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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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Systematic revision and palaeobiology of *Emplastron edwardsi* (Van Straelen, 1928)
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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 (consequently 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.

Key words: *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, 2004; Porter *et al.*, 2005; Crandall and Buhai, 2008). Since they are almost entirely restricted to freshwater environments and devoid of a planktic larval stage, their dispersion 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 astacoid families is puzzling (see Důřiš 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.*, in press). Herein we revise the only known fossil of *Astacus edwardsi* Van Straelen, 1928 from the Upper Palaeocene 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 fauna bore strong affinities (Dollo, 1923), which Van Straelen (1928) corroborated. We reinvestigate the degree to which *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, 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), Mollusca, and flora indicative of a hot, humid climate (Saporta, 1868: Langeron, 1899; Lapparent, 1964), probably tropical (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 (reported by Velain, 1889), both springs and the river deposited the travertines (Velain, 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 both banks did not display similar deposits: the north bank was characterized by a bottom of pebbles, sign of a fast flow of water; the southern bank is characterized by the deposition of travertines (Velain, 1889), sign of a slower flow. Ernest Munier-Chalmas apparently recognized these deposits spreading for over two km (see also the map in Lapparent 1964) and supposed the river to end in the Rilly Lake, as the deposits of this lake contains similar fauna (Velain, 1889). Note that the eponymous locality (Rilly-la-Montagne) of the Rilly lake is situated about 50 km north of Sézanne, and that Velain (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, 2019) 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 Bonfleur, 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 microorganisms 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 wears of the plaster. Thus, Van Straelen (1928), considering the anatomical preservation, or lack thereof, was reticent to assign it to a genus and eluded 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 enough for a precise generic assignment. Therefore, he considered it to be an astacoid *a priori* based on its

palaeogeographic considerations (i.e., 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, this species 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 exhibit 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). It 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 carinae in *Pontastacus*). For all these reasons, we erect the new genus *Emplastron* to accommodate *Astacus edwardsi* Van Straelen, 1928.

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 paired subdorsal carinae and 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 Van Straelen, 2010, Schweitzer *et al.*, p. 32.

Holotype (axiotype sensu Lucas and Harris, 2019).—SU.Pal.2017.2.60 from the Thanetian of Sézanne, Marne department, Grand Est region, North-eastern France; see also discussion.

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

(Cephalothoracic shield outline) Cephalothoracic shield approximately as wide as high, approximately twice as long as high (apex of rostrum incompletely preserved). Short, straight rostrum, subtrapezoidal with smooth lateral margins fringed by subdorsal carinae and bearing no laterorostral spines. Dorsal surface of rostrum slightly concave. Shallow ocular incision fringed by ocular carinae. Shallow antennal incision, smaller than ocular incision. Pterygostomian angle partially obscured by pereopod fragments. Curved ventral margin of shield fringed by thin carinae, wider posteriorly. Posterior margin fringed by carinae, curving anteriorly to accommodate the insertion of pleon.

(Cephalothoracic shield grooves and carinae) Shallow antennal groove extending obliquely from the pterygostomian region toward the cervical groove, largely obscured by a partially preserved pereopod. Cervical groove shallower ventrally, curved and extending 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 carina posterior to the ocular incision, immediately under the subdorsal carina.

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

(Pleon and telson) Pleon subrectangular in dorsal view, narrows distally, subequal in length of cephalothoracic shield including rostrum, approximately as wide as cephalothoracic shield. All pleonites smooth dorsally. Pleonite 1 shorter 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; tergopleura on 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.

(*Eyes and appendages*) 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 width of pleon/postorbital length of cephalothoracic shield is very low (*circa* 0.53) compared to the mean ratio of males (0.56) 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 (Siveter *et al.*, 2001; Sutton *et al.*, 2001), and that some ichnofossils can only be preserved as casts as it is sometimes impractical to recover large surfaces of rock (Lucas and Harris, 2019). 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 (2019) 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 (Arignon, 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 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 the Kazakistan (Pasini and Garassino, 2011), which could very well be a man-made curio from a petrifying spring. This later 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) estimated the Astacidae, Cambaridae, and Parastacidae radiation *circa* 153 Ma, *circa* 90 Ma, and *circa* 161 Ma, respectively. The presence of *E. edwardsi* is of Thanetian age (59.2-56 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 is to be further explored.

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References

- Arrignon, J., 1981: *L'écrevisse et son élevage*, 178 p. Gauthier-Villars, Paris. (in French)
- Audo, D., Schweigert, G. and Charbonnier, S., 2020: *Proeryon*, a geographically and stratigraphically widespread genus of polychelidan lobsters. *Annales de Paléontologie*, vol. 106, doi: 10.1016/j.annpal.2019.102376.
- Bathurst, R. G. C., 1976: *Carbonate Sediments and their Diagenesis, Developments in Sedimentology*, vol. 12, 658 pp., Elsevier, Amsterdam.
- Bell, P. R., Bickmell, R. D. C. and Smith, E. T., in press: Crayfish bio-gastroliths from Eastern Australia and the middle Cretaceous distribution of Parastacidae. *Geological Magazine*, doi: 10.1017/S0016756819001092.

- Bengtson, S., 2000: Teasing fossils out of shales with camera and computer. *Palaeontologica Electronica*, vol. 3, art. 4, p. 1–14.
- Bott, R., 1950: Die Flußkrebse Europas (Decapoda, Astacidae). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, vol. 483, p. 1–36, pls. 1–6.
- Bracken, H. D., Toon, A., Felder, D. L., Martin, J. W., Finley, M., Rasmussen, J., Palero, F. and Crandall, K. A., 2009: The decapod tree of life: Compiling the data and moving toward a consensus of decapod evolution. *Arthropod Systematic and Phylogeny*, vol. 67, p. 99–106.
- Breinholt, J., Pérez-Losada, M. and Crandall, K. A., 2009: The timing of the diversification of the freshwater crayfishes. In, Martin, J. M., Crandall, K. A., Felder, D. L. eds., *Decapod Crustacean Phylogenetics*, p. 343–355. Crustacean Issues, no. 18, CRC Press, Boca Raton.
- Chafetz, H. S., Srdoc, D. and Horvantincic, N., 1994: Early diagenesis of Plitvice Lakes waterfall and barrier travertine deposits. *Géographie physique et Quaternaire*, vol. 48, p. 247–256.
- Cignoni, P., Corsini, M. and Ranzuglia, G., 2008: MeshLab: an open-source 3D mesh processing system. *ERCIM News*, vol. 73, p. 47–48.
- Cohen, K. M., Finney, S. C., Gibbard, P. L. and Fan, J. 2013; updated: The ICS International Chronostratigraphic Chart. *Episodes*, vol. 36, p. 199–204.
- Collomb, F-M., Nel, A., Fleck, G. and Waller, A., 2008: March flies and European Cenozoic palaeoclimates (Diptera: Bibionidae). *Annales de la Société Entomologique de France*, vol. 44, p. 161–179.
- Cope, E. D., 1872: On the Wyandotte Cave and its fauna. *American Naturalist*, vol. 6, p. 406–422.
- Crandall, K. A. and Buhay, J. E., 2008: Global diversity of crayfish (Astacidae, Cambaridae, and Parastacidae—Decapoda) in freshwater. *Hydrobiologia*, vol. 595, p. 295–301.
- Crandall, K. A. and De Grave, S., 2017: An updated classification of the freshwater crayfishes (Decapoda: Astacidea) of the world, with a complete species list. *Journal of Crustacean Biology*, vol. 37, p. 615–653.
- Dana, J. D., 1852: Crustacea, *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U.S.N.*, vol 13., C. Sherman, Philadelphia, p. 1–685.
- Dollo, L., 1923: *Saniwa orsmaelensis*, varanidé nouveau de Landénien supérieur d’Orsmael (Brabant). *Bulletin, Société Belge de Géologie de Paléontologie et d’Hydrologie*, vol. 33, p. 76–82.

- Ďuriš, Z. and Petrusek, A., 2015: Evolution and historical biogeography of crayfishes. *In*, Kozák, P., Ďuriš, Z., Buřič, M., Horká, I., Kouba, A., Kozubíková-Balcarová, E. and Polícar, T. eds., *Crayfish Biology and Culture*, p. 39–58. Faculty of Fisheries and protection of waters, University of South Bohemia, Vodňany.
- Erichson, W. F., 1846: Uebersicht der arten der gattung *Astacus*. *Archiv für Naturgeschichte*, vol. 12, p. 86–103.
- Fabricius, J. C., 1775: *Systema Entomologiae, sistens Insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Flensbergi et Lipsiae [= Leipzig].
- Faxon, W., 1884: Descriptions of new species of *Cambarus*, to which is added a synonymical list of the known species of *Cambarus* and *Astacus*. *Proceedings of the American Academy of Arts and Sciences*, vol. 20, p. 107–158.
- Gingerich, P. D., 2000: Paleocene/Eocene boundary and continental vertebrate faunas of Europe and North America. *GFF*, vol. 122, p. 57–59.
- Gervais P., 1877 : Énumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine. *Journal of Zoology*, vol. 6, p. 74 –79. (*in French*)
- Glaessner, M. F., 1929: Crustacea decapoda. *In*, Pompeckj J. F. ed., p. 1–464. *Fossilium Catalogus I: Animalia*, vol. 41, W. Junk, Berlin.
- Guérin-Méneville, F. E., 1839: Nouveau genre de Crustacé macroure, établissant le passage entre deux familles, les Thalassiniens et les Astaciens. *Revue Zoologique, par la Société Cuvierienne*, vol. 1839, p. 108–109.
- Haug, C. Mayer, G., Kutschera, V., Waloszek, D., Maas, A. and Haug, J. T., 2011: Imaging and documentating gammarideans. *International Journal of Zoology*, vol. 2011, doi:10.1155/2011/380829.
- Hobbs, H. H. Jr., 1942: A generic revision of the crayfishes of the subfamily Cambarinae (Decapoda, Astacidae) with the description of a new genus and species. *American Midland Naturalist*, vol. 28, p. 334–357.
- Hobbs, H. H. Jr., 1969: On the distribution and phylogeny of the crayfish genus *Cambarus*. *In*, Holt, P. C. ed., *The distributional history of the biota of the southern Appalachians*, p. 93–178. Virginia Polytechnic Institute, Blacksburg, VA.

- Hobbs, H. H., 1974: Synopsis of the families and genera of crayfishes (Crustacea: Decapoda). *Smithsonian Contributions to Zoology*, vol. 164, p. 1–32.
- Huxley, T. H., 1879: On the classification and the distribution of the crayfishes. *Proceedings of the Zoological Society of London*, vol. 1878, p. 752–788.
- Huxley, T. H., 1880: *The Crayfish: An introduction to the study of zoology*, 371 p. C. Kegan Paul and co, London.
- ICZN 1999: *International Code of Zoological Nomenclature*. v-xxix, 1-306 p..International Trust for Zoological Nomenclature. Natural Museum, London.
- Kahle, C. F., 1977: Origin of subaerial Holocene calcareous crusts: role of algae, fungi and sparmicritization. *Sedimentology*, vol. 24, p. 413–435.
- Kawai, T., 2012a: Re-description of *Pacifastacus nigrescens* (Decapoda: Astacidae). *Crustacean Research, Special Number*, vol. 7, p. 77–85.
- Kawai, T., 2012b: Re-description of *Pacifastacus gambelii* (Decapoda: Astacidae). *Crustacean Research, Special Issues*, vol. 7, p. 61–70.
- Kawai, T., 2016: Re-examination of species in *Pacifastacus* subgenus *Hobbsastacus* (Decapoda: Astacidae). *Freshwater Crayfish*, vol. 22, p. 61–80.
- Kawai, T., 2018: Observation of museum specimen of genus *Pacifastacus* Bott, 1950 (Decapoda: Astacidae). *Nauplius*, doi: 10.1590/2358-2936e2018001.
- Kerp, H. and Bomfleur, B., 2011: Photography of plant fossils—New techniques, old tricks. *Review of Palaeobotany and Palynology*, vol. 166, p. 117–151.
- Kouba, A., Bůrič, M. and Petrussek, A., 2015: Crayfish Species in Europe. In, Kozák, P., Ďuriš, Z., Bůrič, M., Horká, I., Kouba, A., Kozubíková-Balcarová, E. and Polícar, T. eds., *Crayfish Biology and Culture*, p. 79–164. Faculty of Fisheries and protection of waters, University of South Bohemia, Vodňany.
- Kozák, P., Bůrič, M. and Kouba, A., 2015: Reproduction and life cycle. In, Kozák, P., Ďuriš, Z., Bůrič, M., Horká, I., Kouba, A., Kozubíková-Balcarová, E. and Polícar, T. eds., *Crayfish Biology and Culture*, p. 201–234. Faculty of Fisheries and protection of waters, University of South Bohemia, Vodňany.
- Lapparent, A. F. de., 1964: *Région de Paris. Excursions Géologiques et Voyages Pédagogiques*, 195 p. Herman, Paris. (in French)

- Langeron, M., 1899: Contributions à l'étude de la flore fossile de Sézanne. *Bulletin de la Société d'Histoire Naturelle d'Autun*, vol. 12, p. 1–27. (in French)
- Latreille, P. A., 1802: *Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs Sociétés savantes*, Vol. 3. F. Dufart, Paris. (in French)
- Lucas, S. G. and Harris, J. H., 2020: The “Plastotype problem” in ichnological taphonomy. *Ichnos*, vol. 27 (2), p. 107–110.
- Mai, D. H., 1991: Palaeofloristic changes in Europe and the confirmation of the Arctotertiary-Palaeotropical geofloral concept. *Review of Palaeobotany and Palynology*, vol. 68, p. 29–36.
- Milne-Edwards, A., 1866: Sur une nouvelle espèce de crustacé aquatique découvert de Sézanne. In, Saporta, G. de. eds., Prodrôme d'une flore fossile des Travertins anciens de Sézanne. *Mémoires de la Société Géologique de France*, t. 2, vol. 8, p. 426–427. (in French)
- Munier-Chalmas, E. C. P. A., 1872: Sur la faune des travertins de Sézanne. *Bulletin de la Société Géologique de France, deuxième série*, vol. 29, p. 166. (in French)
- Ortmann, A. E., 1905: The mutual affinities of the species of the genus *Cambarus*, and their dispersal over the United States. *Proceedings of the American Philosophical Society*, vol. 44, p. 91–136, pl. 3.
- Owen, H. G., 1976: Continental displacement and expansion of the earth during the Mesozoic and Cenozoic. *Philosophical Transactions of the Royal Society A*, vol. 281, p. 223–291.
- Nel, A. and Blot, P., 1990: Paléontologie de la paléotufière Éocène de Sézanne (Marne, France) (Insecta Odonata, Trichoptera, Hemiptera, Diptera). *Entomologica gallica*, vol. 2, p. 26–31.
- Pârvulescu, L., 2019: Introducing a new *Austropotamobius* crayfish species (Crustacea, Decapoda, Astacidae): A Miocene endemism of the Apuseni Mountains, Romania: *Zoologischer Anzeiger*, vol. 279, p. 94–102.
- Pasini, G. and Garassino, A., 2011: Unusual scaled preservation samples on freshwater decapods (Crustacea, Decapoda) from the Pleistocene (Late Cenozoic) of Turkey and Kazakhstan. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, vol. 152, p. 13–18.
- Pentecost, A., 1978: *Blue-green algae and freshwater carbonate deposits*. *Proceedings of the Royal Society B*, vol. 200, p. 43–61.

- Pentecost, A., 1992: Growth and distribution of endolithic algae in some North Yorkshire streams (UK).
British Phycological Journal, vol. 27, p. 145–151.
- Pentecost, A., 2005: *Travertine*, 446 p. Springer, Berlin.
- Porter, M. L. Pérez-Losada, M. and Crandall, K. A., 2005: Model based multi-locus estimation of decapod phylogeny and divergence times. *Molecular Phylogenetics and Evolution*, vol. 37, p. 355–369.
- Sabroux, R., Audo, D., Charbonnier, S., Corbari, L. and Hassanin, A., 2019: 150-million-year-old sea spiders (Pycnogonida: Pantopoda) of Solnhofen. *Journal of Systematic Palaeontology*, vol. 17, p. 1927–1938.
- Saporta, G. de., 1868: Prodrome d'une flore fossile des travertins anciens de Sézanne. *Mémoire de la Société Géologique de France*, vol. 8, p. 1–287. (in French)
- Schneider, C. A., Rasband, P. J. and Eliceiri, K. W., 2012: NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, vol. 9, p. 671–675.
- Scholtz, G. and Richter, S., 1995: Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zoological Journal of the Linnean Society*, vol. 113, p. 289–328.
- Schram, F. R. and Dixon, C., 2003: Fossils and decapod phylogeny. *Contributions to Zoology*, vol. 72, p. 169–172.
- Schweitzer, C. E., Feldmann, R. M., Garassino, A., Karasawa, H. and Schweigert, G., 2010: Systematic List of Fossil Decapod Crustacean Species: *Crustaceana Monographs*, vol 10, 1–222 p. Brill, Boston.
- Scotese, C. R., 2000: *Paleocene Climate*. [Online]. [Cited 25 January 2020]. Available from:
<http://scotese.com/paleocen.htm>
- Siveter, D. J., Sutton, M. D., Briggs, D. E. G. and Siveter, D. J., 2004: A Silurian sea spider. *Nature*, vol. 413, p. 978–980.
- Skorikov, A. S., 1907: Contributions à la classification des Potamobiidae d'Europe et d'Asia. *Annuaire du Musée zoologique de l'Académie Impériale de Sciences de St.-Pétersbourg*, vol. 12, p. 115–118. (in Russian)
- Storey, M., Duncan, R. A. and Swisher, C. C. III., 2007: Paleocene-Eocene Thermal Maximum and the Opening of the Northeast Atlantic. *Science*, vol. 316, p. 587–589.

- Sutton, M. D., Briggs, D. E. G., Siveter, D. J. and Siveter, D. J., 2001: Methodologies for the visualisation and reconstruction of three-dimensional fossils from the Silurian Herefordshire Lagerstätte. *Palaeontologia Electronica*, vol. 4 (1), art. 1, p. 1–17.
- Taylor, R. S., Schram, F. R. and Shen, Y., 1999: A new crayfish family (Decapoda: Astacidae) from the Upper Jurassic of China, with a reinterpretation of other Chinese crayfish taxa. *Paleontological Research*, vol. 3, p. 121–136.
- Thoma, R., 2016: The crayfish fauna of Canada and the United States in North America. In, Kawai T., Faulkes, Z. and Scholtz, G. eds., *Freshwater crayfish: A global overview*. p. 369–403. CRC Press, Boca Raton.
- Tshudy, D. and Sorhannus, U., 2003: *Hoploparia*, the best-known fossil clawed lobster (family Nephropidae), is a “wastebasket” genus. *Journal of Crustacean Biology*, vol. 23, p. 700–711.
- Van Straelen, V., 1925: Contribution à l'étude des Crustacés décapodes de la période jurassique. *Mémoires de la Classe des Sciences de l'Académie royale de Belgique*, vol. 7, p. 1–462. (in French)
- Van Straelen, V., 1928: *Astacus Edwardsi* Munier-Chalmas Ms., Astacidae du Paléocène de Sézanne (Champagne). *Bulletin de la Société Géologique de France, quatrième série*, vol. 28, p. 3–6, pl. 1. (in French)
- Vélain, M. C., 1889: Compte rendu de l'Excursion à Rilly-la-Montagne et à Sézanne. *Bulletin de la Société Géologique de France troisième série*, vol. 17, p. 868–870. (in French)
- Villalobos, A., 1955: *Cambarinos de la fauna mexicana: Crustacea Decapoda*. Departamento de Biología, Universidad Nacional Autónoma de México, Ciudad de México [translated by Hobbs, H. H. Jr. 1983. Crayfishes of Mexico (Crustacea: Decapoda). Smithsonian Institution Libraries and National Science Foundation, Washington DC].

Figure captions

Figure 1

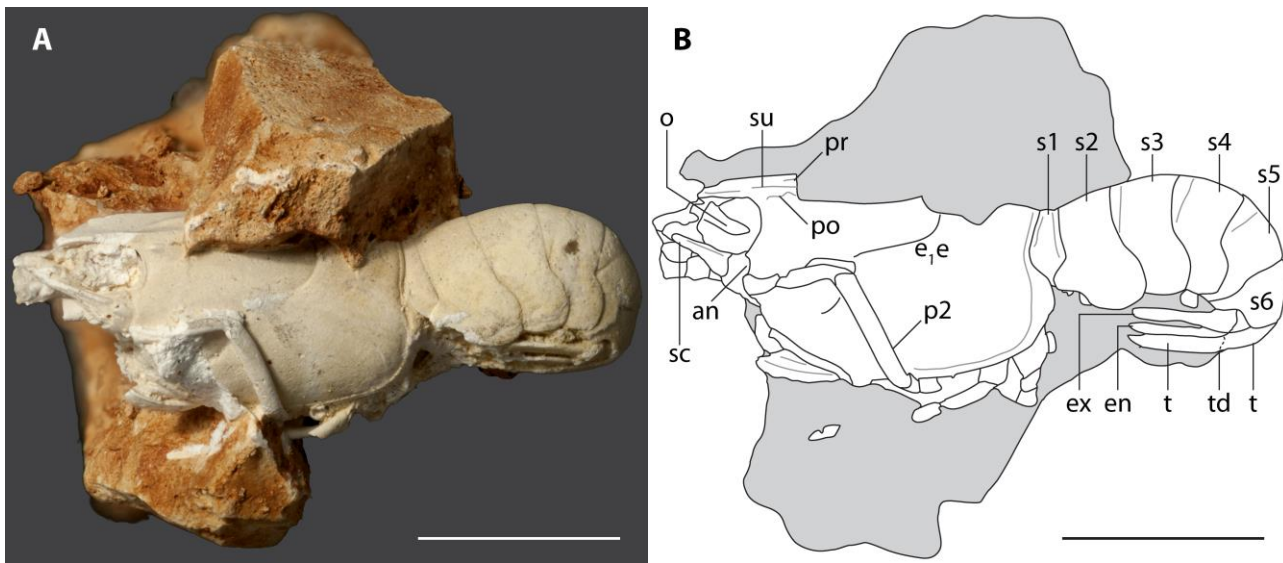


Figure 1. Lateral view of *Emplastron edwardsi* gen. et comb. nov. (SU.Pal.2017.2.60). A, Photographic image; B, interpretative line-drawing of the lateral view. Abbreviations: an, antennal notch; e₁e, cervical groove; en, uropodal endopod; ex, uropodal exopodite; o, eye; p2, second pereiopod (thoracopod 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; Interpretative line-drawing, R. J. O’Flynn and D. Audo. Scale bars represent 10 mm.

Figure 2

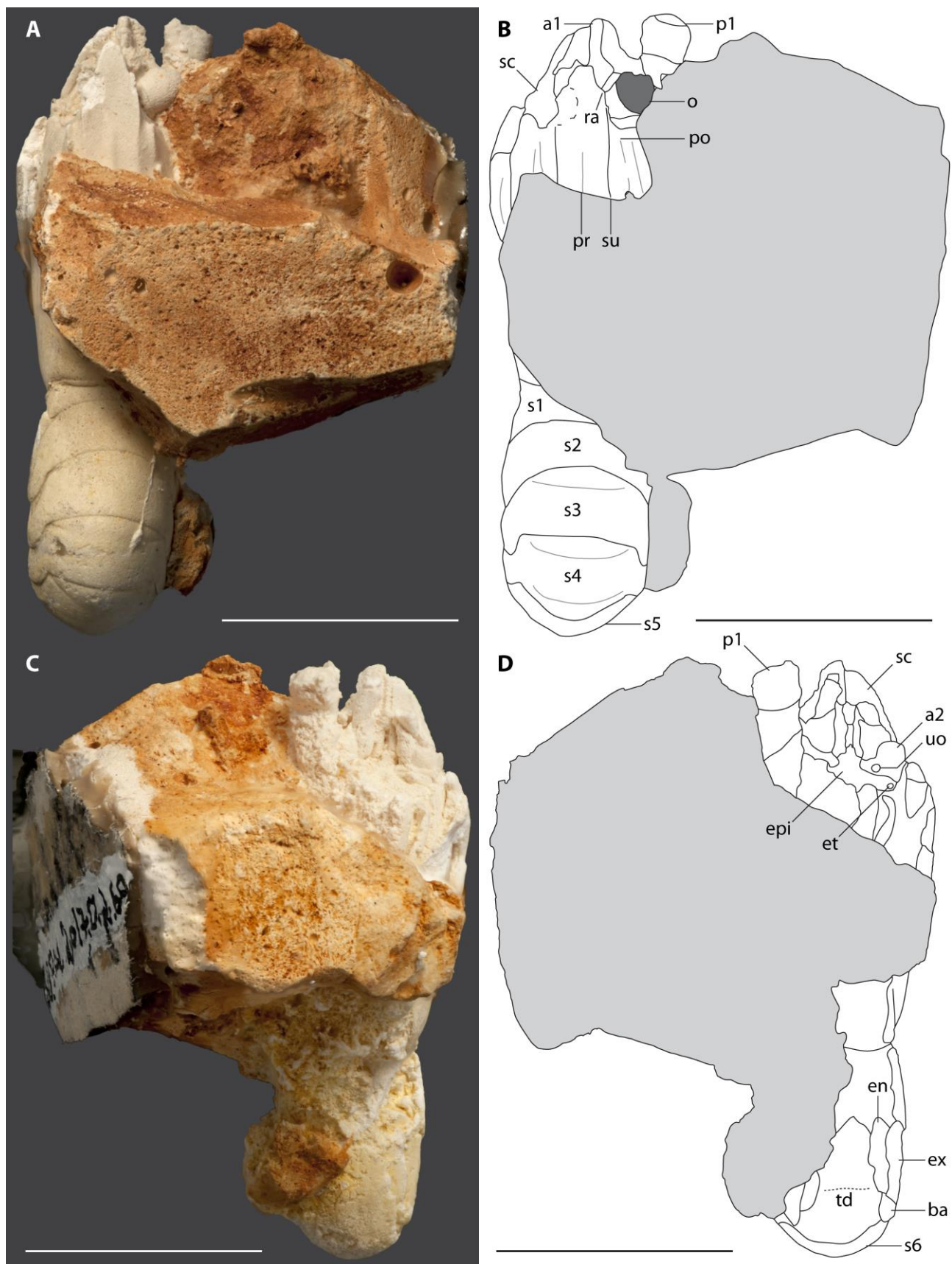


Figure 2. Dorsal and ventral views of *Emplastron edwardsi* gen. et comb. nov. (SU.Pal.2017.2.60). A, Photographic image in dorsal view; B, interpretative line drawing of the dorsal view; C, Photographic image in ventral view, D, and interpretative line drawing. Abbreviations: a1, antennula; a2, antenna; ba, uropodal

basipodite; en, uropodal endopodite; epi, epistome; et, epistome tubercle; ex, uropodal exopodite; o, eye; p1, first pereopod (thoracopod 4); po, postorbital carina; pr, postrostral carina; ra, anterolateral angle of rostrum; s1-s6, pleonites 1-6; sc, scaphocerite; su, subdorsal carina; t, telson; td, telson diaeresis; uo, urinary orifice.

Photo, D. Audo; Interpretative line-drawing, R. J. O’Flynn and D. Audo. Scale bars represent 10 mm.

Table caption

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) 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; MNHM, 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, T. This work; *2, T. Kawai 2018; *3, T. Kawai 2016; *4, T. Kawai 2012a; * T. Kawai 2012b.

| Species name | Males | | | Females | | | | |
|--|-----------------------|--------------------------------------|--------------|--|--------------------------|--------------------------------------|--------------|--|
| | Specimen | Postorbital Shield (carapace) Length | Pleon width | Ratio pleon width / postorbital length | Specimen | 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>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 |
| <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 leniusculus</i> *2 | USNM 2080 Syntype | 49.3 | 28.8 | 0.58 | USNM 2080 Syntype | 33 | 24.3 | 0.74 |
| <i>Pacifastacus connectens</i> *3 | USM 23096 Lectotype | 34.7 | 20.2 | 0.58 | USM 23096 Paralectotype | 21 | 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 nigrescens</i> *4 | USNM 8954 | 46.3 | 25.1 | 0.54 | USNM 4974 | 45.4 | 27 | 0.59 |
| <i>Pacifastacus gambelii</i> *5 | ANSP CA 306 Lectotype | 33.6 | 18 | 0.54 | USNM 117829 | 31.4 | 17 | 0.54 |
| Mean value for extant specimens | | 40.5 | 23.15 | 0.57 | | 36.24 | 23.03 | 0.63 |
| <i>Emplastron edwardsi</i> | SU.Pal.2017.2.60 | 39 | 20.5 | 0.53 | | | | |