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An atypical Silurian myodocope ostracod from the Armorican Massif, France

VINCENT PERRIER



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A new myodocope ostracod *Sineruga insolita* gen. et sp. nov. is herein described from the Armorican Massif (France). *Sineruga* resembles Silurian myodocopes (i.e., bolbozoids and cypridinids) in having anterior features (thinner carapace) possibly related to vision. On the other hand, it resembles entomozoid ostracods in having a bean-shaped outline along with a deep adductorial sulcus and a simple muscle spot, but lacks their characteristic ribbed ornament. The data available suggest that *Sineruga insolita* was probably an atypical, non-ribbed member of the entomozoids thus indicating that early entomozoids may have had smooth representatives. Comparisons with other Recent and fossils ostracods show that the presence of a rostrum and/or symmetrical vision related carapace features (i.e., indicating lateral eyes) can be used as diagnostic characters for myodocope ostracods. The position and shape of the dorsal connection and to a lesser extent that of the sulcus and the adductorial muscle scar can be used to discriminate the higher groups of Silurian myodocopes (bolbozoids, cypridinids, and entomozoids).

Key words: Arthropoda, Crustacea, Ostracoda, Myodocopa, Entomozoidae, taxonomy, Silurian, France.

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Introduction

Silurian myodocope ostracods are very abundant in the Wenlock to Pridoli series of the Armorican Massif (France) and other regions of Europe. This study is a continuation of the revision of this group, initiated during the late 20th century by David J. Siveter, Jean Vannier and co-workers. Siveter (1984), Siveter et al. (1987, 1991), and Vannier and Abe (1992) provided evidence that, taken together, strongly suggested a pelagic lifestyle for Silurian bolbozoids and their myodocope associates. Their hypotheses were based on the functional design of the carapace, and distributional pattern and depositional environments of these ostracods in the Silurian of Europe. More recently, the discovery of soft parts in three Silurian myodocopid ostracods (Siveter et al. 2003, 2007, 2010) opened the way to new interpretations of fossil carapaces (Perrier 2007; Perrier et al. 2007, 2011). Perrier (2007) also showed the high diversity of Silurian myodocopes in the Armorican Massif (more than 12 species) and revealed the remarkable morphological stability of the group over the last 400 million years. As a follow-up to these recent revisions this paper focuses on a particularly interesting new species and examines its external carapace characters and their taxonomic importance.

Institutional abbreviations.—FSL, Faculty of Science, University of Lyon, Lyon, France; LPB, University of Brest, Brest, France; MNHN, Museum d'Histoire Naturelle de Nantes, Nantes, France.

Other abbreviations.—H, valve height; L, valve length.

Geological setting

This study is based on newly collected material from three localities in France (Fig. 1: Loc. 1, 3, 4) and also on the revision of several specimens formerly collected (Fig. 1: Loc. 2). *Sineruga insolita* gen. et sp. nov. occurs in these localities within the Armorican Massif and Normandie and in stratigraphical layers assigned to the Upper Silurian (late Wenlock to early Pridoli Series) based on graptolite biostratigraphy established by Sadler et al. 2009 (Fig. 1). These new specimens are deposited in the collections of the Université Claude Bernard Lyon 1 (FSL). The author also studied two collections from which *Sineruga* ostracods were recovered: the Racheboeuf collection (LPB; Loc. 1) and the De Tro- melin collection (MNHN; Loc. 2). Details of these localities are as follows (see also Fig. 1):

Les Chevrolières.—Exposures at the intersection between the A81/E50 motorway (Laval to Le Mans section) and the departmental road D49 from St. Denis-d'Orques to Brûlon, St. Denis-d'Orques, Sarthe (= Loc. 5 in Siveter et al. 1987; and Loc. 3 in Racheboeuf 1994; herein Fig. 1). Highly deformed siltstone and mudstone rocks containing numerous partly pyritized nodules; Le Val Formation (see Paris 1977). Poorly preserved graptolites indicate the uppermost Ludlow to early Pridoli (Palmer in Siveter et al. 1987; Fig. 1C). *Sineruga* carapaces (3D-preserved single valves and complete closed carapaces in nodules) are associated with other myodocopid ostracods (bolbozoids and cypridinids), numer-

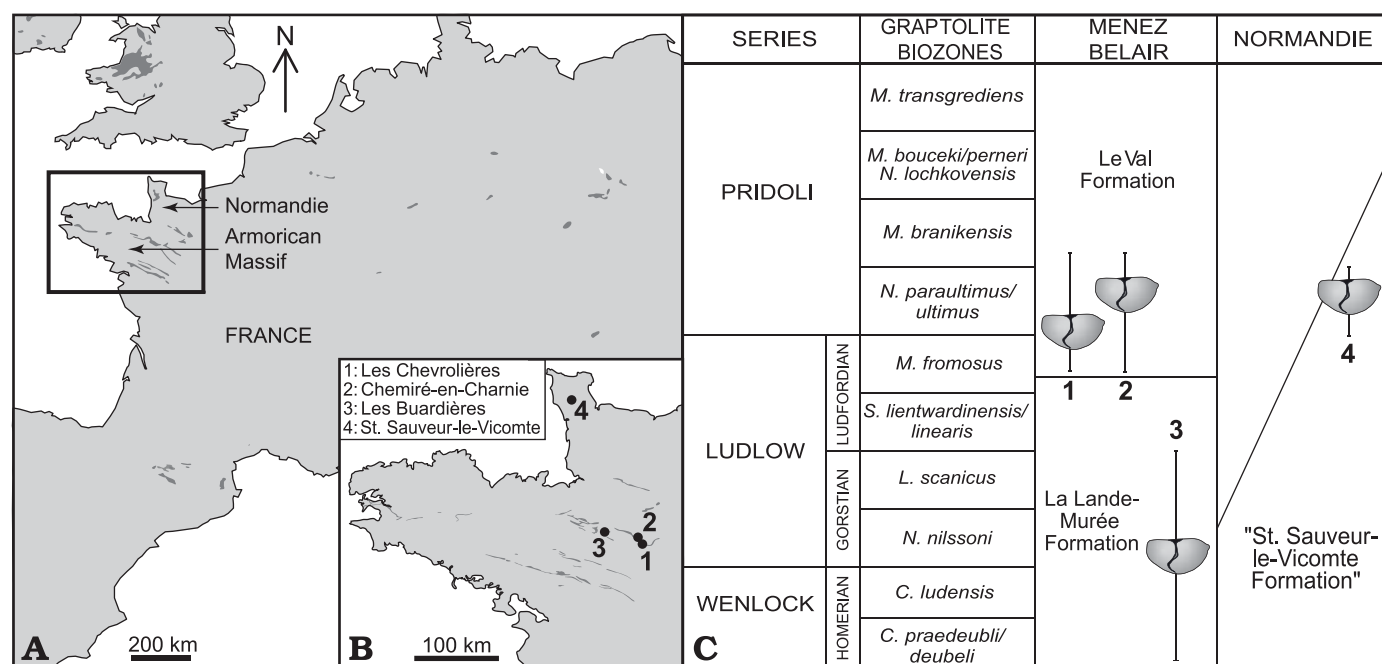


Fig. 1. Geographic and stratigraphic position of studied localities (1–4). **A.** Silurian outcrops in Western Europe. **B.** Localities sampled in the Silurian of the Armorican Massif and Normandie, France. **C.** Approximate stratigraphic position of the localities. Successions after: Paris 1981 (Menez-Belair); Michel Robardet, personal communication 2005 (Normandie). Graptolite zonations from Sadler et al. (2009), not to scale.

ous phyllocarids (mainly tail-pieces of *Ceratiocaris* and *Warneticaris*), bivalves, orthoconic cephalopods, crinoids, gastropods, fragments of eurypterids, bryozoans, and spirorbids.

Chemiré-en-Charnie.—Specimens from the de Tromelin collection (19th century), housed in the Natural History Museum of Nantes (= Loc. 4 in Siveter et al. 1987; herein Fig. 1). Outcrops no longer available. Siltstone and mudstone rocks containing siliceous nodules collected by Albert Guillier in Le Val Formation (Guillier and de Tromelin 1874; Guillier 1896). Graptolites indicate the Ludlow or Pridoli (Palmer in Siveter et al. 1987; Fig. 1C). *Sineruga* (well-preserved and undeformed moulds of single valves) occurs with myodocopes (bolbozoids and cyprinidids), phyllocarids (*Ceratiocaris* and *Schugurocaris*), orthoconic cephalopods, crinoids (*Scyphocrinites*?) and spirorbids.

Les Buardières.—Numerous exposures along the departmental road D104 between St. Germain-le-Fouilloux and Andouillé, Andouillé, Mayenne (= Loc. 1, Armorican Massif in Siveter et al. 1987; Fig. 1). Highly tectonised, fossiliferous, finely laminated grey to black shales in the La Lande Murée and Le Val Formations (see Paris 1981; Siveter et al. 1987). Tectonic deformation prevents accurate determination of graptolites except *Colonograptus. ludensis*, *Mono-graptus haupti*, and *Pristiograptus dubius*, that indicate a range from the late Wenlock into the early Ludlow (Palmer in Siveter et al. 1987 and Mark Williams, personal communication 2005; Fig. 1C). *Sineruga* (flattened single and connected valves) occurs with numerous myodocopes (seven

bolbozoid and cyprinid species; Perrier et al. 2011), thin-shelled bivalves (*Praecardium* or *Dualina*, *Actinopteria*), brachiopods, orthoconic cephalopods, crinoids, and phyllocarids (*Ceratiocaris*).

St. Sauveur-le-Vicomte.—Two exposures, one near the sport field, the other one near the cemetery of St. Sauveur-le-Vicomte, Manche (see Robardet 1981: fig. 31, Loc. 8, 9; Fig. 1). Finely laminated and highly deformed black shales, St. Sauveur-le-Vicomte Formation (Robardet 1981). Graptolites (*Neocolonograptus ultimus*) indicate the early Pridoli (Jaeger in Robardet 1981; Fig. 1C). *Sineruga* gen. nov. (flattened and deformed) is associated with myodocopes (bolbozoids and cyprinidids), bivalves (*Dualina*, *Actinopteria*, and *Praecardium*), orthoconic cephalopods, crinoids, and phyllocarids (*Ceratiocaris*).

Material and methods

Ostracod carapaces were preserved either in shales or in nodules, along with other fossils. Mechanical preparation with a "Vibrotol" and small needles was used with 3D-specimens preserved in nodules, whereas latex and silicon casts were made from external moulds of specimens present in nodules and on the surface of shale slabs. Some key specimens of both types were mounted and coated for scanning electron microscopy (SEM; Hitachi S800, Lyon). The specimens were measured under the binocular microscope using morphometric tools (Scion Image 4.0.2).

Systematic palaeontology

Class Ostracoda Latreille, 1802

Subclass Myodocopa Sars, 1866

Order Myodocopida Sars, 1866

Suborder Entomozocopina? Gründel, 1969

Superfamily Entomozoacea? Přibyl, 1950

Emended diagnosis.—Valves generally thin, weakly calcified, adults usually >1 mm long, characteristically ornamented with longitudinal, concentric or spiral ribs. Lacking a rostrum and rostral incisure. Adductorial sulcus well developed to absent (modified after Gooday 1983).

Remarks.—Herein the term “Entomozoacea” is used in its widespread sense (see Gooday 1983), even though the type species of the type genus of the “Entomozoidae”, namely *Entomozoe tuberosa* (Jones, 1861) from the Silurian of Scotland, is known to be an entirely different form of ostracod (assigned to the myodocope superfamily Bolbozoacea Bouček, 1936; see Groos-Uffenorde and Schindler 1990; Siveter and Vannier 1990; Perrier et al. 2007 for discussion and recommendations).

Sineruga lacks the typical external ribbed ornament characteristic of the entomozoaceans. However, other external morphology (valve shape, dorsal connection, sulcus, and muscle spot) of *Sineruga insolita* gen. et sp. nov. is very similar to that of the Silurian Entomozoidae *Richeria migrans* Barrande, 1872 (see Perrier et al. 2007) or the Devonian Rhomboentomozoidae *Franklinella lysogorensis* Olempska, 2002. The major difference between these two families is the overall valve outline, which is elongated to bean-shaped in the Entomozoidae, and triangular to sub-quadrate in Rhomboentomozoidae (see Gooday 1983). Because *Sineruga* displays an elongated bean-shape carapace it is tentatively placed here within the Entomozoidae.

The classification used for the higher taxa of Ostracoda is that of Horne et al. (2002).

Family Entomozoidae? Přibyl, 1950

(= Entomidae Jones, 1873)

Emended diagnosis.—“Entomozoaceans” with bean-shaped or symmetrically to asymmetrically ovoid lateral outline, rarely with a weak anteroventral indentation; dorsal margin curved or straight, shorter than carapace length. Adductorial sulcus concave toward anterior end or straight; posteroventral sulcus present (subfamily Bouciinae) or absent; muscle scar as a smooth patch (but sometimes composed of many tiny scars), a pit or absent. Ornament usually present, consisting of transverse, longitudinal, spiral, concentric or irregular pattern of ribs, in some cases reduced to minute spines (modified after Gooday 1983).

Genus *Sineruga* nov.

Type species: *Sineruga insolita* gen. et sp. nov.; monotypic, see below.

Etymology: From Latin *sine*, without; *rug*a, ribs.

Diagnosis.—Same as species.

Sineruga insolita gen. et sp. nov.

Figs. 2–5, 7I, J, N.

Etymology: From Latin *insolita*, unusual.

Type material: Holotype: FSL 710900 (Figs. 2F, 3A) right valve preserved in 3D (L = 2.91 mm; H = 1.75 mm). Paratype: FSL 710893 (Fig. 2A) left valve preserved in 3D (L = 3.19 mm; H = 1.96 mm).

Type locality: Les Chevrolières, St. Denis-d’Orques, Sarthe, France (Loc. 1).

Type horizon: Highly deformed siltstone and mudstone beds containing numerous partly pyritized nodules; Le Val Formation; uppermost Ludlow to lower Pridoli.

Referred material.—Hundreds of valves from four localities in France. 3D preserved specimens: the largest and the smallest specimens (respectively FSL 710630, Fig. 2A, L = 3.20 mm, H = 2.03 mm and FSL 710897, Fig. 2A, L = 1.33 mm, H = 0.87 mm) come from Loc. 1. Flattened specimens: the largest specimen (FSL 710533, Fig. 4A, L = 3.96 mm; H = 2.60 mm) comes from Loc. 3, the smallest (FSL 710924, Fig. 4B, L = 1.11 mm; H = 0.70 mm) from Loc. 4.

Diagnosis.—Entomozoidae with reniform outline, rounded to square anterior margin, rounded ventral margin, slightly pointed posterior margin and straight dorsal margin. Anterior half of valves less prominent than posterior. Dorsal connection centred above sulcus. Sinusoidal adductorial sulcus with simple elliptical muscle spot. Ventral and posterodorsal tubercle often present. Valves completely smooth.

Measurements.—See scatterplots diagrams (Fig. 6). Length to height ratios (L:H) were calculated for 39 specimens from four localities. Five to six ontogenetic stages are probably represented (Fig. 6).

Description.—Symmetrical reniform valves. Maximum valve length (L) across the posterior tubercle; maximum valve height (H) at approximately mid-length (ventral tubercle) and maximum width across the centre of the posterior half of the carapace. The lateral outline tapers anteriorly. Valves divided by a subcentral sulcus; anterior part less prominent than posterior part (respectively 1/3 and 2/3 of valve area). Straight dorsal margin showing the dorsal connection (more than half of valve length) centred above the sulcus and the muscle spot. Anterodorsal part of the carapace flattened, rounded to square without rostrum or rostral incisures. Ventral margin perfectly rounded. Posterior margin slightly pointed (tubercle) or rounded when tubercle absent. The entire lateral surface is more or less deeply (deeper in the dorsal part) incised by a narrow sinusoidal sulcus. This sulcus originates in a triangular area (centre of the dorsal connection) and extends from dorsal to ventral margins. The sulcus is concave frontward in the dorsal part, and backward in the ventral part. The sulcus broadens in the muscle spot region, which is located at the inflection point of the sulcus. The muscle spot consists of a single reniform scar. Two small tubercles are often present; they are situated posterodorsally and ventrally. External surface of the valve completely smooth.

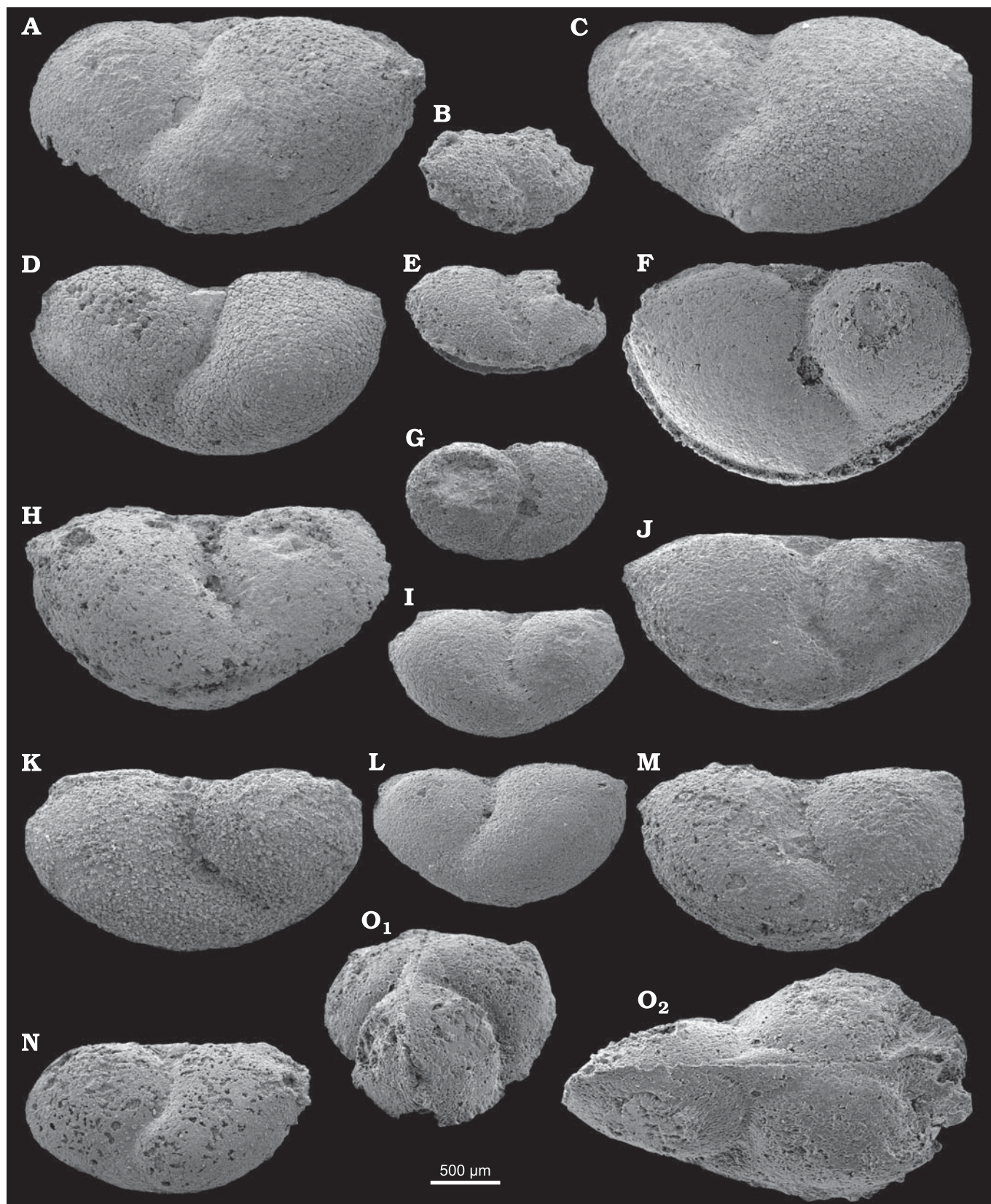


Fig. 2. General views of myodocope ostracod *Sineruga insolita* gen. et sp. nov., Ludlow–Pridoli Silurian. **A.** Paratype, left valve, FSL 710893, Loc. 1. **B.** Smallest specimen, right valve, FSL 710897, Loc. 1. **C.** Left valve, FSL 710630, Loc. 1. **D.** Left valve, LPB 18931b, Loc. 1. **E.** Right valve, FSL 710895, Loc. 1. **F.** Holotype, right valve, FSL 710900, Loc. 1. **G.** Right valve, FSL 710919, Loc. 1. **H.** Right valve, FSL 710631, Loc. 1. **I.** Right valve, FSL 710601, Loc. 1. **J.** Right valve, MNHN 145a, Loc. 2. **K.** Right valve, FSL 710625, Loc. 1. **L.** Left valve, LPB 18926b, Loc. 1. **M.** Right valve, FSL 710898, Loc. 1. **N.** Left valve, LPB 18932b, Loc. 1. **O.** Complete carapace, FSL 710629, Loc. 1, in oblique frontal (O₁) and oblique dorsal (O₂) views.

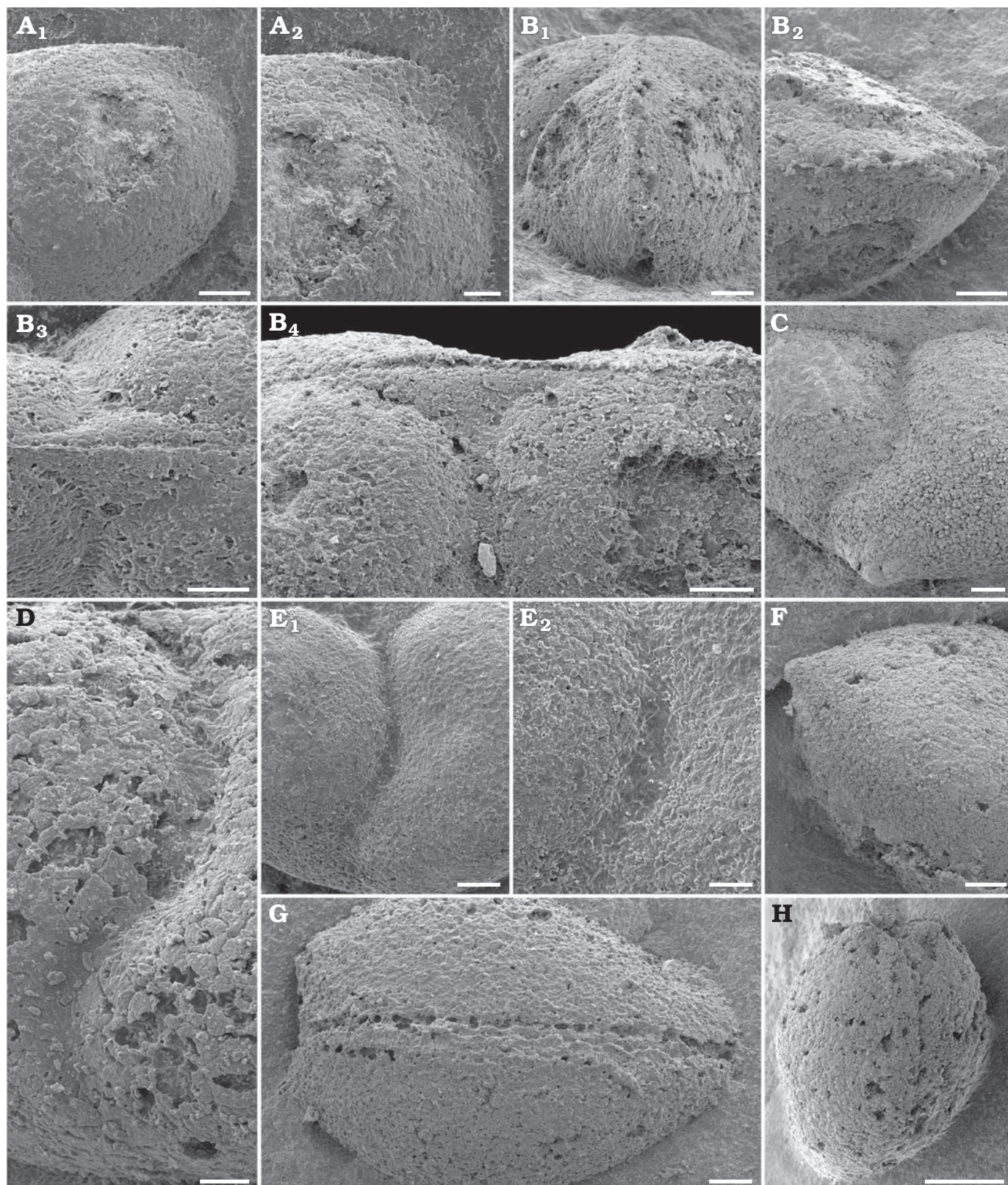


Fig. 3. Details of the carapace of myodocope ostracod *Sineruga insolita* gen. et sp. nov., Ludlow–Pridoli Silurian. **A.** Holotype, right valve, FSL 710900, Loc. 1. Anterior (**A**₁) and anterodorsal (**A**₂) parts of the valve. **B.** Complete carapace, FSL 710629, Loc. 1, in frontal (**B**₁) and dorsal (**B**₂) views; dorsal view of the hinge (**B**₃); oblique left lateral view of the hinge and the dorsal part of the adductor sulcus (**B**₄). **C.** Left valve, adductor sulcus and ventral tubercle, FSL 710630, Loc. 1. **D.** Left valve, adductor sulcus, LPB 18932b, Loc. 1. **E.** Right valve, MNHN 150, Loc. 2. Adductor sulcus showing the central muscle spot (**E**₁), muscle spot (**E**₂). **F.** Right valve, posterior part and posterodorsal tubercle, FSL 710913, Loc. 1. **G.** Complete carapace, ventral view, FSL 710892, Loc. 1. **H.** Complete carapace, posterior view, FSL 710595, Loc. 1. Scale bars: **A**₁, **B**₁–**B**₄, **C**, **E**₁, **F**, **G**, 200 µm; **A**₂, **E**₂, 100 µm; **D**, 50 µm; **H**, 500 µm.

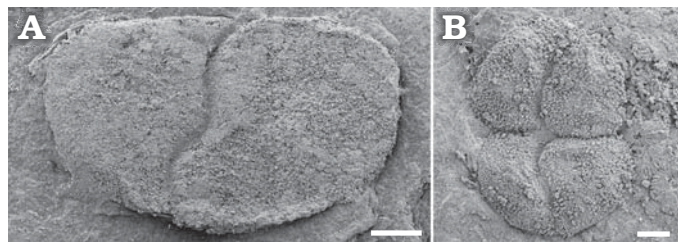


Fig. 4. General views of flattened myodocope ostracod *Sineruga insolita* gen. et sp. nov., Late Wenlock–Pridoli Silurian. **A.** Right valve, FSL 710533, Loc. 3. **B.** Both valves in “butterfly position”, FSL 710924, Loc. 4. Scale bars: A, 500 µm; B, 200 µm.

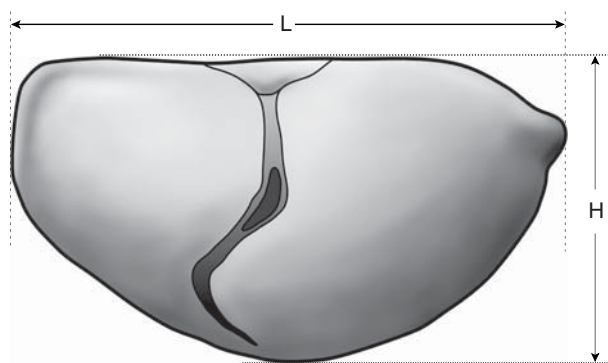


Fig. 5. Parameters used for measurements of *Sineruga insolita* gen. et sp. nov. H, maximum valve height; L, maximum valve length.

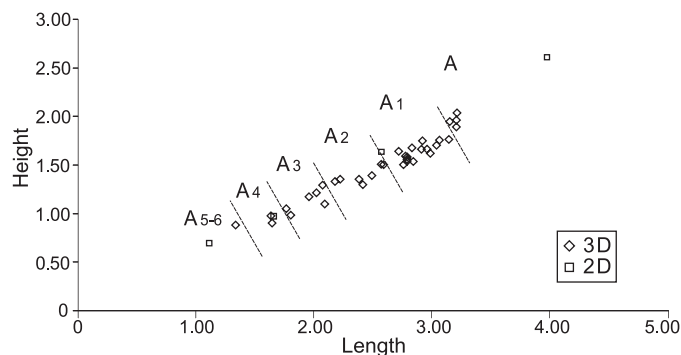


Fig. 6. Measurements of *Sineruga insolita* gen. et sp. nov. Length-height plot of 39 specimens of *S. insolita*. Specimens comprise both latex casts from external moulds and 3-D preserved specimens. L, H as in Fig. 5. A = adults; A₁–A₆ = possible juvenile instars 1 to 6.

Remarks.—*Sineruga insolita* gen. et sp. nov. is difficult to place within a previously described group of Palaeozoic myodocopid ostracods. *Sineruga* definitely belongs neither to the cypridinids (no rostrum, but a sulcus and a straight dorsal margin; compare Fig. 7L and N) nor to the bolbozoids (no rostrum and no bulb, but simple muscle scar and straight dorsal margin; compare Fig. 7K and N). Nevertheless, *Sineruga* shares several characteristics with Silurian and Devonian entomozoids. For example, *S. insolita* gen. et sp. nov. shares several morphological features with *Richteria migrans* (middle Ludlow, Fig. 7G, H; see Perrier et al. 2007), such as a

bean-shaped outline, a straight dorsal connection, and a well-developed adductor sulcus (compare Fig. 7M and N). However, *Sineruga* bears two tubercles and a small frontal projection. These characters are absent in *Richteria*, which displays the typical entomozoid ribbed ornament and an “eye tubercle”. In some features, *Sineruga* is also close to the Devonian Rhomboentomozoidae *Franklinella lysogorensis* from Givetian/Frasnian boundary interval (Olempska 2002). Both the Silurian and the Devonian species display a straight dorsal connection with a small anterodorsal projection and two tubercles situated posteriorly and ventrally. However, *Franklinella* has a ribbed ornament and a nearly circular outline very different from the elongated bean shape of *S. insolita* gen. et sp. nov.

The biggest problem with the entomozoid assignment is that *Sineruga* lacks the typical external ribbed ornament characteristic of the entomozoaceans (see Gooday 1983). However, when Barrande (1872) described the first known entomozoid “*Entomis migrans*” (now known as *Richteria migrans*), he included in this genus three smooth species that clearly belong to the entomozoaceans (see details in Perrier et al. 2007). Their carapaces are smooth, bean shaped with a more or less developed adductor sulcus, and one species bears an anterior tubercle. Other smooth species were described as *Entomis* by Canavari (1900; Ludlow, Sardinia). Within these new Canavari (1900) forms, Perrier et al. (2007) suggested that six of these non-ribbed taxa should be included in the entomozoaceans (see also Gnoli et al. 2009). Among the smooth forms described by Barrande (1872) and Canavari (1900) several poorly preserved specimens may have lost their external ornament. However, some specimens clearly show an unornamented carapace.

The carapace of *Sineruga insolita* gen. et sp. nov. also resembles that of *Colymbosathon ecplecticos* (Wenlock of England; Siveter et al. 2003) in its general outline and shares with this species the possession of a deep dorsal sulcus. However, *S. insolita* gen. et sp. nov. has a much longer S-shaped adductor sulcus that reaches the anteroventral margin, two tubercles located both ventrally and posteriorly (*Colymbosathon* has only an eye tubercle), and a less prominently developed anterior lobe. *C. ecplecticos* was described with its soft parts and placed within the Cylindroleberididae (Myodocopa). In the absence of preserved soft parts the author cannot be precise with the assignment of *S. insolita*, however its general outline shows many similarities with *Richteria migrans* and herein, *S. insolita* is placed within the Entomozoidae where it possibly deserves its own subfamily. Perrier et al. (2007) showed that *R. migrans* has a very similar valve outline and lobal/sulcal morphology to that of *C. ecplecticos*. Moreover, these two taxa lack a rostrum and a rostral incisure. These authors suggested that entomozoaceans may have had strong affinities with myodocopes and perhaps Cylindroleberididae. The same suggestion can be made for *Sineruga* gen. nov.

Stratigraphic and geographic range.—Silurian (late Wenlock to early Pridoli Series), Armorican Massif (France).

Table 1. Characters of “biological importance” in fossil myodocopes and comparison with Recent myodocopes orders and subclass Podocopa. Data concerning *Colymbosathon* after Siveter et al. 2003, *Nymphetelina* after Siveter et al. 2007, Recent myodocopes and podocopes after Horne et al. 2002 and Cohen et al. 2007.

Characters of “biological importance”	Rostrum	Lateral eye related carapace features	Dorsal connection	Sulcus	Muscle scar
Silurian myodocopes					
Bolbozoids	present	bulb or node	curved; anterior	deep; anteriorly curved	complex; numerous paches
Cypridinids	present	visual window if ornamented	curved; posterior	absent	simple; crescent shaped
Entomozoids	absent	unornamented node or absent	straight; central	deep; anteriorly curved	simple; elliptical
Sineruga	absent	weak anterodorsal carapace	straight; central	deep; sinusoid	simple; elliptical
Colymbostahon	absent	eye tubercle	straight; central	deep; vertical	unknown
Nymphetelina	absent	absent	straight; central	shallow; vertical	unknown
Recent myodocopes					
Myodocopina	present	translucent carapace or visual window	curved; central	absent	complex; numerous paches
Halocypridina	present	lateral eye absent	straight; central	shallow or absent	complex; numerous paches
Cladocopina	absent	lateral eye absent	curved; central	absent	complex; numerous paches
Recent podocopes	absent	lateral eye absent	real hinge	present or absent	complex; numerous paches

Discussion

Characters of “biological importance”.—The systematics of fossil ostracods, especially among Palaeozoic taxa, is based on carapace features, the soft parts being unknown in most cases. Therefore, classical taxonomy often relies on a set of morphological characters such as the valve outline, the internal and external relief of the carapace (e.g., lobes, sulcus, and hinge) and ornament (e.g., spines, tubercles, reticulations, see Scott 1961). The robustness of this taxonomy is sometimes questionable; typically, however, there are no alternatives from other sources of information. As a result, the most abundant ostracod group of the lower Palaeozoic, the Palaeocopa, is classified entirely based on carapace characters. No data on the internal anatomy of these ostracods are available. Exoskeletal features provide reliable diagnosis at the specific and generic levels. However, difficulties arise in the use of carapace morphology in the systematics of higher taxa.

The discovery of ostracods with soft tissues in the Silurian of the UK (Herefordshire Lagerstätte; Siveter et al. 2003, 2007, 2010) provides important additional evidence. The myodocope body plan, as it is known in Recent forms, already existed during the early Palaeozoic. For example, the soft parts of *Colymbosathon eplecticos*, clearly indicate that this species is a myodocope and probable member of the extant family Cyndroleberididae (Siveter et al. 2003). It is surprising that the carapace of these ancestral myodocopes was not ovoid as in most Recent (Cypridinidae) and fossil (bolbozoids, cypridinids) myodocopid ostracods. Two of the three species described by Siveter et al. (2003, 2007) bear a large Palaeocopid-like carapace (straight dorsal margin, lobal/sulcal morphology). The straight dorsal margin is one of the main diagnostic characters of the Palaeocopa (Benson et al. 1961). Thanks to the exceptional material from UK, we now know that this character was also shared by several Palaeozoic myodocope species. This indicates that ancestral

myodocopes secreted various exoskeletons of different shape. However, this line of reasoning is not sufficient to conclude that Palaeocopa were also primitive myodocopes.

This exceptional material (Siveter et al. 2003, 2007, 2010) and Recent studies (Perrier 2007; Perrier et al. 2007, 2011) have shown that Silurian myodocopes were very diverse in their external morphology (probably more than Recent forms) even if their internal body plan showed little variation. Some Silurian forms had a carapace very close to that of Recent myodocopes, bearing an ovoid outline and a well-developed rostrum (cypridinids; see Siveter et al. 1991; Perrier et al. 2011). Other species (bolbozoids; see Siveter et al. 1991; Perrier et al. 2011) show some similarities with Recent forms (i.e., outline, rostrum), however, they display a prominent bulb unknown in Recent representatives. Finally, some groups certainly related to myodocopes (*Colymbosathon* and *Nymphetelina*) or thought to be myodocopes (entomozoids; see Gooday 1983; Perrier et al. 2007) bear a morphology distinct from all Recent forms (e.g., straight dorsal margin, lobes/sulci, complex ornament).

The new species described herein is an atypical myodocope ostracod. Its carapace morphology is very different from that of all other known Silurian species and highlights the uncertain taxonomic affinities among bolbozoids, cypridinids and entomozoids. Well-preserved specimens of *Sineruga insolita* gen. et sp. nov., both in three dimensions and in “butterfly position” (i.e., with both valves flattened in connection), show carapace characters of “biological importance” (see Table 1). These characters can be used to differentiate the higher myodocope taxa in the Silurian. The identification of the relationships between internal (soft) and external (hard) morphology provides insight into the taxonomy of the Silurian myodocopes and can help to differentiate myodocopes from other Palaeozoic ostracods:

Rostrum.—*Sineruga* gen. nov. does not bear any rostrum or rostral incisure in the frontal part of its carapace. In place of

these features, this new genus bears a flattened, rounded to square projection (Figs. 2F, J, M; 3A, B) that has no equivalent in any fossil or Recent myodocope.

All swimming myodocopes, including Recent Myodocopina (Fig. 7A) and Halocypridina (Fig. 7B) as well as Silurian bolbozoids (Fig. 7K) and cypridinids (Fig. 7L), bear a well developed rostrum and incisure (Siveter et al. 1991; Vannier and Abe 1992; Siveter et al. 2010). This rostral complex (rostrum + incisure) is an important functional feature in the swimming mechanism of the animal, helping the swimming antennas (A2) to protrude (see Vannier and Abe 1993). However, even in the absence of a rostrum, the swimming antennas can simply protrude from the gaping carapace. This is the case in Recent Cladocopina (Cohen et al. 2007) and in *Colymbosathon ecplecticos* and *Nymphatelinea graviora* (Siveter et al. 2003, 2007). The same assumption was made for entomozoids by Perrier et al. (2007). A similar disposition and extension of soft parts, and hence function, may also have been present in *Sineruga*.

Because no podocopes bear a rostrum, its presence can be used to identify myodocope ostracods. However, the absence of rostrum is not enough to classify a species within the podocopes or the palaeocopes; in fact several Recent (Cladocopina) and fossil (*C. ecplecticos*, *N. graviora*) myodocopid species lack a rostrum. Based upon this association Silurian bolbozoids and cypridinids are probably myodocopes whereas entomozoids (among them *Sineruga* gen. nov.) are possibly myodocopes.

Visual organs.—The anterodorsal part of the carapace of *Sineruga insolita* gen. et sp. nov. is often broken or altered (Figs. 2D–J, O, 3A, B) whereas the rest of the carapace is generally well preserved. This indicates that the carapace was probably thinner and less calcified at this level, allowing light to pass through it. This particular feature seems to have been directly related to vision.

Not all Recent myodocopes have lateral eyes. Halocypridina have no visual organs, whereas lateral compound eyes are frequent in Myodocopina (Land and Nilsson 1990; Cohen et al. 2007). The lateral eye is located in the anterodorsal part of the body and light is received through their translucent carapace (Vannier et al. 1998: fig. 4; Land and Nilsson 1990: fig. 1). Silurian bolbozoids, cypridinids and some entomozoids bear either a prominent unornamented bulb (bolbozoids, Fig. 7C, D, K) or an unornamented area (visual window) in the

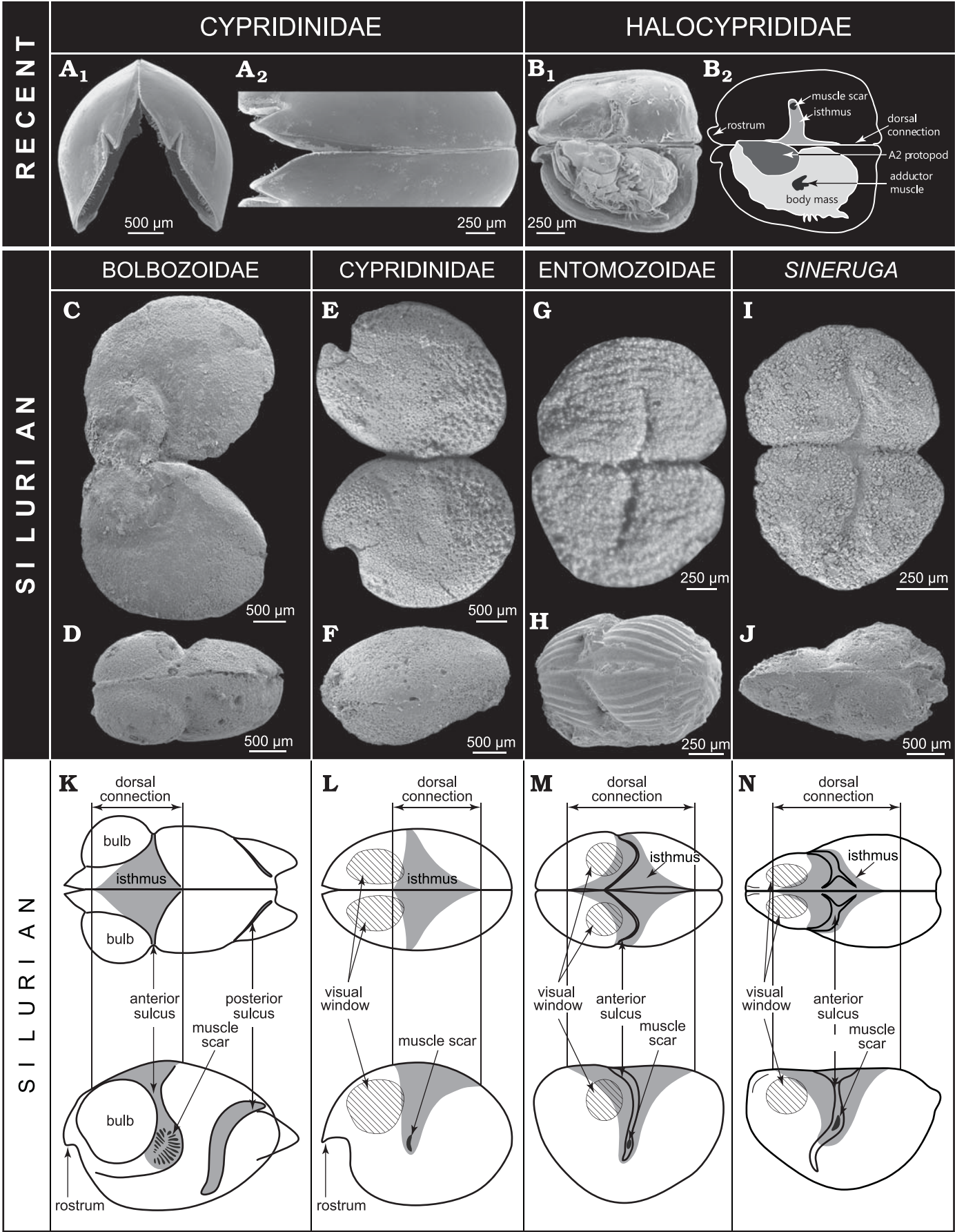
anterodorsal part of their valves (cypridinids, Fig. 7E, L). According to previous studies (Siveter et al. 1991; Vannier and Abe 1992; Perrier 2007; Perrier et al. 2007, 2011) all of these features indicate the possession of visual organs. This hypothesis is strengthened by the presence of a lateral eye in exceptionally preserved Silurian fossils *Colymbosathon ecplecticos*, *Nymphatelinea graviora*, *Nasunaris flata*; Siveter et al. 2003, 2007, 2010), which lies exactly in the same position as the bulb and the visual window. *Sineruga*, with its weakened area in the anterior part of its carapace (Fig. 7N), probably displayed a different kind of visual window that had not been seen previously in the myodocope fossil record. It also suggests the presence of lateral eyes in *Sineruga*.

In Recent ostracods, the lateral eye is present only in myodocopes, podocopes bearing only a naupliar eye (Horne et al. 2002) as probably did palaeocopes (see Tanaka et al. 2009). The presence of symmetrical and well-developed vision-related carapace features that indicate lateral eyes, such as an eye tubercle (*Colymbosathon ecplecticos*), a bulb (bolbozoids) or a visual window (cypridinids, some entomozoids, and *Sineruga* gen. nov.), can be used to identify fossil myodocopes. However, the absence of such characters is not sufficient to discriminate podocopes or palaeocopes; in fact, *Nymphatelinea graviora* (Siveter et al. 2007) possesses well-developed lateral eyes, although no external carapace feature indicates their presence.

Dorsal connection.—The dorsal connection is the articulation between the two valves. In “butterfly position”, the dorsal connection of *Sineruga insolita* gen. et sp. nov. runs the length of the dorsal margin (Figs. 2O₂, 3B₄, 4B). This dorsal connection shows no teeth or dimples and appears to be ligamentous (Fig. 3B₄).

The dorsal connection is very different among Recent myodocopes and podocopes. The podocopes have a hinge with real teeth and dimples (i.e., comparable to that of bivalve molluscs; see Scott 1961). In Recent myodocopes, the dorsal connection is not a true hinge. It consists of a flexible but strong ligament, around which the two valves revolve (Fig. 7A; see Kornicker 1969). This ligamentous dorsal connection was most likely present in Silurian forms, which never show teeth and dimples in the dorsal part of their carapace (Siveter et al. 1991). The dorsal connection is shown in fossil species through the preservation of articulated valves in “butterfly position” (Fig. 7C, E, G, I), and the connection

Fig. 7. Dorsal connection, sulcus and isthmus in Recent and Silurian myodocopes a key to systematic assignation. **A.** Dorsal connection of *Vargula hilgendorffii*, Recent, Japan. Soft parts removed. Frontal (A₁) and anterodorsal (A₂) views. **B.** Dorsal connection, isthmus and muscle position in *Conchoecia atlantica*, Recent, Japan. Valves opened mechanically. SEM picture showing the soft parts inside the carapace (B₁), drawing showing the position of the dorsal connection, the isthmus and the adductor muscle (B₂). “Butterfly position” showing the dorsal connection (**C, E, G, I**). Dorsal (**D, F, I**) and posterodorsal (**H**) views of complete carapace. **C, D.** *Bolbozoe anomala* Barrande, 1872. **C.** FSL 710927, Les Buardières (Loc. 3), late Wenlock–Ludlow. **D.** FSL 710593, Les Chevrolières, France, Ludlow–Pridoli. **E.** *Silurocypridina retroreticulata* Perrier, Vannier, and Siveter, 2011, IRG 33016, Les Buardières (Loc. 3), late Wenlock–Ludlow. **F.** *Silurocypridina calva* Perrier, Vannier, and Siveter, 2011, FSL 710634, Les Chevrolières, France, Ludlow–Pridoli. **G, H.** *Richteria migrans* (Barrande, 1872). **G.** FSL 705028a, La Combe d’Yzarne, France, middle Ludlow. **H.** FSL 705032a, Koukolova Hora Hill, Czech Republic, middle Ludlow. **I, J.** *Sineruga insolita* gen. et sp. nov. from Loc. 1 and 4, Ludlow–Pridoli. **I.** FSL 710925. **J.** FSL 710924. **K–N.** Idealized dorsal and left lateral view of the different Silurian myodocopid groups showing the characters of “biological importance”. **K.** Bolbozoid. **L.** Cypridinid. **M.** Entomozoid. **N.** *Sineruga insolita* gen. et sp. nov. All specimens, except A₁, have their front part on the left.



takes different positions depending on the group. In bolbozoids, the dorsal connection is located in the anterodorsal part of the valve just above the bulb, the adductor sulcus and the muscle scar (Fig. 7C, D, K). In cypridinids it is located in the posterodorsal region of the carapace, above the scar of the adductor muscle (Fig. 7E, F, L). Finally, in Silurian entomozoids the dorsal connection is located along the entire length of the straight dorsal margin (Fig. 7G, H, N). The position of the dorsal connection in *S. insolita* is very close to what is observed in entomozoids (compare Fig. 7G, M and 7I, N).

The ligamentous dorsal connection can be used to recognise myodocopes as podocopes and palaeocopes bear a real hinge (Scott 1961). In addition, the position and extension of the dorsal connection can be used to easily distinguish the three groups of Silurian myodocopes (anterior in bolbozoids; posterior in cypridinids; straight central in entomozoids and *Sineruga* gen. nov.). The position and length of the dorsal connection of Silurian bolbozoids and cypridinids correspond to those found in Recent Myodocopina (e.g., *Vargula*; see Fig. 7A). Those of *Sineruga* and entomozoids correspond more closely to what is observed in Halocypridina (e.g., *Conchoecia*, see Fig. 7B). However, these similarities likely have little- to no taxonomic value as there is no evidence for the existence of fossil halocyprids.

Adductor sulcus and muscle scar.—*Sineruga* gen. nov. bears a well-developed adductor sulcus in the middle/anterior part of the carapace. This sulcus is concave frontward in the dorsal region of the carapace and backward in its ventral part. This particular sinusoidal shape is unknown in all other fossil or Recent myodocopes. A small and simple elliptical muscle scar is present in the middle part of the sulcus.

In Recent myodocopes, the sulcus does not exist except for a slight deformation on the carapace of several forms including Halocypridina (e.g., *Conchoecia imbricata*, see Vannier and Chen 2000: fig. 6). This is a slight sag in the mediodorsal part of the valves, underlining the posterior part of A2 protopod. However, no Recent group bears a sulcus as marked as in the Palaeozoic forms (bolbozoids and entomozoids). The Silurian representatives of these two groups both bear a well-developed frontward concave sulcus. Because the muscle scar is always situated inside the middle part of the sulcus, the sulcus may be the imprint of the isthmus (area of attachment of the body to the carapace; Fig. 7B, K–N) on the carapace. The sulcus, like the dorsal connection, has a different position depending on the group. In bolbozoids it is located in the front half of the carapace, underlining the bulb (Fig. 7C, D, K). In entomozoids it is located in the central part of the valves (Fig. 7G, H, M). The sulcus of *Sineruga* is close to that of entomozoids such as *Richteria migrans*, the only notable difference is its sinusoidal shape. The muscle scar is the imprint of the adductor muscle on the carapace. In Recent myodocopes and in Silurian bolbozoids (Fig. 7K) this scar consists of series of rounded or elongated patches arranged in rosette or disseminated in a small area in the centre of the valve (see

Siveter et al. 1991). In Silurian cypridinids and entomozoids, this scar is very simple consisting of single crescent-shaped (Fig. 7E, L) or elliptical (Fig. 7G, M) spots. The muscle scar of *S. insolita* gen. et sp. nov. is comparable to that of entomozoids in its shape and position (Figs. 3D, E, 7N).

The adductor sulcus is of no real value for recognising myodocopes. It is almost absent in Recent myodocopes whereas it is common in palaeocopes and occurs in Recent podocopes. Its position and extension, however, can be used to differentiate Silurian bolbozoids and entomozoids (including *S. insolita* gen. et sp. nov.). Furthermore, the morphology of the muscle scar is not typically useful for higher taxonomy. The scars of bolbozoids are close to what is observed both in Recent myodocopes and podocopes. On the other hand, the simple spot of Silurian cypridinids and entomozoids has no counterpart in any Recent forms.

Conclusions

Sineruga insolita gen. et sp. nov. is the oldest (upper Wenlock–lower Pridoli) entomozoid reported in the Armorican Massif and is always associated with other myodocopes (bolbozoids and cypridinids).

The data available suggest that *Sineruga insolita* was probably an atypical, non-ribbed member of the entomozoids. This assignment is based mainly on its carapace morphology (i.e., bean shaped valves, adductor sulcus, muscle spot and dorsal connection) and indicates that early entomozoids may have had smooth representatives.

The presence of a rostrum and/or symmetrical vision related organs (i.e., indicating lateral eyes) such as the eye tubercle, the bulb, the visual window or the weakened anterodorsal carapace can be used as diagnostic features for myodocope ostracods.

The position and shape of the dorsal connection and to a lesser extent that of the sulcus and the adductor muscle scar can be used to discriminate the higher groups of Silurian myodocopes (bolbozoids, cypridinids, and entomozoids).

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