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Large polychelidan lobsters with a rounded carapace from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte: taxonomic clarifications

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ABSTRACT
Polychelidan lobsters (Crustacea: Decapoda) are abundant in the celebrated Middle Jurassic (Callovian) Lagerstätte of La Voulte-sur-Rhône (Ardèche, France). Among them, *Eryon giganteus* Van Straelen, 1923, is recognized by its large, rounded carapace. The generic assignment of this species has been particularly complicated, with many conflicting assignments proposed since the first description of the species. The present study reinvestigates *E. giganteus* following the rediscovery of its lectotype. Careful examinations reveal that the type material is composite: the lectotype belongs to a species of eryonid that was described recently as *Cycleryon romani* Audo, Schweigert, Saint Martin & Charbonnier, 2014, and is quite rare (six specimens); the rest of the material, and most specimens formerly assigned to *E. giganteus* correspond to an abundant species of *Proeryon* Beurlen, 1928 (33 specimens) that we herein describe as *Proeryon charbonnieri* n. sp. The present study also allows us to reinvestigate the generic assignment of *E. giganteus*. Detailed observations allowed assigning *E. giganteus* to *Soleryon* Audo, Charbonnier, Schweigert & Saint Martin, 2014 based upon: the grooves marked across the dorsal part of carapace; a posterior carina near the posterior margin; and a hepatic carina between cervical and hepatic grooves. This taxonomic revision also leads to abandon *Proeryon zehentbaueri*, the replacement name which was proposed for *Proeryon giganteus* Beurlen, 1930.

KEY WORDS
Decapoda,
Eryonidae,
Coleiidae,
Callovian,
outcrop with exceptional preservation,
France,
lectotype,
new combination,
new species.

RÉSUMÉ
Les grands Polychelida à carapace arrondie du Jurassique moyen du Lagerstätte de La Voulte-sur-Rhône : clarifications taxonomiques.
Les Polychelida (Crustacea: Decapoda) sont abondants dans le célèbre Lagerstätte Jurassique moyen (Callovien) de La Voulte-sur-Rhône (Ardèche, France). Parmi eux, *Eryon giganteus* Van Straelen, 1923, est reconnaissable à sa grande carapace arrondie. L'assignation générique de cette espèce a été particulièrement complexe, de nombreuses assignations génériques contradictoires ayant été proposées. La présente étude révise cette espèce suite à la redécouverte de son lectotype. Un examen attentif du matériel type démontre qu'il est composite : le lectotype appartient à une espèce d'eryonidé assez rare (six spécimens connus) avec laquelle *Cycleryon romani* Audo, Schweigert, Saint Martin & Charbonnier, 2014 est mis en synonymie ; le reste du matériel type et la plupart des spécimens précédemment assignés à *E. giganteus* correspondent à une nouvelle espèce de *Proeryon* Beurlen, 1928 assez abondante (33 spécimens), ici nommée *Proeryon charbonnieri* n. sp. La présente étude nous permet également de résoudre l'assignation générique d'*E. giganteus*. Cette espèce est assignée à *Soleryon* Audo, Charbonnier, Schweigert & Saint Martin, 2014 en raison de ses sillons marqués sur toute la face dorsale de la carapace, sa carène postérieure près de la marge postérieure de la carapace et sa carène hépatique visible entre le sillon cervical et hépatique. Ces actes taxonomiques impliquent également l'abandon du nom de remplacement *Proeryon zehentbaueri*, qui avait été proposé pour *Proeryon giganteus* Beurlen, 1930.

MOTS CLÉS
Decapoda,
Eryonidae,
Coleiidae,
gisement à conservation exceptionnelle,
France,
lectotype,
combinaison nouvelle,
espèce nouvelle.

INTRODUCTION

The Callovian Lagerstätte of La Voulte-sur-Rhône (about 165 Ma, Ardèche, France) is celebrated because of its exquisitely preserved and diverse fauna dominated by arthropods (Etter 2002; Charbonnier 2009; Charbonnier *et al.* 2010, 2014). Among arthropods, polychelidan lobsters, a group of strange decapod crustaceans characterized by their four to five pairs of claws, are the third group in terms of abundance. The polychelidan lobster occurrence in La Voulte is important in the broader context of their evolutionary history. Indeed, it shows that fossil polychelidan lobsters were not limited to shallow-water environments. La Voulte is considered as a relatively deep marine palaeoenvironment (Charbonnier 2009, Charbonnier *et al.* 2007a, b, 2010), although one recent study questioned this reconstruction based on the occurrence of a species of nektobenthic visual predator, *Dollocaris ingens* Van Straelen, 1923 (Vannier *et al.* 2015).

Polychelidan lobsters in La Voulte are quite diverse, with seven species assigned to as many genera (Audo *et al.* 2014c). Most polychelidans are preserved within sideritic nodules, in volume (albeit slightly compressed), with an exquisite preservation of very fine structures such as ommatidia (Audo *et al.* 2016) and internal organs (Jauvion *et al.* 2016). However, in many cases, the nodules do not encompass the entire animal, and distal parts such as antennae, anterior and lateral parts of carapace, first pair of pereiopods, posterior part of pleon, telson and uropods are missing (Audo *et al.* 2014c). This situation slightly complicates the identification of some specimens, especially the larger ones, which are particularly affected by this phenomenon. Among these, two species of large rounded carapace occur in La Voulte. They are currently known as *Proeryon giganteus* (Van Straelen, 1923) and *Cycleryon romani* Audo, Schweigert, Saint Martin & Charbonnier, 2014. The first species, *P. giganteus*, is the most abundant species (33 specimens), the second one is more rare (six specimens). They belong to distinct families both confused and used in the description of *Eryon giganteus* Van Straelen, 1923, until Audo *et al.* (2014c) noticed the composite nature of the material and resulting reconstructions. Unfortunately, at the time of their review, Audo *et al.* (2014c) were not able to study the lectotype of *Eryon giganteus* considered to be missing or lost. This lectotype has recently been rediscovered by Sylvain Charbonnier (MNHN) in the palaeontological collections of the University Grenoble-Alpes, France. Our observations reveal that this specimen does not correspond to the species which many authors including Audo *et al.* (2014c) called *Coleia gigantea* or *Proeryon giganteus*. The present study focuses on: 1) reinvestigating the lectotype of *E. giganteus*; 2) addressing taxonomic consequence of the rediscovery of this name-bearing specimen; and 3) redescribing specimens that, due to the application of a specific name, are now found not to correspond to any described species.

MATERIAL AND METHODS

This study is based on the type material of three species: *Eryon giganteus* (one lectotype and nine paralectotypes) from the La Voulte Lagerstätte; *Cycleryon romani* (one holotype and three paratypes) also from the La Voulte Lagerstätte; *Proeryon giganteus* Beurlen, 1930 (holotype) from the Toarcian Holzmaden Lagerstätte.

In addition, we also review additional specimens from the La Voulte Lagerstätte which we consider to be conspecific with the paralectotypes of *Eryon giganteus*.

Most specimens from La Voulte are preserved within sideritic nodules, a few are, however, preserved flattened within the marl beds. The holotype of *Proeryon giganteus* Beurlen, 1930 is preserved flattened within bituminous marls.

Specimens from La Voulte were in general studied directly under a stereo microscope. When needed, they were imaged in cross-polarized or fluorescent lights (Bengtson 2000; Tischlinger & Arratia 2013) to enhance the contrast between the fossil and the surrounding sediment. The holotype of *P. giganteus*, being on permanent display in the Urwelt-Museum Hauff, was imaged across a glass using cross-polarized light from a flash, to avoid reflection on the glass (Haug & Haug 2011).

Specimens are stored in several palaeontological collections in: Université Claude Bernard, Lyon 1 (FSL, Lyon, France); Muséum national d'Histoire naturelle (MNHN.F, Paris, France); Staatliches Museum für Naturkunde Stuttgart (SMNS, Baden-Württemberg, Germany); Université Grenoble-Alpes (UJF-ID, Grenoble, France); Université Pierre et Marie Curie (UPMC, Paris, France); Urwelt-Museum Hauff (Holzmaden, Baden-Württemberg, Germany).

The carapace groove nomenclature is based upon Audo *et al.* (2014c).

SYSTEMATIC PALAEONTOLOGY

MALACOSTRACA Latreille, 1802
DECAPODA Latreille, 1802
PLEOCYEMATA Burkenroad, 1963
POLYCHELIDA Scholtz & Richter, 1995
ERYONOIDEA Haan, 1841
ERYONIDAE Haan, 1841
Soleryon Audo, Charbonnier, Schweigert & Saint Martin, 2014

Soleryon giganteus (Van Straelen, 1923) n. comb. (Fig. 1)

Eryon giganteus Van Straelen, 1923: 91, fig. 8 (*pro parte*). — Balss 1924: 175.

Coleia gigantea – Van Straelen 1925: 145-147, fig. 66, pl. 3, fig. 3 (non pl. 3 fig. 4, non pl. 4, figs 1-2). — Roman 1928: 109 (non fig. 18), pl. 3, fig. 1 (non fig. 4). — Glaessner 1929: 127.

Cyclocaris giganteus – Pinna 1968: 103.

Cycleryon gigantea (sic) – Fischer 2003: 241, fig. 27 (genus also misspelled *Glycerion* and *Cyclerion*).

Coleia sp. 1 – Charbonnier 2009: 159, 226, fig. 395. — Charbonnier *et al.* 2010: 115, 117.

Proeryon giganteus – Schweitzer *et al.* 2010: 44 (*pro parte*). — Not Audo *et al.* 2014c: 505-509, figs 2E, 6, 7.

Cycleryon romani Audo, Schweigert, Saint Martin & Charbonnier, 2014: 499, 500, figs 2C, 4. — Audo *et al.* 2016: table 3.

TYPE MATERIAL. — Lectotype, fixation by Van Straelen (1925): UJF-ID.14066 (Fig. 1A, B). Paralectotypes known to date include ten specimens: UJF-ID.11547, 11548, 11549 (part and counterpart), 11550, 11552, 14020, 14023, 14047-14049 (part and counterpart), 14051, 14052, 15050. All these paralectotypes belong to another species and must be excluded from this taxon (see below).

ADDITIONAL SPECIMENS. — Holotype of *Cycleryon romani* (Fig. 1C): FSL 170522 (coll. Marin, part and counterpart). — Paratypes of *C. romani*: UJF-ID.11546ab (coll. Gevrey, part and counterpart), MNHN.F.A50712 (coll. Fischer), SMNS 66652. — specimen MNHN.F.A50728 figured by Audo *et al.* (2014c: fig. 4f).

TYPE LOCALITY. — Ravin des Mines, near La Boissine, La Voulte-sur-Rhône Lagerstätte, Ardèche, Auvergne-Rhône-Alpes, France.

TYPE AGE. — Early Callovian, Gracilis ammonite Zone.

DESCRIPTION (emended from Audo *et al.* 2014c)

Carapace (cephalothoracic shield) outlines (Fig. 1D)

Dorsoventrally flattened carapace, subcircular in outline in dorsal view; concave frontal margin fringed by a row of small tubercles; small subquadrate anterolateral angle; spiny lateral margin, cut by ocular, cervical and hepatic incisions; subcircular ocular incision, slightly convex anterolateral margin, oblique relative to longitudinal axis, fringed by a few small spines and separated from the cervical incision by a large anterolateral cervical spine; cervical, and hepatic incisions opening in the anterior half of the lateral margin; deep and large subrectangular cervical incision; straight mediolateral margin, shorter than anterolateral margin and fringed by a few small spines; subrectangular and large hepatic incision, deeper than cervical incision; slightly convex posterolateral margin fringed with antrorse spines; subquadrate posterolateral angle not contiguous with the pleon; deep posterior margin slightly wider than anterior margin.

Carapace grooves and carinae (Fig. 1D)

Well-marked postrostral and postcervical carinae, not separated by the cervical groove; postrostral carina extending only on the posterior half of cephalic region, with two rows of tubercles connected anteriorly to a wide, roughly subtriangular area covered by coarse tubercles; postcervical carina with two rows of tubercles decreasing posteriorly in size; postorbital carina lacking or completely merged with branchial carina; branchial carina with a single row of tubercles, interrupted by the cervical groove, slightly farther from the median line in front of the cervical groove than behind the cervical groove, slightly sinuous behind the cervical groove, posteriorly forming an angle and extending obliquely toward the posterolateral angle; hepatic carina extending along hepatic groove and merging with branchial carina; posterior carina lying along the posterior margin between the branchial carinae; shallow cervical groove, extending from cervical incision to median line, not cutting the median line; shallow hepatic groove extending from the hepatic incision to the branchial carina; postcervical groove extending obliquely between branchial and postcervical carinae, curving forward (cardiac groove?) near the median line, not cutting the median line; short gastro-orbital groove, extending anteriorly to the cervical groove between the branchial and postrostral carinae; branchiocardiac groove extending posteriorly from the junction between the postcervical groove and the branchial carina, curving towards the median line in the posterior part of the carapace.

Pleon and telson
Pleon half as wide as carapace; subrectangular pleonite 1 slightly shorter than others and narrower than pleonite 2; pleonites 2 to 5 of decreasing in width; pleonites 2 and 3 each crossed by two transverse grooves converging medially, and an axial carina with anterior and posterior spines, cutting the posterior transverse groove; pleonite tergopleura 4 and 5 similar, spines on axial carina indistinct or absent; elongated pleonite 1 tergopleuron; poorly preserved pleonite 2 tergopleuron, with a small lateral process articulating with the carapace on its anterior margin at the beginning of tergopleuron; pleonite 2 tergopleuron with a small lateral process articulating with the preceding pleonite on its anterior margin at the beginning of the tergopleuron (poorly preserved in the available specimens); tergopleura of pleonites 3 and 4 also with similar small lateral processes and a concave margin; telson not preserved in available specimens.

Eyes and cephalic appendages
Eye entirely contained by the ocular incision; antennula with a short peduncle, a thin outer flagella (exopodite) and an endopodite formed by a first podomere characterized by its slightly distal margin wider than the proximal margin, a second subcylindrical podomere and a flagellum; antenna with a wide subtriangular basipodite carrying an elongated and fusiform scaphocerite (exopodite) with carinate margins and an endopodite with a trapezoidal first podomere, a subcylindrical second podomere and a multiarticulated flagellum. Lengths of flagella are unknown because they are not complete in any of our specimens.

Thoracic appendages
Large and chelate first pereiopod (P1); P1 propodus about as long as carapace; subtriangular P1 carpus; pereiopods 2 to 4 (P2-P4) not visible in the available specimens; achelate fifth pereiopod (P5).

Pleonal appendages
Not preserved or visible in the available specimens.

Ornamentation
Dorsal surface of carapace covered with thick tubercles on cephalic region (anterior to postrostral carina), covered with small tubercles on the rest of carapace. Tubercles scarce between branchial carinae.

Discussion

Van Straelen (1923) described *Eryon giganteus* based upon an unspecified number of syntypes. Subsequently, Van Straelen (1925: caption of pl. 3, fig. 3) designated one specimen as "type" (UJF-ID.14066), which, following ICZN (1999: art. 74.5) constitute a fixation of lectotype, other specimens then becoming paralectotypes.

In their recent revision, Audo *et al.* (2014c) noted that the lectotype of *Eryon giganteus* was missing. Therefore, their revision was only based upon the ten available paralectotypes and some new material, all clearly conspecific and which they ascribed to the *Proeryon* Beurlen, 1928.

Our reinvestigation of the lectotype UJF-ID.14066 shows that it differs clearly from all paralectotypes, including all material ascribed to *E. giganteus* by Audo *et al.* (2014c): 1) the cervical groove is straight medially and does not cut the median line (curved and cutting median line in paralectotypes); 2) a faint carina lies along the hepatic groove (no visible carina in the paralectotypes); 3) the postrostral carina is short preceded anteriorly by a flat, tuberculate area (postrostral carina longer, no major change in carapace ornamentation); 4) the median carina (postcervical carina for paralectotypes) is marked by a double row of tubercles (only one row in the paralectotypes); 5) the branchial carina curves obliquely towards the posterolateral angle (more straight in the paralectotypes); 6) the posterior carina extends along the posterior margin; and 7) and the posterior transverse groove on pleonites is cut by an axial carina at least on the second and fourth pleonites (broken on others; posterior transverse groove cuts median line in the paralectotypes). We can therefore conclude that the type material of *Eryon giganteus* is heterogenous.

The morphology of the lectotype of *Eryon giganteus* corresponds more closely to that of a member of Eryonidae (e.g. Fig. 2A, B) than that of Coleiidae Van Straelen, 1925 (e.g. Fig. 2C). Indeed, in the case of eryonids and of the lectotype, the cervical groove tends to be straight and does not cut the median line (Audo *et al.* 2014c). By contrast, in coleiids, the cervical groove cuts the median line deeply and is curved near the median line, as is the case in the paralectotypes, but not the lectotype. Three eryonids have been described from La Voulte: *Eryon ellipticus* Van Straelen, 1923, *Voulteryon parvulus* Audo, Schweigert, Saint Martin & Charbonnier, 2014, and *Cycleryon romani*. The lectotype is clearly distinct from *E. ellipticus* and *V. parvulus* by the shape of the branchial carina (divergent posteriorly on the lectotype, convergent in *E. ellipticus* and *V. parvulus*) and the shape of the median carina (anteriorly straight in the lectotype, anteriorly bifid in *E. ellipticus* and *V. parvulus*). It is also clearly distinguished from *V. parvulus* by its much larger size (carapace length superior to 100 mm for the holotype; between 9.1 and 10 mm for *V. parvulus*). It is, however, similar in every aspects to the specimens of *C. romani*. For this reason, we can infer that *C. romani* is a subjective junior synonym of *E. giganteus*.

The lectotype of *E. giganteus* preserves details that were more difficult to observe on the specimens assigned to the synonymous species *C. romani*. These details allow us to reinvestigate its generic assignment. *Eryon giganteus* has distinctly deep carapace grooves while they are very shallow, barely visible in all species of *Cycleryon* Glaessner, 1965 (Fig. 2A), *Knebelia bilobata* (Münster, 1839), *K. schuberti* (Meyer, 1836) (Audo *et al.* 2014b) and in *Eryon cuvieri* Desmarest, 1817. It possesses a posterior carina between the branchial carinae. This carina is also visible in *Soleryon amicalis* Audo, Schweigert, Saint Martin & Charbonnier, 2014 (Fig. 2B), *S. schorri* Audo, Schweigert, Saint Martin & Charbonnier, 2014, *Cycleryon propinquus* Schlotheim, 1822, but not in other *Cycleryon*, perhaps due to the thinness, poor preservation and strong compaction of many specimens. *E. giganteus* also possesses a hepatic carina merging with the branchial carina. This hepatic carina is visible in *Soleryon amicalis*, *S. schorri*, *E. ellipticus*, *E. sublevis* Carter, 1886,

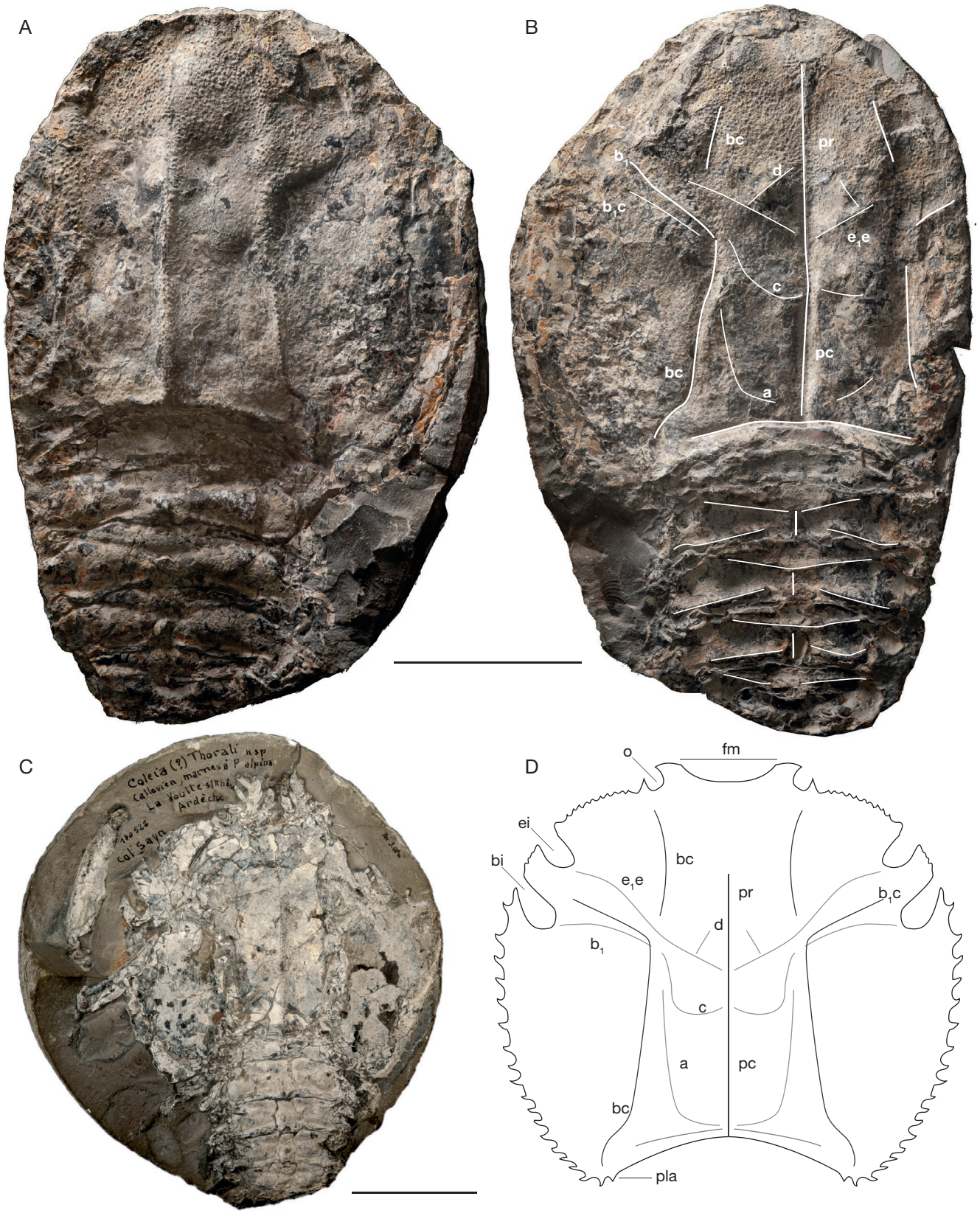

FIG. 1. — *Soleryon giganteus* (Van Straelen, 1923) n. comb. from the La Voulte Lagerstätte: **A**, **B**, lectotype UJF-ID.14066, dorsal view, under polarized light, part (**A**); and counter-part, with line-drawing of grooves and carinae (**B**); **C**, holotype of *Cycleryon romani* Audo, Schweigert, Saint Martin & Charbonnier, 2014 (FSL 170522), dorsal view, under polarized light; **D**, sketch of carapace outline, grooves and carinae adapted from Audo *et al.* (2014c). Abbreviations: **a**, branchiocardiac groove; **b_1**, hepatic groove; **b_1c**, hepatic carina; **bc**, branchial carina; **bi**, hepatic incision; **c**, postcervical groove; **d**, gastro-orbital groove; **e_1e**, cervical groove; **ei**, cervical incision; **fm**, frontal margin; **o**, ocular incision; **pc**, postcervical carina; **pla**, posterolateral angle; **pr**, postrostral carina. Scale bars: 50 mm. Images: D. Audo.

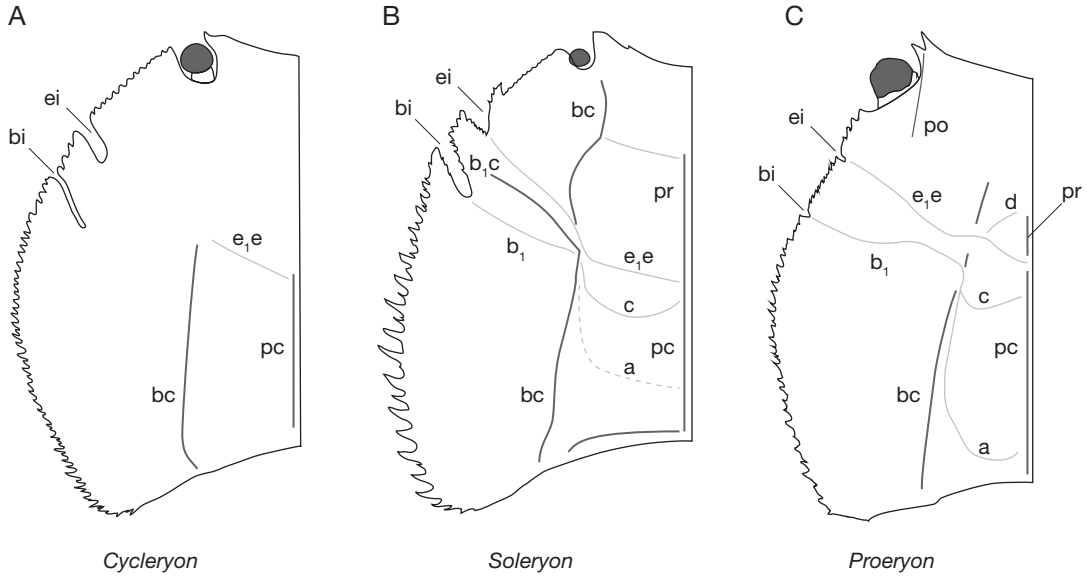

FIG. 2. — Comparison of the carapace shape of the type species of the three herein discussed genera: **A**, *Cycleryon propinquus* (Schlotheim, 1822); **B**, *Soleryon amicalis* Audo, Schweigert, Saint Martin & Charbonnier, 2014; **C**, *Proeryon hartmanni* (Meyer, 1836). Abbreviations: **a**, branchiocardiac groove; **b_1**, hepatic groove; **b_1c**, hepatic carina; **bc**, branchial carina; **bi**, hepatic incision; **c**, postcervical groove; **d**, gastro-orbital groove; **e_1e**, cervical groove; **ei**, cervical incision; **pc**, postcervical carina; **po**, postorbital carina. Illustrations not to scale.

and in *Voulteryon parvulus* – in which it seems to be replaced by a double row of tubercles. While none of these characters alone is diagnostic, they are consistent with an assignment to *Soleryon*. A more definitive proof would be to observe a notch at the tip of the telson, which is typical of *Soleryon* (Audo *et al.* 2014a). However, the telson is not preserved in any of the available specimens, since they are preserved in nodules that did not grow enough to encompass the telson. For these reasons, and in absence of specimens preserving the tip of the telson, we propose to assign *E. giganteus* to *Soleryon*.

COLEIIDAE Van Straelen, 1925
Proeryon Beurlen, 1928

Proeryon charbonnieri n. sp.
(Figs 3-5)

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Eryon giganteus Van Straelen, 1923: 91, fig. 8 (*pro parte*). — Balss 1924: 175.

Coleia gigantea – Van Straelen 1925: 145-147, fig. 66, pl. 3, figs 4 (non fig. 3), pl. 4, figs 1-2. — Roman 1928: 109, fig. 18, pl. 3, fig. 4 (non fig. 1). — Glaessner 1929: 127. — Charbonnier 2009: 158-159, 163, figs 236, 244, 224-229, 393, 394, 399-401. — Charbonnier *et al.* 2010: 115-117, figs 3c, 4c, 11a-c (*pro parte*).

Cyclocaris giganteus – Pinna 1968: 103.

Cycleryon gigantea (sic) – Fischer 2003: 241, fig. 27 (genus also misspelled *Glycerion* and *Cyclerion*).

Proeryon giganteus – Schweitzer *et al.* 2010: 44 (*pro parte*). — Audo *et al.* 2014c: 505-509, figs 2E, 6, 7.

"*Coleia*" *gigantea* – Charbonnier *et al.* 2014: 375, table 1, fig. 4F.

ETYMOLOGY. — The specific epithet honors the French palaeontologist Sylvain Charbonnier, who recently rediscovered the lectotype of *E. giganteus* and published the first comprehensive study of the La Voulte-sur-Rhône Lagerstätte.

TYPE MATERIAL. — **Holotype**: UJF-ID 14023 (Fig. 3A-C). **Paratypes**: MSNM.i20703 (Fig. 3D); UJF-ID.11547, 11548-11549 (part and counterpart, Fig. 4B), 11550, 11552, 14020, 14051, 14052 (Fig. 4C); FSL 170603, 170607-170609 (coll. Marin), 710080; MNHN.F.A50714, A50716-A50719, A50726, A50741 (coll. Fischer, Fig. 4A), B11759 (Fig. 4D); MNHGr.PA.10203 (Fig. 4E), 10276; UPMC-248.

ADDITIONAL SPECIMENS. — FSL 170521, 170610 (coll. Caillet), 71081 (coll. Charbonnier), MNHN.F.A50713, A50727 (coll. Fischer), R03515 (cast); UJF-ID.14026, 14047-14049 (part and counterpart), 15050.

TYPE LOCALITY. — Ravin des Mines, near La Boissine, La Voulte-sur-Rhône Lagerstätte, Ardèche, Auvergne-Rhône-Alpes, France.

TYPE AGE. — Early Callovian, Gracilis ammonite Zone.

DESCRIPTION
Carapace (cephalothoracic shield) outlines (Fig. 5)

Dorsoventrally flattened carapace, pyriform in outline in dorsal view; slightly concave frontal margin; anterolateral angle forming a small spine oriented diagonally; spiny lateral margin, cut by ocular, cervical and hepatic incisions; hemicircular ocular incision, opening laterally; spiny and convex anterolateral margin, oblique compared to longitudinal axis; anterolateral spine as large as the other anterolateral spines; cervical and hepatic incisions opening in the anterior half of the lateral margin; marked, shallow cervical incision; straight mediolateral margin, slightly longer than anterolateral margin and fringed by a few small spines; subtriangular hepatic incision, shallower

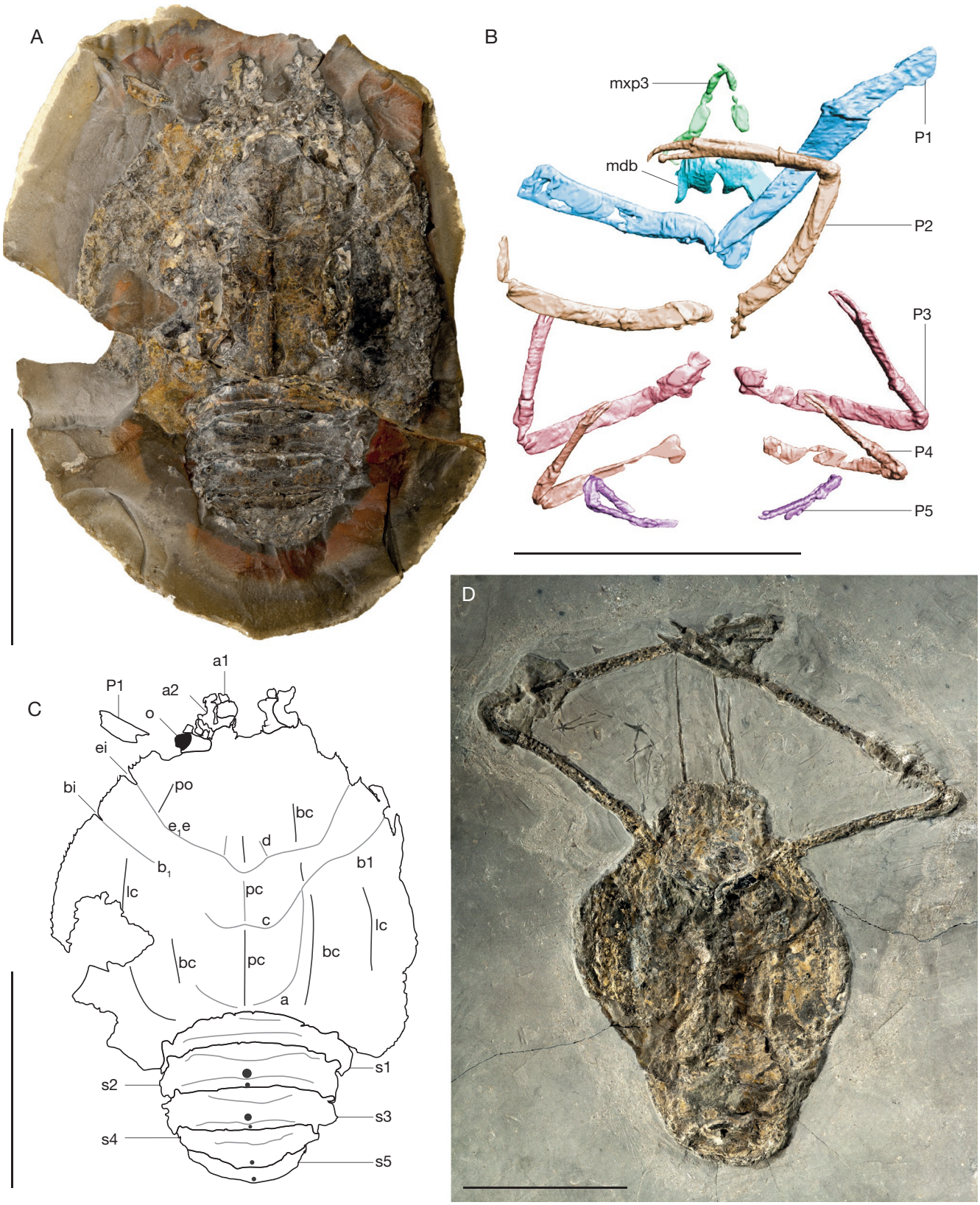

FIG. 3. — *Proeryon charbonnieri* n. sp. from the La Voulte Lagerstätte: **A**-**C**, holotype UJF-ID 14023 (former paralectotype of *S. giganteus* n. comb.); **A**, dorsal view, cross-polarized light; **B**, third maxillipeds and pereiopods, 3D model from CT-scan data, modified from Audo *et al.* (2014c); **C**, interpretative line-drawing; **D**, paratype MSNM i20703, dorsal view, cross-polarized light. Abbreviations: **a**, branchiocardiac groove; **a1**, antennula; **a2**, antenna; **b_1**, hepatic groove; **bc**, branchial carina; **bi**, hepatic incision; **c**, postcervical groove; **d**, gastro-orbital groove; **e_1e**, cervical groove; **ei**, cervical incision; **lc**, lateral carina; **mdb**, mandible; **mxp3**, third maxilliped; **o**, ocular incision; **P1-P5**, pereiopods 1 to 5; **pc**, postcervical carina; **po**, postorbital carina; **s1-s5**, pleonites 1 to 5. Scale bars: 50 mm. Images: D. Audo.

FIG. 4. — *Proeryon charbonnieri* n. sp. from the La Voulte Lagerstätte: **A**, paratype MNHN.F.A50741, dorsal surface, natural light (**A1**) and tail-fan (**A2**); **B**, paratype UJF-ID.11548-49 (former paralectotype of *S. giganteus* n. comb.), partial tail-fan, counterpart, cross-polarized light; **C**, paratype MNHN.F.B11759, dorsal surface, natural light; **D**, paratype UJF-ID.14052 (former paralectotype of *S. giganteus* n. comb.), dorsal surface, cross-polarized light, small-sized specimen; **E**, paratype MHNGr.Pa.10203, dorsal surface, natural light. Abbreviations: **a**, branchiocardiac groove; **b_1**, hepatic groove; **ba**, uropodal basipod; **di**, uropodal diaeresis; **e_1e**, cervical groove; **ei**, cervical incision; **ex**, uropodal exopod; **lc**, lateral carina; **o**, eye; **oph**, ophiuroid; **P1**, pereiopod 1; **s5-s6**, pleonites 5 to 6; **t**, telson. Scale bars: 20 mm. Images: **A1**, **A2**, Peter Massicard (E-Recolnat project); **B**-**D**, D. Audo; **E**, Noël Podevigne.

than cervical incision; curved posterolateral margin fringed with small spines; rounded posterolateral angle contiguous with pleon; slightly concave posterior margin wider than anterior margin.

Carapace grooves and carinae (Fig. 5)
Well-marked postrostral and postcervical carinae, separated by the deep cervical groove; marked postrostral carina, ornamented by a single row of large tubercles, extending only on the posterior half of the cephalic region; postcervical carina with a single row of large tubercles; marked postorbital carina, extending longitudinally from the ocular incision on half the length of the cephalic region, parallel to and not merged with branchial carina; long and straight branchial carina, ornamented with tubercles, interrupted by cervical and hepatic grooves, curving slightly inward at the junction with these grooves, extending to the posterolateral angle; lateral carina extending longitudinally between lateral margin and branchial carina on the branchial region; deep and oblique cervical groove, extending from the cervical incision to the median line, curving slightly posteriorly next to the median line, cutting deeply the median line in the middle of the carapace; deep hepatic groove extending transversally from the hepatic incision to the median line, cutting the branchial carina; curving slightly backward then forward (cardiac groove?) near its junction with the median line (not cutting the median line); shallow, short gastro-orbital groove, extending anteriorly to the cervical groove between the branchial and postrostral carinae; very shallow branchiocardiac groove, originating near the hepatic groove and the branchial carina junction, extending longitudinally along the branchial carina, curving in the posterior part of the carapace to join the median line without cutting it; long submarginal carina marked anteriorly, less so posteriorly, extending on the underside of carapace from the ventral margin near the third maxilliped (mxp3) ischium to the posterolateral angle.

Pleon and telson
Pleon slightly longer than carapace and half as wide as carapace; subrectangular pleonite 1 slightly shorter than others and narrower than pleonite 2; pleonites 2 to 5 of decreasing width, with subrectangular terga; pleonite 6 with subtrapezoidal tergum; pleonite 1 tergum with two transverse grooves converging medially; pleonites 2-6 terga with two transverse grooves converging medially, the anterior one being deeper and separated from the anterior margin by a slightly vaulted area, posterior one being close to the posterior margin; pleonite 1 with a subtriangular tergopleuron with a small lateral process articulating with the carapace posterior margin near the base of the tergopleuron; subtriangular pleonites 2 and 3 tergopleura with a spine in the middle of their lateral margin and a small lateral process articulating with the preceding pleonite near the base of the tergopleura; pleonites 4-6 tergopleura with a small lateral process articulating with the preceding pleonite near the base of the tergopleura, poorly preserved; subtriangular telson strengthened by two longitudinal carinae, with a slightly vaulted anterior region and a small distal groove.

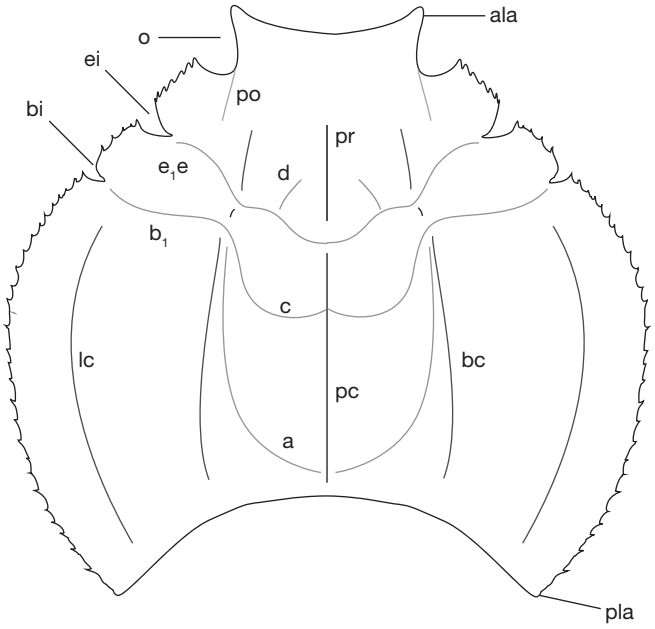

Fig. 5. — Sketch of carapace outline, grooves and carinae of *Proeryon charbonnieri* n. sp. Abbreviations: **a**, branchiocardiac groove; **ala**, anterolateral angle; **b_1**, hepatic groove; **bc**, branchial carina; **bi**, hepatic incision; **c**, postcervical groove; **d**, gastro-orbital groove; **e_1e**, cervical groove; **ei**, cervical incision; **lc**, lateral carina; **o**, ocular incision; **pc**, postcervical carina; **pla**, posterolateral angle; **po**, postorbital carina; **pr**, postrostral carina. Not to scale.

Eyes and cephalic appendages
Large eye with visual surface not entirely contained within ocular incision; quadrate ommatidia with a side measuring 77 to 90 µm (Audo *et al.* 2016); antennula with two flagella, one being at least ⅓ as long as carapace, poorly preserved in all available specimens; antenna comprising a basipodite carrying: 1) a subcircular scaphocerite (exopodite) with a finely spinose distal margin and ornamented by a few tubercles; and 2) an endopodite formed of a long flagellum (length > ⅔ carapace length) carried by two large podomeres, each with a short leaf-like expansion of their inner margin; mandible comprising a hemicircular incisor process forming uneven triangular teeth and a large triangular coxal body.

Thoracic appendages
Third maxilliped comprising a kidney-shaped ischium with a finely serrated inner margin (*crista dentata*) and four stocky podomeres; very long and slender first pereiopod (P1); very thin P1 dactylus and pollex; slender P1 propodus, as long as carapace and three times as long as dactylus; elongated P1 carpus; P1 merus almost as long as propodus, widening distally; short and curved P1 ischium; chelate pereiopods 2-5 (P2-P5) decreasing in size posteriorly; curved P2-P5 dactyli, twice shorter than their propodi.

Pleonal appendages
Elongated and falciform petasma (modified first pleopods of males); uropod comprising: 1) a subrectangular basipod carrying; 2) a wide exopod with a rounded distal margin, a lateral and a median longitudinal carina and an acutely curved diaeresis between these carinae; and 3) a wide endopod with a rounded distal margin, strengthened by a strong median carina which is distally indistinct.

Ornamentation
Densely tuberculate exoskeleton.

Discussion
Until the revision of the La Voulte polychelidans (Audo *et al.* 2014c), all large polychelidan lobsters with a rounded carapace were referred to *E. giganteus* (under various generic assignments). With the rediscovery of the lectotype of *E. giganteus*, we can now observe that the type material was not only composite, but that all paralectotypes belong to a separate species herein described as *Proeryon charbonnieri* n. sp. As explained in Audo *et al.* (2014c), the affinities of *P. charbonnieri* n. sp. have long been debated, in part due confusions with *E. giganteus*. Audo *et al.* (2014c), though mistakenly referring to this species as "*Proeryon giganteus*", justified the assignment to *Proeryon* based upon the following characters: anterolateral angle forming a small spine orientated laterally (more precisely, slightly obliquely); median carina on carapace distinctly cut by cervical groove; ocular incision opening laterally; cervical incision deeper than hepatic incision. We can add that the transverse groove on pleonites cut the axial carina, and that the diaeresis is distinctly curved. All these characters are shared with other species of *Proeryon*¸ notably its type species *Proeryon hartmanni* (Meyer, 1836) and species of two other closely allied genera, *Tethyseryon* Bravi, Garassino, Bartiromo, Audo, Charbonnier, Schweigert, Thévenard & Longobardi, 2014 and *Gabaleryon* Audo, Williams, Charbonnier & Schweigert, 2017. Among these species, *Proeryon charbonnieri* n. sp. resembles more closely species of *Proeryon*, based upon its rounded scaphocerite and the shape of its carapace. However, it distinctly differs from all other species of *Proeryon* by its conspicuously long and slender first pereiopods (stouter in all other species), a wider and more rounded carapace (also pyriform, but slightly more elongated in other species) and a lateral carina on the branchial region (no visible carina in other species).

Proeryon giganteus Beurlen, 1930

Proeryon giganteus Beurlen, 1930: 219-222, fig. 1, pl. 15. — Kuhn 1952: 156, fig. 1. — Garassino & Gironi 2006: 59.

Proeryon laticaudatus – Schweitzer *et al.* 2010: 44.

Proeryon zehentbaueri – Audo *et al.* 2014c: 508.

Type material. — Holotype by monotypy in the collections of Urwelt-Museum Hauff (Holzmaden, Germany), without collection number.

Type locality. — Holzmaden, Baden-Württemberg, Germany.

Type age. — Early Toarcian, Falciferum ammonite Zone.

Discussion
Schweitzer *et al.* (2010) considered *Proeryon giganteus* Beurlen, 1930 as a junior synonym of *P. laticaudatus* Beurlen, 1928. Audo *et al.* (2014c) disagreed with this synonymy and considered *P. giganteus* and *P. laticaudatus* to be separate species. As these authors assigned *Eryon giganteus* to *Proeryon* – based upon the paratypes herein excluded from type material, *Proeryon giganteus* Beurlen, 1930 was considered a secondary homonym of *P. giganteus* Van Straelen, 1923. The rediscovery of the lectotype of *E. giganteus* and the resulting new assignment of *E. giganteus* to *Soleryon* is that this species is no longer homonymous with *P. giganteus* Beurlen, 1930. Therefore, the replacement name *Proeryon zehentbaueri*, for *Proeryon giganteus* Beurlen, 1930 is abandoned (ICZN 1999: article 59.4).

CONCLUSION

The rediscovery of the lectotype of *Eryon giganteus* had a domino effect on the complicated and unstable taxonomy of the "large polychelidans with a rounded carapace" from La Voulte-sur-Rhône. Audo *et al.* (2014c) had already remarked that two species were mingled in the descriptions of these polychelidans, leading to a succession of conflicting generic assignments. Yet, Audo *et al.* (2014c) did not notice that the name *E. giganteus*, as defined by its lectotype, is not attached to the most iconic and abundant species of polychelidan in La Voulte, but rather to a rarer species probably belonging to the genus *Soleryon*.

The present case clearly stresses the possible consequences of the rediscovery of type material, and in this respect, is reminiscent of the rediscovery of the type material of *Eryon cuvieri* (see Charbonnier *et al.* 2012).

This rediscovery of the lectotype of *E. giganteus* will undoubtedly cause some confusion for the specialists and enthusiasts who have been or will be working on the fossil crustaceans from La Voulte. Indeed, the most abundant species was usually referred to as "*Eryon giganteus*" "*Coleia gigantea*" or "*Proeryon giganteus*". Now, the species *giganteus* is relegated to being a rather rare species (six specimens known to date, compared to 33 specimens of *P. charbonnieri* n. sp.). While such a change does not justify a decision of the International Commission on Zoological Nomenclature (ICZN), it still complicates understanding species discussed by previously-published researches, especially so as these two species from La Voulte had been confused for decades. The case of *Proeryon giganteus* Beurlen, 1930 is also confusing, albeit far less, as it was briefly known for another name for a few years.

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