavatum*. The difference between these two types of claws is similar to the‘form I’ (straight fingers) and ‘form II’ (curved fingers) discussed by Hyžný *et al*. (2015), Devillez *et al*. (2016), and Devillez & Charbonnier (2017). If more complete specimens of *Eryma* with the curved claws are found in the Speeton Clay, it may help to better understand the nature of this difference in morphology.

As the origin of crayfishes and the time at which they diverged from their marine relatives is still an ongoing question (Ďuriš, & Petrusek, 2015), our work clears up one possible misunderstanding about the evolutionary history of crayfish: *Eryma multicavatum* is not a late case of marine crayfish but simply a member of the extinct lobster-like Erymidae. Our study has also a broader importance to better understand the evolution of decapods as a whole. *Astacus multicavatus*, interpreted as a crayfish (*Astacus*), was certainly used as a calibration point in Bracken-Grisson *et al.* (2014), it may therefore have affected adversely the estimate for the age of clades presented in this particular study.

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FIGURE CAPTIONS

Figure 1

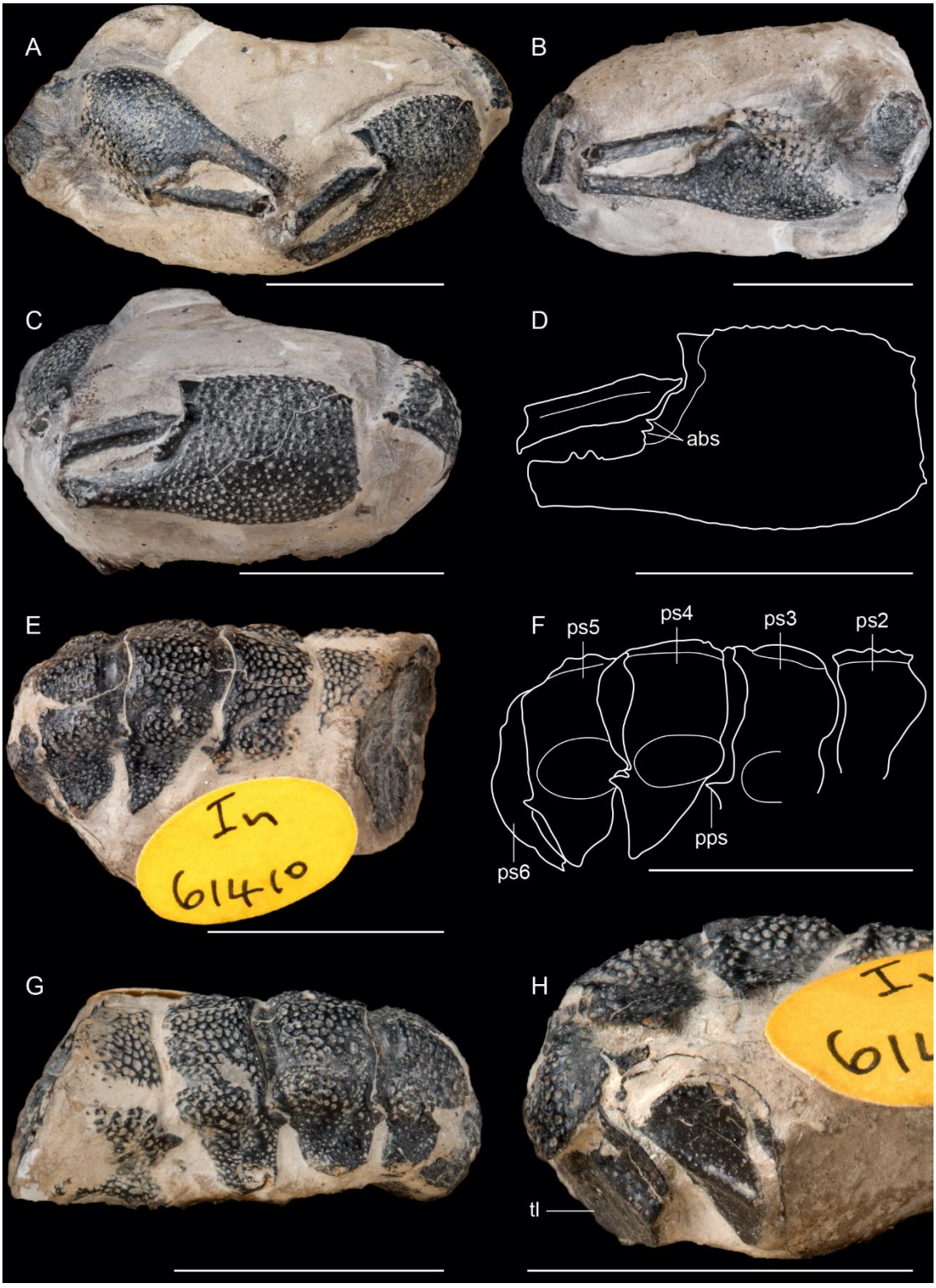

Figure1. Lectotype NHMUK In.61411 and paralectotype NHMUK.In.64410 of *Astacus multicavatus* Bell, 1863 from the Hauterivian of Yorkshire (England). **A**–**D**: P1 chelae and line drawing (**D**); **E**–**H**: fragment of pleon showing the telson and uropod (**H**), and line drawing (**F**). abs, articular bulge spine; pps, post tergopleural spine; ps2-6, pleonal somites 2–6; tl, telson. Scale bars = 1 cm. Photographs K. Webb; ine drawings J. Devillez.

Figure 2

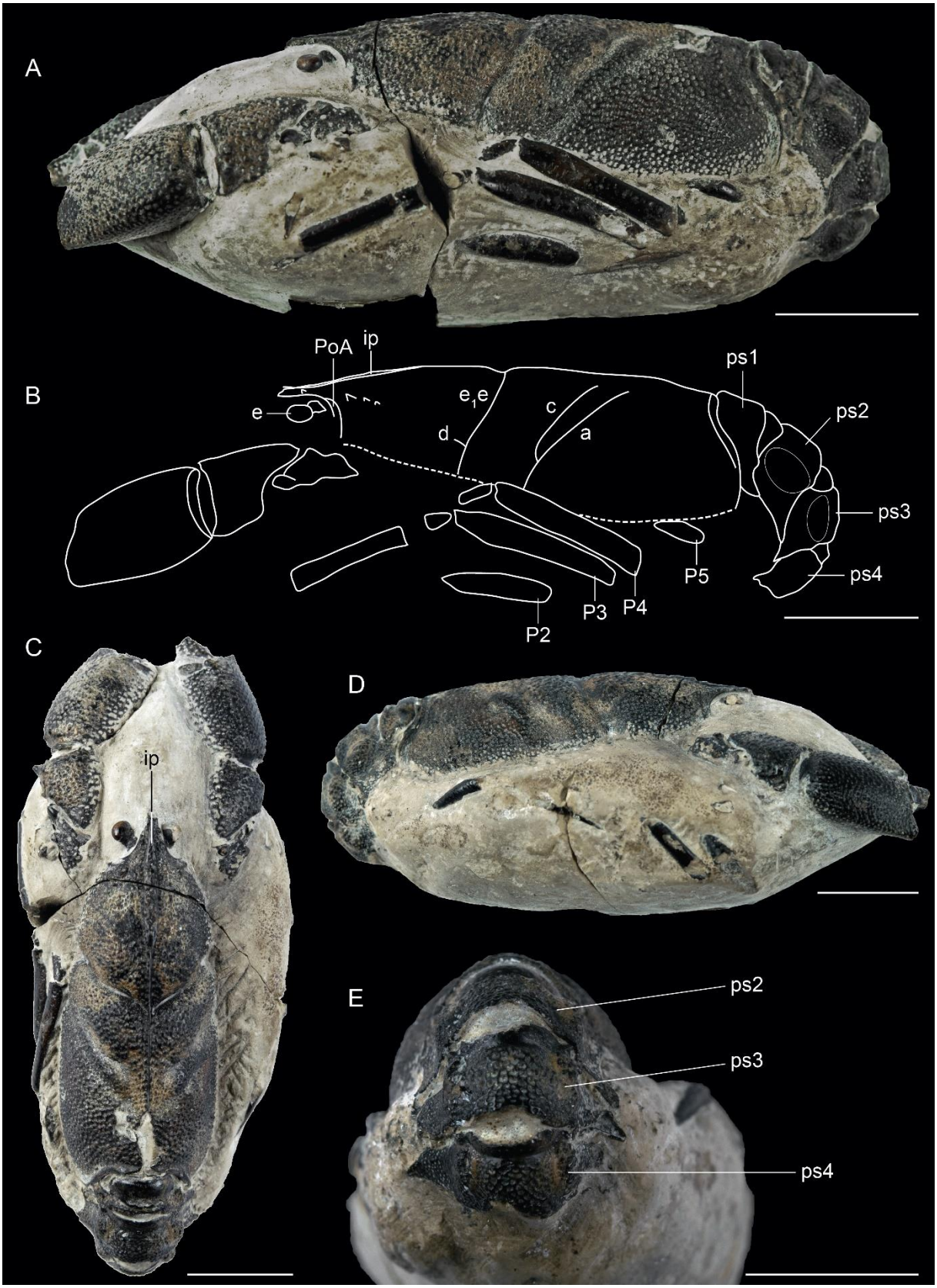

Figure 2. Neotype SM B11437 of *Eryma sulcatum* Harbort,1905 from the Hauterivian of Speeton (England). **L**eft lateral view and line drawing (**A**, **B**); dorsal view (**C**); right lateral view (**D**); detail of the pleon (**E**). a, branchiocardiac groove; c, postcervical groove; d, gastro-orbital groove; e, eye; e_1e, cervical groove; ip, intercalated plate; P2–5, pereiopods 1 to 5; ps1–4, pleonal somites 1 to 4; PoA, post-orbital area. Scale bars =1cm. Photographs and line drawing J. Devillez.

Figure 3

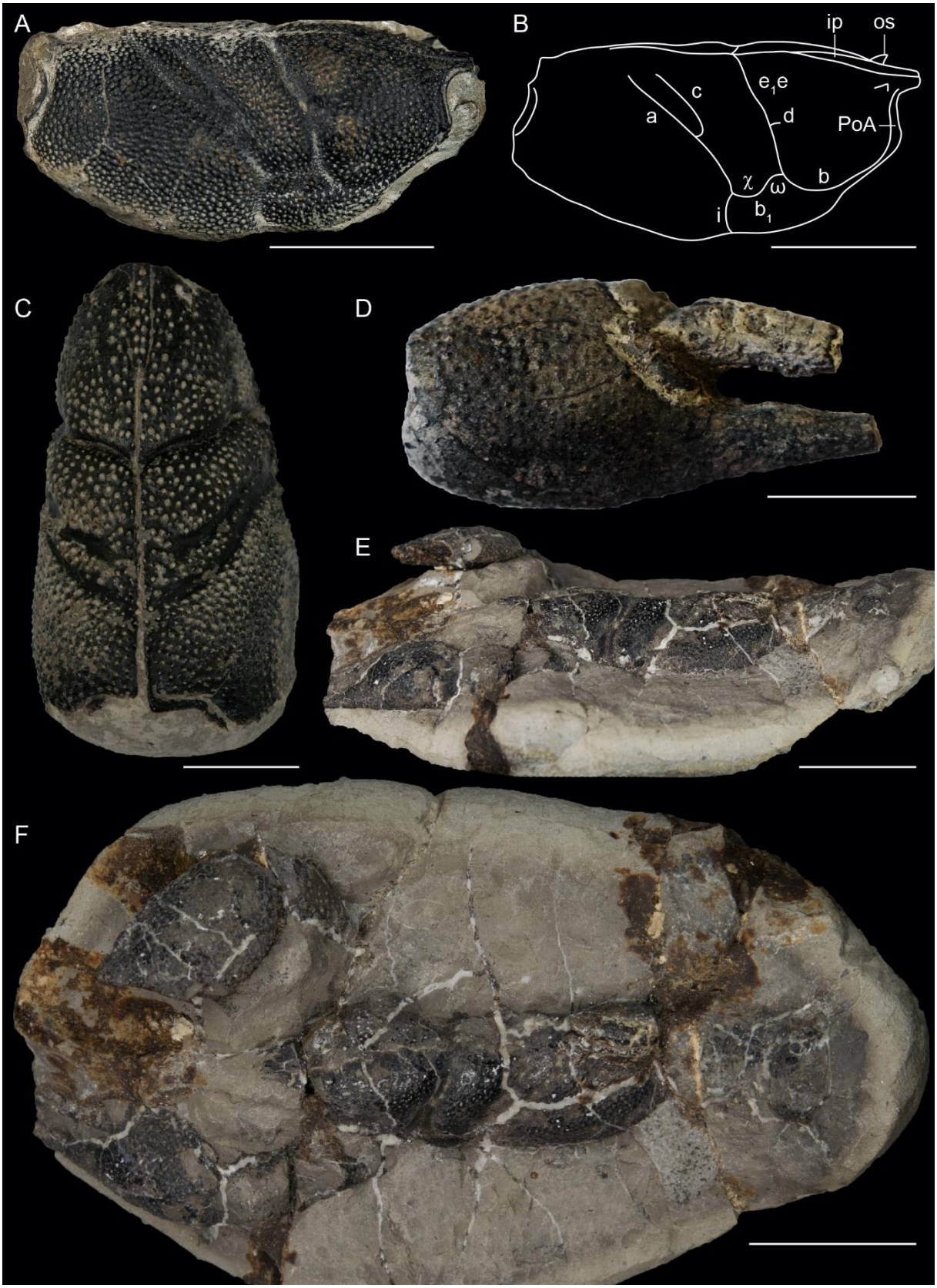

Figure 3. Additional specimens of *Eryma multicavatum* (Bell, 1863) comb. nov. specimen NHMUK In.27837 from the Hauterivian of Speeton (England). Lateral view (**A**) and line drawing showing all the carapace groove pattern (**B**); specimen SM B11438 from the Hauterivian of Speeton (England) (**C**); specimen MFN MB.A.2853 from the Hauterivian of Hilston (England) (**D**); unregistered specimen from the NHMUK collection: lateral (**E**) and dorsal view (**F**). a, branchiocardiac groove; b, antennal groove; b_1, hepatic groove; postcervical groove; d, gastro-orbital groove; e_1e, cervical groove; i, inferior groove; ip, intercalated plate; os, orbital spine; PoA, post-orbital area; χ, attachment site of adductor testis muscle; ω: attachment of mandibular muscle. Scale bars + 1cm. Photographs and line drawing J. Devillez.

Figure 4

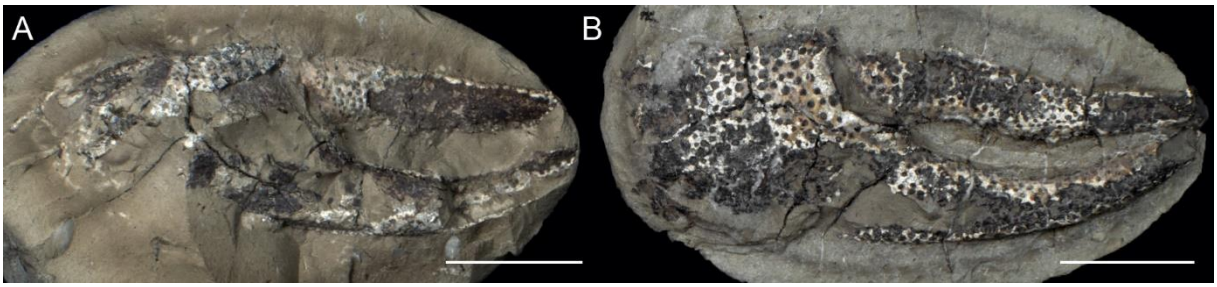

Figure 4. Isolated P1 chelae NHMUK 52081 of *Eryma* aff. *multicavatum* from the Hauterivian of Speeton (England). Scale bars = 1cm. Photographs J. Devillez.

TABLE CAPTION

Table 1. List of the specimens examined in the present work.

Species	Status	Collection number	Origin	Nature	Reference
Astacus multicavatus	Lectotype	NHMUK.In.61411	Speeton, UK	Original	Bell, 1863
Astacus multicavatus	Paralectotype	NHMUK.In.61410	Speeton, UK	Original	Bell, 1863
Eryma sulcatum	Neotype	SM.B11437	Speeton, UK	Original	Devillez *et al*., 2016
Eryma sulcatum	Lectotype	NHMUK.In.27305	Stadthagen, Germany	Cast	Devillez *et al*., 2016
Eryma sulcatum	Paralectotype	NHMUK.In.27307	Stadthagen, Germany	Cast	Devillez *et al*., 2016
Eryma sulcatum	Paralectotype	NHMUK.In.27308	Stadthagen, Germany	Cast	Devillez *et al*., 2016
Eryma sulcatum	Paralectotype	NHMUK.In.27309	Stadthagen, Germany	Cast	Devillez *et al*., 2016
Eryma sulcatum	Paralectotype	NHMUK.In.27310	Stadthagen, Germany	Cast	Devillez *et al*., 2016
Eryma multicavatum	Specimen	NHMUK.In.27837	Speeton, UK	Original	Devillez *et al*., 2016
Eryma multicavatum	Specimen	Unnumbered	?	Original	Herein
Eryma multicavatum	Specimen	SM.B11438	Speeton, UK	Original	Herein
Eryma multicavatum	Specimen	MFN.MB.A.2853	Hilston, UK	Original	Herein
Eryma aff. *E. multicavatum*	Specimen	NHMUK.52081	Speeton, UK	Original	Herein
Eryma aff. *E. multicavatum*	Specimen	NHMUK.52081	Speeton, UK	Original	Herein