A new look at the shrimps (Crustacea, Decapoda, Penaeoidea) from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte

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ABSTRACT
The Middle Jurassic La Voulte-sur-Rhône Lagerstätte yields fossils with remarkable morphological details. Those depict a highly diversified bathyal palaeocommunity dominated by arthropods. Amongst them, shrimps are very abundant. We hereby redescribe the two most abundant species of shrimps (Dendrobranchiata, Penaeoidea), *Aeger brevirostris* Van Straelen, 1923 (Aegeridae), and *Archeosolenocera straeleni* Carriol & Riou, 1991 (Solenoceridae). This leads us to consider *Antrimpos secretaniae* Carriol & Riou, 1991 as a junior synonym of *A. straeleni*. The latter is the only fossil representative of its family.

KEY WORDS
Solenoceridae,
Aegeridae,
Mesozoic,
Callovian,
France,
new synonyms.

RÉSUMÉ
Un nouveau regard sur les crevettes (Crustacea, Decapoda, Penaeoidea) du Lagerstätte de La Voulte-sur-Rhône (Jurassique moyen).
Le Lagerstätte de La Voulte-sur-Rhône (Jurassique moyen) livre des fossiles présentant des détails morphologiques remarquables. Ces fossiles dépeignent une paléocommunauté bathyale hautement diversifiée, dominée par les arthropodes. Parmi ceux-ci, les crevettes sont particulièrement abondantes. Nous redécrivons ici les deux espèces de crevettes (Dendrobranchiata, Penaeoidea) les plus abondantes, *Aeger brevirostris* Van Straelen, 1923 (Aegeridae), et *Archeosolenocera straeleni*, Carriol & Riou, 1991 (Solenoceridae). Ce travail nous amène à proposer la mise en synonymie d'*Antrimpos secretaniae* Carriol & Riou, 1991 avec *A. straeleni*. Cette dernière est la seule représentante fossile de sa famille.

MOTS CLÉS
Solenoceridae,
Aegeridae,
Mésozoïque,
Callovien,
France,
synonymes nouveaux.

INTRODUCTION

Shrimps are abundant and diverse in the fossil record (Schweitzer *et al.* 2010). However, the two most abundant species of penaeoidean shrimps (Dendrobranchiata, Penaeoidea) from the Konservat-Lagerstätte of La Voulte-sur-Rhône (Ardèche, France) have not captured a lot of attention from specialists. First described by Van Straelen (1922, 1923, 1925) as *Aeger brevirostris* Van Straelen, 1923 and *Antrimpos kiliani* Van Straelen, 1923, they were only briefly revised in a small paper by Carriol & Riou (1991). We propose herein a new revision of *Aeger brevirostris* (Aegeridae) and *Archeosolenocera straeleni* Carriol & Riou, 1991 (Solenoceridae).

La Voulte Biota

The fossiliferous deposits of the La Voulte Lagerstätte are dated from the Middle Jurassic (Callovian) based on ammonite biostratigraphy (Roman 1928; Elmi 1967, 1990). They consist in relatively thin interval of marls (thickness: *c.* 4-5 m) topped by iron ore bodies (thickness: *c.* 15 m). There are two types of fossil preservation: either in early diagenetic concretions within which they are three-dimensionally preserved or in surrounding marls where they are flattened and likely preserved in pyrite and phosphate. The La Voulte Lagerstätte is renowned for the exceptional preservation of a highly diverse decapod crustacean fauna (e.g., dendrobranchiate shrimps, astacidean, polychelidan, erymidan and glypheidean lobsters; Charbonnier *et al.* 2010, 2013). Other arthropod groups are also present in this locality such as thylacocephalans (Secrétan 1985; Vannier *et al.* 2006, 2016) and pycnogonids (Charbonnier *et al.* 2007b). Soft-bodied animals are also remarkably well preserved, including a rare octopod related animal (Wilby 2001; Etter 2002; Fischer 2003; Kruta *et al.* 2016), annelids, sipunculid worms, and hemicordates (Alessandrello *et al.* 2004). Very abundant echinoderms are present in the form of fully articulated brittle stars and multi-armed sea stars (Villier *et al.* 2009). Vertebrates are also reported, such as actinopterygian fishes, coelacanths, sharks, and a marine crocodile (Charbonnier 2009). The abundance of brittle stars indicates eutrophic conditions (Cartes & Sardà 1992), common in modern marine environments. Palaeogeographic reconstructions for the Callovian place the La Voulte locality along the western margin of the Tethys Ocean (Enay *et al.* 1993). It is depicted as a complex submarine palaeotopography of tilted blocks (Charbonnier *et al.* 2007a). Thus, the La Voulte palaeoenvironment was close to the slope-basin transition with a water depth most probably exceeding 200 m (Charbonnier *et al.* 2007a). Hydrothermal activity might have played an important role in the mineralization of soft tissues that probably occurred via diverse and complex pathways (Wilby *et al.* 1996). The La Voulte biota is a wonderful mine of information for the understanding of past marine deep environments, for it is one of the most complete and richest locality for the Mesozoic known to date (Charbonnier 2009).

MATERIAL AND METHODS

The entire material includes 42 specimens mainly preserved in nodules (some compressions are also considered). They were observed under binocular microscope and camera lucida drawings were made by the first author.

Abbreviations

Institutional abbreviations

FSL	Université Claude Bernard Lyon 1, Lyon;
MNHN	Muséum national d'Histoire naturelle, Paris;
UJF-ID	Observatoire des Sciences de l'Univers de Grenoble (ex Institut Dolomieu), Grenoble.

Morphological abbreviations

a1	antennula;
a2	antenna;
CH	carapace height;
CL	carapace length;
Mxp3	third maxilliped;
P1-P5	pereiopods 1 to 6;
s1-s6	pleonal somites 1 to 6.

SYSTEMATIC PALAEONTOLOGY

Class MALACOSTRACA Latreille, 1802
Order DECAPODA Latreille, 1802
Suborder DENDROBRANCHIATA Spence Bate, 1888

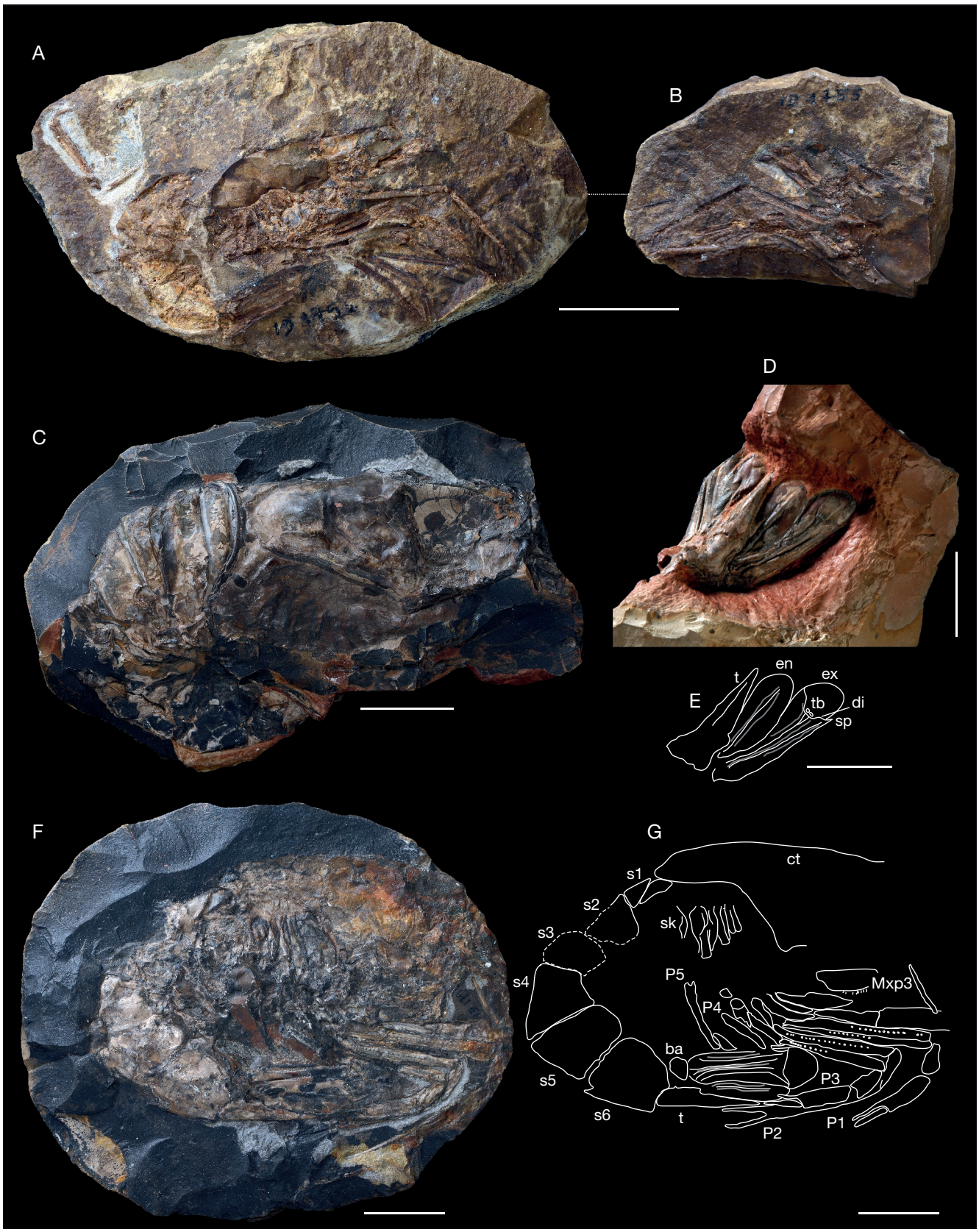


Fig. 1. — *Aeger brevirostris* Van Straelen, 1923 from the La Voulte Lagerstätte: **A**, **B**, specimen UJF-ID.1754-55 (lectotype; coll. Gevrey), right lateral view, part (**A**, UJF-ID.1755) and counterpart (**B**, UJF-ID.1754); **C**-**E**, specimen UJF-ID.14031 (paralectotype; coll. Gevrey), right dorsolateral view (**C**), detail (**D**) and line drawing (**E**); **F**, **G**, specimen UJF-ID.1790 (lectotype of *Antrimpos kiliani* Van Straelen, 1923; coll. Gevrey), right lateral view (**F**), line drawing (**G**). Abbreviations: **ba**, basipodite; **ct**, cephalothorax; **di**, diaeresis; **en**, uropodal endopod; **ex**, uropodal exopod; **Mxp3**, third maxilliped; **P1**-**P5**, pereiopods 1 to 5; **s1**-**s6**, pleonal somites 1 to 6; **sk**, endophragmal skeleton; **sp**, spine; **t**, telson; **tb**, tubercles. Photographs: **A**-**C**, **F**, L. Cazes; **D**, N. Podevigne. Line drawings: C. Jauvion. Scale bars: 20 mm.

Superfamily Penaeoidea Rafinesque, 1815

Family Aegeridae Burkenroad, 1963

Emended diagnosis by Tavares & Martin (2010). — Carapace lacking hepatic spine, but with postorbital spine. Rostrum with ventral tooth, dorsally unarmed. Third maxilliped hypertrophied. First pleomere somewhat reduced.

Remark

The presence of a ventral tooth on the rostrum should not be characteristic, since, according to Schweigert *et al.* (2016), the type species *Aeger tipularius* Schlotheim, 1822 does not display one. The lack of a hepatic spine is not clear since *Acanthochirana* Strand, 1928 and some species of *Aeger* display one.

Genus *Aeger* Münster, 1839

Aeger Münster, 1839: 64, 65.

Type species. — *Aeger tipularius* Schlotheim, 1822, by subsequent designation of Woods (1925). See Schweigert *et al.* (2016) for an updated revision of this species.

Emended diagnosis by Charbonnier *et al.* (2017). — Rostrum with one infrarostral spine; cervical groove steeply inclined, not joined to the dorsal margin, joined to antennal groove; oblique and sinuous branchiocardiac groove, crossing all the carapace from the posterior margin to the hepatic region; convex hepatic groove joined anteriorly to cervical groove and posteriorly to branchiocardiac groove; short inferior groove backward directed, not joined to ventral margin; hypertrophied Mxp3 with rows of movable spines; branch-like Mxp3 dactylus; chelate P1-P3 with chelae bearing movable spines on outer margins; achelate P4-P5, smooth; uropodal exopod with diaeresis.

Aeger brevirostris Van Straelen, 1923
(Figs 1; 2)

Aeger brevirostris Van Straelen, 1923: 87, fig. 4; 1925: 91-93, fig. 54, pl. 2, fig. 4. — Roman 1928: 108, fig. 14. — Förster 1967: 164; 1980: 84. — Carriol & Riou 1991: 149-151, fig. 2, pl. 2, fig. 4, pl. 3, figs 1-4. — Fischer 2003: 241, figs 25, 26. — Charbonnier 2009: 15, 17, 18, 158, 219, 221-223, figs 240, 383-386, 388, tables 14, 24, 25. — Schweitzer *et al.* 2010: 8. — Charbonnier *et al.* 2010: 115, 121, 123-125, 129, figs 4a, 9b, 10a-d, tables 1-4. — Robin *et al.* 2015a: 465, fig. 1c, d; 2015b: 490, fig. 1b.

Antrimpos kiliani Van Straelen, 1923: 84, 85 (partim), fig. 1; 1925: 67-70 (partim), pl. 1, figs 1, 2 (non fig. 3), pl. 2, fig. 2 (non fig. 1).

Aeger sp. – Van Straelen 1922: 982.

Archeosolenocera straeleni – Charbonnier *et al.* 2014: 375, 378, fig. 4d, table 1.

Type material. — Lectotype UJF-ID.1754-1755 (coll. Gevrey, part and counterpart) designated by Van Straelen (1925) (ICZN 1999: article 74.5); paralectotype UJF-ID.14031 (coll. Gevrey, figured by Van Straelen 1923: fig. 4).

Type locality. — Ravin des Mines, near La Boissine, La Voulte-sur-Rhône Lagerstätte, Ardèche, Rhône-Alpes, France.

Type age. — Early Callovian, Gracilis ammonite Zone.

Additional examined material. — *Aeger brevirostris*: UJF-ID.1757, 11561, 14060, (coll. Gevrey), MNHN.F.A58216, A58644, MNHN.F.R61852, R61853, R61854, R61855, R61856, R61857, R61858, R61859, R61860, R61862, R61863 (figured as *Archeosolenocera straeleni* by Charbonnier *et al.* 2014), R61865. — *Antrimpos kiliani*: lectotype UJF-ID.1790, paralectotypes UJF-ID.1789, 1792, 1924.

Description

Carapace

Subrectangular carapace (specimen MNHN.F.R61860, CL = 55 mm; CH = 29 mm); elongate, laterally flattened, dorsally smooth rostrum with one infrarostral spine medially; posterior margin dorsally concave with marginal ridge; anterior margin with deep antennal notch and shallow orbital one; straight dorsal margin; rimmed ventral margin; cervical groove steeply inclined, not joined to the dorsal margin, joined to short curved antennal groove; oblique and sinuous branchiocardiac groove, crossing all the carapace from the posterior margin to the hepatic region; very short inferior groove backward directed, not joined to ventral margin; almost straight hepatic groove joined anteriorly to cervical groove, and posteriorly to branchiocardiac groove; small hepatic spine near the junction between cervical and hepatic grooves; cephalic region with elongate postorbital spine.

Ornamentation of carapace

Smooth carapace.

Pleon

Subrectangular somites; s1 shorter than the others; s3 larger than the others; s1-s6 with smooth terga and pleura; rounded s1-s5 pleura; ventral margin of s1 pleuron with anterior process; s4 and s5 with posterior margin showing median articulation between s4-s5 and s5-s6 respectively; short and subquadrate s6; narrow, triangular telson with median longitudinal carina and acute distal extremity; telson shorter than uropods.

Cephalic appendages

Antennula (a1) with two long (*c.* carapace length) multi-articulated flagella; antenna (a2) with wider flagellum of undetermined length, long lamellar scaphocerite with dorsal longitudinal groove.

Thoracic appendages

Hypertrophied Mxp3 with rows of movable spines; branch-like Mxp3 dactylus; chelate P1-P3 with outer margins bearing a single row of spines; P2 longer than P1 and P3; achelate, smooth and slender P4-P5, shorter than P1-P3.

Pleonal appendages

Multi-articulated pleopods; uropods longer than telson with row of setae on distal margin; uropodal endopod shorter than uropodal exopod; uropodal endopod with longitudinal median carina flanked by longitudinal grooves; uropodal exopod with longitudinal median carina flanked by longitudinal grooves, the outer being deeper; uropodal exopod with

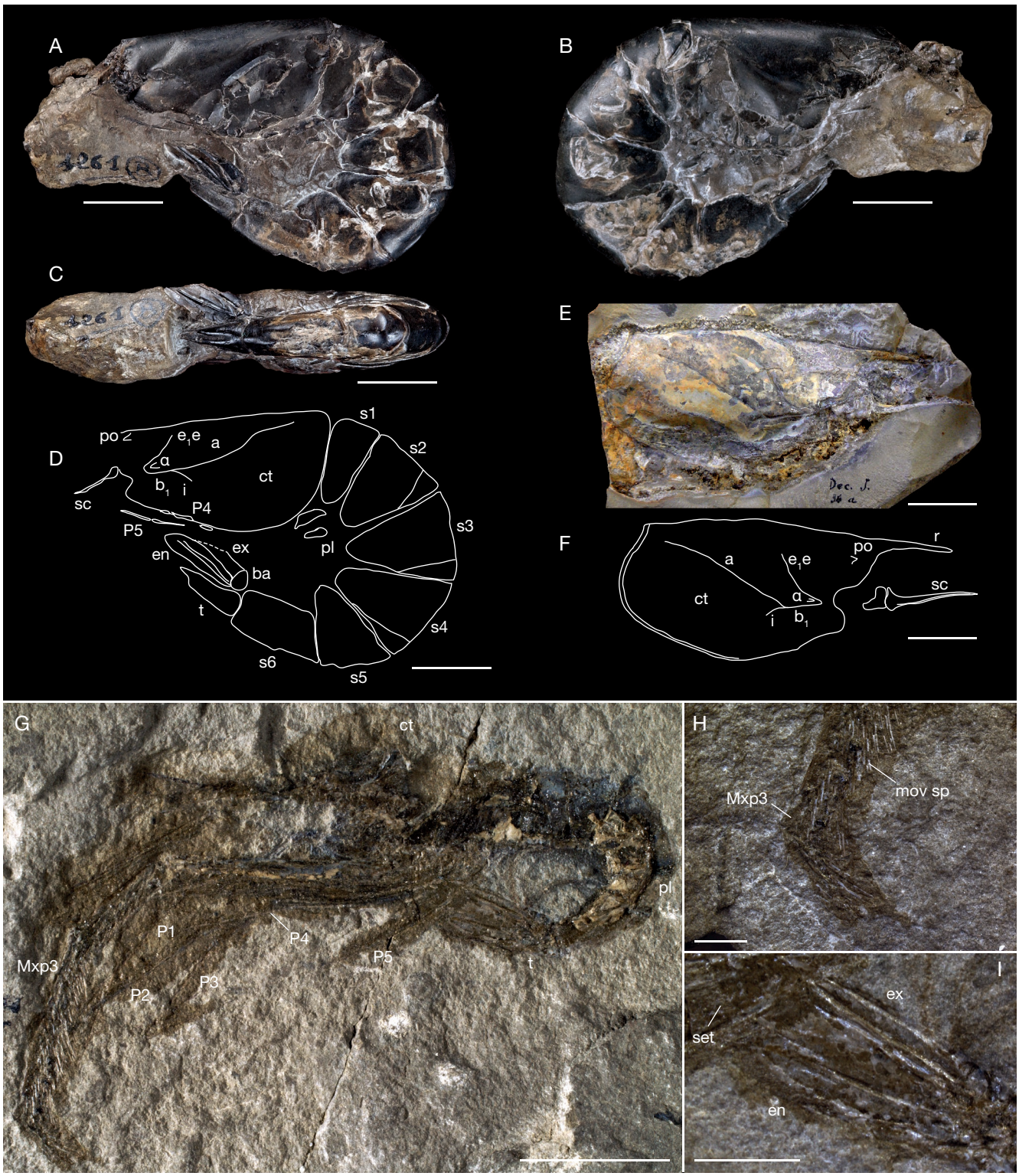


Fig. 2. — *Aeger brevirostris* Van Straelen, 1923 from the La Voulte Lagerstätte: **A**-**D**, specimen MNHN.F.R61863, left lateral view (**A**), right lateral view (**B**), ventral view (**C**), line drawing (**D**); **E**, **F**, specimen FSL 170532, right lateral view (**E**), line drawing (**F**); **G**-**I**, specimen MNHN.F.R61852, right lateral view (**G**), details (**H**-**I**). Abbreviations: **a**, branchiocardiac groove; **α**, hepatic spine; **b_1**, hepatic groove; **ct**, cephalothorax; **e_1e**, cervical groove; **en**, uropodal endopod; **ex**, uropodal exopod; **i**, inferior groove; **mov sp**, movable spines; **Mxp3**, third maxilliped; **P1**-**P5**, pereiopods 1 to 5; **pl**, pleon; **po**, postorbital spine; **r**, rostrum; **s1**-**s6**, pleonal somites 1 to 6; **sc**, scaphocerite; **set**, setae; **t**, telson. Photographs: **A**, **C**-**E**, N. Podevigne; **H**, **I**, C. Jauvion; **G**, P. Massicard (e-recolnat Project, MNHN). Line drawings: C. Jauvion. Scale bars: A-G, 10 mm; H, I, 2 mm.

crenel-shaped diaeresis showing one median pair of tubercles; outer margin of uropodal exopod confluent with diaeresis in strong distal spine.

Discussion

Van Straelen (1923) described *Antrimpos kiliani* based upon an undetermined number of type specimens from the Gevrey

collection. Actually, the original type material was composed of 24 specimens, and Van Straelen (1925) designated specimen UJF-ID.1790 as the lectotype (Fig. 1F). Later, Carriol & Riou (1991) identified it as *Aeger brevirostris* and synonymized *Antrimpos kiliani* with *Aeger brevirostris*. Our examination of the lectotype reveals Mxp3 with rows of spines, P1-P3 outer margins bearing a single row of spines, and P2 longer than P1 and P3 (Fig. 1F, G). All these characters are diagnostic of *Aeger brevirostris* and leads us to confirm the proposed synonymy. Moreover, three paralectotypes (UJF-ID.1789, 1792, 1924) are also representatives of *Aeger brevirostris*.

Family Solenoceridae Wood-Mason, 1891

Genus *Archeosolenocera* Carriol & Riou, 1991

Archeosolenocera Carriol & Riou, 1991: 145. — De Grave *et al.* 2009: 14. — Schweitzer *et al.* 2010: 9.

Type species. — *Archeosolenocera straeleni* Carriol & Riou, 1991, by monotypy.

Original diagnosis by Carriol & Riou (1991). — Rostre non bombé ventralement ; sillon cervical court ; sillon antennaire présent ; flagelles antennulaires longs d'environ la moitié de la carapace ; telson sans sillon dorsal médian.

Literal translation. — Rostrum ventrally not rounded; short cervical groove; antennal groove present; antennular flagella of approximately half the carapace in length; telson without median dorsal groove.

Emended diagnosis. — Laterally flattened rostrum with suprarostral spines; epigastric spine antennal and pterygostomian spines; inclined cervical groove, not joined to the dorsal margin; antennal groove, widening towards antennal notch; elongate, subhorizontal hepatic groove; inferior groove directed frontward; hepatic spine; postorbital spine; long, very thin and delicate P4-P5.

Discussion

Carriol & Riou (1991) placed *Archeosolenocera* within the Solenocerinae among the Aristeidae, but with unclear justification. Actually, their original diagnosis does not present any diagnostic characters (see literal translation above). Later, De Grave *et al.* (2009) placed *Archeosolenocera* within Aristeidae but without real justification. Schweitzer *et al.* (2010) followed this placement and indicated that Solenoceridae had no fossil representatives.

Our examination of the type material reveals that *Archeosolenocera* possesses anatomical characters typical of Dendrobranchiata Spence Bate, 1888 *sensu* Pérez Farfante & Kensley (1997), a subrectangular s2 not overlapping s1 pleuron, s1-s6 locked to each other by midlateral hinges, chelate P1-P3 (Figs 3; 4). The key to the two superfamilies of the Dendrobranchiata (Penaeoidea Rafinesque, 1815 and Sergestoidea Dana, 1852) proposed by Pérez Farfante & Kensley (1997) and updated by Tavares & Martin (2010) is based upon gill characters, which are not visible on fossil specimens. However, *Archeosolenocera* cannot be assigned within Sergestoidea due to its elongate rostrum (short in sergestoid shrimps, Figs 3-5), its well-developed antennular flagellum (modified or absent in sergestoid shrimps, Fig. 4B), and its well-developed P4 and P5 (reduced or absent in most sergestoid shrimps). Besides, the well-developed P1-P5 of *Archeosolenocera* indicates an affinity with the Penaeoidea (Fig. 4C, D).

According to the key to the families of the Penaeoidea proposed by Pérez Farfante & Kensley (1997), the presence of a postorbital spine in *Archeosolenocera* is a diagnostic character of Solenoceridae (Figs 3; 5). Moreover, the carapace groove pattern (Figs 3-5) is close to those observed in several solenocerid genera such as *Cryptopenaeus* De Freitas, 1979, *Mesopenaeus* Pérez Farfante, 1977 and *Solenocera* Lucas, 1849. The very elongate and thin P4-P5 (Fig. 4C, D) are also present in the solenocerid shrimps *Hadropenaeus* Pérez Farfante, 1977, *Haliporoides* Stebbing, 1914 and *Hymenopenaeus* Smith, 1882.

In conclusion, *Archeosolenocera* is to this date the sole fossil representative of Solenoceridae.

Archeosolenocera straeleni Carriol & Riou, 1991
(Figs 3; 4; 5)

Archeosolenocera straeleni Carriol & Riou, 1991: 146-148, fig. 1, pl. 1, figs 1-3, pl. 2, figs 1-3. — Charbonnier 2009: 15, 17, 18, 158, 219, 221, 223, 230, figs 232, 238, 241, 379-382, 387, tables 14, 24, 25. — Charbonnier *et al.* 2010: 115, 121-123, 125, 129, figs 3, 4, 8, 9, tables 1-4; 2014: 375, 378, table 1. — Schweitzer *et al.* 2010: 9. — Robin *et al.* 2015a: 465, fig. 1a, b, table 1; 2015b: 490.

Antrimpos kiliani Van Straelen, 1923: 84-85 (partim), fig. 1; 1925: 67-70 (partim), fig. 40, pl. 1, fig. 3 (non figs 1, 2), pl. 2, fig. 1 (non fig. 2). — Roman 1928: 107, fig. 12, pl. 3, figs 2, 3. — Glaessner 1969: R447, fig. 252.1. — Pinna 1974: 13, 14, 19, fig. 3 — Schweitzer *et al.* 2010: 9.

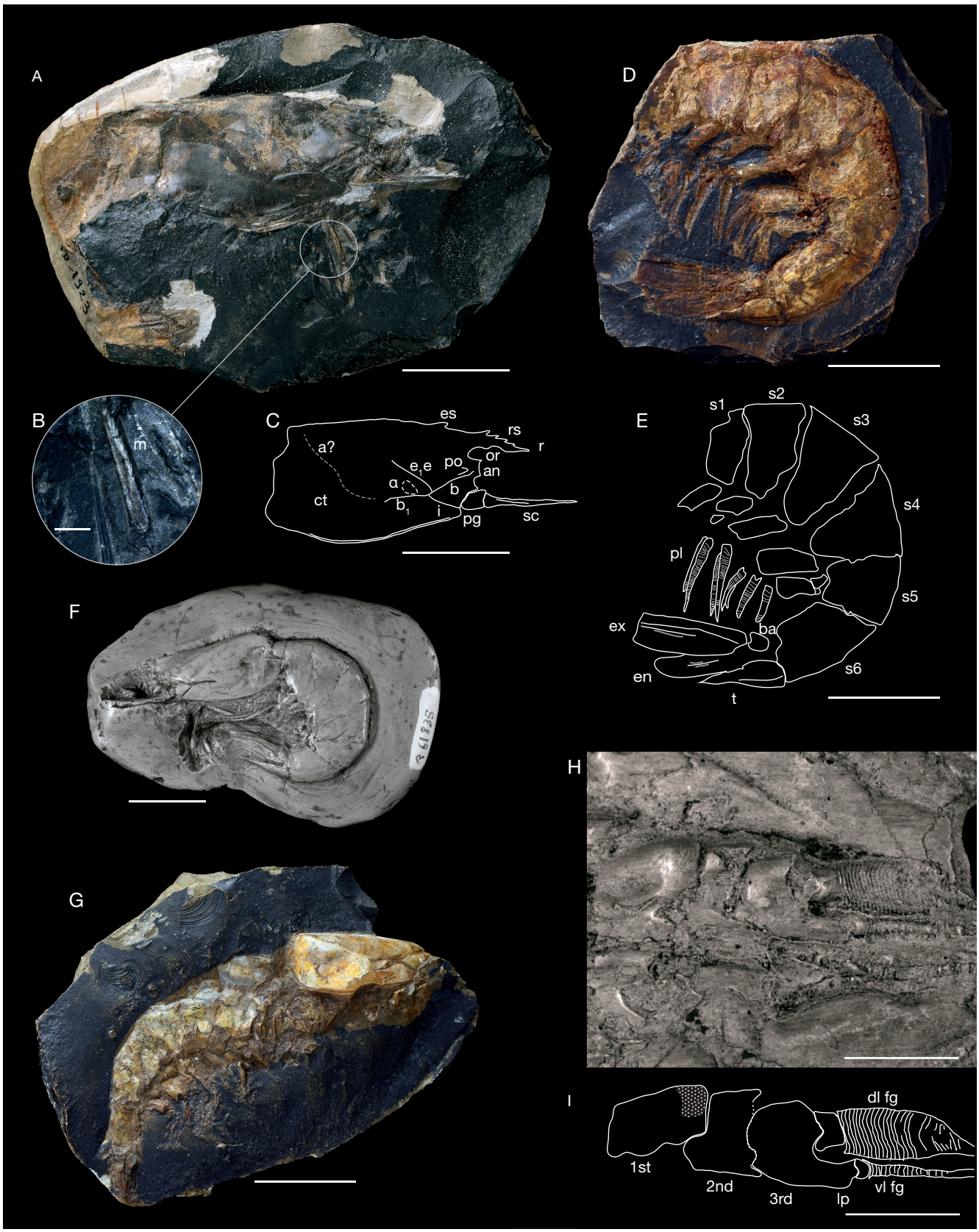
"*Antrimpos*" *secretaniae* Carriol & Riou, 1991: 151-153, fig. 3, pl. 4, figs 1-4, **n. syn.**

Antrimpos secretaniae – Fischer 2003: 241. — Charbonnier 2009: table 14. — Charbonnier *et al.* 2010: tables 1, 2; 2014: table 1 — Schweitzer *et al.* 2010: 9.

Antrimpos sp. – Van Straelen 1922: 982.

Type material. — Holotype UJF-ID.1923 (coll. Gevrey); paratypes UJF-ID.1791 and 1793 (*ex* paralectotypes of *A. kiliani*, coll. Gevrey), MNHN.F.R61835, R61836, R61837, R61838, R61839, R61840, R61841, R61842, R61843 and R61851.

Fig. 3. — *Archeosolenocera straeleni* Carriol & Riou, 1991 from the La Voulte Lagerstätte: **A**-**C**, specimen UJF-ID.1923 (holotype; coll. Gevrey), right lateral view (**A**), detail (**B**) and line drawing (**C**); **D**-**E**, specimen UJF-ID.1793 (paratype; coll. Gevrey), left lateral view (**D**) and line drawing (**E**); **F**, specimen MNHN.F.R61835 (paratype), left lateral view; **G**, specimen UJF-ID.1791 (paratype; coll. Gevrey), right lateral view; **H**-**I**, detail of specimen MNHN.F.R61836, dorsal view (**H**) and line drawing (**I**). Abbreviations: **a?**, possible branchiocardiac groove; **an**, antennal notch; **α**, hepatic spine; **b**, antennal groove; **b_1**, hepatic groove; **ba**, basipodite; **ct**, cephalothorax; **dl fg**, dorsolateral flagellum; **e_1e**, cervical groove; **end pl**, pleopodal endopod; **end u**, uropodal endopod; **ex**, pleopodal exopod; **es**, epigastric



spine; **i**, inferior groove; **lp**, lateral process; **m**, muscle fibres; **or**, orbital spine; **pg**, pterygostomian spine; **pl**, pleopod; **po**, postorbital spine; **r**, rostrum; **rs**, rostral spines; **s1**-**s6**, pleonal somites 1 to 6; **sc**, scaphocerite; **t**, telson; **vl fg**, ventrolateral flagellum; **1st**, first segment of antennular peduncle; **2nd**, second segment of antennular peduncle; **3rd**, third segment of antennular peduncle. Photographs: **A**, **D**, **G**, L. Cazes; **H**, J.-P. Cuif; **B**, C. Jauvion; **F**, P. Massicard (e-recolnat Project, MNHN). Line drawings: C. Jauvion. Scale bars: A, C-G, 20 mm; B, 2 mm; H, I, 10 mm.

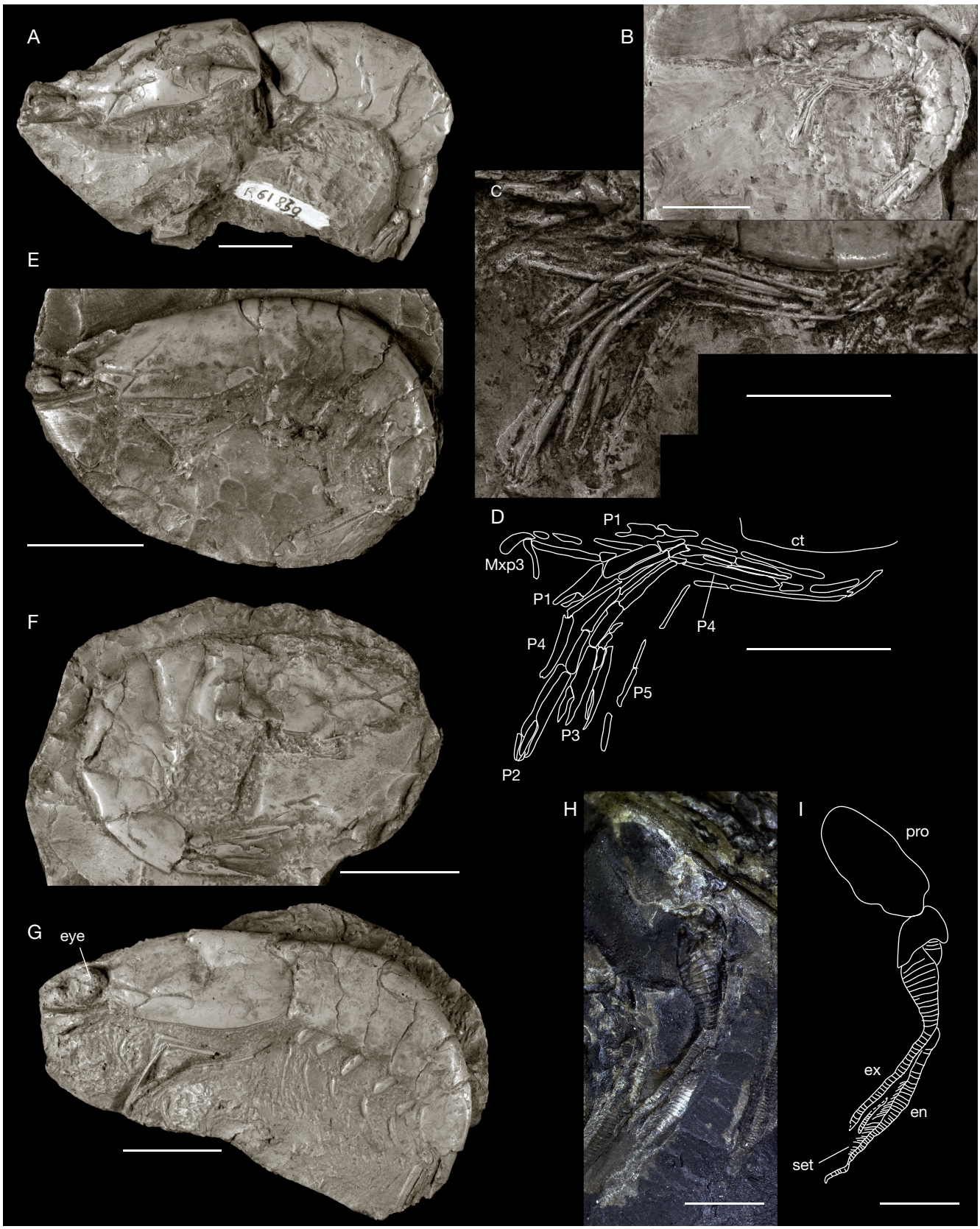


FIG. 4. — *Archeosolenocera straeleni* Carriol & Riou, 1991 from the La Voulte Lagerstätte: **A**, specimen MNHN.F.R61839 (paratype), left lateral view; **B**, specimen MNHN.F.R61837 (paratype), left lateral view; **C**, **D**, detail of specimen MNHN.F.R61837 (paratype), left lateral view (**C**) and line drawing (**D**); **E**, specimen MNHN.F.R61840 (paratype), left lateral view; **F**, specimen MNHN.F.R61842 (paratype), right lateral view; **G**, specimen MNHN.F.R61843 (paratype), left lateral view **H**-**I**, detail of specimen UJF-ID.1748 (coll. Gevrey), right lateral view (**H**) and line drawing (**I**). Abbreviations: **ct**, cephalothorax; **en**, pleopodal endopod; **ex**, pleopodal exopod; **Mxp3**, third maxilliped; **P1**-**P5**, pereiopods 1 to 5; **pro**, pleopodal protopod; **set**, setae; **s6**, pleonal somite 6; **t**, telson. Photographs: **A**, **B**, **E**-**G**, P. Massicard (e-recolnat Project, MNHN); **C**, **H**, C. Jauvion. Line drawings: C. Jauvion. Scale bars: A, B, E-G, 20 mm; B, C, 10 mm; H, I, 5 mm.

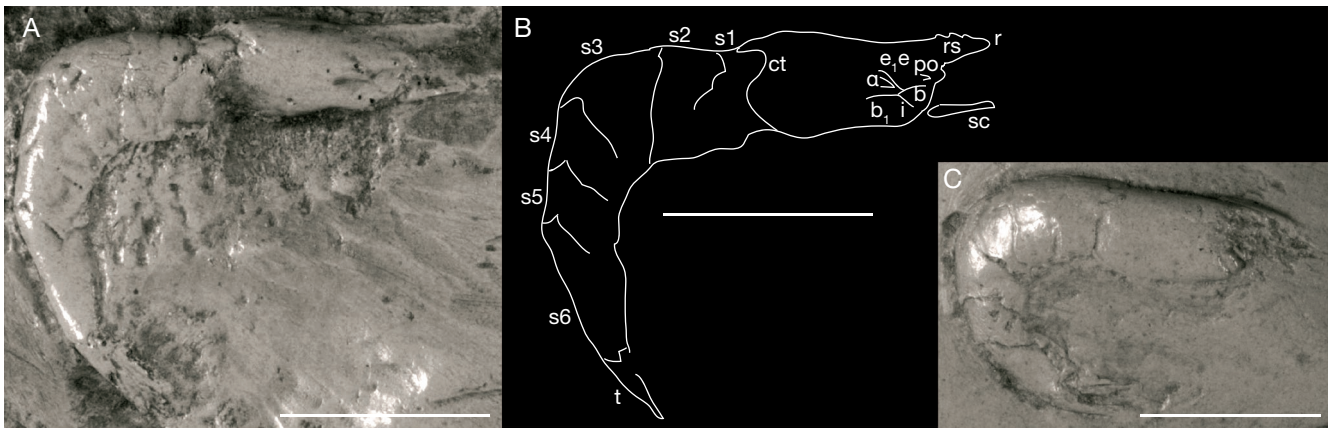


Fig. 5. — *Archeosolenocera straeleni* Carriol & Riou, 1991, from the La Voulte Lagerstätte. **A**, **B**, specimen MNHN.F.R61868 (holotype of *Antrimpos secretaniae*), right lateral view (**A**) and line drawing (**B**); **C**, specimen MNHN.F.R61870 (paratype of *A. secretaniae*), right lateral view. Abbreviations: **α**, hepatic spine; **b**, antennal groove; **b**$_1$, hepatic groove; **ct**, cephalothorax; **e**$_1$**e**, cervical groove; **i**, inferior groove; **po**, postorbital spine; **r**, rostrum; **rs**, rostral spines; **s1**-**s6**, pleonal somites 1 to 6; **sc**, scaphocerite; **t**, telson. Photographs: P. Massicard (e-recolnat Project, MNHN). Line drawings: C. Jauvion. Scale bars: 10 mm.

Type locality. — Ravin des Mines, near La Boissine, La Voulte-sur-Rhône Lagerstätte, Ardèche, Rhône-Alpes, France.

Type age. — Early Callovian, Gracilis ammonite Zone.

Additional examined material. — ***Archeosolenocera straeleni***. 19 *ex* paralectotypes of *A. kiliani* UJF-ID.1748, 1749 (3 specimens), 1756, 11897, 11898, 11900-11902, 11922, 14053-14059, 14061 and specimen UJF-ID.11907; MNHN.F.A32532, A58275, A59351, MNHN.F.R61847, R61850, R61864.
Antrimpos secretaniae. Holotype MNHN.F.R61868, paratypes MNHN.F.R61869, R61870, R61871.

Description

Carapace

Subrectangular carapace (holotype, CL = 40 mm; CH = 23 mm); short, strong, laterally flattened, rostrum with four suprarostral spines; straight dorsal margin with one epigastric spine at a third of CL; posterior margin dorsally concave with marginal ridge; ridged ventral margin (continuous with posterior margin ridge); anterior margin with antennal and orbital notches ventrally delimited respectively by antennal and pterygostomian spines; inclined cervical groove, not joined to the dorsal margin (interrupted at one third of CH), joined to straight antennal groove, widening towards antennal notch; elongate, subhorizontal hepatic groove, joined anteriorly to cervical and antennal grooves and stretching posteriorly until small ventral-directed inflexion in branchiocardiac region; wide straight inferior groove, frontward directed to antennal notch, joined to hepatic groove at level of hepatic spine (i.e. just posteriorly to junction of hepatic, cervical and antennal grooves); faint possible branchiocardiac groove of inclined sigmoidal shape revealed by a weak line on crushed carapaces, from the hepatic groove almost to dorsal margin; strong hepatic spine at the junction between cervical and hepatic grooves; strong postorbital spine above distal extremity of antennal groove.

Ornamentation of carapace

Carapace uniformly covered by small granules.

Pleon

Subrectangular somites; s1-s6 with posterior margin showing median articulation among somites; s1 as large as s2 and s3; s1 pleura overlapping s2 pleura; long and subquadrate s6; s1-s6 terga and pleura uniformly covered with small granules; triangular telson, evenly covered with small granules, with a fixed median spine, posteriorly directed, on each outer margin, acute distal extremity; telson shorter than uropods.

Cephalic appendages

Prominent eyes (paratype MNHN.F.R61843, diameter = 8 mm for CL = 35 mm); antennula (a1) with strong antennular peduncle composed of three segments, first one displaying small granules as ornamentation, second and third ones almost equal in size, third segment bearing two flagella: wide and thick dorsolateral flagellum (diameter *c.* 3 mm), thin ventrolateral flagellum (diameter *c.* 0.5 mm) fixed on lateral process as long as the rest of third segment; both flagella of undetermined length; antenna (a2) with thick flagellum approximately as long as carapace, and elongate scaphocerite, dorsoventrally flattened, with deep dorsal longitudinal groove.

Thoracic appendages

Long, thin and smooth Mxp3 (longer than P1); slender chelate P1-P3, P2 longer than P1 and P3, P3 longer than P1; achelate P4-P5, very thin and delicate, longer than P2; P5 longer and thinner than P4; smooth P1-P5.

Pleonal appendages

Pleopods composed of elongate and strong protopod bearing two multiarticulated flagella (*c.* 30 segments) with setae; uropods longer than telson; uropodal endopod shorter than uropodal exopod; uropods with median deep groove, evenly covered with small granules; uropodal exopod with one row of setae on distal and inner margins.

Discussion

Carriol & Riou (1991) described *Antrimpos secretaniae* based on four small specimens. However the examination of the type specimens reveals morphological characters diagnostic of *Archeosolenocera* (Fig. 5): rostrum with suprarostral spines, epigastric spine; inclined cervical groove not joined to dorsal margin, antennal groove, subhorizontal hepatic groove, joined anteriorly to cervical and antennal grooves and stretching posteriorly, frontward directed inferior groove, strong hepatic spine at junction between cervical and hepatic grooves, postorbital spine. For all these reasons, we think that the type specimens of *Antrimpos secretaniae* are only small-sized or juvenile members of *Archeosolenocera straeleni*. Therefore, we consider them conspecific, the name *A. straeleni* being chosen as the valid name, based on the Principle of the First Reviser (ICZN 1999: article 24.2).

DISCUSSION

Palaeobiology and palaeoecology

Arthropods are a major component of the La Voulte biota, in terms of diversity and abundance (Charbonnier 2009). *Aeger brevirostris* and *Archeosolenocera straeleni* were very common species. For instance, *A. straeleni* represents 22% of the arthropods preserved in La Voulte nodules (Charbonnier *et al.* 2010).

Aeger brevirostris is a quite large shrimp with robust thoracic appendages (Figs 1; 2). The hypertrophied Mxp3 with movable spines suggests suspension feeding animal. The shrimp may have been feeding by catching small animals and food particles from water, by moving around this potential specialized filtering structure. Moreover, its seemingly elongate pleopods (Fig. 2A, D) and well-developed uropods (Figs 1; 2) suggest well-developed swimming capacities, compatible with a filter feeder animal.

Archeosolenocera straeleni had quite large eyes for a shrimp of its size (see Fig. 4G). This could be an adaptation to a dim, but not completely dark, environment (close to the inferior limit of the photic zone). As the La Voulte palaeoenvironment was a deep-water setting (probably exceeding 200 m; Charbonnier *et al.* 2007a) and therefore dark, *A. straeleni* probably migrated in the water column for foraging, or reproduction for instance. A similar behaviour was proposed for the polychelidan *Voulteryon parvulus* Audo, Schweigert, Saint Martin & Charbonnier, 2014, by Jauvion *et al.* (2016).

Preservation

These shrimps display a very exquisite preservation, typical of the La Voulte Lagerstätte. Indeed muscle fibers seem to be discernable on one of these specimens (Fig. 3B). An investigation on the internal organs and other fine anatomic details is therefore possible, as already published for two other arthropods from La Voulte (Jauvion *et al.* 2016; Vannier *et al.* 2016). Wilby *et al.* (1996) proposed briefly a synthetic taphonomical pathway to explain this delicate preservation. Further investigations such as characterization on the mineral phases composing these fossils are in progress.

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