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Ecological significance of the arthropod fauna from the Jurassic (Callovian) La Voulte Lagerstätte

SYLVAIN CHARBONNIER, JEAN VANNIER, PIERRE HANTZPERGUE, and CHRISTIAN GAILLARD

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The La Voulte Lagerstätte is remarkable for its unique soft-bodied fauna (e.g., worms, coleoid squids) and its exceptionally preserved arthropods mainly found in small sideritic concretions. This arthropod fauna includes 30 different species assigned to the crustaceans, the thylacocephalans and the pycnogonids. Crustaceans are the most diversified group with 23 species distributed in a dozen families. Quantitative analyses based on 388 nodules reveals four dominant groups: (i) the enigmatic thylacocephalan arthropods (33%), (ii) the Solenoceridae shrimps (22%), (iii) the Coleiidae crustaceans (15%), and (iv) the Penaeidae shrimps (10%). Converging lines of evidence from depositional environment and modern analogues, indicate that this arthropod fauna probably inhabited a deep water setting most probably exceeding 200 m (= bathyal zone) under dysphotic or aphotic conditions. This new set of data sheds new light on the deep-sea colonisation by animal communities in the Mesozoic.

Key words: Arthropoda, Crustacea, Thylacocephala, Lagerstätte, Jurassic, Callovian, La Voulte, France.

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Introduction

The celebrated Jurassic La Voulte-sur-Rhône Lagerstätte (Ardèche, SE France) is known to yield an exceptionally preserved fauna mainly composed of ophiuroids and arthropods, but also numerous others invertebrates (e.g., coleoid cephalopods). Among arthropods, crustaceans (mainly decapods) are the most diverse and abundant group of fossils. They are often three-dimensionally preserved in sideritic nodules. They were preliminarily studied by Van Straelen (1922, 1923a, b, 1925), and more recently by Secrétan (1983), Secrétan and Riou (1983, 1986), Carriol and Riou (1991) and Schweigert et al. (2006). The most enigmatic faunal elements of the La Voulte Lagerstätte are "bivalved" arthropods known as thylacocephalans (Secrétan 1985; Vannier et al. 2006). The soft-bodied organisms are mainly represented by coleoid cephalopods (Fischer and Riou 1982a, b, 2002). Marine worms also occur (possible sipunculans; Alessandrello et al. 2004). Among the unusual fossils from La Voulte, three new species of sea spiders (Pycnogonida) have recently improved our knowledge on this enigmatic group of marine arthropods (Charbonnier et al. 2007a).

In this paper we use the arthropods preserved in nodules as an important source of information to reconstruct key aspects of the La Voulte marine palaeoenvironment. We present the updated faunal inventory of the La Voulte arthropods and analyse their biodiversity. We also propose the first quantitative data on these arthropods based on 388 specimens. We make detailed comparisons between the major arthropod groups represented in the La Voulte Lagerstätte and their present-day analogues. These comparisons lead to discussions on the ecology of the arthropods and to interpretations concerning the palaeoenvironment (e.g., bathymetry).

Institutional abbreviations.—FSL, Faculté des Sciences de Lyon, Université Lyon 1, France; MNHN, Muséum national d'Histoire naturelle, Paris, France; MHNGr.PA, Muséum d'Histoire naturelle de Grenoble, France; MHNL, Musée des Confluences, Lyon, France; UJF-ID, Université Joseph Fourier, Institut Dolomieu, Grenoble, France.

Other abbreviations.—CL, cephalothoracic length; TL, total length.

Geological setting

The La Voulte Lagerstätte is located southeast of the French Massif Central (= hercynian crystalline basement) along the right bank of the Rhône valley (ca. 150 km south of Lyon; Fig. 1A). The fossiliferous deposits belong to the eastern sedi-

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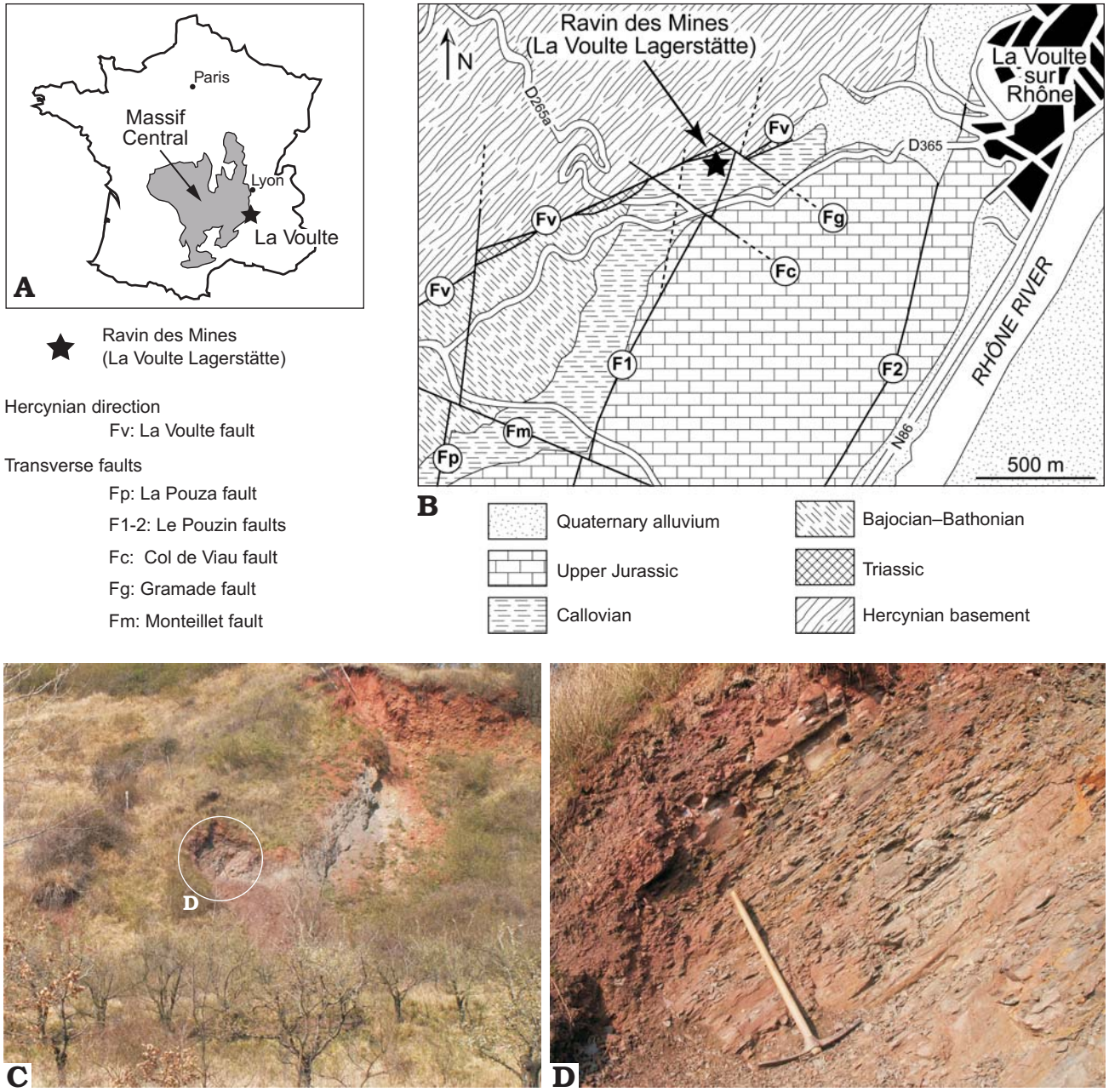

Fig. 1. Geological setting of the La Voulte Lagerstätte. **A**. Map of France. **B**. Geological map of the La Voulte area (modified from Elmi 1967 and Charbonnier et al. 2007b). **C**. Main outcrop corresponding to site A of Fischer (2003); note the reddish iron ore overlying the fossiliferous basal marls. **D**. Recent excavation in the basal marls showing all the fossiliferous beds, note the strong dip (ca. 60°) that makes difficult the sampling of fossils (pick = 1 m).

ment cover of the Massif Central (Elmi 1967; Charbonnier et al. 2007b). They are separated from the basement by a major hercynian sub-vertical fault, the so-called La Voulte fault (N54°, inherited hercynian direction) which was very active during the Jurassic and cuts through the whole area (Fig. 1B). Palaeogeographic reconstructions for the Callovian place the La Voulte area along the western margin of the Tethys, adjacent to the Massif Central which was probably submerged at that time (Enay et al. 1993a, b). The La Voulte area was situated in the bathyal zone near the slope-basin transition with a water depth most probably exceeding 200 m (Enay et al. 1993a, b; Charbonnier et al. 2007b). This margin running east of La Voulte was characterised by a complex submarine palaeotopography of tilted blocks generated by a series of inherited hercynian and transverse faults (e.g., Col de Viau fault, Le Pouzin faults; Fig. 1B) (see Charbonnier et al. 2007b for more details). The fossiliferous deposits of the La Voulte Lagerstätte have been dated to the Lower Callovian *Macrocephalites* (*Dolikephalites*) *gracilis* Biozone (Elmi 1967) (Fig. 2) based on abundant ammonite faunas (Roman 1930, Elmi 1967). They crop out in the Ravin des Mines southwest of the town of La Voulte-sur-Rhône (Fig. 1B, C). They consist in relatively thin interval (ca. 4–5 m; Figs. 1D, 2A) of marls topped by iron ore bodies (thickness: ca. 15 m; Fig. 2A) which

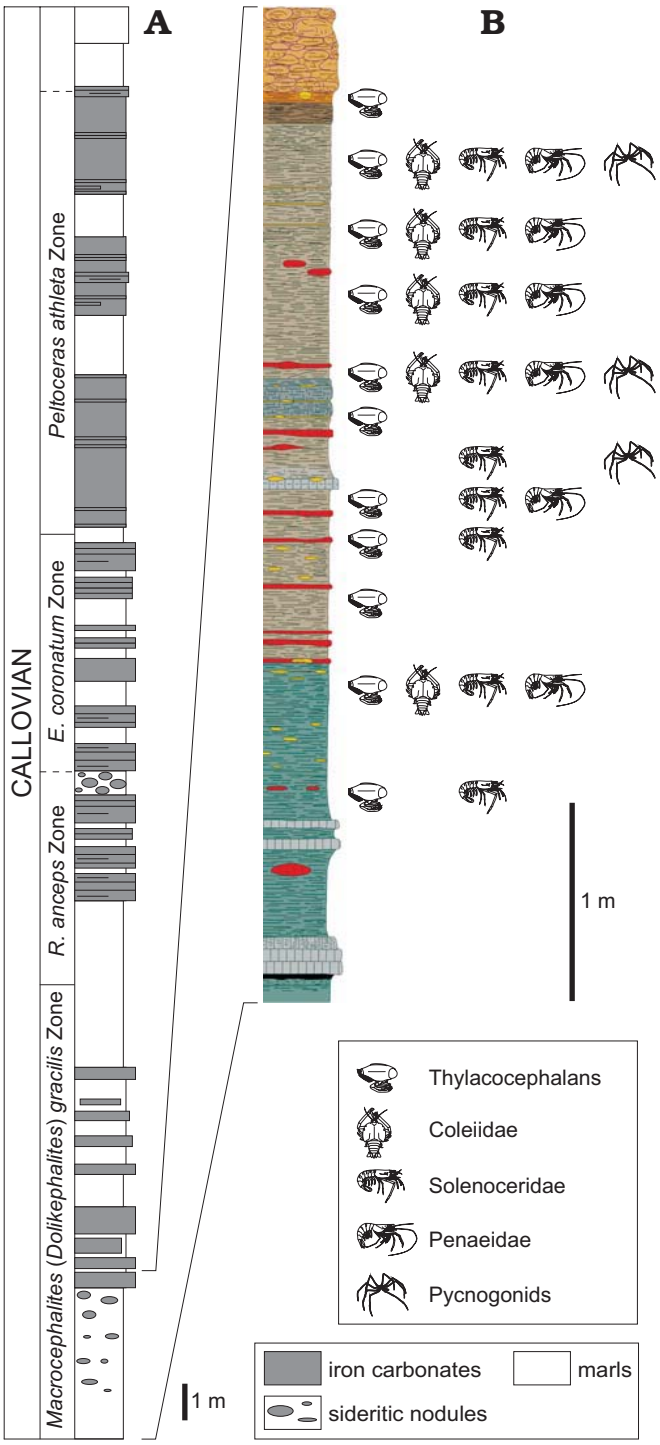

Fig. 2. Lithological logs of the La Voulte Lagerstätte (Lower Callovian, *Macrocephalites* (*Dolikephalites*) *gracilis* Biozone). **A**. Historical section and biostratigraphy of the "Ravin des Mines" beds, note the thickness of the iron ore bodies (ca. 15 m) overlying the basal marls. **B**. Detailed section of the basal marls rich in nodules and distribution of the main arthropod groups (new excavation). Abbreviations: *E.*, *Erymnoceras*; *R.*, *Reineckeia*.

were exploited during the 19th century (Fournet 1843; Ledoux 1868). The basal marls yield numerous sideritic nodules which most of the time are fossiliferous. They principally contain three-dimensional preserved arthropods (ca. 95% of nodules: crustaceans, thylacocephalans; Fig. 2B). The remaining nodules (ca. 5%) bear some fragments of fishes (actinopterygians, sarcopterygians, sharks) but also superbly 3D-preserved coleoid cephalopods. The basal marls are locally rich in soft-bodied fossils such as coleoid cephalopods and marine worms (see Fischer 2003; Alessandrello et al. 2004). Some arthropods occur also in the marls where they are usually very flattened. The basal marls are punctually reddened by small iron carbonate layers very rich in ophiuroids (Valette 1928; Hess 1960; Dietl and Mundlos 1972).

Material and methods

Arthropods are the most abundant and diverse organisms of the La Voulte Lagerstätte. They occur either in early diagenetic concretions where they are three-dimensionally preserved (Fig. 3A–C) or in surrounding marls where they are flattened and preserved in pyrite and phosphate (Fig. 3D, E). The specimens preserved in marly levels are relatively rare. They were collected during excavations made by the Muséum national d'Histoire naturelle, Paris in the 1980s (see Fischer 2003). Unfortunately, no precise stratigraphic information is available for these specimens. Most of them are also excessively flattened and others are very small-sized for a specific identification. For instance, when the specimens are flattened, the distinction between a juvenile penaeid shrimp (length: 3–4 cm) and an adult eucopid mysid (length: 3–4 cm) is difficult. Moreover, some of these flattened arthropods might be exuviae which would not have been included within a concretion and that consequently would not have resisted compaction. Therefore, the small number of arthropods preserved in marls was not integrated into the quantitative analyses. We reasonably decided not to include these specimens which absence should not introduce strong sampling bias. On the other hand, the arthropods three-dimensionally preserved in nodules show generally numerous anatomical details (e.g., eyes, articulated appendages, soft tissues including gills, stomach and muscles) that greatly facilitate the determinations. The exceptional preservation of the La Voulte arthropods coupled with the presence of their internal organs (for details see Secrétan 1985; Wilby et al. 1996) clearly indicates that they are autochthonous. The distribution of the nodules is relatively homogeneous within the 4–5 m thick sediments of the La Voulte Lagerstätte (Fig. 2B). The process through which these nodules were formed is uncertain but probably results from punctual chemical conditions and microbial activity in the surroundings of the decaying carcasses (Wilby et al. 1996). The formation of the nodules seems to be independent from a specific stratigraphic layer. Thus the nodules supply a significant overview on the La Voulte arthropods. Only palaeontological excavations integrating both arthropods preserved in nodules and as pyritised and phosphatised bodied in the marly levels will be susceptible to precise the abundance of the La Voulte arthropods.

This study is based on fossils collected during field excursions in 2005 and 2006 (SC, 76 nodules) from several sections

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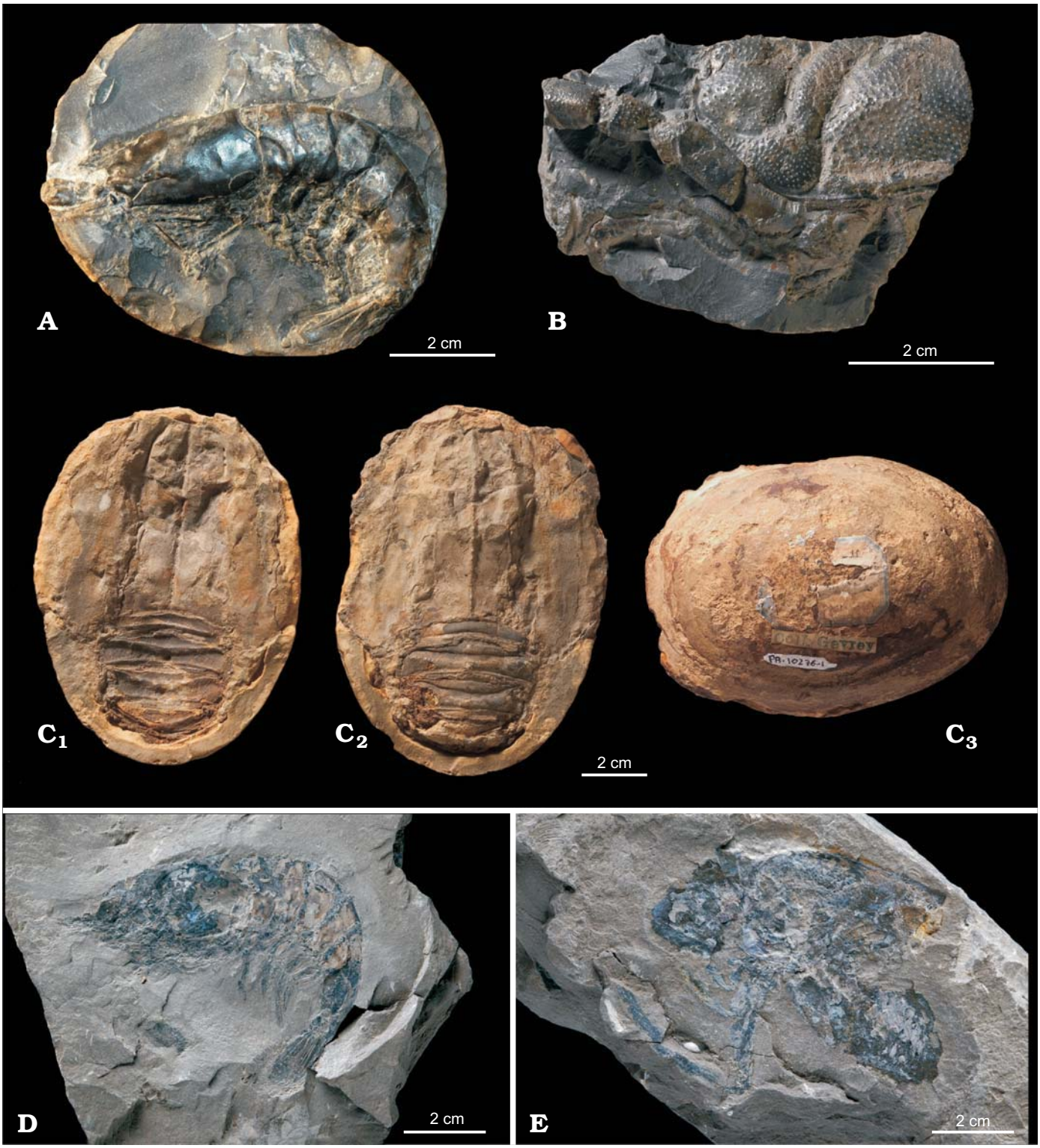

Fig. 3. Types of preservation for the La Voulte arthropods. **A**. 3D-preserved shrimp in sideritic nodule (*Archeosolenocera straeleni* Carriol and Riou, 1991, MNHN R61840), lateral view, note the stalked eye and the pleopods. **B**. Exceptionally 3D-preserved fragment of shrimp (*Eryma cumonti* Van Straelen, 1921, UJF-ID.11906), lateral view, note the appendages and the finely granular carapace. **C**. Sideritic nodule with 3D-preserved crustacean (*Coleia gigantea* [Van Straelen, 1923a], MHNGr.PA.10276-1,2), dorsal (C_1, C_2) and upper (C_3) views, note the ovoid shape. **D**. Phosphatised and pyritised compression of shrimp (*Archeosolenocera straeleni*, MNHN R61847), lateral view. **E**. Phosphatised and pyritised compression of thylacocephalan arthropod (*Dollocaris ingens* Van Straelen, 1923b, MNHN A29148), lateral view, note the large eye and the well-developed prehensile appendages.

of the Ravin des Mines. This new material adds to fossil arthropods deposited in the collections of the Université Lyon 1 (65 nodules), the Institut Dolomieu, Université de Grenoble (96 nodules), the Muséum d'Histoire naturelle de Grenoble

(6 nodules), the Muséum d'Histoire Naturelle de Lyon (9 nodules), the Musée de La Voulte (54 nodules) and the Muséum national d'Histoire naturelle, Paris (82 nodules). The whole material consists of 388 specimens three-dimensionally preserved in sideritic nodules.

We revised and updated the previous inventories made by Van Straelen (1922, 1923a, 1925) in the light of personal observations (SC, JV) and the most recent systematic studies on the La Voulte arthropods (Secrétan 1983, 1985; Secrétan and Riou 1983, 1986; Carriol and Riou 1991; Schweigert et al. 2006; Vannier et al. 2006). The taxonomic richness and relative abundance of arthropod species were calculated in order (i) to establish the palaeobiodiversity and (ii) to enable comparisons with Recent crustacean communities. Biometric measurements on two species of penaeid shrimps from La Voulte (*Archeosolenocera straeleni*, *Aeger brevirostris*) were made on 24 complete specimens. These measurements correspond to the cephalothoracic length, excluding rostrum (= CL, linear distance between the post-orbital margin and the posterior margin of the cephalothorax) and to the total body length including rostrum (= TL, linear distance between the anterior part of the cephalothorax and the extremity of the telson). In order to compare the morphometric relationships with Recent shrimps and to interpret the palaeobiology of the La Voulte species, the results obtained were plotted graphically and regression coefficients describing these morphometric relationships were calculated using a linear model.

The La Voulte arthropods

Diversity and relative abundance.—The La Voulte arthropod fauna as a whole includes 30 different species (Table 1) assigned to the crustaceans, the thylacocephalans and the pycnogonids. The crustaceans are the most diversified group with 23 species distributed in about 12 families (e.g., Penaeidae, Eryonidae, Mysidae). Decapods (17 species) are remarkably diverse and most species such as *Aeger brevirostris* Van Straelen, 1923a (Fig. 4A), *Archeosolenocera straeleni* Carriol and Riou, 1991 (Fig. 4B), *Coleia gigantea* (Van Straelen, 1923a) (Fig. 4C), *Eryma mandelslohi* (von Meyer, 1837) (Fig. 4D), *Eryma cumonti* Van Straelen, 1921 (Fig. 4E), *Eryon ellipticus* Van Straelen, 1923a (Fig. 4F), *Hellerocaris falloti* (Van Straelen, 1923a) (Fig. 4G), and *Willemoesiocaris ovalis* (Van Straelen, 1923a) (Fig. 4H) are characteristic for the La Voulte Lagerstätte. Mysidaceans (Lophogastrida: 2 species; Mysida: 2 species) and cumaceans (1 species) are less diverse. Note that several crustaceans (e.g., *Coleia* sp. 1, sp. 2) exhibit very unusual anatomical characters and may represent new taxa. The thylacocephalan arthropods are represented by 4 species: *Dollocaris ingens* Van Straelen, 1923b (Fig. 5A, B), *Kilianicaris lerichei* Van Straelen, 1923b (Fig. 5C), *Clausocaris ribeti* (Secrétan, 1985) (Fig. 5D), and *Paraostenia voultensis* Secrétan, 1985 (Fig. 5E). The pycnogonids (sea spiders) are very rare and include 3 species (*Palaeopycnogonides gracilis* Charbonnier, Vannier, and Riou, 2007a; *Colossopantopodus boissinensis* Charbonnier, Vannier, and Riou, 2007a, *Palaeoendeis elmii* Charbonnier, Vannier, and Riou, 2007a). Among the 30 arthropod species of La Voulte, six of them have, so far, never been found preserved in nodules. These are the sea spiders, the cumacean *Palaeocuma hessi* Bachmayer, 1960; the decapod *Stenochirus vahldieki* Schweigert, Garassino, and Riou, 2006; and the thylacocephalan *Clausocaris ribeti*. Their absence in nodules

Table 1. List of fossil arthropods from the La Voulte Lagerstätte (Lower Callovian, *Macrocephalites* (*Dolikephalites*) *gracilis* Biozone).

CRUSTACEA
DECAPODA
Penaeidae
Aeger brevirostris Van Straelen, 1923a
"Antrimpos" secretaniae Carriol and Riou, 1991
"Antrimpos" sp. 1
Rhodanicaris depereti Van Straelen, 1925
Solenoceridae
Archeosolenocera straeleni Carriol and Riou, 1991
Erymidae
Eryma cumonti Van Straelen, 1921
Eryma mandelslohi (von Meyer, 1837)
Stenochiridae
Stenochirus vahldieki Schweigert, Garassino, and Riou 2006
Coleiidae
Coleia gigantea (Van Straelen, 1923a)
Coleia sp. 1
Coleia sp. 2
Coleia sp. 3
Hellerocaris falloti (Van Straelen, 1923a)
Eryonidae
Eryon ellipticus Van Straelen, 1923a
Polychelidae
Willemoesiocaris ovalis (Van Straelen, 1923a)
Glypheidae
Trachysoma ornata (Quenstedt, 1858)
Family uncertain
Udora gevreyi Van Straelen, 1923a
Udora minuta Van Straelen, 1923a
LOPHOGASTRIDA
Lophogastridae
Lophogaster voultensis Secrétan and Riou, 1986
Eucopiidae
Eucopia praecursor Secrétan and Riou, 1986
MYSIDA
Mysidae
Siriella antiqua Secrétan and Riou, 1986
Siriella carinata Secrétan and Riou, 1986
CUMACEA
Famille incertaine
Palaeocuma hessi Bachmayer, 1960
THYLACOCEPHALA
ORDER AND FAMILY UNCERTAIN
Dollocaris ingens Van Straelen, 1923b
Kilianicaris lerichei Van Straelen, 1923b
Clausocaris ribeti (Secrétan, 1985)
Paraostenia voultensis Secrétan, 1985
PYCNOGONIDA
Family uncertain (possibly Ammotheidae)
Palaeopycnogonides gracilis Charbonnier, Vannier, and Riou, 2007
Family uncertain (possibly Colossendeidae)
Colossopantopodus boissinensis Charbonnier, Vannier, and Riou, 2007
Family uncertain (possibly Endeidae)
Palaeoendeis elmii Charbonnier, Vannier, and Riou, 2007

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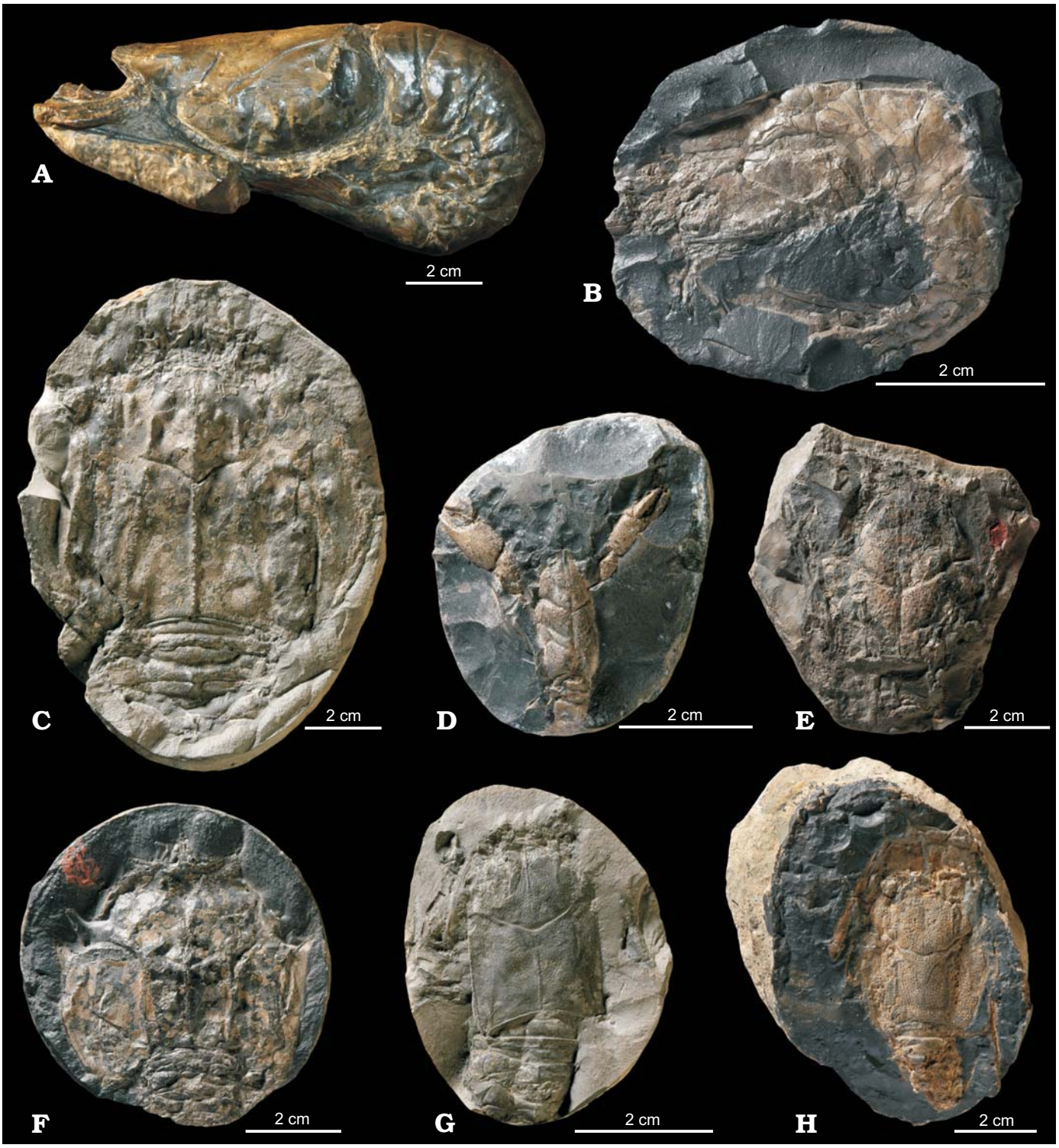

Fig. 4. Decapod crustaceans from the La Voulte Lagerstätte: three-dimensionally preserved specimens in sideritic nodules. **A**. *Aeger brevirostris* Van Straelen, 1923a, MNHN R61860, lateral view. **B**. *Archeosolenocera straeleni* Carriol and Riou, 1991, UJF-ID.11901, lateral view, note the lateral flattening. **C**. *Coleia gigantea* (Van Straelen, 1923a), UJF-ID.11547, dorsal view, cephalothorax and abdomen. **D**. *Eryma mandelslohi* (von Meyer, 1837), UJF-ID.11543, dorsal view. **E**. *Eryma cumonti* Van Straelen, 1921, UJF-ID.11895, dorsal view, cephalothorax with granular surface. **F**. *Eryon ellipticus* Van Straelen, 1923a, UJF-ID.11540, dorsal view cephalothorax and fragmentary abdomen. **G**. *Hellerocaris falloti* (Van Straelen, 1923a), UJF-ID.11553, dorsal view, cephalothorax and abdomen. **H**. *Willemoesiocaris ovalis* (Van Straelen, 1923a), UJF-ID.11542, dorsal view, cephalothorax and abdomen.

might be due to their weakly sklerotised carapaces (Secrétan 1985; Vannier et al 2006; Charbonnier et al. 2007a) although this requires further taphonomic studies.

The quantitative analysis based on 388 nodules (Table 2, results expressed as percentages of specimens included by family) shows four dominant groups: (i) the thylacocepha-

Table 2. Arthropods preserved in sideritic nodules (La Voulte Lagerstätte): results of quantitative analysis (number of nodules and percentages).

Taxa (nodules)	This work	Collections FSL	Collections UJF-ID	Collections MNHN	Collections MHNGr	Collections MHNL	Musée La Voulte	Total samples	Percentages (%)
Dollocaris ingens	50	7	9	40	-	7	1	114	29.4
Kilianicaris lerichei	0	2	2	4	-	-	1	9	2.3
Paraostenia voultensis	1	-	-	2	-	-	-	3	0.8
Total thylacocephalans	-	-	-	-	-	-	-	-	**32.5**
Archeosolenocera straeleni	11	23	26	10	1	1	15	87	22.4
Total Solenoceridae	-	-	-	-	-	-	-	-	**22.4**
Coleia gigantea	4	16	13	1	3	-	10	47	12.1
Coleia sp. 1	-	2	-	-	-	-	1	3	0.8
Coleia sp. 2	-	1	-	-	-	-	-	1	0.3
Coleia sp. 3	-	-	1	-	-	-	-	1	0.3
Hellerocaris falloti	1	2	3	-	-	-	2	8	2.0
Total Coleiidae	-	-	-	-	-	-	-	-	**15.5**
Aeger brevirostris	2	6	6	4	1	-	6	25	6.4
Rhodanicaris depereti	-	-	7	-	-	-	-	7	1.8
"Antrimpos" secretaniae	-	-	-	3	-	-	-	3	0.8
"Antrimpos" sp. 1	-	1	-	-	-	-	-	1	0.3
Total Penaeidae	-	-	-	-	-	-	-	-	**9.3**
Eryma cumonti	-	-	5	-	-	-	4	9	2.3
Eryma mandelslohi	-	1	5	-	1	-	-	7	1.8
Total Erymidae	-	-	-	-	-	-	-	-	**4.1**
Eryon ellipticus	-	2	3	-	-	-	10	15	3.9
Total Eryonidae	-	-	-	-	-	-	-	-	**3.9**
Siriella antiqua	-	-	-	9	-	-	1	10	2.6
Siriella carinata	-	-	-	2	-	-	-	2	0.5
Total Mysidae	-	-	-	-	-	-	-	-	**3.1**
Lophogaster voultensis	-	-	-	5	-	-	-	5	1.3
Total Lophogastridae	-	-	-	-	-	-	-	-	**1.3**
Udora gevreyi	-	-	1	-	-	-	-	1	0.3
Udora minuta	-	-	2	-	-	-	-	2	0.5
Total family uncertain	-	-	-	-	-	-	-	-	**0.8**
Willemoesiocaris ovalis	-	-	1	-	-	-	1	2	0.5
Total Polychelidae	-	-	-	-	-	-	-	-	**0.5**
Trachysoma ornata	-	-	1	-	-	-	1	2	0.5
Total Glypheidae	-	-	-	-	-	-	-	-	**0.5**
Eucopia praecursor	-	-	-	2	-	-	-	2	0.5
Total Eucopiidae	-	-	-	-	-	-	-	-	**0.5**
Undentifiable remains	7	2	11	-	-	1	1	22	**5.7**
Total specimens	**76**	**65**	**96**	**82**	**6**	**9**	**54**	**388**	**100.0**

lans (32.5% of nodules), (ii) the Solenoceridae (22.4%), (iii) the Coleiidae (15.5%), and (iv) the Penaeidae (9.3%). All the other arthropods are minor elements of the fauna with relative abundances lower than 5%. Most of the remaining families are often represented by a small number of fossils (e.g., Erymidae, 16 specimens: 4.1%; Lophogastridae, 5 specimens: 1.3%). A small number of nodules (5.7%) contain unidentifiable remains of arthropods (e.g., fragments of carapace or abdomen, or isolated appendages).

Thylacocephalans.—A taxonomic revision of this group requires new detailed observations of the appendages (especially the cephalic ones) and other key-anatomical features (e.g., digestive system, gills). New techniques such as the X-ray microtomography are being used in order to provide accurate reconstructions of these enigmatic animals and firm evidence of their affinities within or without the Crustacea. We present here a summary of the previous works on thylacocephalans that add to several personal observations.

The thylacocephalans are "bivalved" arthropods with a distinctive morphology characterised by hypertrophied visual organs and long raptorial appendages (see Secrétan 1985; Vannier et al. 2006; Fig. 5A). In the nodules, the most frequent and well-preserved species is *Dollocaris ingens* (114 nodules, Table 2). This species is represented by juvenile (Fig. 5B) and adult specimens exceeding 30 cm in length (Fig. 5A). The association in situ of these different stages of growth probably indicates autochthonous assemblages. The other thylacocephalan species from La Voulte (*Kilianicaris lerichei*, Fig. 5C; *Clausocaris ribeti*, Fig. 5D; *Paraostenia voultensis*, Fig. 5E) are less frequent and relatively smaller than *Dollocaris*. The following palaeoecological interpretations are based on *Dollocaris ingens* which is presently the best known species (Secrétan and Riou 1983; Secrétan 1985) and a short description of its general morphology is proposed below. The bivalved carapace of *D. ingens* is laterally compressed and encloses the whole body except the caudal part. The carapace presents on both sides a typical lateral carina

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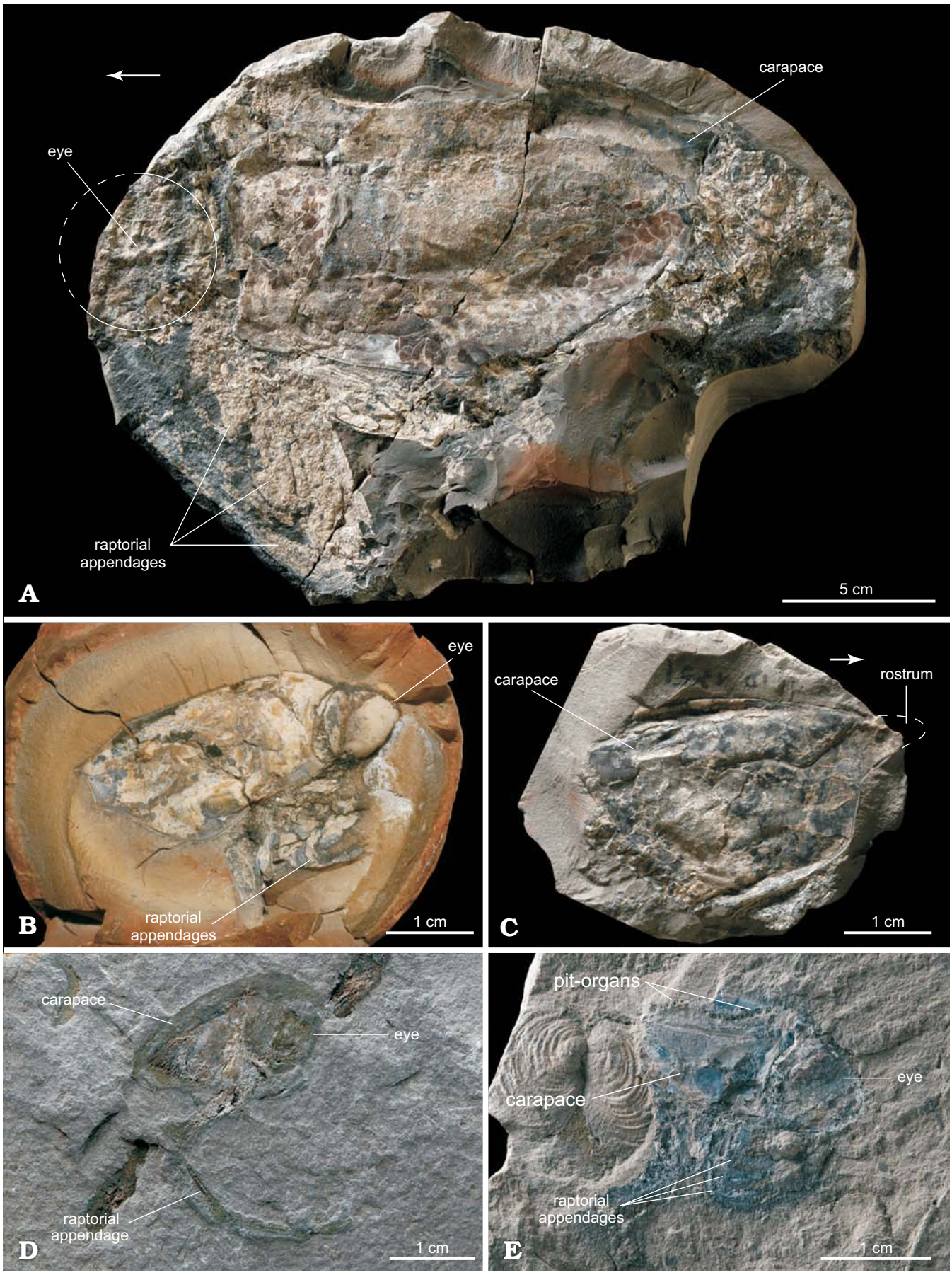
carapace
eye
raptorial
appendages
A
5 cm
eye
raptorial
appendages
B
1 cm
carapace
rostrum
C
1 cm
carapace
eye
raptorial
appendage
D
1 cm
pit-organs
eye
carapace
raptorial
appendages
E
1 cm

and an elliptical protuberance in the antero-ventral margin (Fig. 6A). The concave dorsal margin separates the carapace in two identical valves and bears frontally a crest prolonged by a short sharp rostrum. The anterior part is concave and shows two pairs of globular eyes protruding through the notch formed between the rostrum and a short antero-ventral spine (Figs. 5B, 6B, C).

There is a lack of information concerning the anterior appendages of the animal—i.e., those that are assumed to have been present in front of the three pairs of raptorial appendages (for discussion, see Schram et al 1999; Lange et al. 2001; Vannier et al. 2006). It is possible that some of these cephalic appendages were very short. The anterior part of the trunk shows three pairs of raptorial appendages with geniculate shape and spiny features (Figs. 5A, 6D). They decrease in size from front to rear (Fig. 6E). The posterior part of the trunk is concave, limited by dorsal and ventral spines and bears a series of pleopod-like appendages (= trunk limbs of Schram et al. 1999; Lange et al. 2001; Fig. 6F).

Dollocaris ingens has a pair of extremely prominent bulbous eyes in the front part of its body (e.g., Vannier et al. 2006). These eyes protrude the cararape margin and show a regular network of small ommatidia over their external surface. The detailed structure of these huge visual organs was first studied by Fröhlich et al. (1992) who recognised in *D. ingens* some of the typical structural elements (e.g., ommatidial facets, retinal rosettes) of the present-day crustaceans. Externally, the eyes of *D. ingens* resemble those of present-day crustaceans (Hiller-Adams and Case 1985; Brusca and Brusca 2002), for example the huge eyes of the deep-sea hyperiid amphipods (Crustacea: Peracarida; Fig. 7A, B) that are extremely prominent. Hyperiids such as *Hyperia macrocephala* (Dana, 1853) (Fig. 7A) and *Cystisoma neptunus* Guérin-Méneville, 1842 (Fig. 7B) are two examples of Recent deep-sea amphipods with bulbous pigmented eyes that occupy almost half of its otherwise transparent body (Land 1981, 1989). Hyperiids inhabit epi- and mesopelagic environments from the surface down to 1000 m (Bowman and Gruner 1973). A major function of the huge eyes of some of them seems to be the location of objects that are small and/or of low contrast (e.g., transparent prey against a dark or low-illuminated background). For instance, with enormous upward-looking eyes, the deep-sea-living amphipod *Cystisoma neptunus* is well-adapted to its dim world (Fig. 7B). It needs such large eyes to detect the little light available in its midwater environment (ca. 800 m), and red eyes look black and invisible at that depth (Laurence P. Madin, Woods Hole Oceanographic Institution, personal communication 2008). The visual organs of hyperiid amphipods show striking external ressemblances with those of thylacocephalans (Fig. 7C). It is plausible that *Dollocaris* had eyes with similar properties but requires more detailed fossil evidence from the ommatidial and retinal structures and appropriate comparisons with Recent analogues. Based on these similarities, the giant eyes of *D. ingens* are likely an indicator of dim-light conditions and deep water setting at La Voulte. In *D. ingens*, the density of ommatidia is relatively high (ca. 15 per mm^2; Vannier et al. 2006). The high density of ommatidia together with the extremely large size of the eyes themselves indicate well-developed visual capabilities, either high resolution and/or high sensibility (Dan-E. Nilsson, personal communication to JV 2007). The presence in *D. ingens* and other thylacocephalans of both huge eyes and a set of powerful prehensile appendages strongly suggest that these animals were visual predators and possibly able to detect prey in dim light conditions (relatively deep environment and/or turbid waters). Comparable functional associations of visual and predatory organs are known to occur in the Cambrian arthropod *Isoxys* (Vannier and Chen 2000) and Recent crustaceans (e.g., mantis shrimps, Wortham-Neal 2002; Marshall et al. 2007).

The exact mode of life of thylacocephalans remains an open question. For some authors (Secrétan and Riou 1983; Secrétan 1985; Schram 1990), thylacocephalans were benthic animals with reduced capabilities for swimming due to the absence of a flexible abdomen and the small size of their posterior trunk limbs. Some important features of *D. ingens* would suggest that thylacocephalans could swim: (i) the absence of walking limbs that always characterise benthic arthropods, (ii) their relatively thin carapace (see thin sections in Secrétan 1985), and (iii) the presence of a repeated series of styliform trunk limbs that protrude beyond the postero-ventral margin of the carapace that suggest a locomotory function (Fig. 6F).

Dollocaris ingens has long been considered as a predator (Secrétan and Riou 1983; Vannier et al. 2006), the most convincing evidence being the presence of three pairs of robust raptorial appendages armed with spines. Their geniculate posture indicates (i) that they could probably be projected forwards in order to catch prey and (ii) that they were possibly used to maintain prey close to the mouth parts (Figs. 6E, 8C). The predatory habits of thylacocephalans are confirmed by the stomach contents of Sinemurian *Ostenocaris* (Pinna et al. 1985) that preserves mainly remains of fishes and hooks of cephalopods and fragments of carapaces of crustaceans and small thylacocephalans.

The raptorial appendages of *D. ingens* may be compared with those of the Recent mantis shrimps (Stomatopoda). The first pair of raptorial appendages of *D. ingens* closely resem-

← Fig. 5. Thylacocephalan arthropods from the La Voulte Lagerstätte, Lower Callovian, *Macrocephalites* (*Dolikephalites*) *gracilis* Biozone. **A**, **B**. *Dollocaris ingens* Van Straelen, 1923b. **A**. FSL 170759, general view, large-sized specimen showing enormous eye and the robust raptorial appendages. **B**. FSL 710064, lateral view, 3D-preserved juvenile specimen showing a bulbous eye with no spherical curve. **C**. *Kilianicaris lerichei* Van Straelen, 1923b, UJF-ID.1751, lateral view, incomplete carapace showing lateral carina curved anteriorly and fragmentary encapsulating rostrum-notch complex typical of the species. **D**. *Clausocaris ribeti* (Secrétan, 1985), MNHN A29149, lateral view, note the large eye and the well-developed prehensile appendages, phosphatised and pyritised compressed specimen. **E**. *Paraostenia voultensis* Secrétan, 1985, MNHN A29150, lateral view, phosphatised compressed specimen showing large eye and series of small pit-organs laterally aligned along the surface of the carapace; note the articulated valves of *Bositra buchi* (Roemer, 1836) to the left.

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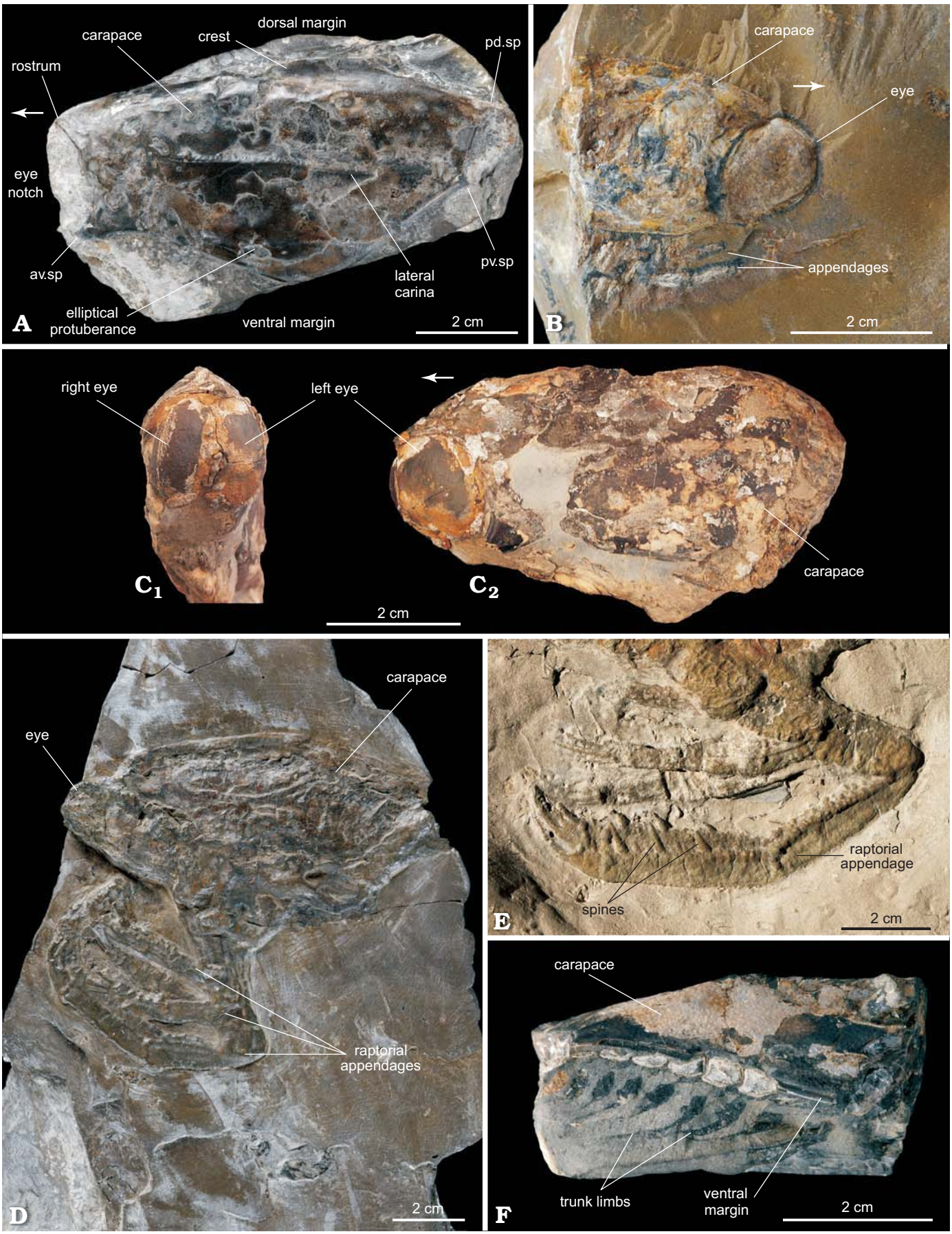

A
carapace
crest
dorsal margin
pd.sp
rostrum
eye notch
av.sp
elliptical protuberance
ventral margin
lateral carina
pv.sp
2 cm
B
carapace
eye
appendages
2 cm
C1
right eye
left eye
C2
carapace
2 cm
D
carapace
eye
raptorial appendages
2 cm
E
raptorial appendage
spines
2 cm
F
carapace
trunk limbs
ventral margin
2 cm

bles the second pair of thoracopods of mantis shrimps (Fig. 7D–F) that is used to stab and snag prey (Wortham-Neal 2002). It is possible that thylacocephalans could unfold their appendages very rapidly in the same way as do Recent mantis shrimps when catching their prey.

Kilianicaris lerichei, *Clausocaris ribeti*, and *Paraostenia voultensis* are less well documented than *Dollocaris ingens*. The series of small pit-organs (= "craters" of Secrétan 1985; Fig. 5E) that run along the lateral surface of the carapace of *P. voultensis* evoke bioluminescent organs comparable with those of Recent deep sea bioluminescent ostracodes (Angel 1993). If this interpretation is correct, then *P. voultensis* may have used bioluminescence either as lures to attract prey or as sexual signals or, alternatively to deter predators (Vannier et al. 2006).

In summary, thylacocephalans dominate the arthropod fauna in numerical abundance. They are mainly represented by *D. ingens*. Several key-features of *Dollocaris* such as huge eyes, raptorial appendages strongly suggest that these arthropods were visual predators living in dim-light conditions. These conclusions support with the current interpretations of the La Voulte biota in relatively deep setting, possibly exceeding 200 m (Charbonnier et al. 2007a, b).

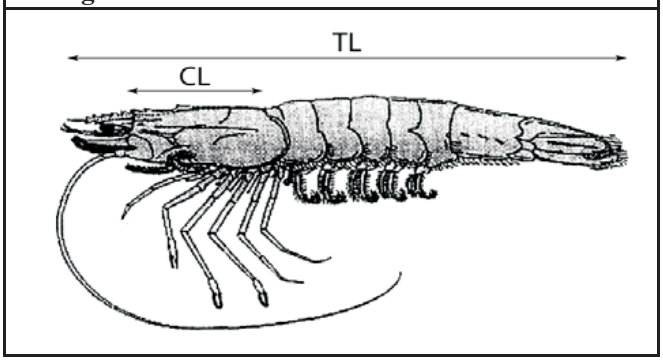
Solenoceridae and Penaeidae shrimps.—The decapod shrimps are the second dominant group of the La Voulte arthropods. Two families are represented: the Solenoceridae (22.4% of specimens) and the Penaeidae (9.3%). By far, *Archeosolenocera straeleni* (87 nodules, Table 2) and *Aeger brevirostris* (25 nodules, Table 2) are the most frequent species.

Archeosolenocera straeleni (Fig. 8A–D) is considered as the only fossil representative of the extant family Solenoceridae (Carriol and Riou 1991). This species is easily recognizsable by typical anatomical features such as the cervical and hepatic grooves both present on each side of the cephalothorax (Fig. 8B). The hepatic groove divides into inferior and antennal grooves that extend towards the orbital notch. The angle between the cervical and hepatic grooves is also occupied by a strong hepatic spine typical of the species (Van Straelen 1925; Carriol and Riou 1991; Fig. 8D, C).

Biometric measurements (Table 3) on 16 complete specimens show that *Archeosolenocera straeleni* is a medium-sized shrimp (TL = 12.8 cm average) the largest specimens being less than 18 cm (Fig. 8C). The relation between the cephalothorax length and the total length of *A. straeleni* is described by a linear model (y = ax + b; Fig. 9A) as observed for many extant penaeoidean shrimps (e.g., Guégen 1997; Table 4). The model clearly indicates that small and/or juve-

Table 3. Measurements of cephalothorax lengths (CL) and total lengths (TL) for *Archeosolenocera straeleni* (16 samples) and *Aeger brevirostris* (8 samples) (schematic drawing indicates the measurements).

Specimens	CL Cephalothoracic length (mm)	TL Total length (mm)
Archeosolenocera straeleni		
MNHN R61839	47.3	180.0
FSL 170546	32.3	152.0
FSL 170547	34.2	147.0
MNHN R61843	36.8	140.0
FSL 170558	32.4	136.0
UJF-ID.11897	31.6	133.0
MHNGr.PA.10231	29.7	132.0
Musée La Voulte	29.0	131.0
UJF-ID.11900	34.7	130.0
MNHN R61840	27.6	124.0
UJF-ID.11898	24.6	121.0
FSL 170560	29.0	118.0
FSL 170524	25.4	106.0
UJF-ID.1791	24.4	105.0
UJF-ID.11901	26.7	99.3
Musée La Voulte	21.6	93.9
Average	**30.5**	**128.0**
Aeger brevirostris		
Musée La Voulte	71.2	313.0
Musée La Voulte	68.0	294.0
FSL 170540	67.6	279.0
UJF-ID.1924	66.0	278.0
FSL 170543	64.7	251.0
MNHN R61860	46.2	215.0
UJF-ID.1790	39.3	195.0
Musée La Voulte	31.5	152.0
Average	**56.8**	**247.1**



← Fig. 6. *Dollocaris ingens* Van Straelen, 1923b (La Voulte Lagerstätte): general morphology and detailed anatomy. **A**. Carapace of specimen MNHN R50930, lateral view, appendages and soft parts are not preserved. **B**. Small-sized specimen MNHN R50954, lateral view (posterior part absent), note the large eye. **C**. 3D-preserved specimen MHNL 20293244 showing a pair of bulbous eyes, frontal (C_1) and left lateral (C_2) views. **D**. Large-sized specimen MNHN R06203, lateral view, note the robust prehensile appendages, pyritised compressed specimen in relief. **E**. Large-sized specimen MNHN R06202, lateral view, detail of articulated raptorial appendages, note the robust spines of the most massive pair of anterior appendages, pyritised compressed specimen in relief. **F**. Fragmentary specimen MNHN R50957 showing caudal region with trunk limbs (= pleopod-like appendages). Abbreviations: av.sp, antero-ventral spine; pd.sp, postero-dorsal spine; pv.sp, postero-ventral spine.

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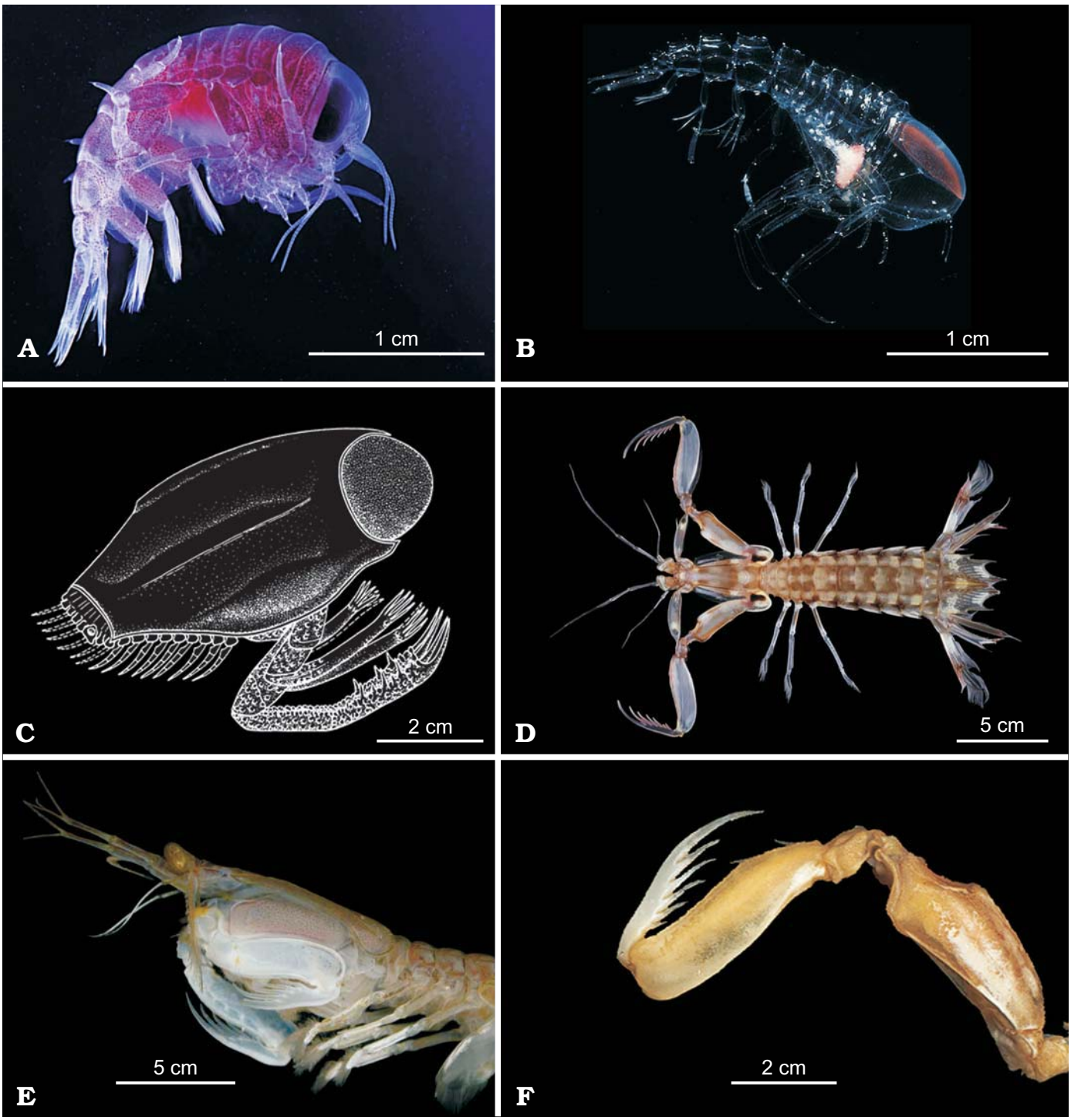

Fig. 7. General morphology of present-day crustaceans: comparisons with thylacocephalan arthropods. **A**. Recent hyperiid amphipod *Hyperia macrocephala* (Dana, 1853), general view, note the very large eyes (courtesy Uwe Kils, Rutgers [The State University of New Jersey, New Brunswick, USA]). **B**. Recent hyperiid amphipod (*Cystisoma neptunus*), general view, note the enormous upward-looking eyes (depth: 500 m; courtesy Laurence P. Madin [Woods Hole Oceanographic Institution, Woods Hole, USA]). **C**. Reconstruction of *Dollocaris ingens* Van Straelen, 1923b, note the large eye, the raptorial appendages and the pleopod-like appendages (modified from Secrétan 1985). **D**–**F**. Recent Stomatopoda (mantis shrimps). **D**. Complete specimen, dorsal view, note the well-developed and spiny second thoracopods (courtesy Mitsuhashi Masako [National Taiwan Ocean University, Keelung, Taiwan], Mission Santo 2006, Vanuatu Island, SW Pacific). **E**. Specimen in lateral view showing the second thoracopod tucked under the body (courtesy Susan DeVictor [Southeast Regional Taxonomic Center, Charleston, USA]). **F**. Detail of the second thoracopod ("spearing" claw), lateral view showing the articulations and the spines (courtesy S. DeVictor).

nile specimens of *A. straeleni* are absent. Juvenile specimens do not appear in the model due to the difficulty to identify the small shrimps to the generic or specific level. Sexual dimorphism expressed by size differences is frequent among Re-

Table 4. Biometric measurements and ecological data for several Recent deep-sea shrimps (references in the text) and comparison with the fossil shrimps from La Voulte.

Taxa		CL (mm)	TL (mm)	Linear equation	TL maximum	bathymetry (m)	abondance peak bathymetry (m)	mode of life	substrate	References
Archeosolenocera straeleni		21–47 (32)	94–180 (128)	TL= 3.2074CL + 30.327	18 cm					
Solenocera acuminata	♀	13–44	55–160	TL= 3.3973CL + 17.219	16 cm	200–300	200–300	benthic endobenthic	continental slope muddy bottoms	Guégen 1997, 1998b
	♂	16–32	65–130	TL= 3.81153CL + 9.507	13 cm					
Aristeus antillensis	♀	26.7–44.6	118–171	TL= 2.4822CL + 57.837	17 cm	450–800	500–600	-	muddy bottoms	Guégen 2001
	♂	25.1	104	-	-					
Aristeus varidens	-	-	-	-	19 cm	300–1134	400–600	-	muddy bottoms	Holthuis 1980, 1991
	-	-	-	-						
Aeger brevirostris		31–71 (57)	152–313 (247)	TL= 3.4992CL + 48.325	31 cm					
Aristaeomorpha foliacea	♀	20–65 (37.9)	95–259 (164.2)	-	26 cm	150–1850	300–700	nectobenthic	muddy bottoms	Ragonese et al. 1997
	♂	20–43 (29.9)	97–174 (132.9)	-	17 cm					
Aristaeopsis edwardsiana	♀	22–84	90–285	TL= 3.0363CL + 46.155	28.5 cm	400–900	700	epibenthic	muddy bottoms	Guégen 1997, 1998b
	♂	22–58	85–230	TL= 3.4033CL + 33.528	23 cm					

cent Solenoceridae (e.g., *Solenocera acuminata* Pérez, Farfante, and Bullis, 1973; for details see Guégen 1998a). Our diagram plots do not show separate clusters that might be interpreted as being due to sexual dimorphism. The number of complete specimens is probably insufficient to reveal separate clusters including males and females respectively. *Archeosolenocera straeleni* is relatively similar in proportions and general morphology to several extant Solenoceridae [e.g., *Solenocera acuminata*, *S. membranacea* (Risso, 1816); Fig. 8E] and Aristeidae [e.g., *Aristeus varidens* Holthuis, 1952, *A. antillensis* Milne-Edwards and Bouvier, 1909, *A. antennatus* (Risso, 1816); Fig. 8F]. These species are deep-water shrimps that are being intensely fished through different areas of the world (Holthuis 1980). Despite their commercial interest, only few biological and ecological data on these species are available because they live at depths where in situ observations are rare and dependent of submersibles or camera sledges. *Solenocera acuminata* (FAO name: orange shrimp; Table 4) is a medium-sized shrimp (TL = 6–16 cm) mainly captured along the continental slope of French Guinea (Western Tropical Atlantic) at depths ranging from 200 m to 300 m where its maximum abundance is reached (Guégen 1997). *S. acuminata* is benthic in the night and endobenthic during the daytime (Guégen 1998a); it lives in dense swarms on muddy sediments and is only captured at night. *Aristeus varidens* (FAO name: striped red shrimp) and *Aristeus antillensis* (FAO name: purplehead gamba prawn) are also medium-sized shrimps (TL: 17–19 cm; Table 4). They are commercially exploited along the continental slope where their maximum abundances are reached at depths between 400 to 600 m. As numerous Aristeidae, these two species are benthic and strictly live on soft muddy bottoms (Guégen 2001). Their feeding diet is principally composed of small crustaceans (e.g., euphausids, mysids), marine worms (e.g., polychaetes), small echinoderms (e.g., holothurians) and also plant debris (Kapiris 2004; Chartosia et al. 2005; Cartes et al. 2008). The comparisons with Recent Solenoceridae seem to indicate that *Archeosolenocera straeleni* was benthic. The prevalence of marly sediments at La Voulte indicates that the bottom conditions were muddy. Recent analogues of *A. straeleni* have also ecological preferences for muddy substrates. The absence of bioturbation in the laminated sediments of La Voulte strongly suggests that *A. straeleni* was not a burrower but more likely lived at the water-sediment interface as a vagile member of the epibenthic community. No direct evidence is available concerning the diet although potential prey is abundant in the La Voulte biota. As most of the extant deep-water shrimps, *A. straeleni* was probably gregarious and lived in dense aggregates.

Aeger brevirostris Van Straelen, 1923a (Fig. 10A–D) is affiliated with the Penaeidae. Despite its name, this species is characterised by a well developed rostum (Fig. 10A). *A. brevirostis* is characterised by a cephalothorax with a hepatic spine surrounded dorsally by a cervical groove and ventrally by a hepatic groove prolonged posteriorly in ventral groove (Fig. 10B, D). A typical branchiocardiac groove crosses diagonally the whole cephalothorax from the postero-dorsal angle to the separation of the hepatic and ventral grooves (Van Straelen 1925; Carriol and Riou 1991). The first three pairs of pereiopods are armed by spines and long chelae (Van Straelen 1925; Carriol and Riou 1991; Fig. 10D). *Aeger brevirostris* had a large size compared to *Archeosolenocera straeleni* (TL = 24.7 cm average, max. 30 cm; Table 3) the largest specimens being more than 30 cm (Figs. 9B, 10C). The relation between the cephalothorax length and the total length of *Aeger brevirostris* is also described by a linear model (Fig. 9B). Juveniles are absent probably due to difficulties for the identification of small specimens.

Aeger brevirostris is relatively similar in size and general morphology to some extant Aristeidae such as *Aristaeomorpha foliacea* (Risso, 1827) (FAO name: giant red shrimp; Fig. 10E) or *Aristaeopsis edwardsiana* (Johnson, 1868) (FAO name: scarlet shrimp; Fig. 10F). These two species are large-sized shrimps that commonly reach 20–30 cm in total length (Table 4). They live in the Mediterranean Sea, Atlantic, Western Pacific and in the Indian Ocean (Ragonese et al. 1997).

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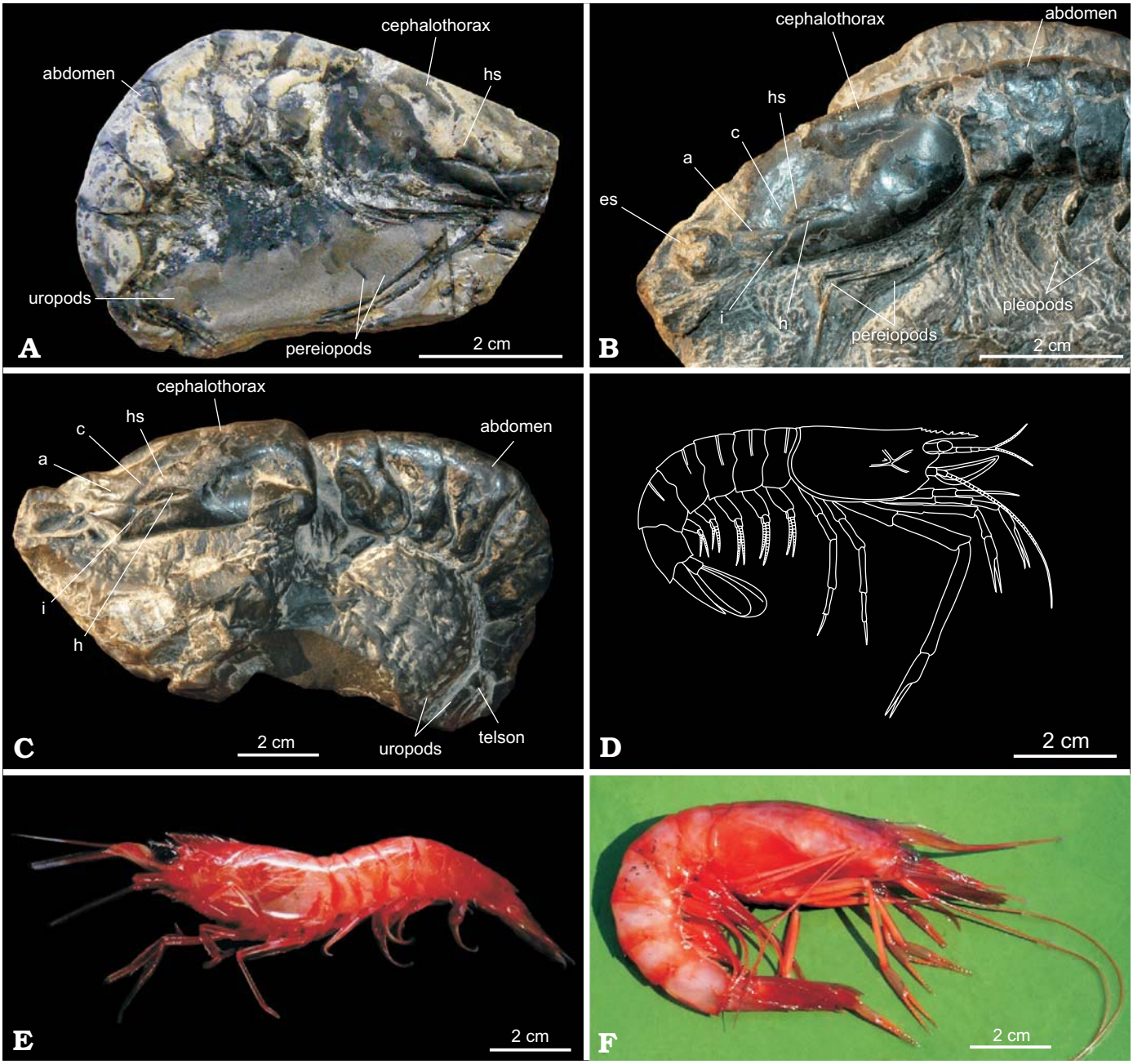

Fig. 8. Solenocerid shrimps from the La Voulte Lagerstätte and Recent representatives. **A**–**D**. *Archeosolenocera straeleni* Carriol and Riou, 1991, Lower Callovian, La Voulte. **A**. Medium-sized specimen FSL 170560, general view. **B**. Detail of cephalothorax MNHN R61843, lateral view, note the different grooves and the well-developed hepatic spine. **C**. Very large-sized specimen MNHN R61839, general view. **D**. Synthetic reconstruction [composite line drawing from Van Straelen (1923), Carriol and Riou (1991), and personal observations]. **E**. *Solenocera* sp., general view, medium-sized species (LTmax = 15 cm; courtesy of Database of Crustacea, http://decapoda.free.fr). **F**. *Aristeus antennatus* (Risso, 1816), general view, medium-sized species (LTmax = 19 cm; courtesy Pere Abelló [Institut de Ciències del Mar, Barcelona, Spain]). Abbreviations: a, antennal groove; c, cervical groove; es, eye-stalk; h, hepatic groove; hs, hepatic spine; i, inferior groove.

They are deep-water organisms commercially fished along the continental slope at depths ranging from 300 to 700 m where peaks of abundance are reached (Ragonese et al. 1997; Guégen 1998b; Papaconstantinou and Kapiris 2003). They live on muddy grounds and move in dense aggregates along the steep reliefs of the continental slope (Pérez Farfante 1988; Bianchini and Ragonese 1994). *Aristaeomorpha foliacea* is nektobenthic (Ragonese et al. 1997) and *Aristaeopsis edwardsiana* is strictly benthic (Guégen 1998b). These shrimps are active predators and principally feed on small-sized crustaceans (e.g., euphausids, mysids), small fishes and cephalopods (Bello and Pipitone 2002). The comparisons with Recent Aristeidae seem to indicate that *Aeger brevirostris* was a benthic shrimp moving on muddy substrate typical of the marly sediments of La Voulte. More precisely, *A. brevirostris* was most probably nectobenthic as its long pleopods suggest well

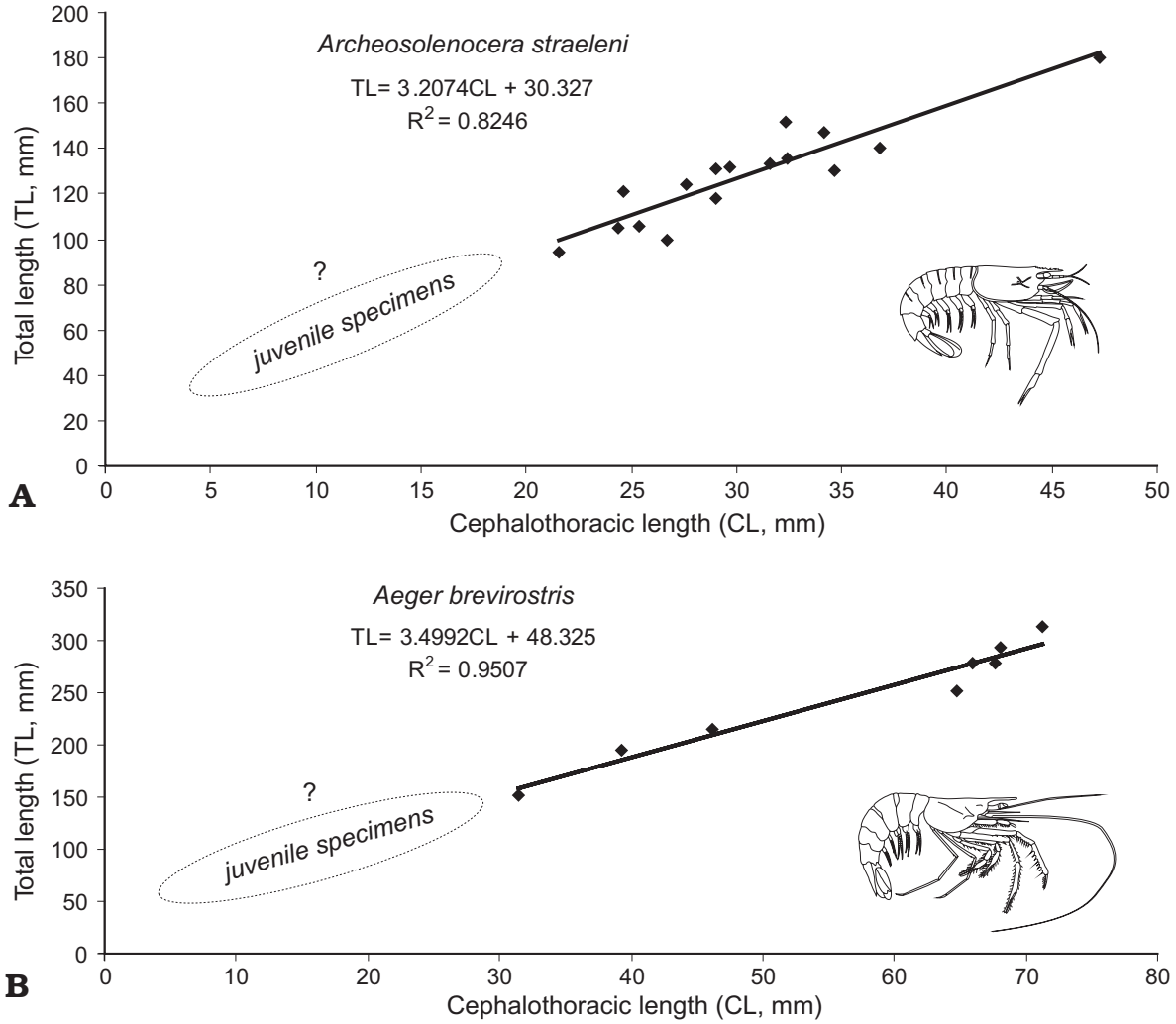

Fig. 9. Results of biometric analyses on the La Voulte shrimps. Linear relation between the cephalothoracic length (CL) and the total length (TT), note the absence of small-sized specimens (probable juveniles) in *Archeosolenocera straeleni* (**A**) and *Aeger brevirostris* (**B**).

developed swimming capacities. As *Archeosolenocera straeleni*, *Aeger brevirostris* might have been an active predator.

In summary, *Archeosolenocera straeleni* and *Aeger brevirostris* are important components of the La Voulte arthropod fauna that have morphological and possible ecological analogues among the Recent deep-water giant shrimps. That these two fossil shrimps lived in similar bathyal conditions as their modern analogues is plausible and confirmed by other fossils such as crinoids, siliceous sponges (Charbonnier et al. 2007b), sea spiders (Charbonnier et al. 2007a) and sea stars (Villier et al. 2009). All these organisms support the notion that the La Voulte area was situated in the upper bathyal zone with a water depth most probably exceeding 200 m.

Coleiidae crustaceans.—The Coleiidae crustaceans (15.5% of the specimens) are the third dominant group of the La Voulte arthropods after the thylacocephalans and the Solenoceridae (Table 2). The Coleiidae belongs to the superfamily Eryonoidea (Glaessner 1969). By contrast with coleiids, eryonids have extant representatives all grouped within the single family Polychelidae. The coleiids from La Voulte are represented by several species (Table 1). The most abundant and the best preserved is *Coleia gigantea* (Van Straelen, 1923a) (Figs. 3C$_2$, 4C, 11A; see also Van Straelen 1925) whereas *Hellerocaris falloti* (Van Straelen, 1923a) (Fig. 4G; see also Van Straelen 1925) is a poorly documented species (3 specimens available).

Coleia gigantea is characterised by a dorsoventrally flattened carapace and a large first pair of chelate pereiopods often lacking in specimens preserved in nodules. The cephalothorax is subcircular and bears (i) laterally two narrow marginal incisions, (ii) frontally two circular orbital sinuses and (iii) dorsally a spiny median carina well-marked from the posterior margin to the first lateral incision (Fig. 11A–C). This carina is flanked by two branchial carinae. These three carinae are stopped by a cervical groove deep and V-shaped, very characteristic of the species (Figs. 4C, 11B). The abdomen, mostly folded back under the cephalothorax, is composed of 6 spiny somites dorsoventrally depressed. The telson is triangular and each uropodal exopod bears a diaeresis (see Van Straelen 1925: pl.3: 4). All the pereiopods are chelate and the first pair of them, very long and armed with strong chelae, is

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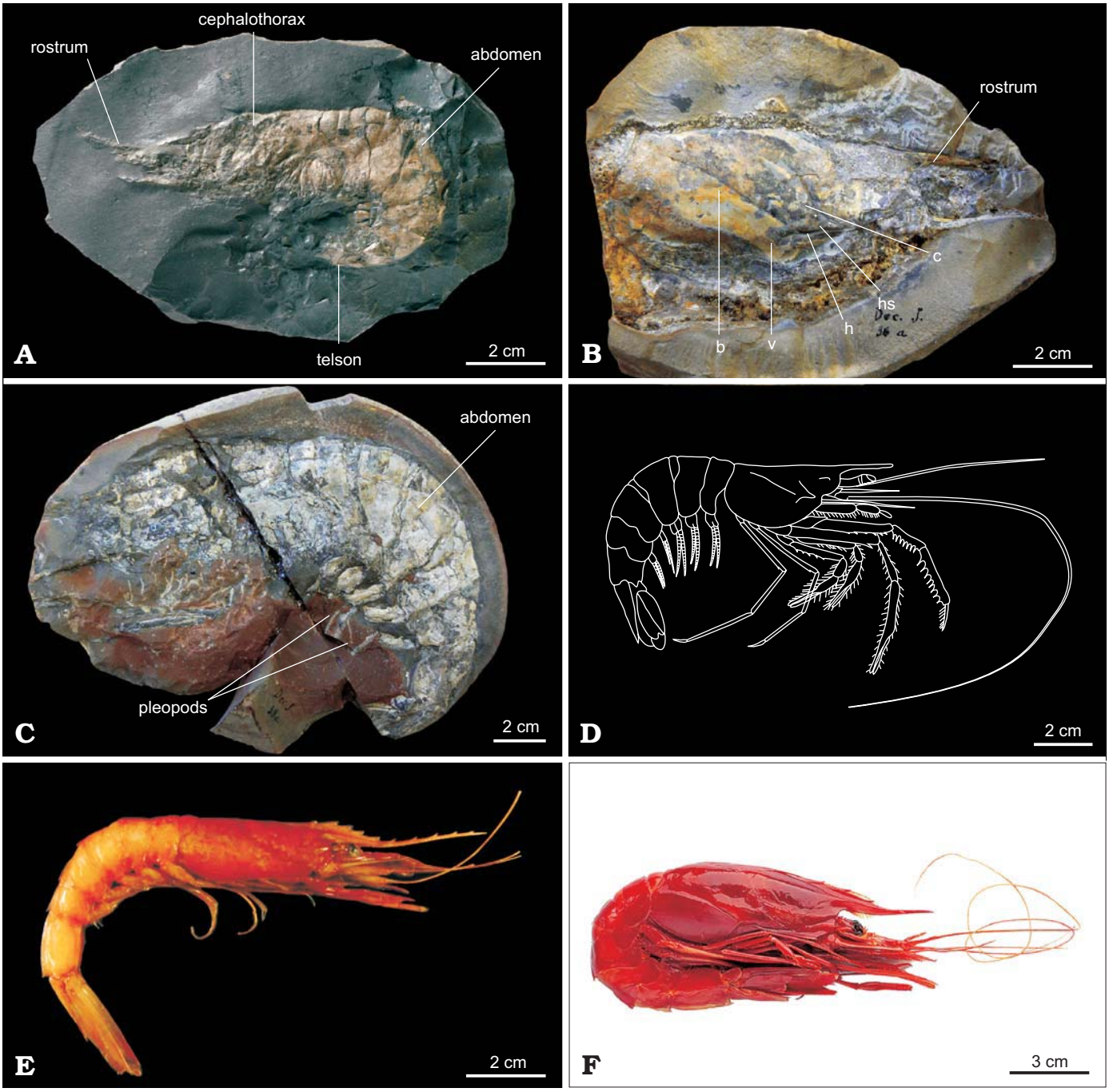
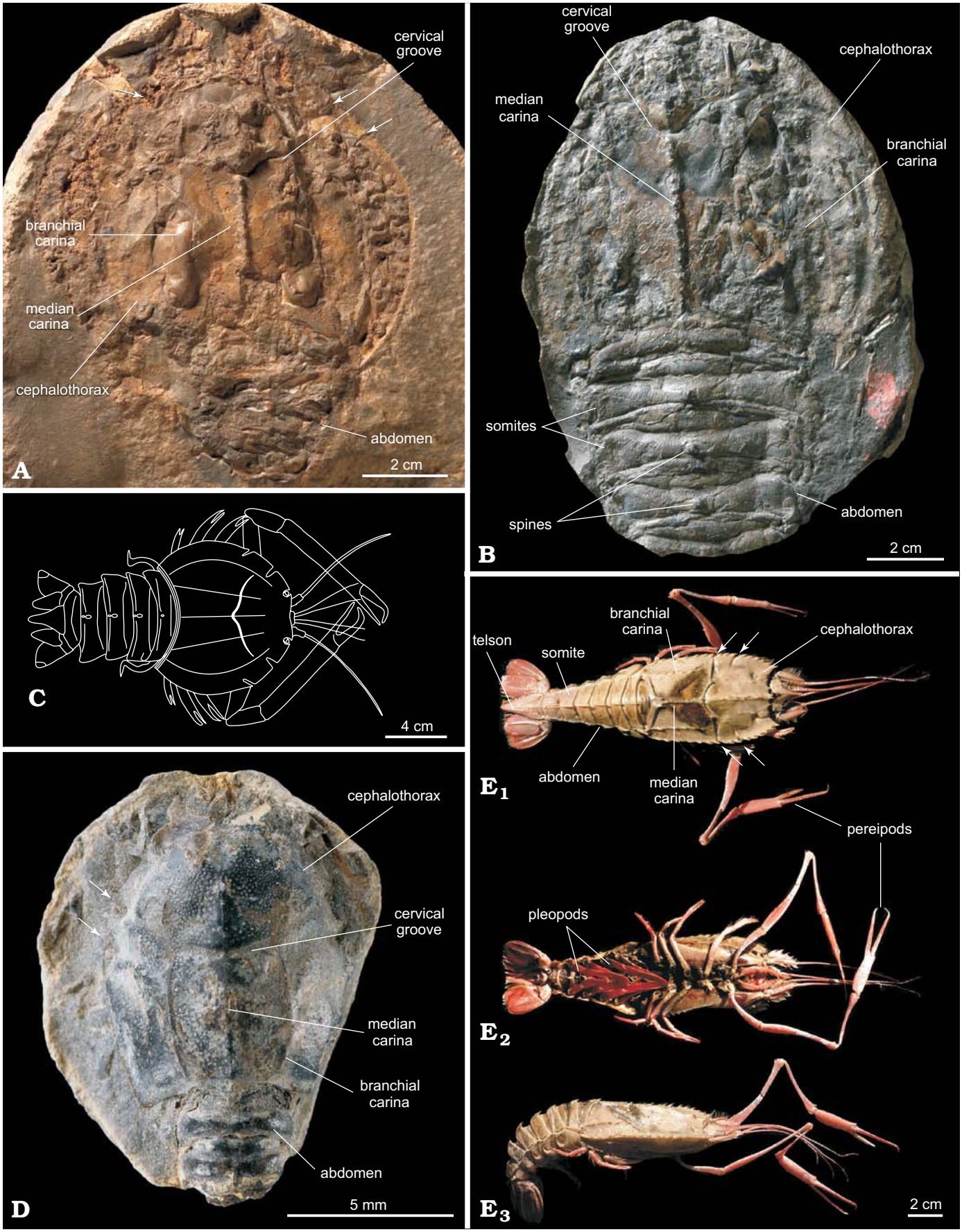


Fig. 10. Penaeid shrimps from the La Voulte Lagerstätte and Recent deep-sea representatives. **A**–**D**. *Aeger brevirostris* Van Straelen, 1923a, Lower Callovian, La Voulte. **A**. Medium-sized specimen UJF-ID.11561, general view, note the lateral flattening and the well-developed rostrum. **B**. Detail of cephalothorax of large-sized specimen FSL 170532, showing the elongate rostrum and the lateral grooves. **C**. Very large-sized specimen FSL 170540, general view. **D**. Synthetic reconstruction [composite line drawing from Carriol and Riou (1991) and personal observations]. **E**. *Aristaeomorpha foliacea* (Risso, 1827), giant red shrimp (LTmax = 26 cm, from Perry and Larsen 2004). **F**. *Aristaeopsis edwardsiana* (Johnson, 1868), scarlet shrimp (LTmax = 34 cm) (courtesy Sanchez y Guzman S.A. [Fischeries Company, Las Palmas de Gran Canaria, Canary Islands, Spain]).

Fig. 11. Coleiid crustaceans from the La Voulte Lagerstätte and Recent deep-sea representatives. **A**–**C**. *Coleia gigantea* (Van Straelen, 1923a), Lower Callovian, La Voulte. **A**. Specimen MHNGr.PA.10203, dorsal view, carapace subcircular, dorsoventrally flattened with two lateral incisions (white arrows). **B**. Specimen UJF-ID.11552, dorsal view, note the spiny median carina, the deep V-shaped cervical groove and the median tubercles on the somites. **C**. Synthetic reconstruction (personal line drawing) of *Coleia gigantea*. **D**. Very small-sized Eryonoidea, MNHN A29151, dorsal view, possibly juvenile state of *Coleia gigantea*. **E**. Recent polychelid crustacean (*Polycheles sculptus* Smith, 1880, NW Ireland; courtesy Cédric d'Udekem d'Acoz [Institut royal des Sciences naturelles de Belgique, Brussels, Belgium]), in dorsal (E_1), ventral (E_2) and right lateral (E_3) views, note the dorsoventrally flattened carapace and the lateral incisions (white arrows). →



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typical of the Eryonoidea (Fig. 11C). *Coleia gigantea* is represented by specimens of various sizes, the largest one exceeding 30 cm long (Van Straelen 1925). It is not clear if the smallest specimens of Eryonoidea from La Voulte (Fig. 11D) belong to *C. gigantea* or a different species. Matching juvenile forms with adult ones is a recurrent problem with extant Eryonoidea that led to excessive taxonomic splitting (Holthuis 1991). However, the most recent revisions of the family Polychelidae came to the conclusion that only 37 species were valid but the assignment of the larval forms to such or such species remains unresolved (Galil 2000; Ahyong and Brown 2002; Boyko 2006). The Coleiidae are relatively similar in size and general morphology with the extant Polychelidae, which are also known from the fossil record (Glaessner 1969). The polychelids have a subrectangular or oval, dorsoventrally flattened carapace (Fig. 11E). The lateral margins show cervical and postcervical incisions dividing it into three parts. The frontal margin is often characterised by two orbital sinuses with eyestalks lacking cornea (Galil 2000). The first pair of pereiopods is very slender and bears robust chelae. Therefore, comparisons between the Coleiidae and the Polychelidae are possible and allow precise discussions on the possible lifestyle and ecology of *C. gigantea*.

The polychelids are large and very uncommon decapods that inhabit the depths of the world oceans (Galil 2000). They are prominent members of the deep sea biota and principally live in the bathyal and abyssal zones. They are considered as rare crustaceans and none are of commercial value (Galil 2000). Nevertheless, some species can be caught in considerable quantities. During the 1964 cruises of R.V. John Elliot Pillsbury, the catch of *Polycheles talismani* (Bouvier, 1917), at one of the stations off West Africa, was so large that the surplus specimens were shoveled overboard (Holthuis 1991).

These crustaceans may be grouped in aggregates at the time of reproduction and are probably relatively solitary the rest of the time. Most of the polychelids live on muddy substrates in the mesobathyal zone (ca. 500–1500 m of depth) where they show high diversity and abundance. Some species live at depths between 150 and 200 m, near the distal limit of the platforms, along the upper part of continual slope. Some others are abyssal and occur exclusively at depths greater than 2000 m (Galil 2000).

The comparisons with Recent Polychelidae suggest that *C. gigantea* and the other eryonoids from La Voulte may be indicators of deep sea conditions and a bathyal environment.

Originality and environmental significance of the La Voulte arthropods

Comparison with other famous Jurassic crustacean faunas.—The La Voulte fauna as a whole contains nearly 60 different species (see Fischer 2003; Charbonnier 2007) and is largely dominated by arthropods (30 species, ca. 50% of the species richness) while other groups (e.g., cephalopods, marine worms, ophiuroids) taken separately do not exceeded 12% of the total biodiversity. The high percentage of arthropod species is the most original characteristic of the La Voulte fauna that is found nowhere else in the Jurassic deposits except in the Solnhofen Lagerstätte (see Van Straelen 1922, 1925; Etter 2002). Because of their specific richness (30 species), their abundances (hundreds of specimens) and their probable endemism (ca. 10–12 species only described from La Voulte), the La Voulte arthropod fauna may be considered as the richest and the most diverse fauna after that of Solnhofen (ca. 70 crustacean species; Frickhinger 1994, 1999; Schweigert and Garassino 2004; Garassino and Schweigert 2006). However, the biodiversity of the La Voulte fauna is relatively low compared with that of other Mesozoic Lagerstätten such as (i) Holzmaden (Toarcian, Germany) with more than 100 species recognised in bituminous shales (Gall and Blot 1980; Hauff and Hauff 1981), (ii) Solnhofen (Kimmeridgian–Tithonian, Germany) with more than 500 species in limestone (Barthel 1978; Frickhinger 1994, 1999), and (iii) Cerin (Kimmeridgian, France) with ca. 120 species in the lithographic limestone (Bernier et al. 1991). These differences of biodiversity must be balanced by the sampling methods and the outcrop surfaces. The fossiliferous beds from La Voulte crop out only in the Ravin des Mines (some hectares) and occur within a relatively thin interval (ca. 4–5 m; Fig. 2B) whereas for instance, the Solnhofen limestone, intensely quarried for centuries, comprise a large set of localities extending over several hundreds of square kilometers (Frickhinger 1994, 1999; Garassino and Schweigert 2006). The low biodiversity of the fauna from La Voulte is possibly linked to reduced outcrops but more certainly reflects major differences in palaeoecological and palaeoenvironmental conditions. Indeed, the Late Jurassic lithographic limestone was deposited in very shallow carbonate platforms and coastal lagoons where high biodiversity is commonly observed such as in southern Germany (e.g., Eichstätt, Solnhofen, Nusplingen; Frickhinger 1994; Garassino and Schweigert 2006), in Lebanon (Hakel, Hadjula, Sahel Alma; Garassino 1994; Gayet et al. 2003) or in France (Cerin: Bernier et al. 1991; Canjuers: Roman et al. 1994; Carriol and Secrétan 1998). The majority of the taxa that occurred in these Lagerstätten correspond to relatively shallow water organisms. Other crustacean faunas contemporaneous of that of La Voulte but mainly composed of fragmentary specimens are known from the Etrochey area (NE France, Callovian) and are also considered to have inhabited shallow depths in the circalittoral zone (ca. 40–80 m, Crônier and Courville 2004).

Recent deep-sea crustacean faunas.—Today, the most diversified arthropod faunas occur in the bathyal zone, along the continental slope (Abelló et al. 1988). The environmental conditions of the slope areas seem to be propitious to the development of rich and diversified communities of decapod crustaceans (Pérès 1985; Abelló et al. 1988). Recent studies on the distribution and abundance patterns of decapods, chiefly in

deep waters, revealed clear evidence of bathymetric zonation (Fariña et al. 1997). The parameters that control the community structure are mainly the depth but also the submarine topography, the type of substrate and the seasonal fluctuations of water temperature (Fariña et al. 1997, Fanelli et al. 2007). In the NW Mediterranean, four distinct crustacean assemblages are classically distinguished (Abelló et al. 1988): (i) shallow shelf assemblage (depth: 0–100 m) with littoral communities over sandy bottoms, (ii) deep shelf assemblage (depth: 100–150 m) characterised by terrigenous muds, (iii) upper slope assemblage (depth: 150–400 m) characterised by muddy sediments and rocky substrates linked to the steepness of the continental slope, and (iv) lower slope or bathyal assemblage (depth: 400–800 m) with only fine muds. Each community comprises typical species whose abundance is variable according to the depth. The upper and lower slope crustacean assemblages present the highest species richness (Abelló et al. 1988). Thus 32 species are recognised along the continental slope in French Guyana by Guégen (1995) and 30–40 species along the Western Mediterranean slopes by Abelló et al. (1988) and Fariña et al. (1997). Among these species, the Solenoceridae shrimps (e.g., *Solenocera membranacea*, *S. acuminata*) principally inhabit the upper slope (Maynou et al. 1996; Guégen 1997, 1998a) and the Aristeidae shrimps (e.g., *Aristeus antennatus*, *Aristaeopsis edwardsiana*,) principally live on the lower slope (Guégen 1997, 1998b; Sardà et al. 2004). Moreover, the lower slope constitutes also the area where polychelids (e.g., *Polycheles typhlops*) become abundant (Galil 2000; Company et al. 2004). These observations may be balanced by the proportions of certain species within the different crustacean assemblages. Indeed, in a well diversified assemblage, only 3–4 crustacean species show very high numerical abundances whereas all the others are only represented by a few sparse specimens. For instance, along the continental slope of French Guyana (Western Central Altantic) the specific richness is high (32 species) but only 5 species comprised 80% of total biomass for decapod crustaceans. Among these 5 species, the Aristeidae *Aristaeopsis edwardsiana* (33% of the biomass) and Solenoceridae *Solenocera acuminata* (27%) are clearly dominant (Guégen 1995). Similarly, the lower slope of Western Mediterranean shows very high specific richness of decapod crustaceans (30–40 species; Fariña et al. 1997; Abelló et al. 1988) but, in most places, only two species represent the quasi-totality of the biomass: the so-called deep sea shrimps *Aristaeomorpha foliacea* and *Aristeus antennatus* (Abelló et al. 1988; Company et al. 2004; Sardà et al. 2004).

Probable environmental setting of the La Voulte fauna.—Convergent palaeoenvironmental evidence obtained from both stalked crinoids, siliceous sponges (Charbonnier et al. 2007b), sea spiders (Charbonnier et al. 2007a), asterids (Villier et al. 2009) and cephalopods (Fischer and Riou 1982a, b, 2002) support the hypothesis that the La Voulte area was situated in the bathyal zone, around the slope-basin transition. The reconstruction proposed by Charbonnier et al. (2007b) shows a depositional environment along the external part of the slope where steep topographies and tilted block generated heterogeneous bottom conditions. This setting was probably favourable to the numerous animals—including arthropods— because it provides appropriate trophic and ecological conditions (temperature, salinity, currents, food abundance, obscurity?) and adequate substrates (fine sediments, muds, steep reliefs). The comparisons with the ecological parameters and the structure of the Recent crustacean communities seem to indicate that the La Voulte arthropods may be interpreted as a characteristic continental slope assemblage. This hypothesis is based both on the palaeobiodiversity and on the remarkable abundances observed at La Voulte. The fossil fauna is diverse but only four species (*Dollocaris ingens*, 32.4% of specimens; *Archeosolenocera straeleni*, 22.4%; *Coleia gigantea*, 15.5%; *Aeger brevirostris*, 9.3%) are numerically very abundant. These observations suggest that during the Callovian, the structure of the La Voulte arthropod fauna might be very similar to that noticed in the Recent decapod crustacean faunas from the continental slope (bathyal zone?). As the Recent deep sea crustaceans from the continental slope, the La Voulte arthropods might benefit of propitious ecological conditions that allowed the settlement and the development of a long lasting community. Each of the four studied groups presents a wide range of specimens from probable juvenile to adult stages. These three-dimensionally preserved arthropods—with their internal organs (see Secrétan 1985; Wilby et al. 1996)—are obviously autochthonous and might indicate relatively stable ecological conditions that characterise the Recent deep marine environments (Gage and Tyler 1991).

The La Voulte Lagerstätte: a Jurassic hydrothermal site?—By comparison with Recent hydrothermal communities, the La Voulte Lagerstätte might also correspond to a fossil oasis possibly linked to hydrothermal activity. This hypothesis is supported by different arguments such as (i) the high abundance of arthropods very similar to some remarkable concentrations of crustaceans specific to extant hydrothermal vents (Rona et al. 1986; Segonzac 1992; Segonzac et al. 1993; Desbruyères et al. 2000, 2001) and (ii) the probable high endemism of the La Voulte arthropod fauna that comprise ca. 10–12 species only described in this Lagerstätte. These taxa may represent highly adapted species as commonly observed in numerous deep sea hydrothermal settings where ca. 82% of species appear to be endemic (McArthur and Tunnicliffe 1998; Van Dover 2000). Although direct evidence of hydrothermal vents at La Voulte has not been found yet, the hydrothermal hypothesis is also supported by mineralogical and sedimentological clues. The presence of substantial iron deposits (thickness: ca. 15 m; Fig. 2A) clearly related to the activity of the La Voulte fault reinforces the hypothesis of hydrothermal activity (Fournet 1843; Wilby et al. 1996; Charbonnier et al. 2007b). Moreover, many of the minerals (e.g., pyrite, siderite, galena, sphalerite; see Wilby et al. 1996 for details) preserving the La Voulte arthropods are often present at marine hydrothermal settings

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where fluids distributed onto the sea floor are enriched in various metals (especially Fe, Zn, Cu, and Mn; Little and Vrijenhoek 2003; Little et al. 2004).

In summary, a possible occurrence of hydrothermal activity in the vicinity of the La Voulte Lagerstätte may have created conditions favourable to the settlement of a specific marine community dominated by arthropods and ophiuroids. This activity might also be the origin of the exceptional preservation of the arthropods and other animals by the introduction in the environment of high concentrations of dissolved metals, sulfides and sulfates inducing early diagenetic mineralisation.

Conclusions

The study of the fossils three-dimensionally preserved in nodules from the La Voulte Lagerstätte shows that the arthropods are major components of the fauna. Represented by 30 different species, these arthropods constitute one of the most diverse fossil faunas for the Mesozoic, even rivaling the decapod crustacean fauna of Solnhofen. Quantitative analysis of the nodule contents reveals four dominant groups of arthropods: the thylacocephalans, the Solenoceridae and Aristeidae and the Coleiidae.

Convergent lines of fossil evidence, based on detailed comparisons with modern morphological and ecological analogues, support the hypothesis that this arthropod fauna inhabited deep water setting most probably exceeding 200 m (= bathyal zone) under dysphotic or aphotic conditions. If our interpretations are correct, the La Voulte arthropods may be considered reliable indicators of a deep sea setting possibly with hydrothermal conditions. They provide key-information on the deep marine palaeobiodiversity during the Mesozoic and make the La Voulte fauna a very rare and precious window into the bathyal Mesozoic communities.

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