The euthycarcinoid arthropods from Montceau-les-Mines, France: functional morphology and affinities

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ABSTRACT: New three-dimensionally preserved specimens of two euthycarcinoid arthropods, namely *Schramixerxes gerem* and *Sottyxerxes multiplex*, allow complete description of both the dorsal and ventral sides of the exoskeleton. The functional morphology is tentatively interpreted for the first time. In *S. gerem*, the 'thirteenth somite', or 'monosomite' is fully described and re-interpreted as the main articulatory process of the body, between the cephalic region and the preabdomen. The morphology and arrangement of the two parts of the process clearly indicate that the anterior cephalic region of the body could move laterally and bend ventrally, while posterior somites could only move ventrally. Unlike several other euthycarcinoid species, the ventral side of the head area exhibits one or two plates instead of mandibles; such distinct morphologies are indicative of different feeding mechanisms and behaviours among euthycarcinoid arthropods. Possible homologies with the labrum of Hexapoda support the hypothesis that euthycarcinoids have hexapod affinities.

KEY WORDS: Anatomy, preservation, environment, mode of life, Stephanian

A series of recently published papers over the last few years has shed new light on the floral and faunal components of the Montceau-les-Mines biotopes (Morvan area, Saône-et-Loire, northern Massif Central, France: see Racheboeuf *et al.* 2002, text-fig. 1, p. 126; coordinates : Lat. 46°40′N–Long. 2°0′E), highlighting their diversity and aspects of their lifestyles. Whilst the whole flora preserved in concretions has been thoroughly revised (Charbonnier 2004; Charbonnier *et al.* 2008), the revision of the fauna is still in progress, based on a new collection of abundant complete specimens, preserved in three dimensions. Since 2001, the hagfish *Myxineidus gononorum* (Poplin *et al.* 2001); the xiphosuran *Alanops magnificus* (Racheboeuf *et al.* 2002); the spinacaudatans *Euestheria feysi* and *Montcestheria orri* and the ostracod *Carbonita* sp. aff. *salteriana* (Vannier *et al.* 2003); the diplopod *Amynilyspes fatimae* (Racheboeuf *et al.* 2004); the syncarid *Palaeocaris secretanae* (Perrier *et al.* 2006), and the annelid *Palaeocampa* (Pleijel *et al.* 2004) have been first described and/or revised. Other papers dealing with groups such as the polychaetes, myriapods, insects, isopods, and amphibians are in progress. This paper reveals important information on the morphology and anatomy of the exoskeleton of the euthycarcinoids *Schramixerxes gerem* (Schram & Rolfe, 1982), and *Sottyxerxes multiplex* Schram & Rolfe, 1982. The new material described here adds to our understanding of the morphology of both species, and they pose questions as to past assumptions about the mode of life, the feeding mechanisms, and the behaviour of euthycarcinoids in general. A broader implication of this work concerns the taxonomic affinities of the Subclass Euthycarcinoidea. *Schramixerxes gerem* (Schram & Rolfe, 1982), and *Sottyxerxes multiplex* Schram & Rolfe, 1982 are fully described below according to the newly discovered, three-dimensionally (3D) preserved specimens, and measurements of the exoskeleton of *Schramixerxes gerem* are given for the first time.

The occurrence of euthycarcinoids in the Montceau Lagerstätte was first mentioned by Secrétan (1980), then by Pacaud *et al.* (1981). *Schramixerxes gerem* (Schram & Rolfe, 1982) was initially described based on only nine specimens. Twelve complete or almost complete, and 27 partly preserved new specimens of *S. gerem* have been positively identified among the newly processed fossils. In the same way, 49 new specimens of *Sottyxerxes multiplex* Schram & Rolfe, 1982 add to the 11 previously known. The incomplete nature of several specimens at hand mainly results from the risk inherent in the processing of concretions.

The number of euthycarcinoid specimens now available represents the largest population of Euthycarcinoidea known from a single locality (Wilson & Almond 2001), apart from the 100+ specimens of *Euthycarcinus kessleri* from the Triassic of eastern France (Gall & Grauvogel 1964). This exceptionally well-preserved material has no equivalent in the fossil record
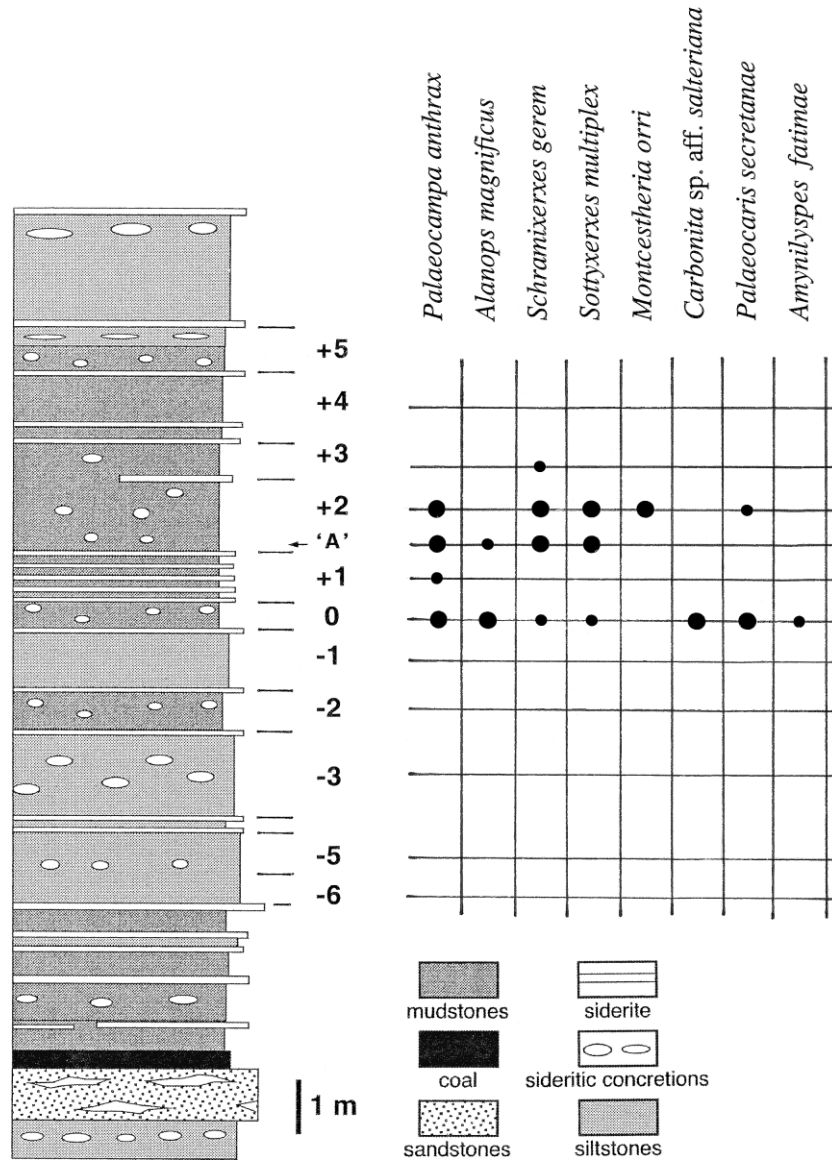
Figure 1 Lithological succession in the Saint-Louis open-cast pit with the relative abundance and vertical distribution of the recently studied faunal components in the twelve identified and sampled fossiliferous concretion-bearing beds (−6 to +5): polychete (*Palaeocampa*); xiphosuran (*Alanops*); euthycarcinoids (*Schramixerxes*, *Sottyxerxes*); ostracodes (*Montcestheria*, *Carbonita*); syncarid (*Palaeocaris*), and diplopod (*Amynilyspes*). Small rounded dots: up to ten specimens; large rounded dots: tens to thousands of specimens. Mudstones and siltstones are massive, and devoid of lamination of lacustrine type. For further sedimentological data see Poplin & Heyler 1994.

of the group for the Palaeozoic (the same can be said of the xiphosuran from the site). Some 108 specimens (48 *Schramixerxes gerem* and 60 *Sottyxerxes multiplex*) have been firmly recognised as euthycarcinoids among the 74,731 fossiliferous processed concretions present in the collections. Representing presently only 0·0014% of the fossil population, euthycarcinoids appear as a minor component of the Montceau-les-Mines biota. This very low percentage possibly reflects the real relative scarcity of euthycarcinoids within the biota, but it could also possibly reflect a taphonomic bias correlated with their mode of life.

In fact, several levels of the Montceau-les-Mines section (among which beds 0 to +2, and +3; see Fig. 1) provided us with a biota which is a mixture of both strictly aquatic, freshwater faunal components and terrestrial ones. Among aquatic components are the xiphosuran (Racheboeuf *et al.* 2002), the hagfish (Poplin *et al.* 2001), fireworms (Pleijel *et al.* 2004), bivalve molluscs, shrimps – often with eggs preserved *in situ* – which are the most abundant invertebrates among the Montceau biota (e.g. more than 5,000 specimens of the

syncarid *Palaeocaris*; see Perrier *et al.* 2006). Terrestrial faunal components include abundant insect remains, millipedes, spiders and scorpions, as well as abundant plant remains. Were euthycarcinoids aquatic or terrestrial living faunal components? Most probably they were aquatic, if we consider the lack of 'accessory foramina' (Schram 1971), or 'sternal pores' (Edgecombe & Morgan 1999) on the exoskeleton of the two euthycarcinoids from Montceau. Such features are considered to be directly associated with water absorption in terrestrial arthropods (see below). This observation is highly interesting when comparing the Montceau biota with the Early Devonian Rhynie chert of Scotland, where the branchiopod *Lepidocaris*, which can primarily be considered as a probable equivalent of *Palaeocaris*, is far more abundant than the euthycarcinoid *Heterocrania* (Scourfield 1926; Anderson & Trewin 2003). This last point would strongly suggest that euthycarcinoids were always rare faunal components of the freshwater Upper Carboniferous biota at Montceau-les-Mines and through the world.

The material belongs to the D. Sotty collection of the Muséum National d'Histoire Naturelle of Paris (MNHN-SOT); it is deposited in the Museum d'Histoire Naturelle, 14 rue Saint-Antoine, F-71400 Autun (Chabard & Poplin 1999).

1. Material and methods

Between 1998 and 1999, A. and D. Sotty processed in the region of 29,000 concretions of their collection (Chabard & Poplin 1999) which were added to the 45,731 concretions processed prior to 1982 (some 31,006 concretions remain unprocessed). This valuable work provided the present authors not only with abundant new fossil remains that greatly increase the biodiversity as well as the number of specimens of previously known organisms, but also with better preserved and/or more complete specimens, including the euthycarcinoid representatives. This new material gives important preliminary information about the most abundant organisms, and about the dominance ranking of faunal components. However, such data will be published when the remaining 31,000 concretions have been processed.

Specimens were carefully prepared under the microscope, using dental tools, a compressed-air engraver pen and fine needles, in order to remove sediment infilling and mineral deposits from both external and internal moulds. Chemical treatment was also used (dilute hydrochloric acid, or acetic acid) in order to dissolve out calcitic and carbonate infillings, and the soap-like 'Quaternary O' to loosen phyllosilicate minerals. Final preparation was undertaken with fine needles in order to remove insoluble minerals without damage to the fossil remains. Latex replicas of both internal and external moulds were made, examined and photographed. Morphological details were drawn using a camera lucida.

Segmentation and terminology used for the description of euthycarcinoids has been a matter of debate for several years, as well as their affinities and relationships among arthropods. The present paper uses the terminology applied to euthycarcinoid cephalic and preabdominal tergites as recently proposed by Edgecombe & Morgan (1999) and Wilson & Almond (2001).

2. Preservation

Sideritic concretions from the Montceau Lagerstätte undoubtedly developed under excellent conditions for the preservation of organic remains (Couvrat-Desvergnes 1981; Poplin & Heyler 1994; Charbonnier 2004; Perrier et al. 2006; Charbonnier et al. 2008). Most animals are complete, wholly 3D-preserved, still articulated, with attached appendages and sometimes with eggs preserved in situ. This is the case for chelicerates (Racheboeuf et al. 2002), spinacaudatans and ostracods (Vannier et al. 2003), diplopods (Racheboeuf et al. 2004), syncarids (Perrier et al. 2006), and euthycarcinoids (this paper). Such preservation implies little, if any, transportation, and it strongly suggests that death and burial of the organisms was almost simultaneous. It should be noted that all the complete specimens of both Schramixerxes gerem and Sottyxerxes multiplex exhibit a pronounced ventral bending of the exoskeleton, which probably reflects either a last defensive reflex attitude when the organism died (Figs 5, 6), or is due to post-mortem relaxation of muscles. The wholly articulated nature and 3D-preservation of most euthycarcinoid specimens implies a very early and rapid post-mortem microbial activity which occurred prior to scavenging. The development of concretions around carcasses and plant remains results from microbial activity prior to burial (Charbonnier 2004, fig. 13; Perrier et al. 2006). The 3D-preservation of the euthycarcinoids from the Montceau Lagerstätte is comparable to that of the Pragian Heterocrania rhyniensis from the Rhynie chert of Scotland (Anderson & Trewin 2003), but in the Rhynie chert euthycarcinoids are preserved in 3D in siliceous matrix, and can only be studied in thin sections.

3. Environmental conditions

Some 100,000 concretions were collected from the eleven concretion-bearing levels that were exposed in the various opencast pits before they shut down in 1993 (Fig. 1). Others concretions were recovered from excavations of spoil tips without any indication of the concretion-bearing horizon they came from. A large number of concretions whose precise origin has been carefully noted by field collectors are still awaiting preparation. This unstudied material deposited at the Autun Museum has great potential for the study of the composition of fossil assemblages from the aforementioned 11 concretion-layers of the Montceau Lagerstätte.

An important question raised by Rolfe et al. (1982) and Poplin (1994, p. 299), and others, was the possible periodical presence of marine incursions during the deposition of the Stephanian clastic sediments in the Blanzy/Montceau-les-Mines Basin. It is clear that there is no sedimentological evidence of any Upper Carboniferous open marine deposits in the Montceau area. According to available data, the closest Upper Carboniferous marine deposits were located at least several hundred kilometres SW of Montceau (Debelmas & Ellenberger 1974; Courel et al. 1994). Such a situation led to the suggestion that the genus Alanops was possibly the first xiphosuran freshwater representative (Racheboeuf et al. 2002, p. 144).

If any marine influence in the Montceau-les-Mines area during the Stephanian depositional time interval can definitely be excluded, the apparent marine character and/or affinities of some of the faunal components requires an explanation. Researchers are still faced with an apparent 'mixture' of marine and freshwater faunal components, as expressed above and below, mainly because evidence is still being sought for the age of the marine to freshwater shift for the faunal elements under consideration.

Marine influences were recently questioned again with the description of the craniate Myxineidus by Poplin et al. (2001), and again with the revision of the annelid worm Palaeocampa by Pleijel et al. (2004). No recent representatives of these two animal groups live in strictly freshwater environments. Neither do the Carboniferous mixinids and annelids from the Mazon Creek Lagerstätte that occur in marine to brackish environments. In the Montceau Lagerstätte crustaceans are dominated by the syncarid Palaeocaris secretanae (Perrier et al. 2006) that closely resembles syncarids from present-day freshwater environments (e.g. Anaspides tasmaniae Thompson, 1893 from the freshwater streams of Australia). Recent syncarid crustaceans live in a variety of freshwater environments, although the early ancestors of the group were probably marine to brackish in habit (Schram 1981; Briggs et al. 1991). Spinicaudatans (='conchostracans') and ostracods (Vannier et al. 2003) of the Montceau Lagerstätte similarly indicate freshwater environments. The presence of representatives of many animal groups in present-day freshwater environments is indeed the result of an initial ecological shift from marine to freshwater that took place in the Palaeozoic (such as crustaceans and fishes).

Rolfe (1985, p. 72) wrote that most euthycarcinoids from Montceau originated from the 'Horizon A' located at the base

Table 1 Euthycarcinoid fossil record. List of taxa in stratigraphic order, geographic distribution, and environmental setting

Genera and species	Age	Distribution	Environment
Apankura machu	Cambrian	Argentina	Marine
Kalbarria brimmellae	Ordov.* or Late Sil.	Australia	Freshwater
Heterocrania rhyniensis	Lower Devonian	UK	Freshwater
Smithixerxes pustulosus	Westphalian A,B	UK	Brackish to Freshwater
Kottixerxes anglicus	Westphalian B	UK	Brackish to Freshwater
Kottyxerxes gloriosus	Westphalian D	USA	Brackish to Freshwater
Smithixerxes juliarum	Westphalian D	USA	Brackish to Freshwater
Pieckoxerxes pieckoae	Westphalian D	USA	Brackish to Freshwater
Euthycarcinus ibbenburensis	Westphalian D	Germany	Freshwater
Sottyxerxes multiplex	Stephanian B-C	France	Freshwater
Schramixerxes gerem	Stephanian B-C	France	Freshwater
Euthycarcinus martensi	Permian	Germany	Freshwater
Synaustrus brookvalensis	Triassic	Australia	Freshwater**
Euthycarcinus kessleri	Triassic	France	Freshwater
Euthycarcinoid?			
Arthrogyrinus platyurus	Westphalian B	UK	Brackish to Freshwater

*Following Edgecombe & Morgan 1999. **According to Riek 1968.

of the concretion-bearing level '2', where they co-occur with amphibians, millipedes, syncarids and estherid spinacaudatans (see Sotty 1980, p. 13; Pacaud & Sotty 1994, p. 28). Euthycarcinoids were considered by Schram & Rolfe (1997, p. 211). ". . . as marine cousins of myriapods and insects." However, the association of euthycarcinoids with syncarids (Perrier *et al.* 2006), and estherids (Vannier *et al.* 2003), together with the lack of 'accessory foramina' in euthycarcinoids, and of any sedimentological evidence for marine influence in the Montceau-les-Mines area, establishes that euthycarcinoids were animals living in freshwater environments. In the same way, the occurrence of *Heterocrania rhyniensis* (Hirst & Maulik 1926) in the Lower Devonian Windyfield cherts of Scotland (Anderson & Trewin 2003), indicates that euthycarcinoids were members of a freshwater community in water bodies with no external drainage. This ecological shift may have occurred within the Upper Cambrian–Ordovician time interval, according to literature (see Table 1).

The very low latitude position of the Massif Central during the Upper Carboniferous (Poplin & Heyler 1994) must be taken into account. Due to this geographic location, it is suggested that equatorial rainfalls were abundant enough to prevent the intramontane basin of Blanzy-Montceau from becoming more saline, and even more from drying up. The abundance and diversity of plant remains preserved in concretions attests to such wet and hot, equatorial environmental conditions (Charbonnier *et al.* 2008). The exceptional preservation, added to the vertical distribution in eleven distinct levels (-6 to $+5$; see Fig. 1) of the organic remains in concretions attests to rapid, sudden events, and would strongly support episodic climatic events which would fit well with seasonal heavy rainfall and storms (Couvrat-Desvergnes 1981; Charbonnier 2004; Charbonnier *et al.* 2008; Perrier *et al.* 2006). Both faunal and floral inventories, and to a lesser extant sedimentological data, attest that the Montceau Basin included a wide range of palaeoenvironments from terrestrial to paludal, deltaic lacustrine, and/or fluvial. In this way the upper Stephanian Montceau biota seems to have been more closely allied with the freshwater Lagerstätten of Sosnowiec (Westphalian A) of Poland (Krawczynski *et al.* 1997); the Bickershaw (Westphalian A) Lagerstätten of Lancashire in Great Britain (Anderson *et al.* 1997); the Braidwood facies

(Westphalian D) of Mazon Creek in Illinois (Shabica & Hay 1997); etc.

The fauna that originally inhabited the regressive marine settings probably responded to these sudden environmental changes in various ways (e.g. migrations, extinctions), one of them being to have adapted first to low-salinity then to freshwater conditions. These assumed adaptations would have required a series of changes in the physiology (e.g. osmoregulation) and behaviour of the animals concerned by this ecological shift. Such a simple scenario would explain the presence of 'unusual' faunal elements at Montceau, for example the xiphosurans. Recent limulids live in marine conditions but migrate to estuarine areas for mating. They experience major seasonal environmental changes during their life span and provide an example of remarkable physiological adaptations to salinity variations. This also supports the present authors' environmental model for the Blanzy-Montceau Basin. The unique xiphosuran representative from Montceau possibly originated from marine or brackish ancestors to eventually adapt to strictly freshwater conditions in lakes. The very small size and peculiar morphology of the exoskeleton of *Alanops magnificus* (see Racheboeuf *et al.* 2002) would possibly reflect such an adaptive process. The xiphosuran from Montceau may be a rare case of a freshwater limulid in the whole evolutionary history of the group; *Valoisella lievinensis* from the Westphalian C of northern France could be another example (Racheboeuf 1992). In a similar way, this scenario would make the presence of myxinoids and annelids much less odd than previously thought.

The influence of the Andean orogeny on the geomorphology, climates and environment of the Amazonian Basin during the Neogene, inducing the shift from marine to freshwater of many organisms (gastropods, dolphins, among others), may provide a modern analogue that would lead credence to this scenario (Hoorn 2006; Hoorn & Vonhof 2006). The Amazonian Basin is at a very low, equatorial latitude, as was the Montceau-Blanzy Basin during the Upper Carboniferous. It must be supposed that abundant equatorial rainfall in the small intramontane Blanzy-Montceau Basin (as compared with the Amazonian Basin) would have substituted for the influence of freshwater streams. The shift from marine to

freshwater conditions in the Amazonian Basin began about 23 Ma ago, and its duration was about 16 Ma (Hoorn 2006). According to the Global Stratigraphic Chart, concerning the Massif Central of France and its intramontane basins, the time interval between the Viséan, when the last marine conditions prevailed, and the Stephanian B or C, when the Montceau Lagerstätte deposited, is about 20 to 25 Ma (Gradstein & Ogg 2004).

4. Systematic palaeontology

Order Euthycarcinoidea Gall & Grauvogel, 1964
Family Euthycarcinidae Handlirsch, 1914
Genus *Schramixerxes* Starobogatov, 1988

Type species. *Kottyxerxes gerem* Schram & Rolfe, 1982.

Schramixerxes gerem (Schram & Rolfe, 1982)
(Figs 2–6, 7A; Table 2)

v.1980 Euthycarcinoidea (?); Secrétan, p. 34, Pl. 4, fig. 1.
v.1982 *Kottixerxes gerem* n. sp.; Schram & Rolfe, p. 1437.
v.1985 *Kottixerxes gerem* Schram & Rolfe; Rolfe, pp. 71–73.
?1988 *Schramixerxes gerem* (Schram & Rolfe); Starobogatov, pp. 72–73.
v.1994 *Schramixerxes gerem* (Schram & Rolfe); Schram & Rolfe, pp. 140, 142, Figs 1, 3.

Type material. Previously known specimens with new collection numbers and equivalent (see Schram & Rolfe 1982): MNHN-SOT 1564 (=AM 27916); 3661, holotype (=AM53175); 3663a–b (=AM 52271–52272); 3364 (=AM 10065–10066); 3666a–b (=AM 52651); 3668 (=AM52922); 3671a–b (=AM 53532–53533); 3673 (=AM 4682); 3676a–c (Don Montagne coll.).

Additional material. Thirty-nine new specimens have been made available by recent processing of concretions (Chabard & Poplin 1999). New complete or almost complete specimens: MNHN-SOT 2513a–b; 3039a–b; 3661; 3985a–b; 74698a–b; 83726a–c; 84846a–b; 84851a–c; 89291a–b; 89300a–c; 91759a–b; 101710a–b.

New fragments and/or poorly preserved specimens: MNHN-SOT 1564; 1828a–b; 1878a–b; 1893a–b; 1919; 1949; 2115; 5149a–b; 5211a–b; 5212a–c; 5221a–b; 5507a–b; 5574a–e; 6259a–b; 7458a; 7459a–b; 13406; 24770a–b; 24846a–b; 27031; 27797a–b; 84842a–e; 85460a–e; 86476a–c; 92940a–c; 97033a–b; 100737a–b; 101729a–b.

Type locality and horizon. Most specimens of *S. gerem* are from the Saint-Louis opencast pit, north of Montceau-les-Mines (Saône-et-Loire, France), Assise de Montceau lower part of bed +2 ('horizon A') of Stephanian B–C age; the species also occurs in beds 0 and +3 (Fig. 1) of the same locality; another specimen (MNHN-SOT 27031) comes from the Saint-François open-cast pit.

Emended diagnosis. *Schramixerxes* with no mandibles, with unpaired trapezoidal buccal plate on ventral side of head; five preabdominal tergites; 12 preabdominal sternites; 11 pairs of uniramous, antenniform legs; postabdomen of five somites which decrease in width and increase in length posteriorly; telson long and narrow terminating in a movable spine.

General features. The maximum length of the exoskeleton can be estimated as about 60 mm, with a corresponding width of 10 mm. In MNHN-SOT 89291, the total length of the head area plus preabdomen is 24·8 mm (straight line measurement) for a maximum width of 9·8 mm (tergite T3); the postabdomen is 24·6 mm long and 4·0 mm wide (PA1), and the

telson+terminal spine is about 5·8 mm long. The whole body is markedly flattened dorso-ventrally; its maximum thickness can be estimated as between 2·5 mm and 3 mm at the level of tergite 3 for specimen MNHN-SOT 89291. Figure 7A gives a complete reconstruction of the whole body of *S. gerem* in dorsal, ventral and lateral views.

Head and cephalic region. Complete and detailed observation of the head of *S. gerem* is always difficult because the anterior part of the body is always, to some degree, flexed ventrally. The bending of the body is invariably situated between the anterior cephalic region and the preabdomen, i.e. between the posterior cephalic tergite and tergite 1. Thus, even when well preserved, the head and the anterior cephalic tergite are often buried deep in the concretion, making preparation and casting a particularly delicate and difficult process.

A pair of antennae are inserted on the head, beneath the anterior cephalic tergite, in a dorsal, anterolateral position (Fig. 2). Only basal articles of the right and left antennae are preserved in specimen MNHN-SOT 89291 (Fig. 5d). In a same manner, the two sphaeroidal processes (? lateral eyes) are inserted on the lateral head walls, beneath the anterior cephalic tergite, in a posterodorsal position (Fig. 2). Ventrally the head area is covered by a rounded, elongate, moderately convex subtrapezoidal plate which covers posteriorly the anterior margin of sternite 1. This plate is tentatively interpreted herein as a labrum covering the mouth (Fig. 2).

The anterior cephalic tergite (ACT; see Figs 2, 3) (Edgecombe & Morgan 1999) [=head/procephalon (Schram & Rolfe 1982);=procephalon (McNamara & Trewin 1993)] is subtriangular to broadly rounded in dorsal view, with a straight or weakly concave posterior margin. In anterior view it is gently arched dorsally in cross section, as well as longitudinally, with a moderately concave ventral margin. It is much shorter and narrower than the posterior cephalic tergite (Edgecombe & Morgan 1999) [=tergite 1 (Schram & Rolfe 1982); =gnathocephalon/tergite 1 (McNamara & Trewin 1993)], which it overlaps posteriorly. In MNHN-SOT 89291, the anterior cephalic tergite is 2·6 mm long and 3·7 mm wide. Its surface is smooth, devoid of any ornament. The width of the posterior cephalic tergite (PCT; see Figs 2, 3) does not exceed 8 mm; it markedly differs from the following tergites in that it bears a well developed, convex ventral doublure which gives it the volume to accommodate the cephalic organs inside. The maximum thickness of the PCT is about 2 mm. The doublure extends posteriorly to the free margin of the posterior cephalic tergite which is about 0·5 mm thick at its postero-lateral extent, and rounded in cross section, whilst the posterior margin of the following tergites is very thin and lamellar. Beneath the posteromedian part of the PCT is inserted the sub-semi sphaeroidal process of the anterior articulating process.

Anterior articulating process. Schram & Rolfe (1982, pl. 2, fig. 4, and text-fig. 2B; 1994, fig. 3B) described this feature as ". . . a thirteenth monosomite tucked under the posterior margin of tergite 1 . . ." (p. 1439) and which they named tergite 2 ". . . t2=second tergite (monosomite) . . ." (pl. 2, fig. 4, figure caption). Although available specimens are numerous, this morphological feature could only be observed on specimen MNHN-SOT 3676 (Figs 3, 6a, b), and it is incompletely visible on the new specimens MNHN-SOT 84851 and 89291. It can only be observed in strongly ventrally flexed exoskeletons. Such a bending, inducing a break of the exoskeleton between the posterior cephalic tergite (PCT) and the first preabdominal tergite (T1), results from postmortem attitude, possibly accentuated by post-mortem decay.

The so-called 'monosomite', as cited in the literature, clearly belongs to the posterior part of the PCT, the posterior margin
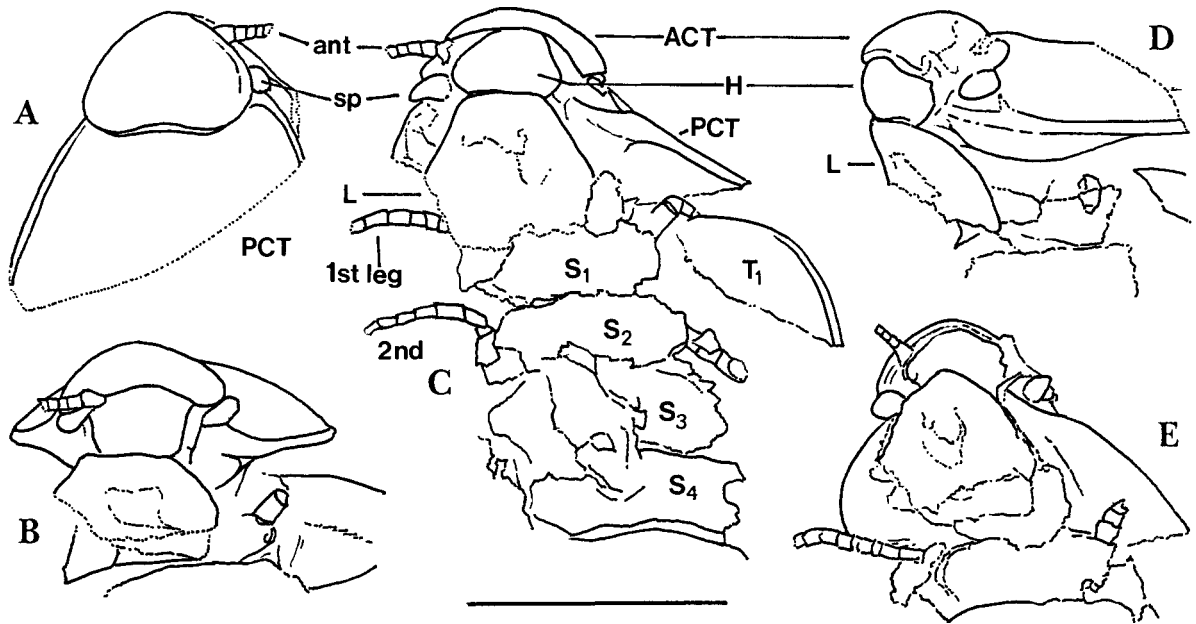
Figure 2 *Schramixerxes gerem* (Schram & Rolfe, 1982). Camera lucida drawings of a latex cast of the anterior region of the exoskeleton of specimen MNHN-SOT 89291 in dorsal (A), anterior (B), anteroventral (C), anterolateral (D), and ventral (E) views. Scale bar=5 mm. Abbreviations: (ACT) anterior cephalic tergite; (PCT) posterior cephalic tergite; (H) head; (L) (?) labrum; (ant) antenna; (sp) spheroidal process; (T1) tergite 1; (S1–4) sternites 1–4.
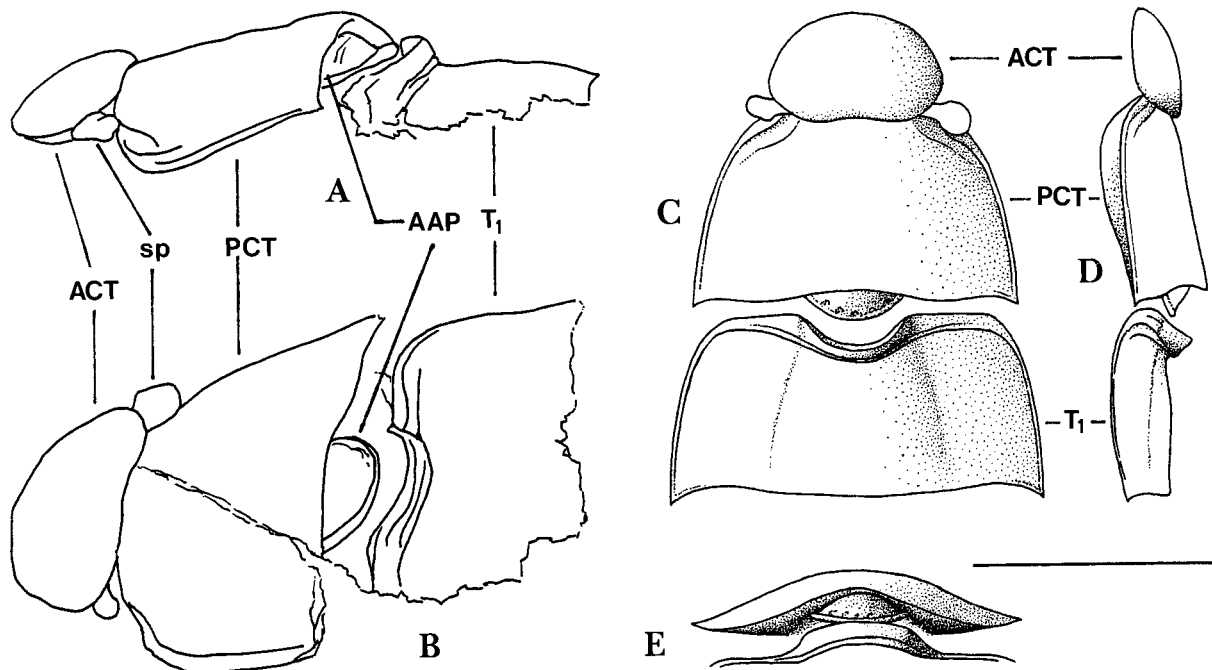

Figure 3 *Schramixerxes gerem* (Schram & Rolfe, 1982). Schematic camera lucida drawings of the anterior and posterior cephalic tergites, and tergite 1 of specimen MNHN-SOT 3676 in latero-posterior (A), and dorsal (B) views. Reconstruction of the same part of the body in dorsal (C), lateral (D), and posterior (E) views, showing the morphology of the two parts of the anterior articulating process. The posterior cephalic tergite and tergite 1 (T1) have been intentionally spaced to exhibit articulating features. Compare the morphology of the anterior margin of T1 with that of T3–5 on Figure 4. Reconstruction after specimens MNHN-SOT 3676, 84851 and 89291. Scale bar=5 mm. Abbreviations: (AAP) anterior articulating process; (ACT) anterior cephalic tergite; (PCT) posterior cephalic tergite; (sp) spheroidal process; (T1) tergite 1.

of which is thickened, unlike the thin, lamellar structure of the following tergites. It appears as a 2·5 mm to 3·0 mm-wide, sub-semisphaeroidal process situated in a median, postero-ventral position beneath the posterior margin of the PCT, and extends about 1 mm posterior of the posterior margin of the PCT.

In addition, the anterior margin of the first preabdominal tergite (T1) is morphologically distinct from that of tergites T2 to T5 (compare Fig. 3C–D and Fig. 4). MNHN-SOT 3676, 84851, and 89291, exhibit a narrow, markedly convex, short and prominent half-ring that is 1·5 mm long and about 2·5 mm to 3 mm wide, i.e. not exceeding one-third of the width of the tergite (Fig. 6a, b). Size and morphology of both the semi-sphaeroidal process of the PCT and the half-ring of T1, clearly indicate that they constitute an articulating process. The present authors name this the **anterior articulating process**
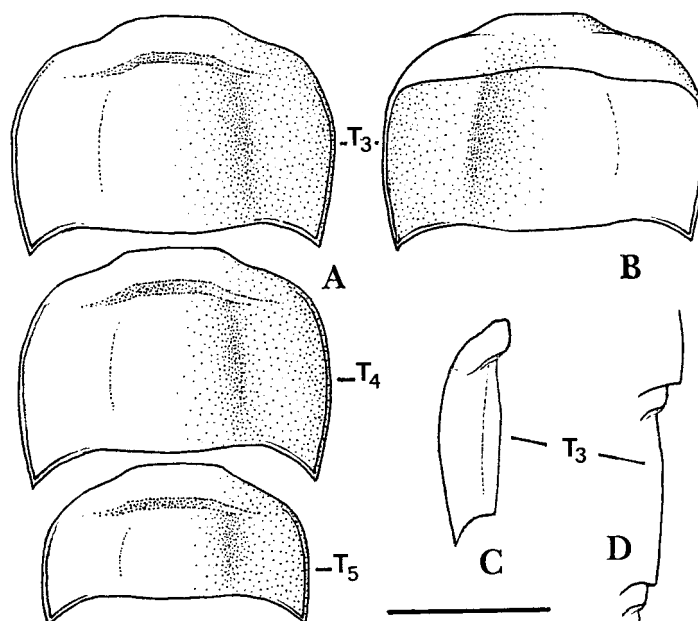
Figure 4 *Schramixerxes gerem* (Schram & Rolfe, 1982): (A) reconstruction of tergites 3 to 5 in dorsal view; (B) tergite 3 in ventral view; (C) tergite 3 in lateral view; (D) lateral view of dorsal profile of tergites in connection. Scale bar = 5 mm.

(AAP), lying between the anterior cephalic region of the body, and the trunk. In this way, the articulation of this part of the exoskeleton is very similar to that described in many other arthropods, such as the microtergite in the xiphosuran limulid *Alanops magnificus* (Racheboeuf *et al.* 2002, pl. 3, fig. 6).

Preabdominal tergites (T1–T5). Each of the five tergites is wider than long, flattened and laterally extended. The maximum width is located either in tergite 2 (MNHN-SOT 84851), or in tergite 3 (MNHN-SOT 89291) and it coincides with the maximum width of the exoskeleton which is about 10 mm. The tergites are uniformly almost subrectangular in outline, with maximum width located at two thirds of their length from the anterior margin (Figs 4, 5f). The anterolateral margins are markedly rounded; the lateral margins are very weakly convex, bearing a very thin marginal ridge, and extend backwards in short, wide, pointed expansions. The posterior margin is sinuous, weakly convex medially. The anterior margin is very weakly convex, almost straight medially, between the rounded anterolateral margins, except for the anterior margin of tergite T1 that definitely differs from that of the following tergites (see above). The anteromedian part of tergites T2–T5 bears a moderately convex transverse ridge corresponding to an articulating half-ring elevated above the surface of the tergite; the length of the articulating half ring is about 1 mm, for a width varying between 4·0 mm and 5·0 mm. The half ring is posteriorly bounded by a transverse marked slope that tapers laterally and parallels the anterior margin of the tergite and weakly bends posteriorly to parallel the posterolateral border of the somite. In ventral view, each tergite exhibits in its anterior part a well developed doublure, the length of which about equals that of the so-called articulating half ring; this feature has been previously illustrated by Schram & Rolfe (1982, pl. 1, fig. 1; 1994, fig. 3C). The surfaces of tergites are smooth and devoid of any ornamentation. Each tergite exhibits a weakly convex, medial longitudinal area occupying about one-third of maximum width, and laterally bounded by two curved, shallow furrows delineating the weakly convex or flattened lateral expansions of the tergite.

Preabdominal sternites (S1–S12). Schram & Rolfe (1982, p. 1439) recognised 12 somites, and suspected the presence of "a thirteenth monosomite tucked under the posterior edge of tergite 1" (now the anterior articulating process). The present detailed study of new material reveals that there are no more than 12 somites. Each ventral somite is identified by its wide, subrectangular, very weakly concave transversely, almost flat, and smooth sternal plate. Each sternal plate is weakly arched, with a convex anterior margin and a concave posterior margin. A low and narrow transverse ridge parallels the anterior margin. Despite the very fine preservation, no sternal pores could be observed on the ventral side of sternites *sensu* Edgecombe & Morgan (1999) as described in *Synaustrus brookvalensis*, or 'accessory foramina' *sensu* Schram (1971) as described in *Kottyxerxes gloriosus*.

Schram & Rolfe (1982) described (p. 1439, text-fig. 1) an oval, concave depression, on the second preabdominal sternite of a specimen of Don Montagne's collection. The restudy of MNHN-SOT 3676 confirms the presence of such a structure (Fig. 6e). In the present authors' opinion, its location in the middle part of the somite, as well as its regular outline and profile, preclude any artefact. Although the function of such a feature remains unknown, it is noted that none of the specimens that show the ventral side of the exoskeleton exhibits the same structure. The length/width ratio of the anterior cephalic tergite of MNHN-SOT 3676 is much more transverse in outline (0·586) than that of MNHN-SOT 89291 (0·712), which is devoid of a concave depression. The posterior cephalic tergite is more transverse in MNHN-SOT 89291 (0·444) than in MNHN-SOT 3676 (0·538). Could this concave depression, associated to different size and outline of ACT and PCT be possibly related to some from of dimorphism? In such an enigmatic organism it is impossible to state the likelihood of this but it is clear that the cephalic region (ACT+PCT) is longer and wider in MNHN-SOT 89291 than in MNHN-SOT 3676 (length: 6·2 instead of 5·85; maximum width: 8·1 instead of 6·76; corresponding ratios: 0·76 instead of 0·86).

Postabdominal somites (PA1–PA5). The postabdomen (PA) is narrow, less than half the width of the tergites. The five postabdominal somites are devoid of appendages, and are subcylindrical, ventrodorsally flattened, and oval to elliptical in cross section. Their ventral side is smooth and very weakly convex; their dorsal side is more convex, and some specimens exhibit some longitudinal and posteriorly weakly divergent
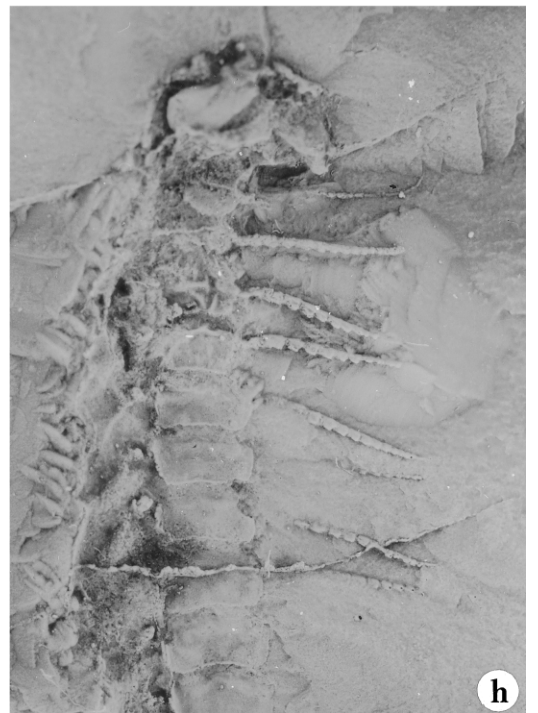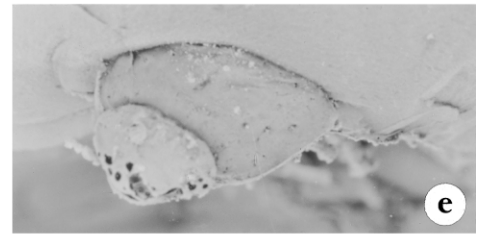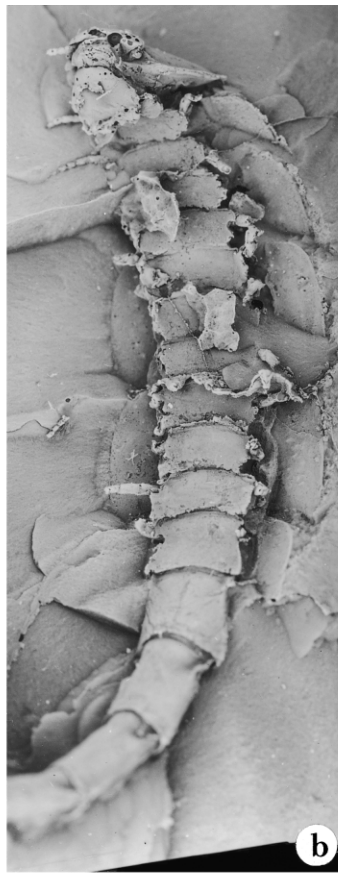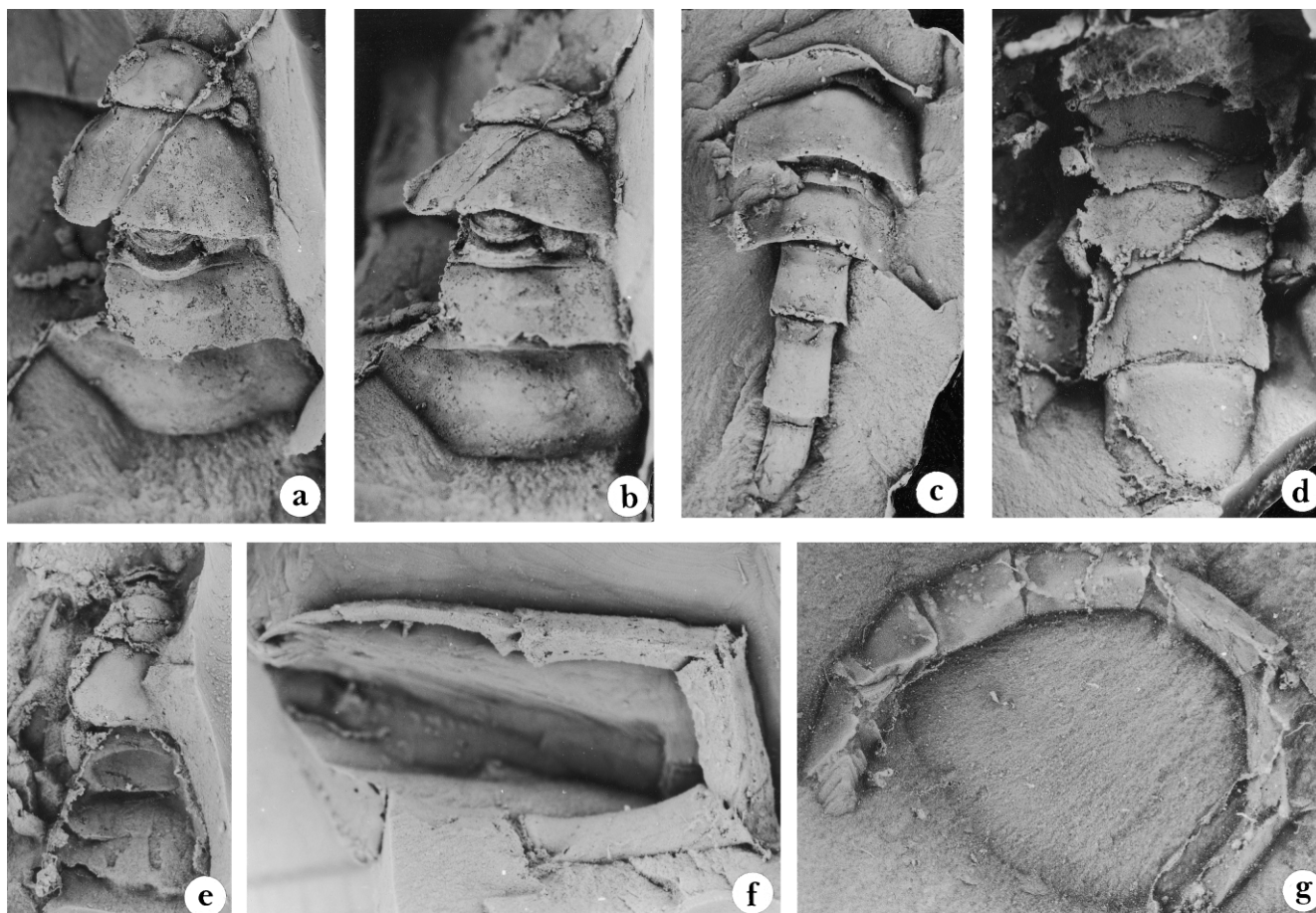
Figure 6 *Schramixerxes gerem* (Schram & Rolfe, 1982). (a–f) latex peels of specimen MNHN-SOT 3676; (a–b) cephalic tergites and tergites 1 and 2 of the preabdomen in (a) dorsal and (b) posterodorsal views. Note the convex articulating process at the posterior margin of the posterior cephalic tergite which articulates with the concave part at the anterior margin of tergite 1, × 5; (c) tergites 3 to 5 and postabdominal somites 1 to 3, × 5; (d) ventral side of the exoskeleton with the last preabdominal sternites and first postabdominal somite; (e) ventral side of the anterior part of the exoskeleton showing the "oval cavity" on sternite 2, × 5; (f) postabdominal somites 3 to 5, telson, and terminal moveable spine, × 7. (g) specimen MNHN-SOT 2115, postabdominal somites in lateral view × 5.

rough ridges. However it cannot be positively stated that such features represent some kind of ornamentation or if they result from the burial process or preservation. The length of the PA somites in general increases posteriorly, while their width and thickness decrease backwards. In MNHN-SOT 89291, the length of postabdominal somites PA1 to PA5 progressively increases from 3·9 mm to 5·52 mm, while the width decreases from 4·03 mm to 1·56 mm (see Table 2). Consequently, the length/width ratio of the same increases from 0·96 (PA1), 1·45 (PA2), 1·97 (PA3), 2·65 (PA4) to 3·37 (PA5). The thickness of each somite equals about one-third its width. The postero-lateral extremities of somites PA1 to PA3 bear short, postero-laterally weakly divergent, pointed expansions; somites PA4 and PA5 lack such spines. The ventral posterior margin of each somite is concave posteriorly; such a notched morphology enables ventral flexure of the postabdomen, while the dorsal posterior margin is straight to weakly convex. At the antero-lateral part of each somite, a pair of rounded articulatory processes enables the articulation of the somite with the

preceding one, and the ventral flexure of the postabdomen. The dorsal posterior margin of each somite is straight to weakly convex posteriorly, precluding dorsal flexure. The telson is relatively stout, 4·16 mm long, for a width of 1·30 mm in MNHN-SOT 89291. The dorsal side is weakly convex, while the ventral side is semicircular, with two dorsolateral carinae. The anal opening is large and well defined. The terminal moveable spine is cylindrical, and 1·62 mm to 1·82 mm long (specimens MNHN-SOT 89291 and 2115, respectively).

Preabdominal appendages. Eleven pairs of ventral, uniramous, antenniform leg appendages occur. Each pair is inserted on the lateral body walls, probably unsclerotised, of each somite, near the anterior margin of each sternal plate. Appendages are composed of 12 to 15 podomeres, subtriangular in cross section, and weakly flattened dorso-ventrally; proximal podomeres are about three times longer than the distal ones. They are devoid of any setae. The posterior leg appendages are shorter than the anterior ones. It seems that the length of leg appendages weakly decreases progressively

Figure 5 *Schramixerxes gerem* (Schram & Rolfe, 1982). (a–f) specimen MNHN-SOT 89291, latex peels of a complete exoskeleton: (a–c) three variable latero-ventral to almost ventral views, × 2·5 (a), and × 3 (b, c); (d) enlargement of the cephalic region in antero-ventral view exhibiting the left sphaeroidal process, the basis of the right antenna, the head, the unpaired convex, elongated ventral plate, and the first sternites, × 5; (e) anterior cephalic tergite and anterior part of the posterior cephalic tergite in dorsal view, × 5; (f) preabdominal tergites 1 to 5. (g) MNHN-SOT 91759, ventral side of a nearly complete exoskeleton, × 3; (h) anterior left limbs, and sternites of specimen MNHN-SOT 3666, × 5.

Table 2 Measurements (in mm) of elements of the exoskeleton of *Schramixerxes gerem* (Schram & Rolfe, 1982) for seven well-preserved specimens. For preabdominal tergites T1 to T5, the first length value corresponds to the total length of the tergite along the longitudinal axis; the second value refers to the length from the furrow of the half ring to the posterior margin of the tergite. Abbreviations: (ACT) anterior cephalic tergite; (PCT) posterior cephalic tergite; (T) thoracic somites; (PA) preabdominal somites; (S) sternites

Spec. nb	89291		91759		84851		3661	2115	89300		3676 (hol.)	
	L	W	L	W	L	W	L	L	L	W	L	W
ACT	2·60	3·70	–	–	–	–	–	–	–	–	2·21	3·77
PCT	3·6	8·1	–	–	–	–	–	–	–	–	3·64	6·76
T1	3·12/2·66	8·51	–	–	– /3·25	–	–	–	–	–	– /2·99	–
T2	3·96/3·44	9·23	–	–	– /4·35	8·77	–	–	–	–	– /3·25	–
T3	5·91/4·81	9·81	–	–	– /4·35	8·58	–	–	–	–	– / –	8·71
T4	5·91/4·81	9·29	–	–	– /3·90	8·12	–	–	–	9·42	4·16/ –	8·45
T5	4·09/2·92	8·45	–	–	– / –	6·89	–	–	–	7·80	3·51/2·86	7·28
PA1	3·90	4·03	3·57	4·09	3·25	–	3·25	2·79	3·57	4·29	3·51	3·25
PA2	4·74	3·25	4·35	4·25	4·35	–	3·57	3·70	–	–	4·55	2·86
PA3	5·26	2·66	5·33	2·92	4·68	–	4·29	4·16	–	–	4·68	2·08
PA4	5·52	2·08	5·85	2·08	3·90	–	4·22	4·68	–	–	–	–
PA5	5·26	1·56	4·74	1·56	3·70	–	–	4·55	–	–	–	–
Telson	4·16	1·30	–	–	–	–	–	4·29	–	–	–	–
Spine	1·62	–	–	–	–	–	–	1·82	–	–	–	–
S1	1·62	–	–	–	–	–	–	–	–	–	–	–
S2	1·65	–	1·36	–	–	–	–	–	–	–	–	–
S3	1·75	–	1·49	–	–	–	–	–	–	–	–	–
S4	1·80	–	1·59	–	–	–	1·56	–	–	–	–	–
S5	1·82	–	1·75	–	–	–	1·69	–	–	–	–	–
S6	1·82	–	1·75	–	–	–	1·69	–	–	–	–	–
S7	1·95	–	1·95	–	–	–	1·95	–	–	–	–	–
S8	1·95	–	1·96	–	–	–	1·95	–	–	–	–	–
S9	1·95	–	1·95	–	–	–	1·95	–	–	–	–	–
S10	1·95	–	1·92	–	–	–	2·01	–	–	–	–	–
S11	1·95	–	1·95	4·09	–	–	2·01	–	–	–	–	–
S12	2·60	–	2·60	3·77	–	–	2·86	–	–	–	–	–

along the body from the anterior to the posterior, but this cannot be clearly established owing to the variably curved position of the appendages.

Order Sottyxerxiformes Starobogatov, 1988
Family Sottyxerxidae Schram & Rolfe, 1982
Genus *Sottyxerxes* Schram & Rolfe, 1982

Type species.   *Sottyxerxes multiplex* Schram & Rolfe, 1982

Sottyxerxes multiplex Schram & Rolfe, 1982
(Figs 7B–10)

v.1982 *Sottyxerxes multiplex* n. sp.; Schram & Rolfe, p. 1445.
v.1985 *Sottyxerxes multiplex* Schram & Rolfe; Rolfe, pp. 71–73.
v.1994 *Sottyxerxes multiplex* Schram & Rolfe; Schram & Rolfe, p. 142, fig. 4.

Type material.   Previously known specimens with new collection numbers and equivalents (see Schram & Rolfe 1982): MNHN-SOT 3662, 3665, 3667 (AM 46504), 3669, 3670, 3672, 3675, 3677–3680.

Additional material.   To the 11 previously known specimens, 49 new specimens have been added (Chabard & Poplin 1999). However, before preparation and owing to the elongated and segmented nature of the body, some specimens were provisionally considered to be myriapods, and it is expected

that other specimens may have been provisionally catalogued under other faunal names.

New complete or almost complete specimens: MNHN-SOT 21763, 78001, 80185, 83723, 89968, 89974, 91726, 94611.

New fragments and/or poorly preserved specimens: MNHN-SOT 6297, 7037, 19041, 19809, 23869, 24769, 73826, 77215, 77230, 80209, 80935, 81536, 83719, 84389, 84835, 85456, 86018, 86491, 87637, 89280, 89950, 91099, 91734, 92357, 92362, 92250, 93517, 93518, 94615, 94627, 95659, 95676, 96570, 96574, 97031, 97033, 99332, 99347, 99350, 99677, 100110.

Type locality and horizon.   Specimens originate from the Saint-Louis opencast pit, north of Montceau-les-Mines (Saône-et-Loire, France), Assise de Montceau; all are from bed +2 (most of them from the lower part, namely 'horizon A'), apart from bed 0.

Emended diagnosis.   *Sottyxerxes* with anterior cephalic region relatively small, with posteriorly rounded PCT; lacking mandibles but with two unpaired buccal plates; 14 preabdominal tergites; 28 preabdominal sternites; 28 pairs of uniramous, antenniform legs; six postabdominal somites, posterolaterally produced, with two proximal somites shorter than wide; telson short; no movable spine.

General features.   The maximum length of the exoskeleton may have been about 35 mm, the preabdomen being 3·0 mm wide. The length of the cephalic region (ACT+PCT) is about 2·4 mm; that of the preabdomen about 20 mm, the postabdomen about 12 mm and the telson is 1 mm long. The whole
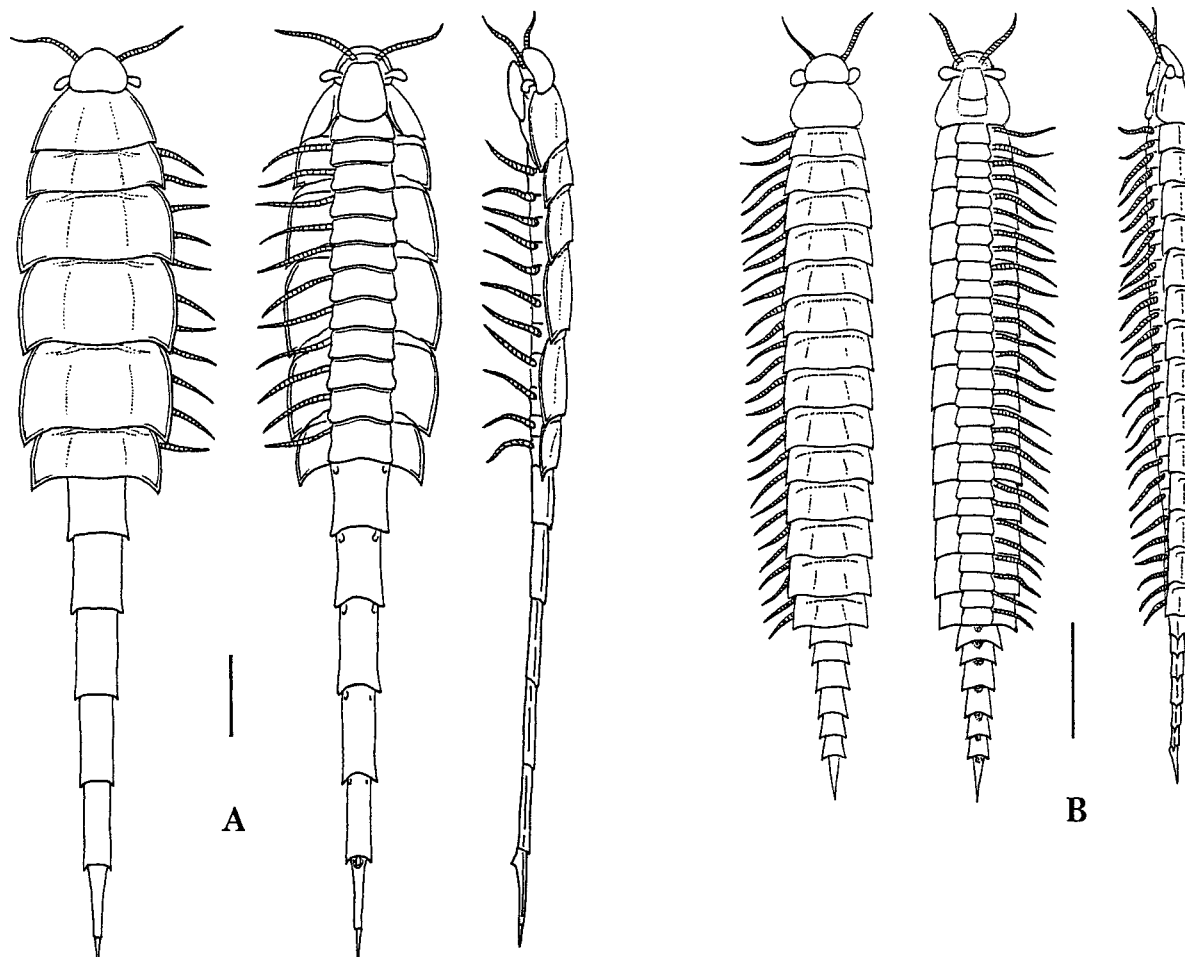
Figure 7 Reconstructions of the complete exoskeletons of *Schramixerxes gerem* (Schram & Rolfe, 1982) (A), and *Sottyxerxes multiplex* Schram & Rolfe, 1982 (B), in dorsal, ventral and lateral views. Scale bars = 5 mm.
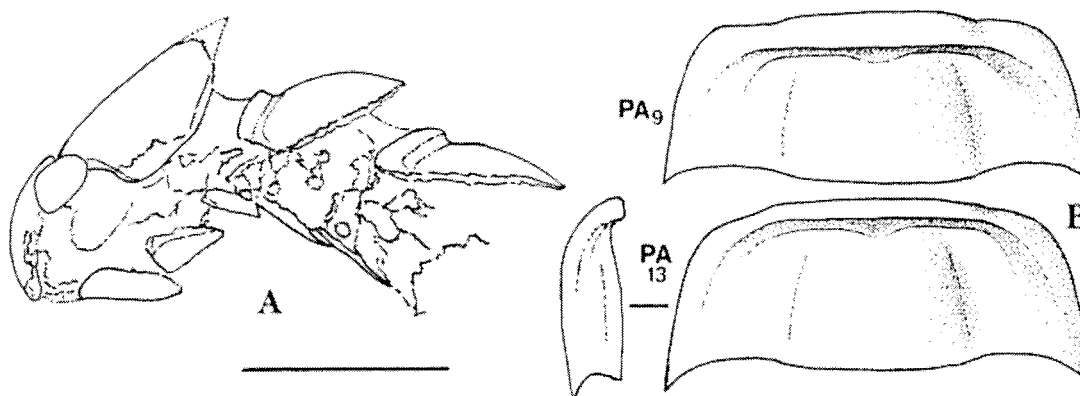

Figure 8 *Sottyxerxes multiplex* Schram & Rolfe, 1982. (A) Camera lucida drawing of the latex cast of specimen MNHN-SOT 83723 showing the head area with ACT and PCT, the sphaeroidal process (sp), and the two ventral plates, with the (?) labrum (L), and preabdominal tergites PA1 and PA2. (B) Reconstructions of preabdominal tergites PA9 and PA13 in dorsal view, and PA13 in lateral view. Scale bar = 1·5 mm.

body is markedly flattened dorso-ventrally; its maximum thickness can be estimated as about 1·5 mm at the level of tergites 3 to 10 for specimen MNHN-SOT 83723. Figure 7B gives a complete reconstruction of the whole body in dorsal, ventral and lateral views.

Head and cephalic region. The head of this species is poorly preserved in all specimens. The anterior cephalic tergite (ACT) is rounded in outline, moderately convex both longitudinally and in cross section, and about 1 mm long for a corresponding width of about 1·6 mm. The posterior cephalic tergite (PCT) is about 1·5 mm long; its width remains unknown, but it probably equals that of the first tergite, i.e.

about 3 mm. The sphaeroidal processes are relatively stout and prominent. In specimen MNHN-SOT 83723, the ventral side of the head bears two weakly convex, unpaired plates, the posterior margin of the second one partly covering the first preabdominal sternite (Fig. 10c, d). The size and outline of these two plates, possibly corresponding to the 'labrum' of *S. gerem* (see above) remain unknown.

Preabdominal tergites (T1–T14). Schram & Rolfe (1982) mentioned the presence of a monosomite plus 14 diplotergites; later (1994), the same authors listed 15 tergites. Detailed observations of newly available specimens reveals that the monosomite is in fact an articulating process between the
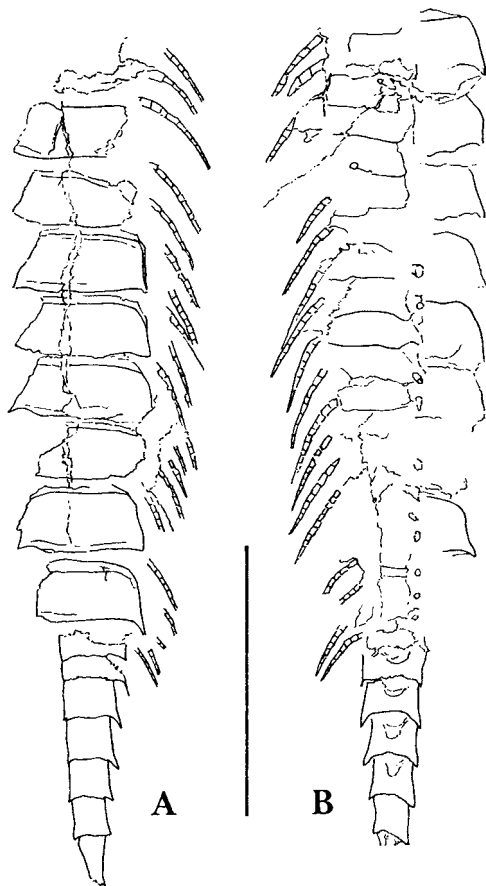
Figure 9 *Sottyxerxes multiplex* Schram & Rolfe, 1982. Camera lucida drawings of latex casts of specimen MNHN-SOT 3667: (A) dorsal side; (B) ventral side. Scale bar = 4 mm.

cephalic region and the preabdominal region. So it is established herein that the exoskeleton of *S. multiplex* includes fourteen tergites (diplotergites). All tergites are very similar in size and outline, except for T14. The length of T1 to T13 varies between 1·15 mm and 1·3 mm, for a corresponding width of about 3 mm; T14 is shorter (1·1 mm) and narrower (2·6 mm). Tergites are subrectangular in outline, with a weakly convex anterior margin and a sinuous posterior margin; lateral margins are oblique, weakly convex and posteriorly acuminate. The anterior margin of each tergite bears a narrow, well differentiated half-ring, which articulates with the posterior margin of the preceding tergite. The half ring is weakly convex, and posteriorly bounded by a transverse, subvertical wall which parallels the anterior margin and bends posteriorly along the lateral margins of the tergite in its distal, lateral parts. The half ring of the first tergite (T1) appears narrower, but it is much more developed and prominent than that of the more posterior tergites. Dorsally, each tergite exhibits a slightly convex, median longitudinal area laterally bounded by two wide and shallow furrows delineating the lateral expansions of the tergites.

Preabdominal sternites (S1–S28). The presence of 28 preabdominal sternites fits with the 28 pairs of limbs as previously established by Schram & Rolfe (MNHN-SOT 3667 = AM 46505; 1982, p. 1445). In ventral view, each sternite is subrectangular, markedly transverse in outline, with a very weakly convex anterior margin, and a weakly concave posterior margin. Their longitudinal profiles are very weakly concave to flat. Most sternites are between 0·6 mm and 0·7 mm long, except for sternite S1 which is 0·5 mm long; posteriorly the length of sternites progressively decreases from sternite S23 (0·66 mm) to sternite S28 (0·43 mm) (MNHN SOT 21763 and

83723). The width of the preabominal sternites is almost constant and about 1·3 mm to 1·4 mm. Each somite bears a pair of relatively long, articulated limbs.

Postabdominal somite (PA1–PA6). The two first somites are short (0·50 mm long) and transverse (1.25 mm and 1·15 mm for PA1 and PA2, respectively). From somites PA3 to PA6, length and width progressively decrease from 0·8 mm to 0·65 mm, and from 1·0 mm to 0·65 mm, respectively (MNHN-SOT 21763). The somites are dorso-ventrally flattened, with a sinuous posterior margin, and each somite bears a pair of posterolateral acuminate expansions, the development of which decreases from PA1 to PA6. Ventrally, the antero median part of each somite exhibits a depressed, semicircular area which allowed ventral bending of the postabdomen. The telson is straight, needlelike, subcylindrical, 1 mm long, and with a diameter of about 0·15 mm (MNHN-SOT 21763). The anal opening is subcircular. No moveable spine was observed.

Preabdominal appendages. Twenty-eight pairs of ventral, uniramous, antenniform leg appendages occur, all devoid of setae. Each pair is inserted on the lateral body walls, probably unsclerotised, of each somite, near the anterior margin of each sternal plate. Appendages are uniramous and antenniform and composed of more than 13 subcylindrical podomeres, that are weakly flattened dorso-ventrally. Proximal podomeres are about three times longer than the distal ones. The posterior leg appendages are shorter than the anterior ones. The length of leg appendages decreases progressively along the body from the anterior to the posterior.

5. Position of euthycarcinoids within Arthropoda

5.1. The euthycarcinoid record

From the initial description of Handlirsch (1914) until the present, fourteen taxa have been described and/or revised, and assigned to euthycarcinoids; another taxon (*Arthrogyrinus platyurus* Wilson & Almond, 2001) still remains questionably assigned to this arthropod group. Table 1 summarises their occurrence in stratigraphical order and their geographic distribution, as well as their environmental setting, as gained from the literature. Euthycarcinoids have probable Cambrian ancestors, the oldest representative of the group being *Apankura machu* Vaccari, Edgecombe & Escudero, 2004, from the late Cambrian of Argentina, which occurs in marine facies (Vaccari *et al.* 2004). Due to the patchy fossil record of euthycarcinoids, it is not possible to state precisely when euthycarcinoids first invaded freshwater environments. The clear implication is that the marine–freshwater shift occurred very early in the history of the euthycarcinoid group, this depending, of course, on whether or not the euthycarcinoids are accepted as a homogenous arthropod group.

5.2. Environmental setting and behaviour

The preabdominal appendages of *Kottyxerxes gloriosus* are feather-like, bearing "... flap-like setae, one on each joint of the leg." (Schram & Rolfe 1982, p. 1437); such a morphology undoubtedly suggests "... that this species might have been capable of swimming in addition to pushing along the bottom with its limbs." (Schram & Rolfe 1982, p. 1437). *Schramixerxes gerem* and *Sottyxerxes multiplex* lack setae, flat-like setae or other swimming adaptations, and their podomeres are subtriangular, weakly flattened, in cross-section. In this way, *Schramixerxes gerem* and *Sottyxerxes multiplex* were probably not capable of swimming, like the Lower Devonian form *Heterocrania rhyniensis* (Hirst and
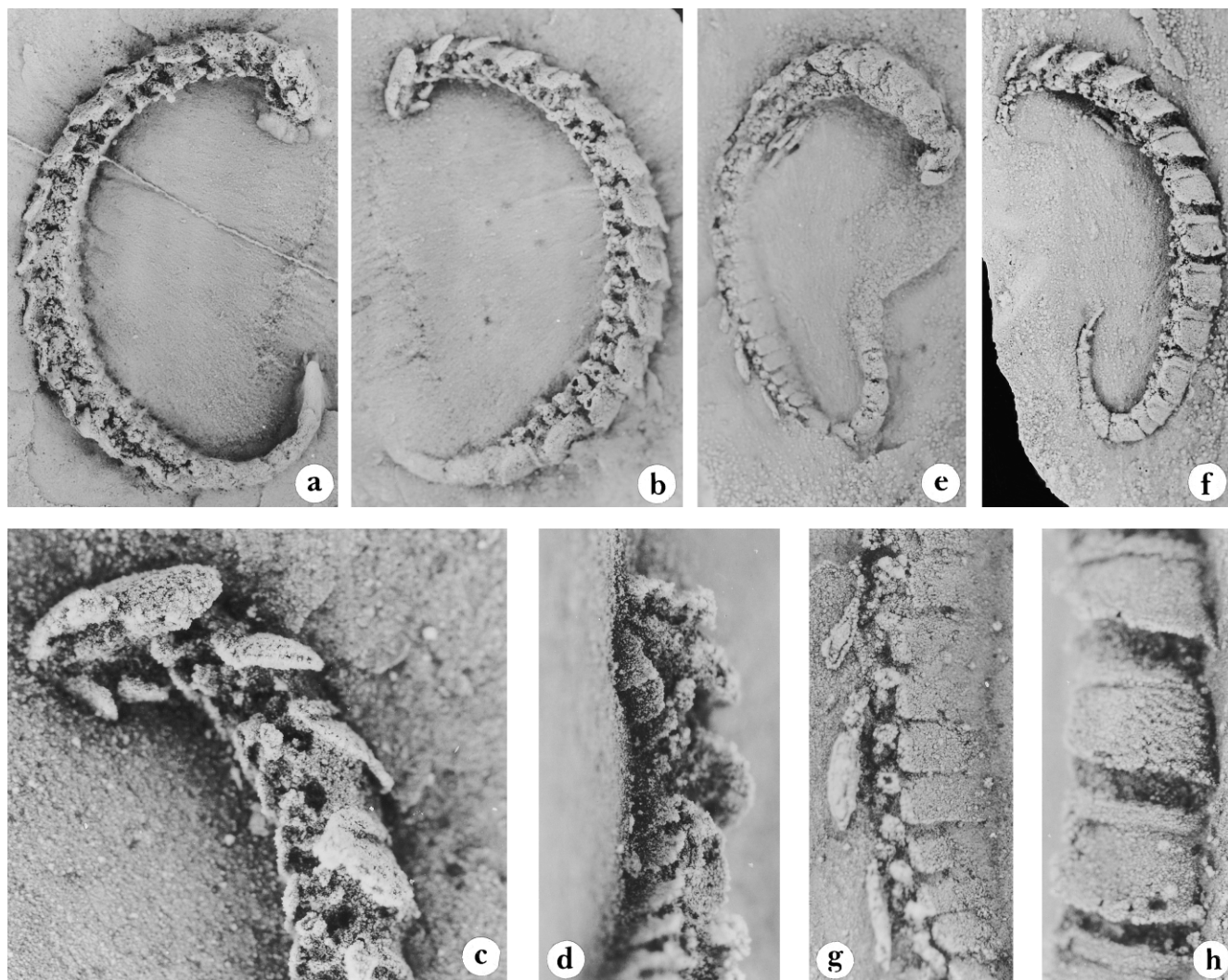
Figure 10 *Sottyxerxes multiplex* Schram & Rolfe, 1982. (a–d) latex peels of specimen MNHN-SOT 83723: right (a) and left (b) sides, × 4; (c–d) detail of the anterior part of the exoskeleton in lateral (c) and ventral (d) views, showing the anterior and posterior cephalic tergites, the tergites 1 to 4, the sternites 1 to 7, and the two unpaired ventral plates below the head, × 10. (e–h) latex peels of specimen MNHN-SOT 21763: right (e) and left (f) sides, × 4; (g–h) lateroventral and laterodorsal views of the preabdomen showing tergites 5 to 8 with their anterior and posterior ridges (g), corresponding sternites, and insertion of limbs (h), × 10.

Maulik, 1926), but they were capable of living in water, "pushing along the bottom with their limbs" (Anderson & Trewin 2003). It should be noted that the limbs of the Cambrian marine *Apankura machu* show no special adaptation to the aquatic environment. Moreover, due to their distinct size and morphology, it appears likely than *K. gloriosus*, *Smithixerxes juliarum* and *Schramixerxes gerem* on the one hand, and *Pieckoxerxes pieckoae*, and *Sottyxerxes multiplex* on the other, occupied different ecological niches.

Three euthycarcinoid species occur in the Westphalian D non-marine Braidwood facies of Mazon Creek, namely *Kottyxerxes gloriosus* Schram, 1971; *Smithixerxes juliarum* Schram & Rolfe, 1982; and *Pieckoxerxes pieckoae* (Schram & Rolfe, 1982). The Montceau-les-Mines Lagerstätte (Stephanian B or C), provides us with two taxa, namely *Schramixerxes gerem* (Schram & Rolfe, 1982), and *Sottyxerxes multiplex* Schram & Rolfe, 1982. Initially, one might compare *P. pieckoae*, and *Sottyxerxes multiplex*, as they share a similar morphology and both exhibit 14 'tergites', but the exoskeleton of *S. multiplex* is much smaller than that of *P. pieckoae* (see Schram & Rolfe 1982, text-fig. 2). Similarly, the exoskeletons of *Kottyxerxes gloriosus*, and *Smithixerxes juliarum*, with five or six 'tergites', exhibit a similar whole outline to the smaller *Schramixerxes gerem* (after Schram & Rolfe 1982, text-fig. 2).

Thus the two Montceau euthycarcinoids were undoubtedly smaller than their Mazon Creek homologues (see Schram & Rolfe 1982, text-fig. 2).

Another point of interest relates to sternal pores. Each sternite of the preabdomen of *Kottixerxes gloriosus* and *Synaustrus brookvalensis* (see Riek 1968) bears a pair of small circular pits that have been described as 'accessory foramina' in *K. gloriosus* by Schram (1971), and as 'sternal pores' in *S. brookvalensis* by Edgecombe & Morgan (1999). Such features have been compared with coxal vesicles of ". . . many atelocerates, . . . [in which they] . . . are associated with water absorption in terrestrial arthropods." (Edgecombe & Morgan 1999). The lack of sternal pores in *Schramixerxes gerem* and *Sottyxerxes multiplex* at Montceau, supports an aquatic mode of life for these two taxa.

5.3. Previous work on euthycarcinoid affinities
The position of euthycarcinoids within Arthropoda is still a matter of debate. They have been assigned to several groups such as copepods, branchiopods, as an independant group of crustaceans, as trilobitoids, merostomoids or possibly merostomes (see Bergström 1980, p. 14). Bergström concluded (p. 15) that euthycarcinoids represent a distinct uniramian group comparable in rank with the Myriapoda and Hexapoda.

Schram & Rolfe (1982) suggested that euthycarcinoids ". . . might be regarded as an interim stage en route to hexapody . . ." (1982, p. 1449), and that they ". . . may represent the remnants of an ancestral uniramian, or proto-antennate, marine stock, rather than being crustaceans or merostomoideans." (1982, abstract). For McNamara & Trewin ". . . euthycarcinoids belong in the same phylum as the hexapods and myriapods . . ."; they evolved from the latter and were at the origin of the former (1993, p. 327). The cladistic analysis of Edgecombe & Morgan (1999) shows that euthycarcinoids are allied with Atelocerata (=Uniramia), but they only noticed analogous characters with symphylans. Wilson & Almond (2001) did not exclude possible euthycarcinoid–crustacean relationships and suggested that euthycarcinoids may be a sister group of the Branchiopoda; however they concluded that the status of euthycarcinoids remained uncertain and should be provisionally left as Arthropoda *incertae sedis*. Another interesting point was introduced by Anderson & Trewin (2003), who suggested a desiccating egg stage to explain the occurrence of an euthycarcinoid in ephemeral pools at Rhynie.

Several euthycarcinoids have well-developed mandibles, for example *Euthycarcinus martensi* Schneider, 1983, *E. ibbenburensis* Schultka, 1991, *Heterocrania rhyniensis* (Hirst & Maulik, 1926). Others, such as *Synaustrus brookvalensis*, lack these appendages. Mandibles are also absent in *Schramixerxes gerem* and *Sottyxerxes multiplex* from Montceau. They are replaced by a unique, unpaired labrum-like plate in *Schramixerxes gerem*, similar to that of *Kottyxerxes anglicus* described by Wilson & Almond (2001), and by two plates (an anterior one and a posterior one) in *Sottyxerxes multiplex*.

The unique ventral plate of *Schramixerxes gerem* closely resembles the labrum of hexapods and branchiopods (among others) in its morphology as well as in its location on the ventral side of the head, and it is provisionally considered herein to be homologous with a labrum. The two plates of *Sottottyxerxes multiplex* do not further argue for such a homology; they would provide a compelling apomorphy to ally euthycarcinoids with hexapods. This last point would strongly suggest two styles of feeding behaviour, as well as questioning phyletic relationships between the genera *Schramixerxes* and *Sottyxerxes*.

The Montceau-les-Mines representatives of the euthycarcinoid group do not provide a solution to the problem of the phylogenetic position of these arthropods. It should be noted here that on the whole the exoskeleton of *Schramixerxes gerem* resembles some insect larvae (nymphs), such as those of cockroaches, especially in lateral view. Indeed, as a first approximation, the cockroach has a head morphology that is pretty close in morphology to the bipartite head of euthycarcinoids, and cockroaches are considered to lie near the base of Dictyoptera among insects. This could lend some further support for atelocerate affinities. On the other hand, the distinction between Sottyxerxiformes and Euthycarcinifomes appears to be a real one, fundamentally dividing the euthycarcinoids into two quite distinct groups. It cannot yet be said which is the more primitive.

6. Acknowledgements

7. References

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