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Systematic revision and palaeobiology of *Emplastron edwardsi* (Van Straelen, 1928) gen. et comb. nov. (Crustacea, Decapoda, Astacidae) entombed within travertine, from Sézanne, France

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Abstract. Crayfish are rare in the fossil record and therefore it is important to investigate each occurrence in detail. The only known fossil crayfish from France, *Astacus edwardsi* Van Straelen, 1928, is known from a replica made by pouring plaster of Paris inside the holotype (subsequently destroyed), an external mould extracted from a travertine cavity from the Thanetian of Sézanne. An evaluation of the taxonomic name, *A. edwardsi*, is provided; *A. edwardsi* is considered valid in accordance with ICZN rulings. It possesses atypical features for all other astacid genera, thus *Emplastron* gen. nov. is erected. *Emplastron edwardsi* gen. et comb. nov. inhabited a warm climate with calm waters, abundant food sources, and an ample supply of calcium carbonate: so much so that it is surprising that it is the only recovered specimen. Despite apparent North American faunal and floral affinities in the vicinity, *E. edwardsi* is more closely related to European crayfishes than it is to American ones.

Keywords: *Astacus edwardsi*, freshwater crayfish, palaeogeography, Sézanne, Thanetian, travertine

Introduction

Astacoidea Latreille, 1802 and Parastacoidea Huxley, 1879 (crayfishes) are diverse superfamilies of decapod crustaceans that have played a central role in biology for over 130 years since being proposed as a model organism (Huxley, 1880). Crayfishes likely diverged from marine lobsters (Nephropoidea Dana, 1852) during the Permian or Triassic, resulting in their radiation and dispersal before the breakup of Pangaea (Schram and Dixon, 2003; Porter *et al.*, 2005; Crandall and Buhay, 2008). Since they are almost entirely restricted to freshwater environments and devoid of a planktic larval stage, their dispersal potential is poor compared to that of marine lobsters. Therefore, they are good palaeogeographical indicators (Pârvulescu, 2019).

Of the two superfamilies, Astacoidea inhabits the Northern Hemisphere and Parastacoidea inhabits the Southern Hemisphere. Astacoidea contains four families (Crandall and De Grave, 2017): the extant Astacidae Latreille, 1802, Cambaridae Hobbs, 1942, Cambaroididae Villalobos, 1955 and the extinct Cricoidoscelosidae

Taylor *et al.*, 1999. The biogeography of extant astacid families is puzzling (see Dürš and Petrusek, 2015): *Pacifastacus* Bott, 1950 from western North America and Astacidae from Europe are united by their mutual lack of female spermatheca (*annulus ventralis*) and male coxal hooks, but they are separated geographically by the Cambaridae of eastern North America. Their relationships are also unclear: according to Breinholt *et al.* (2009), astacids and cambarids are more closely related to each other than they are to *Pacifastacus*; according to Bracken *et al.* (2009), conversely, astacids are more closely related to *Pacifastacus* than they are to cambarids.

Fossil data would help resolve these relationships, but fossil crayfishes are rare (Bell *et al.*, 2020). Herein we revise the only known fossil of *Astacus edwardsi* Van Straelen, 1928 from the upper Paleocene freshwater travertine deposits of Sézanne, France. Even at the time of its original description, its generic assignment was in doubt. It had been reported that contemporary continental European and North American faunas bore strong affinities (Dollo, 1923), which Van Straelen (1928) corroborated. We reinvestigate *A. edwardsi*, in light of recent

progress in freshwater crayfish systematics (notably the understanding that there are three astacid genera in Europe), and investigate whether this species might be related to North American genera, as suggested by Van Straelen (1928).

We demonstrate that *Emplastron edwardsi* gen. et comb. nov. is sufficiently dissimilar to all astacid genera to warrant the erection of *Emplastron* gen. nov., which seems to be more closely related to *Astacus* Fabricius, 1775, *Austropotamobius* Skorikov, 1907 and *Pontastacus* Bott, 1950 than it is to any other genus, placing it confidently within European astacids.

Geological setting

The holotype of *Emplastron edwardsi* gen. et comb. nov. was recovered by Ernest Munier-Chalmas in 1872 (see Vélain, 1889) from travertine beds situated in Sézanne (Marne department, France; see Van Straelen, 1928). These travertines were deposited in a river flowing in carbonate landscapes (Thanetian age: Van Straelen, 1928; Gingerich, 2000). This period was warmer than the current climate with evergreen broad-leaf forests present in the area and temperate conditions extending up to high latitudes (Mai, 1991; Scotese, 2000; Collomb *et al.*, 2008). The simoedosaurid choristoderan *Simoedosaurus lemoinei* Gervais 1877, representatives of other crustaceans, i.e., isopods (e.g., Milne-Edwards, 1866), insects (see Nel and Blot, 1990), molluscs, and plants indicative of a hot, humid, and probably tropical climate (Saporta, 1868; Langeron, 1899; Lapparent, 1964; Pentecost, 2005), coexisted.

Travertines are chemical deposits of calcium carbonate as calcite or aragonite that can occur in various bodies of waters (seepage, streams, rivers, and springs) (Pentecost, 2005). In the case of Sézanne, as reported by Ernest Munier-Chalmas (in Vélain, 1889), both springs and the river deposited the travertines (Vélain, 1889). The abundance of calcium carbonate in the water of the river and springs may well have come from dissolution of the surrounding chalk. The river bend was probably a meandering one, as banks do not display similar deposits: the northern bank is characterized by a bottom of pebbles, a sign of a fast flowing water; the southern bank is characterized by the deposition of travertines (Vélain, 1889), a sign of slower flow. Ernest Munier-Chalmas apparently recognized these deposits extending for over 2 km (see also the map in Lapparent, 1964) and supposed the river to end in the Rilly lake, as the deposits of this lake contain a similar fauna (Vélain, 1889). Note that the eponymous locality (Rilly-la-Montagne) of the Rilly lake is situated about 50 km north of Sézanne, and that Vélain (1889) indicated that further away the lake transitioned to the

'sea of sands', an epicontinental sea.

Material and methods

The holotype of *Astacus edwardsi* Van Straelen, 1928 (SU.Pal.2017.2.60) was an external mould, which Munier-Chalmas infilled with plaster of Paris (axiotype *sensu* Lucas and Harris, 2020) before he dissolved the surrounding limestone with hydrochloric acid to make a replica of the original morphology of the crayfish (Vélain, 1889). This axiotype is housed at Sorbonne University (SU).

The specimen was imaged with a digital single-lens reflex camera equipped with a 105 mm macro lens. In capturing photographic stills of the specimen, cross-polarised light was employed to avoid reflection of light on the surface of the specimen; images were combined using image stacking software to obtain a satisfactory depth of field (Bengtson, 2000; Haug *et al.*, 2011; Kerp and Bomfleur, 2011). Some of the images were variously coloured prior to the stacking process to produce microtopographical maps (see Sabroux *et al.*, 2019). The three-dimensional model was a product of 75 photographs that had been captured in natural, non-polarised light and combined with Agisoft LLC Agisoft PhotoScan. The model was then processed in MeshLab (Cignoni *et al.*, 2008), the open source system for processing and editing three-dimensional triangular meshes. Measurements were made on digital photographs using the image processing software ImageJ (Schneider *et al.*, 2012).

The terminology developed by Van Straelen (1925) and Tshudy and Sorhannus (2003) is followed wherever possible. The term cephalothoracic shield, and not carapace, is applied herein.

Systematic palaeontology

Order Decapoda Latreille, 1802
 Infraorder Astacida Scholtz and Richter, 1995
 Superfamily Astacoidea Latreille, 1802
 Family Astacidae Latreille, 1802
 Genus *Emplastron* gen. nov.

Type species.—*Astacus edwardsi* Van Straelen, 1928.

Diagnosis.—Cephalothoracic shield with well-developed anterior and posterior postorbital carinae; epistome without spine or ridge posterior to urinary orifice; wide rostrum flanked by well-marked lateral carinae without spines; subdorsal carinae extending on the shield (as far as it is possible to observe); postrostral carina raised above the cephalic area; postorbital carinae subdivided into anterior and posterior postorbital carinae; tergopleurae of pleonites 2-5 rounded.

Occurrence.—Travertine from Sézanne (Marne department, *circa* 100 km east of Paris, France).

Etymology.—(Gr. *Emplastron*), n. plaster-of-Paris.

Remarks.—*Emplastron edwardsi* gen. et comb. nov. was described based upon a single specimen, which had been recovered 56 years prior to the work of Van Straelen (1928) (see Munier-Chalmas, 1872). The study of this specimen is complicated due to the incomplete preservation of the axiotype. For instance, some structures that are invaluable for systematic placement (Hobbs, 1974) are not visible or preserved: the first maxilliped, the carpal hook on the pereopods, the first and second pleopods, and spermatheca. Some of these structures may have been lost to sparmicritisation, destructive activities of micro-organisms etching sparry carbonate rocks, e.g. in travertine, by cyanobacteria (see Bathurst, 1976; Kahle, 1977; Pentecost, 1978, 1992; Chafetz *et al.*, 1994). Furthermore, it is probable that some of these missing structures may be due to the casting process: the plaster of Paris might not have reached delicate structures, e.g. appendages. Further details may also have been obscured due over the years to abrasion of the plaster. Thus, Van Straelen (1928), considering the anatomical preservation, or lack thereof, was reticent to assign it to a genus and alluded to no characters in its generic assignment.

Nevertheless, *Emplastron* gen. nov. is ascribed to Astacoidea because it has a telson divided by a transverse suture (see Hobbs, 1974, p. 5). However, it would be a weakly substantiated assignment to rely on one distinguishing character, hence our decision to compare the specimen to all genera of Astacoidea and Parastacoidea.

Van Straelen (1928) considered the axiotype to have too few diagnostic characters preserved for a precise generic assignment. Therefore, he considered it to be an astacoid *a priori* based on its palaeogeographic considerations (a supposition, however logical, but without empirical evidence). Furthermore, of the three genera restricted to Eurasia and North America that had been described prior to his 1928 publication (*Astacus*, *Cambarus* Erichson, 1846 and *Cambaroides* Faxon, 1884), he considered his new species to be *Astacus*, again *a priori* and further to his original assumption, the modern-day distribution of which overlaps the locality where *Emplastron* gen. nov. had been recovered. Conversely, Van Straelen (1928) noted in addition that the continental fauna of the area at the time had North American affinities and that it might, consequently, belong to a North American genus. Freshwater crayfish taxonomy has, since then, been subject to splitting of both *Astacus* and *Cambarus*, which significantly complicates the assignment of *Emplastron edwardsi* gen. et comb. nov.

Since its first description, *Emplastron edwardsi* gen. et comb. nov. has never been studied in detail. Our revision

of the axiotype of *Emplastron edwardsi* gen. et comb. nov. and comparison with all genera led to a reconsideration of its generic assignment. Most characters listed by Van Straelen (1928) are common within Astacoidea: the rostrum is generally subtriangular, *Astacoides* Guérin-Méneville, 1839 being an exception. The triangular rostrum and the absence of conspicuous spines or tubercles on the cephalothoracic shield first exclude an assignment to *Cambaroides*, which exhibits a subrectangular rostrum and conspicuous tubercles on the cephalothoracic shield. *Orconectes* Cope, 1872, *Astacopsis* Huxley, 1879, *Cambarellus* Ortmann, 1905, *Procambarus* Ortmann, 1905, *Astacus*, *Pacifastacus*, *Barbicambarus* Hobbs, 1969, and *Emplastron* gen. nov. all possess marked anterolateral angles of rostrum. By contrast, other genera do not have such marked anterolateral angles of rostrum (see Hobbs, 1974). *Emplastron* gen. nov. is distinguished from: *Orconectes* by the absence of cephalothoracic spiniform tubercles (present in *Orconectes*); from *Cambarellus* and *Astacopsis* by the presence of a postrostral carina (absent in *Cambarellus* and *Astacopsis*); from *Procambarus* by postorbital carinae that do not taper anteromedially (tapering anteromedially in *Procambarus*); from *Barbicambarus* by the absence of posterior carinae (present in *Barbicambarus*). It probably also differs from *Astacopsis* by the presence of a telson with a transverse suture (thin line suggesting a suture in *Emplastron*, absent in *Astacopsis*); *Emplastron* gen. nov. is distinguished from all other astacids by the combination of a postrostral carina, postorbital carinae, and anterior and posterior subdorsal carinae. It differs from *Astacus* by the smooth surface between the postrostral and postorbital carinae (in *Astacus*, a groove lies longitudinally, inward from the postorbital carina). *Astacus* and *Emplastron* gen. nov. differ in other aspects: (1) the rostrum, anterior of the rostral anterolateral angle, is broad in comparison with *Astacus* (and most other genera of Astacoidea), the medial surface of the rostrum is convex, which is also atypical; (2) postrostral carina of *Astacus* adorns the anterior half of the rostrum, whereas it adorns the posterior half in *Emplastron* gen. nov., extending beyond the posterior margin of the postorbital carinae; (3) the eye to ocular incision ratio in *Astacus* is *circa* 1:1, as opposed to *circa* 6:1 in *Emplastron* gen. nov. (see Hobbs, 1974, p. 8–27). *Emplastron* gen. nov. also differs from *Austropotamobius* by its paired subdorsal carinae and postrostral carina (single subdorsal carina and no postrostral carinae in *Austropotamobius*). It also differs from *Pontastacus* by its postrostral carina not visible on the rostrum, but further back (present on the rostrum but not further back in *Pontastacus*) and the paired subdorsal carinae (single subdorsal carina in *Pontastacus*). For all these reasons, we erect the new genus *Emplastron* to accommodate *Astacus edwardsi* Van Straelen, 1928.

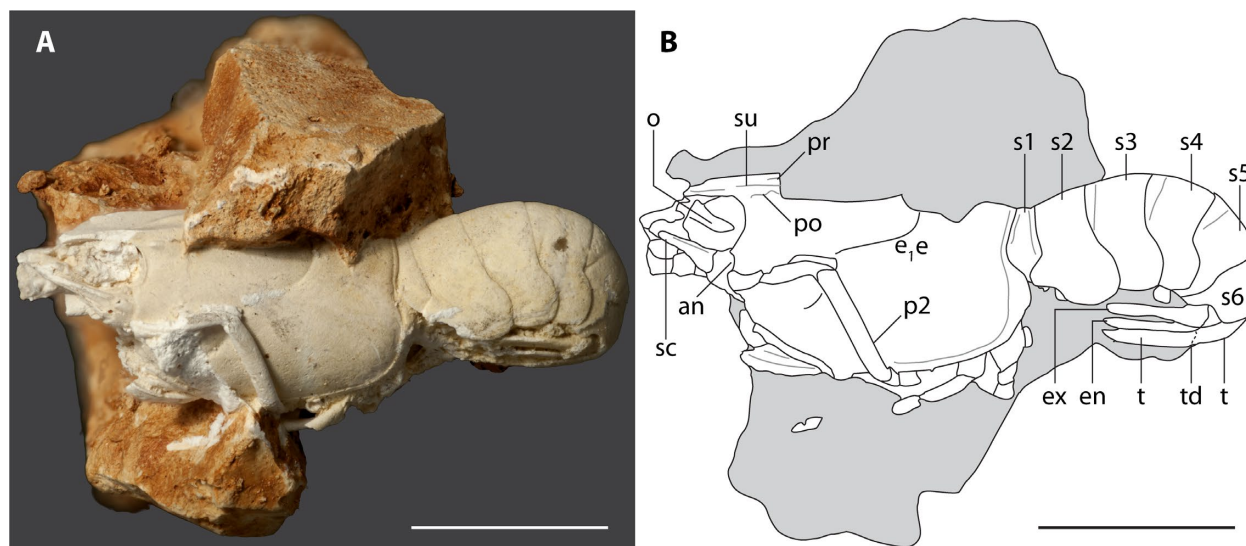


Figure 1. Lateral view of *Emplastron edwardsi* gen. et comb. nov. (SU.Pal.2017.2.60). **A**, Photographic image; **B**, interpretive line-drawing of the lateral view. Abbreviations: an, antennal notch; e,e, cervical groove; en, uropodal endopod; ex, uropodal exopodite; o, eye; p2, second pereiopod (thoracopod 5); po, postorbital carina; pr, postrostral carina; s1-s6, pleonites 1-6; sc, scaphocerite; su, subdorsal carina; t, telson; td, telson diaeresis. Photo, D. Audo; interpretive line drawing, R. J. O'Flynn and D. Audo. Scale bars represent 10 mm.

Nevertheless, *Emplastron* gen. nov. seems to combine characters of *Austropotamobius*, *Astacus* and *Pontastacus*: the postrostral carina like *Austropotamobius* and *Pontastacus* (albeit in a different position in the case of *Pontastacus*) and the general shape of the rostrum of *Pontastacus* and the general shape of the rostrum of *Astacus*. This suggests that *Emplastron* gen. nov. is probably more closely related to these three European astacids than it is to other crayfishes.

Emplastron edwardsi (Van Straelen, 1928) comb. nov.

Figures 1–3

Astacus Munier-Chalmas, 1872, p. 166. [nomen nudum]

Astacus edwardsi Vélain, 1889, p. 870. [nomen nudum]

Astacus edwardsi Van Straelen, 1928, p. 4, pl. 1.

Astacus edwardsi Glaessner, 1929, p. 60.

Astacus edwardsi Lapparent, 1964, p. 105.

Astacus edwardsi Schweitzer *et al.*, 2010, p. 32.

Holotype (*axiotype* sensu Lucas and Harris, 2020).—SU.Pal.2017.2.60 from the Thanetian of Sézanne, Marne department, Grand Est region, northeastern France; see also discussion.

Description.—medium-sized crayfish, *circa* 11 mm total length of cephalothoracic shield (CL: from the ocular incision to the opposing margin). Cephalothoracic shield (carapace) globally smooth; pleon smooth.

Cephalothoracic shield approximately as wide as high, approximately twice as long as high (apex of rostrum

incompletely preserved). Short, straight rostrum, subtrap-
ezoidal with smooth lateral margins fringed by subdorsal
carinae and bearing no laterorostral spines. Dorsal sur-
face of rostrum slightly concave. Shallow ocular inci-
sion fringed by ocular carinae. Shallow antennal inci-
sion, smaller than ocular incision. Pterygostomian angle par-
tially obscured by pereiopod fragments. Curved ventral
margin of shield fringed by thin carinae, wider posteri-
orly. Posterior margin fringed by carinae, curving anteri-
orly to accommodate the insertion of pleon.

Shallow antennal groove extending obliquely from
the pterygostomian region toward the cervical groove,
largely obscured by a partially preserved pereiopod.
Cervical groove shallower ventrally, curved and extend-
ing obliquely on the shield, reaching medial line at CL.
Cephalic regions with prominent subdorsal, postorbital,
and postrostral carinae. Postrostral carina raised in the
cephalic region, not extending to the rostrum. Subdorsal
carinae extending from the lateral margin of the rostrum
as far as can be observed. Paired postorbital carinae pos-
terior to the ocular incision, immediately under the sub-
dorsal carina.

Epistome formed of a transverse bar with one tuber-
cle on either side located behind antennal insertion, with
anterior medial process.

Pleon subrectangular in dorsal view, narrows distally,
subequal in length of cephalothoracic shield includ-
ing rostrum, approximately as wide as cephalothoracic
shield. All pleonites smooth dorsally. Pleonite 1 shorter

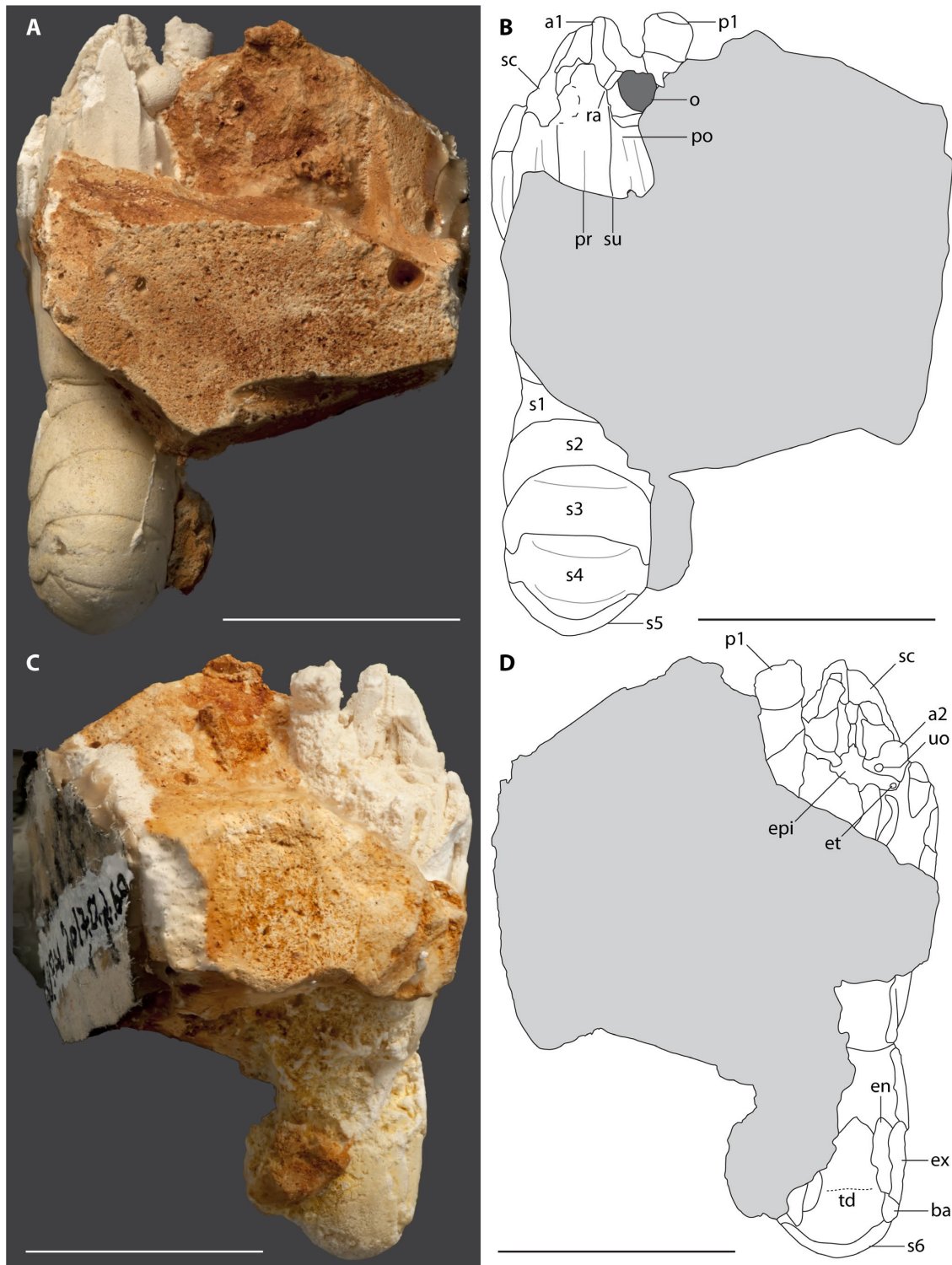


Figure 2. Dorsal and ventral views of *Emplastron edwardsi* gen. et comb. nov. (SU.Pal.2017.2.60). **A**, Photographic image in dorsal view; **B**, interpretive line drawing of the dorsal view; **C**, Photographic image in ventral view; **D**, interpretive line drawing of the ventral view. Abbreviations: a1, antennula; a2, antenna; ba, uropodal basipodite; en, uropodal endopodite; epi, epistome; et, epistome tubercle; ex, uropodal exopodite; o, eye; p1, first pereiopod (thoracopod 4); po, postorbital carina; pr, postrostral carina; ra, anterolateral angle of rostrum; s1-s6, pleonites 1-6; sc, scaphocerite; su, subdorsal carina; td, telson diaeresis; uo, urinary orifice. Photo, D. Audo; interpretive line drawing, R. J. O'Flynn and D. Audo. Scale bars represent 10 mm.

Table 1. Proportions in mm of the pleon as compared to the postorbital length of shield (carapace) of several males (left side) and females (right side) in Astacidae. Collection acronyms: ANSP CA, Academy of Natural Science of Philadelphia, Philadelphia, USA; MHNLM, Musée Vert/Natural History Museum of Le Mans, Le Mans, France; MNHN, Muséum national d’Histoire naturelle, Paris, France; NMPC, Národní Muzeum, Prague, Czech Republic; SU, Sorbonne University; USNM, National Museum of Natural History, Washington D. C., USA. Sources of data: *1, This work; *2, Kawai, 2018; *3, Kawai, 2016; *4, Kawai, 2012a; *Kawai, 2012b.

Species name	Specimen	Males			Specimen	Females		
		Postorbital Shield (carapace) Length	Pleon width	Ratio pleon width/ postorbital length		Postorbital Shield (carapace) Length	Pleon width	Ratio pleon width/ postorbital length
<i>Astacus astacus</i> *1	NMPC P6E 1511/2.3	33.7	19.2	0.57	NMPC P6E 1511/2.3	28.8	17.3	0.60
<i>Astacus astacus</i> *1	MNHN IU BA320	49.7	31.5	0.63	—	—	—	—
<i>Austropotamobius pallipes</i> *1	NMPC P6F6 4053	36.8	20.8	0.57	NMPC P6F6 4053	36.6	21.5	0.59
<i>Austropotamobius torrentium</i> *1	NMPC 6PE 1495	34.5	17.4	0.50	NMPC 6PE 1495	27.7	16.5	0.60
<i>Pacifastacus connectens</i> *3	USM 23096 Lectotype	34.7	20.2	0.58	USM 23096 Paralectotype	21.0	12.3	0.59
<i>Pacifastacus fortis</i> *3	USNM 44404 Lectotype	39.8	24.3	0.61	USNM 44404 Paralectotype	28.6	20.7	0.72
<i>Pacifastacus gambelii</i> *5	ANSP CA 306 Lectotype	33.6	18.0	0.54	USNM 117829	31.4	17.0	0.54
<i>Pacifastacus leniusculus</i> *2	USNM 2080 Syntype	49.3	28.8	0.58	USNM 2080 Syntype	33.0	24.3	0.74
<i>Pacifastacus nigrescens</i> *4	USNM 8954	46.3	25.1	0.54	USNM 4974	45.4	27.0	0.59
<i>Pontastacus leptodactylus</i> *1	NMPC P6 d-31/2003	50.2	28.6	0.57	NMPC P6 d-31/2003	41.2	27.5	0.67
<i>Pontastacus leptodactylus</i> *1	—	—	—	—	MHNLM 2010.9.3	55.2	33.7	0.61
<i>Pontastacus pachypus</i> *1	NMPC P6E 4940	36.9	20.7	0.56	NMPC P6E 4940	49.7	35.5	0.71
Mean value for extant specimens		40.5	23.1	0.57		36.2	23.0	0.63
<i>Emplastron edwardsi</i>	SU.Pal.2017.2.60	39.0	20.5	0.53				

than others, with tergopleuron covered by tergopleuron of pleonite 2; pleonite 2 with saddle-shaped tergopleuron; pleonites 3 and 4 tergopleura rounded and similarly shaped; pleonite 5 with tergopleuron hidden; pleonite 6 with reduced tergopleura, spine-like to accommodate uropods.

Telson subtriangular, tapering slightly posteriorly, approximately as wide as long, posterior margin poorly preserved; slight bend of telson, possibly corresponding to distal membranous part.

Large eyes in comparison with the cephalothoracic shield (diameter > CL), round with hemispherical cornea and short stalk. Antennula fragmentary. Antenna with coxa carrying distinct urinary orifice, basipod, ischium, merus, and carpus. Subtriangular scaphocerite reinforced by thick carina on outer lateral margin, slightly curved mesial inner margin. Maxilliped 3 (thoracopod 3) well developed, reaching anteriorly to partially preserved antennal peduncle. Basis of pereopod 1 subelongate, subrectangular. Fragmentary pereopods 5–8 and pleopods 1–5. Uropodal endopod and exopod with straight

outer margins.

Remarks.—The axiotype seems to be male: the width of the pleon compared to postorbital length differ substantially between male and female crayfishes (Kouba *et al.*, 2015; Pârvulescu, 2019). Female crayfishes require an enlarged pleon to carry a sufficient number of their large eggs. In the axiotype the ratio pleon width/postorbital length of cephalothoracic shield is very low (*circa* 0.53) compared to the mean ratio of males (0.57) and even more compared to that of females (0.63)—see Table 1.

The specimen does not present any traces of disarticulation between the cephalothorax and the pleon, suggesting it may well be a corpse, as opposed to an empty exuvia. However, we cannot exclude this last option because discarded exoskeletons of decapod crustaceans sometimes can close back and give the appearance of a whole animal (D. A. pers. obs.)

Discussion

Nature of the specimen

Due to the method by which the specimen was recovered and prepared, only a replica of the original external mould is available. In accordance with ICZN rulings, the name-bearing type can be ‘a natural replacement, natural impression, natural mould, or natural cast of an animal [*sic*]’ following ICZN (1999) article 72.5.3. The material attributed to *Emplastron edwardsi* gen. et comb. nov. used by Van Straelen (1928) is not a natural cast, but a replica made by pouring plaster of Paris inside the original external mould. Does this mean that *E. edwardsi* is devoid of a name-bearing type and/or worse that *Astacus edwardsi* Van Straelen, 1928 is an invalid taxonomic name? No: ‘an animal, or any part of an animal, or an example of the fossilized work of an animal, or of the work of an extant animal if the name based on it was established before 1931 [*sic*]’ following ICZN (1999) article 72.5.1 are eligible to be a name-bearing type. With *E. edwardsi*, a natural object used to exist. Furthermore, ICZN (1999) article 72.5.6 indicates that a type material can be initially based on an illustration or description, in which case the type material would be the physical specimen on which said depiction was based. In the case of the publication of *E. edwardsi* by Van Straelen (1928), deductive logic dictates that the holotype was the original external mould that was destroyed during extraction of the plaster cast we herein refer to as the name-bearing type (Vélain, 1889). Given the possibility that we consider the holotype lost, following what is arguably a contrived line of thought, we further argue that the replacement of said holotype by a natural specimen would not be recommended: ICZN (1999) article 75 states that a neotype is only justified to clarify the taxonomy, i.e., if insufficient diagnostic characters were available from the existing documentation. Such is not the case for *E. edwardsi*, which is satisfyingly documented by the cast and, hopefully, the present work. Another important point to consider is that in some cases, original physical specimens are destroyed for study, e.g. the case of fossils from the Herefordshire Lagerstätte (Sutton *et al.*, 2001; Siveter *et al.*, 2004), and that some ichnofossils can only be preserved as casts as it is sometimes impractical to recover large surfaces of rock (Lucas and Harris, 2020). For these reasons, we consider the original cast made by Ernest Munier-Chalmas directly from the natural specimen represent a good substitute to the *E. edwardsi* holotype, as it links the name to a physical specimen with substantial detail. On a side note, we also observe that casts of type specimens subsequently destroyed or lost (Audo *et al.*, 2020) are probably preferable to a neotype for nomenclatural stability, if they provide enough diagnostic characters. Therefore, we agree

with the evaluation of the ‘plastotype’ problem as stated by Lucas and Harris (2020) and refer herein to the plaster cast as an axiotype, a specimen which we in practice use as a holotype, but isn’t recognized by the code as such.

Palaeoecology

Crayfishes, as most reptantian decapods are not strong swimmers, the slow current of the south bank of the river (Vélain, 1889) was probably more suitable to *Emplastron edwardsi* gen. et comb. nov. than the faster flow of the northern bank. This environment was also favourable as *E. edwardsi* would have had good access to calcium for use in exoskeleton construction. The palaeoenvironment of Sézanne also provided numerous food sources for crayfishes in general: numerous insects, i.e. stinkbugs, dragonfly larvae, Diptera, Trichoptera (Nel and Blot, 1990), and numerous plants (Saporta, 1868; Lapparent, 1964). All these are known food sources for extant crayfishes (Arrignon, 1981; Kozák *et al.*, 2015; Thoma, 2016), for these reasons, the palaeoenvironment of Sézanne seems to have been ideal for crayfishes and it is surprising more specimens have not been recovered from the locality. Surprisingly too, no other fossil crayfish has been reported from travertine so far, with the possible exception of one specimen of *Austropotamobius*? from Kazakhstan (Pasini and Garassino, 2011), which could very well be a man-made curio from a petrifying spring. This latter specimen is indeed not fully entombed in the travertine as the name-bearing type of *E. edwardsi* was: it is covered by a thin layer of travertine deposit and lying beautifully, fully on the ventral side. Although this cannot be verified, it seems possible that this specimen was deliberately man-made.

Place of *Emplastron* gen. nov. within crayfish evolution and biogeography

At the time of the original description, Van Straelen (1928) was correct in assigning *Emplastron edwardsi* gen. et comb. nov. to Astacidae. More precisely, *Emplastron* gen. nov. appears to be more closely related to *Astacus*, *Austropotamobius* and *Pontastacus* than it is to any other genus; we do not see substantial evidence of cambarid affinities in *E. edwardsi*, which is not in accordance with the argument presented by Van Straelen (1928): no close relationship between eastern North American cambarid and European astacid crayfishes is evinced by the occurrence of *E. edwardsi* from the Thanetian of France, despite a warm temperate zone and close proximity of North America, Greenland, Scandinavia and the remainder of western Europe (see Scotese, 2000; Storey *et al.*, 2007). Breinholt *et al.* (2009) dated the radiations of Astacidae, Cambaridae, and Parastacidae at *circa* 153 Ma, *circa* 90 Ma, and *circa* 161 Ma, respectively. The presence of *E. edwardsi* is of Thanetian age (59.2–56.0 Ma: see Cohen *et*

al., 2013), after the initial split of Laurasia had begun (see Owen, 1976); therefore, its only known occurrence is at a time after *Pacifastacus*, *Astacus*, *Cambarellus* and *Orconectes* had already diversified (American and European crayfishes: see Breinholt *et al.*, 2009, fig. 1).

The recovery of *Emplastron edwardsi* gen. et comb. nov. provides additional data on crayfish diversity and diversification: the discovery of *E. edwardsi*, a lineage distinct from other astacids shows that European crayfishes were more diverse than had been considered previously. The specimen is important, but the recovery and reinvestigation of more fossil crayfishes is necessitated if the affinities between North American and European crayfishes are to be further explored.

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R. J. O. and D. A. wrote the manuscript with input from T. K. The figures were prepared by R. J. O. and D. A. All authors discussed and approved the manuscript.