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Systematic Palaeontology (Invertebrate Palaeontology)

New xiphosuran merostomata from the Upper Carboniferous of the Graissessac Basin (Massif Central, France)

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Abstract

Carboniferous merostome arthropods are relatively diversified, but their remains are rare, especially in France. A new specimen has been collected from the southern part of the Massif Central (France). This new taxon of xiphosurid, assigned to *Euproops mariae* n. sp. from Graissessac, is described; comparisons with closely allied species from Europe are discussed. Based on the associated macroflora, the material is considered to be Stephanian B–C in age. **To cite this article:** C. Crônier, P. Courville, *C. R. Palevol* 4 (2005).

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Résumé

Un nouveau mérostome xiphosure du Carbonifère supérieur du bassin de Graissessac (Massif central, France). Les arthropodes mérostomes du Carbonifère sont relativement diversifiés, mais leurs restes sont rares, notamment en France. Un nouveau xiphosure, attribué à *Euproops mariae* n. sp., récolté dans le bassin de Graissessac, au sud du Massif central (France) est décrit. Ses affinités avec les espèces proches de l'Europe sont discutées. D'après la macroflore, le matériel est daté du Stéphanien B–C. **Pour citer cet article :** C. Crônier, P. Courville, *C. R. Palevol* 4 (2005).

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Mots clés : Carbonifère ; Stéphanien ; Massif central ; France ; Merostomata ; Xiphosures

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Version française abrégée

1. Introduction

Les mérostomes (Arthropoda) sont des organismes présents dès le Cambrien. Globalement, il s'agit d'un groupe essentiellement paléozoïque, rassemblant les euryptérides (surtout siluriens) et les xiphosures (surtout carbonifères). Depuis leur radiation, les xiphosures n'ont guère montré de changement morphologique notable. Souvent considérés comme des « fossiles vivants » [15], ils ont persisté, avec une morphologie conservatrice et une faible diversité : actuellement, les xiphosures ne sont représentés que par trois genres et quatre espèces de « limules ».

Néanmoins, les détails anatomiques fournissent des informations précieuses pour l'identification ou la compréhension des phénomènes évolutifs chez les mérostomes xiphosures. L'évolution de leurs caractères pendant le Carbonifère – période correspondant à un pic de diversité pour le groupe – renseigne donc sur les relations phylogénétiques au sein des xiphosures.

Trois grands traits évolutifs marquent le groupe : accroissement spectaculaire de la taille, perte de la segmentation de l'opisthosome et restriction à des habitats marins après le Jurassique. De nombreuses formes furent inféodées à des eaux saumâtres, voire douces, entre le Carbonifère et le Jurassique. Tous les xiphosures actuels sont marins. Dans tous les cas, ces animaux benthiques, fouisseurs et se nourrissant de petits invertébrés, se rencontrent dans les régions tropicales [15,30].

En Europe, le Carbonifère se signale surtout par ses dépôts de marais limniques ou paraliques tropicaux. Dans le bassin houiller de Graissessac (Stéphanien du Sud-Est du Massif central, France), un tel dépôt a fourni un exceptionnel reste de xiphosure.

Le fossile décrit ci-après, rapporté à *Euproops mariae* n. sp., contribue à la connaissance anatomique, biologique et systématique des xiphosures carbonifères de France et d'Europe. Au sein des mérostomes, cette forme fait partie des xiphosures les plus primitifs inféodés à des eaux non marines.

2. Graissessac : contexte géologique

Cadre général

À l'échelle de l'Europe, l'intervalle Carbonifère supérieur/Permien inférieur est caractérisé par de nom-

breux bassins houillers intramontagneux, liés à des fossés structuraux isolés, mais reliés par des zones de fractures [5,7,11,13]. Le développement des bassins stéphanio-permiens est contrôlé par l'extension tardive liée aux stades tardifs de la surrection de la chaîne Varisque [11]. Au nord de l'extrémité orientale de la Montagne noire, le bassin de Graissessac (Sud du Massif central français, Fig. 1) est attribué au Stéphanien B–C d'après la flore [5].

Données paléobiologiques et contexte paléo-environnemental

À Graissessac, la faune connue est rare et dispersée, avec quelques lamellibranches, insectes et poissons [5]. En revanche, les faisceaux exploités pour la houille sont caractérisés par la présence de très nombreux végétaux fossiles, même si les différents sites à végétaux semblent livrer une flore relativement peu variée localement. Des peuplements végétaux différents devaient caractériser différents secteurs du bassin. Cette distribution pourrait être le résultat d'un tri mécanique et non d'une « phytazonéographie » [23].

Selon Becq-Giraudon et Van Den Driessche [6] et Becq-Giraudon et al. [7], certains faits sédimentologiques (cratères d'échappement, coulées de solifluxion, fantômes de cristaux de glace), ainsi qu'une flore caractérisée par son homogénéité, sa faible diversité et son extension géographique limitée, traduisent un climat à saisons et hivers froids. Ces faits seraient liés à des effets périglaciaires de haute altitude. Au regard de la position équatoriale de la chaîne Hercynienne, ce type de climat n'existerait qu'à une altitude supérieure à 4500 m. De façon contradictoire et pertinente, Puaud [23], note, d'une part, que les végétaux ne montrent aucun caractère anatomique témoignant de l'existence de saisons et, d'autre part, qu'il n'existe pas actuellement de végétaux, au port comparable à ceux des sigillaires (30 m de haut), se développant à une altitude supérieure à 4000 m.

3. Matériel

Il s'agit d'un céphalothorax lié à un abdomen, bien conservé, appartenant à la nouvelle espèce *Euproops mariae* n. sp., collecté par Mme Maria Ménard (Rennes). Le support argileux noir montre de nombreux fragments, permettant de préciser l'âge de l'échantillon.

Le matériel est déposé au laboratoire de paléontologie de l'université de Lille-1 (France).

4. Systématique

La terminologie utilisée est basée sur les travaux de Størmer [31], Selden et Siveter [28], et Filipiak et Krawczyński [14].

Ordre Xiphosurida Latreille, 1802

Sous-ordre Bellinurina Zittel & Eastman, 1913

Famille Euproopidae Eller, 1938

Genre *Euproops* Meek, 1867

Euproops mariae n. sp. (Figs. 2–3)

Derivatio nominis : prénom de l'inventeur, Mme Maria Ménard.

Holotype : Carapace USTL-CC026 (Figs. 2–3).

Locus typicus : déblais d'un puits situé à Graissessac, Sud du Massif central (France) ; Stéphanien B–C, Carbonifère supérieur.

Diagnose : prosome étiré (tr.) ; lobe cardiaque trapézoïdal et massif, délimité par des sillons dorsaux profonds ; lobe axial opisthosomal marqué et étroit, à cinq anneaux bombés, suivis postérieurement d'une portion terminale élargie, plus étroit entre le quatrième et le cinquième anneau ; lobes latéraux avec une légère segmentation ; limbe opisthosomal à épines marginales courtes et massives.

Description : la carapace, non ornée, étirée (tr.) et comprimée dorso-ventralement, mesure 2 cm de long et 2,5 cm de large.

Le prosome, de contour semi-circulaire, est trois fois plus large que long, convexe, et plus large que l'opisthosome. Le lobe cardiaque, trapézoïdal, est relativement long et large postérieurement. Les sillons dorsaux sont bien distincts et profonds. La région interophtalmique ne montre pas de sillons. Les crêtes ophtalmiques sont concaves vers l'avant et vers l'extérieur. Les épines ophtalmiques sont effilées. La partie antérieure des crêtes ophtalmiques semble proche du rebord antérieur. Les yeux latéraux, non distincts, sont probablement situés loin vers avant, à l'endroit où les crêtes ophtalmiques tournent vers l'intérieur. Les épines génales sont relativement longues, atteignant le quatrième anneau de l'opisthosome. L'étroite marge latérale du prosome est partiellement conservée.

L'opisthosome semi-elliptique est totalement fusionné. Il est plus large (tr.) que long (sag.). Il est pres-

que deux fois plus long que le prosome. Le lobe axial de l'opisthosome est marqué et étroit. Il comprend cinq anneaux enflés et une portion terminale élargie. Il est plus étroit entre le quatrième et le cinquième anneau. Les anneaux 2, 4 et 5 possèdent un petit tubercule médian. Les lobes latéraux montrent une légère segmentation. Le limbe opisthosomal, mal conservé, porte des épines courtes et massives. Le telson est brisé.

Remarques : jusqu'ici, seules trois espèces sont rapportées au genre *Euproops* : *E. danae* (Meek & Worthen, 1865), du Westphalien D du Pays de Galles (Angleterre) et du Mazon Creek (Illinois), du Westphalien d'Angleterre, du Nord de la France et de Belgique; *E. anthrax* Prestwich, 1840, du Westphalien A–B de Belgique; *E. rotundatus* (Prestwich, 1840) du Westphalien A du Lancashire (Angleterre), du Westphalien B de Silésie (Pologne), du Westphalien D du Pays de Galles (Angleterre), et du Westphalien du Nord de la France et de Belgique.

Euproops mariae n. sp. diffère de *Euproops danae* par un lobe cardiaque plus développé, non « étranglé » postérieurement et sans tubercule médian, par un étroit lobe axial opisthosomal « étranglé » entre le quatrième et le cinquième anneau, par une segmentation des lobes latéraux du thoracétron moins bien définie, et par un limbe opisthosomal avec des épines courtes et massives. Cette nouvelle espèce diffère de *E. rotundatus* par son lobe cardiaque mieux défini, sans ride médiane, des épines génales plus longues. À l'instar de *E. rotundatus*, *E. anthrax* possède une crête médiane sur le lobe cardiaque, qui prolonge l'axe opisthosomal.

5. Conclusions

- *Euproops mariae* n. sp. fournit un jalon supplémentaire pour l'étude de la diversité des xiphosures carbonifères.
- *E. mariae* n. sp., attribué au Stéphanien B–C est l'*Euproops* le plus récent connu.
- Dans un contexte environnemental et stratigraphique analogue, d'autres espèces ou genres de xiphosures ont été découverts en France ; les formes les plus proches de notre espèce sont connues dans le Nord de la France, en Belgique, en Angleterre, en Pologne et aux USA. Les différences entre les faunes connues ne sont pas attribuables à des problèmes de préservation : les divers taxons existent aussi bien dans des nodules que dans les argilites. Quelle

que soit la nature de la roche, les taxons peuvent être bien ou mal conservés. Les différences entre les faunes préservées localement sont sans doute artificielles, et liées à la très grande rareté des xiphosures. La probabilité de l'endémisme ne peut être évaluée.

- Très probablement, en liaison avec ce qui est actuellement connu du contexte de Graissessac, *E. mariae* n. sp. semble lié à des environnements d'eau douce.

1. Introduction

Merostomata are benthic organisms that originated in the Early Cambrian, and remained an important aquatic life form in the world until the Permian. They lived in both marine and brackish to fresh water environments. Merostomata include two quite different groups of marine organisms, the eurypterids or sea scorpions, and the xiphosurans or horseshoe crabs [30].

Xiphosurans can be found in the fossil record from Cambrian to Present, but only three genera and four species exist today. These burrowing organisms feed on small invertebrates. Xiphosurans live in shallow-water normal marine environments. Nowadays, horseshoe crabs (*Limulus polyphemus*) live in shallow marine waters, close to the western Atlantic coasts and the Gulf of Mexico [11]. Three other species (genera *Tachypleus* and *Carcinoscorpio*) are found in southern and eastern Asian waters, from Japan to Indonesia and India. Normally living at depths around 30 meters, they move into shallow water to spawn and lay eggs in beach sand [12,15].

Xiphosurans have been reported from European deposits of Late Palaeozoic age notably by Woodward [34], Oplustil [19], Pruvost [21,22], Remy and Remy [27], Vandenberghe [33], Müller [18], Simon [29], Racheboeuf [24], Malz et Poschmann [16], Poplin et Heyler [20], Anderson [1,2], Filipiak & Krawczyński [14], Anderson et al. [4] and Racheboeuf et al. [25]. In addition, publications of Dix and Pringle [8], Raymond [26], and Anderson and Selden [3] have been major contributions to our current knowledge of Carboniferous limulid xiphosurans.

Since their first appearance during the Palaeozoic, xiphosurans have undergone with few morphological changes. They always remained conservative in morphology and of low diversity. They have been cited as an example of a 'living fossil' group [15].

Nevertheless, they provide minutely detailed information about the anatomy and biology of this group of arthropods. Structural details, e.g. ridges, spines, furrows located on the carapace concealing the prosomal appendages, opisthosomal tergites fused or not, and a styliform tail spine are important for systematic discrimination of the species and for an understanding of their evolution. The evolution of the distinctive features during the Carboniferous, when the group was apparently much more diverse than it is today provides information relevant to phylogenetic relationships between the limulid xiphosurid Merostomata.

Three main trends characterize the evolution of the xiphosurans: increasing size, loss of segmentation of the opisthosoma, and restriction to marine habitats. Whereas all living xiphosurans are marine, it seems that some Late Palaeozoic and Mesozoic forms inhabited brackish or even fresh water. It is generally agreed that Merostomata were marine until the Devonian, and then became mainly freshwater during Carboniferous. In Europe, the Upper Carboniferous period is marked by a tropical climate and swampy environments.

The present paper deals with the systematic study of the Upper Carboniferous limulid Merostomata of France. The discovery of a new limulid form assigned to *Euproops mariae* n. sp., from the Stephanian in the southern part of the French Massif Central, gives us the opportunity to understand these forms better. These xiphosurids lend a particular dimension to the Merostomata fauna of the Carboniferous, since they belong to the most primitive limulids living in freshwater.

2. Geological setting

2.1. Geographical and stratigraphic location

The French Massif Central includes one of the most important exposures of the Internal Zone of the Variscan belt of Europe [17]. The Late Carboniferous/Early Permian time interval is characterized by numerous coal-bearing intramontane basins, such as the Graissessac basin, which consists of isolated troughs closely associated with fault zones [5,7,11,13]. The development of the Stephano-Permian continental sedimentary basin controlled by extensional faulting occurred during the late stages of the collapse of the Variscan Belt [11].

The Graissessac coalfield is located on the northeast of the southern edge of the Variscan Massif Central, i.e. of the Montagne Noire area (Fig. 1).

The ‘Sillon houiller’, asymmetrical in form, lies parallel to trend of major extensional structures (Fig. 1). From west to east, Stephanian conglomeratic alluvial deposits grade progressively into sandy pelitic lacustrine sediments with interbedded coal formations [11]. To the east, the Permian continental sedimentary region (Lodève Basin) lies unconformably on Stephanian deposits [11].

An Upper Stephanian age [5] is indicated by palaeofloral evidence.

2.2. Palaeontology and palaeoenvironment

2.2.1. Palaeofloral content

To the east, the area bearing coal-seams is characterized by the presence of numerous layers of coal, with white arkosic sandstones, black silts and shales that represent flood-plain facies interbedded between the coal seams. Floral remains are abundant and quite well preserved. These belong to two main groups: Pteridophytes, with the genera *Sphenophyllum*, *Annularia*, *Asterophyllites*, *Pecopteris*, *Calamites* and Prephanerogams, with *Dadoxylon* and *Araucarioxylon* [23]. The sampled flora from different areas of the basin is always less diversified, and it is probable that local areas carried separate plant communities. According to Puaud [23], however, this specific distribution might be the result of a mechanical sorting, and not of a ‘phytozoneography’.

According to Becq-Giraudon and Van den Driessche [6] and Becq-Giraudon et al. [7], the high-altitude sedimentological evidence (water-escape craters, solifluction flowage, ghosts of ice crystals), and the flora characterised by its homogeneity, low diversity, and limited geographical extension, indicate a seasonally variable climate with cold winters. This may be related to high-altitude periglacial effects. In view of the equatorial palaeogeographic position of the Hercynian belt, this type of climate could exist only at altitudes higher than 4500 m. But according to Puaud [23], wood such as that of *Dadoxylon* shows no anatomical features related to seasonally variable climate. Moreover, in the literature, there is no example of any plant such as *Sigillaria* (30 m tall), developing at altitude higher than 4000 m. The biological data do not agree with the tectono-sedimentological interpretations.

Faunal content: Very scarce and scattered; only few bivalves, insects and fishes are known [5].

Merostomata content: No xiphosuran remains were collected from the Graissessac area, but some have been found in other outcrops as the Montceau-les-Mines basin (NE Massif Central, Fig. 1). From the Stephanian Konservat-Lagerstätte of Montceau-les-Mines, numerous specimens of the genus *Alanops* were reported by Racheboeuf et al. [25].

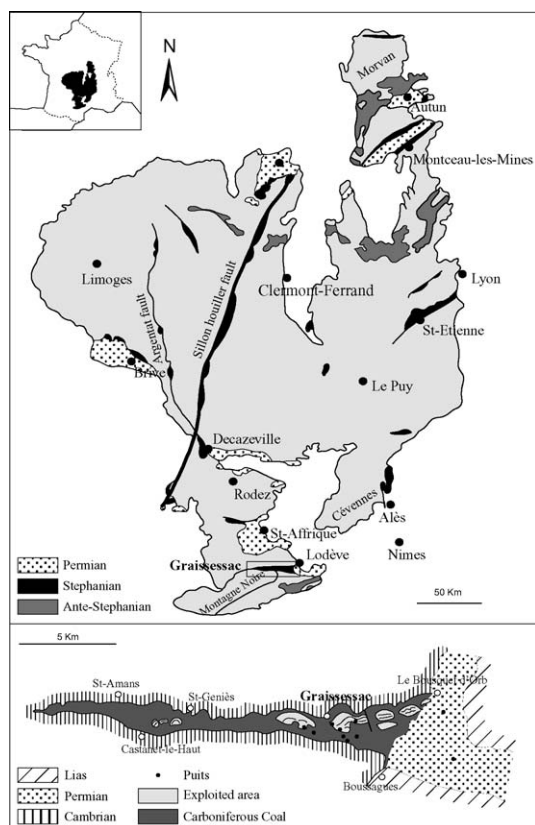


Fig. 1. Geographical location of (a) the main Stephanian/Permian basins of the Massif central (France); (b) the Graissessac Basin (northeast of the Montagne Noire, Hérault, France).

Fig. 1. Localisation géographique (a) des principaux bassins stéphanico-permiens du Massif Central (France) ; (b) du bassin de Graissessac (Nord-Est de la Montagne noire, Hérault, France).

3. Material

This consists of one well-preserved whole carapace, belonging to the species *Euproops mariae* n. sp.;

it was collected by Mrs. Maria Ménard (Rennes) at Graissessac. The black carbonaceous sample exhibits numerous fragments of plants though without well-preserved cuticle (Fig. 3). The material was collected in the rubble of a coal tip. The plant assemblage comprises notably *Sphenophyllum oblongifolium*, *Pecopteris* sp. and *Asterophyllites equisetiformis* leafy stems and *Calamites* sp. stems (determination Laveine, University of Lille-1). It is indicative of a Stephanian B–C age (or ‘Forezian’) according to the recent revision of the Saint-Étienne flora [9,10].

The material described and figured herein, is housed in the laboratoire de paléontologie de l’université de Lille-1 (France).

4. Systematics

The morphological terminology of xiphosuran Merostomata is based on the works of Størmer [31], Selden and Siveter [28], and Filipiak and Krawczyński [14].

Class Xiphosura Latreille, 1802

Order Xiphosurida Latreille, 1802

Suborder Bellinurina Zittel & Eastman, 1913

Diagnosis (emended by Anderson [2]): “Fixed lateral opisthosomal spines, lacking a free lobe and movable, opisthosomal spines; tergite 1 reduced to a microtergite and lacking lateral fields; posterior axial lobe triangular in shape; ophthalmic ridges produced posteriorly to form sharp, carinate, ophthalmic spines.”

Remarks on the systematic validity of suborder Bellinurina and the position of family Euproopidae: The current state of the suborder Bellinurina follows Anderson and Selden [3].

Traditionally, three distinct groups of Carboniferous Xiphosura are generally recognized, the superfamilies Bellinuroidea Zittel & Eastman, 1913, Euproopidea Eller, 1938, and Limuloidea Zittel, 1885. The latter two groups share the possession of a fused opisthosoma, whilst bellinuroidea have hitherto been distinguished by their free opisthosomal tergites.

After the re-examination of the type material of the Upper Carboniferous Bellinuroidea, Anderson and Selden [3] suggested that all true members of the Bellinuroidea exhibit full fusion of the opisthosoma into a thoracetrone. Consequently, they gave a revised classification in which Bellinuridae Packard, 1885 are grouped with Euproopidae Eller, 1938 [2,3].

Family Euproopidae Eller, 1938

Diagnosis (emended by Anderson [2], from Raymond [26]): “Bases of the opisthosomal lateral spines fused distally to form a lateral flange; path of the ophthalmic eyes concave in outline posterior to the lateral compound eyes.”

Genera: *Euproops* Meek, 1867; *Liomesaspis* Raymond, 1944; *Alanops* Racheboeuf *et al.*, 2002; *?Prolimulus* Frič, 1899.

Remarks: Genera previously included in Family Euproopiidae are *Euproops*, *Pringlia*, *Anacontium*, *Prolimulus*, *Palatinaspis*, and more recently *Alanops*. According to Anderson [2], *Pringlia*, *Anacontium* and *Palatinaspis* are junior synonyms of *Liomesaspis*. The genus *Prestwichianella* was synonymised with *Euproops* by Stubblefield [32] and the genus *Prestwichia* was renamed *Prestwichianella* [1].

Genus *Euproops* Meek, 1867

1867a – *Euproops* Meek; Meek, p. 394; 1867b – *Euproops* Meek; Meek, p. 320; 1867 – *Prestwichia* Meek; Meek, p. 257; 1868 – *Euproops* Meek; Woodward, p. 2; 1868 – *Euproops* Meek; Meek & Worthen, p. 547; 1880 – *Anthracopeltis* Boulay; Boulay, p. 277; 1884 – *Euproops* Meek; White, p. 170; 1885 – *Euproops* Meek; Packard, p. 292; 1886 – *Prestwichia* Meek; Packard, p. 146, 148, 150; 1889 – *Euproops* Meek; Ebert, p. 218; 1893 – *Prestwichia* Meek; Bergeron, p. 342; 1895 – *Prestwichia* Meek; Bergeron, p. 480; 1907 – *Prestwichia* Meek; Zalesky, p. 423; 1911 – *Euproops* Meek; Baldwin, p. 75; 1911 – *Prestwichia* Meek; Pruvost, p. 295–296; 1915 – *Prestwichia* Meek; Bolton; 1918 – *Euproops* Meek; Woodward, p. 465; 1918 – *Prestwichianella* Woodward; Woodward, p. 469; 1919 – *Prestwichia* Meek; Pruvost, p. 333; 1927 – *Prestwichianella* Woodward; Tchernechev, p. 648., 653; 1928 – *Prestwichia* Meek; Tchernechev, p. 526; 1929 – *Euproops* Meek; Dix & Pringle, p. 103; 1929 – *Prestwichianella* Woodward; Dix & Pringle, p. 92, 101; 1930 – *Euproops* Meek; Pruvost, p. 201; 1930 – *Prestwichianella* Woodward; Pruvost, p. 200; 1933 – *Euproops* Meek; Kobayashi, p. 178; 1935 – *Euproops* Meek; Willard & Jones, p. 127; 1938 – *Euproops* Meek; Eller, p. 152; 1938 – *Prestwichia* Meek; Renier *et al.*, p. 204; 1944 – *Euproops* Meek; Raymond, p. 484; 1944 – *Prestwichianella* Woodward; Raymond, p. 482–483; 1972 – *Euproops* Meek; Ambrose & Romano. 1994 – *Euproops* Meek; Anderson, p. 270; 1996 – *Euproops* Meek; Filipiak & Krawczyński, p. 270.

Type species: Euproops danae (Meek & Worthen, 1865), Upper Carboniferous of Mazon Creek, Illinois, USA.

Species: Euproops danae (Meek & Worthen, 1865); *Euproops anthrax* (Prestwich, 1840); *Euproops rotundatus* (Prestwich, 1840).

Diagnosis (emended by Anderson [1]): “Opisthosomal axis comprised of nine segments, of which the first segment is reduced to a microtergite, lacking adjacent pleural fields; second and fourth segments possess a spine-bearing tubercle; terminal fused segments 7–9 give rise to a single, large tubercle from which a sharp, posteriorly-directed spine projects.”

Occurrence: Euproops originated in the Lower Carboniferous (Visean) where this genus is common and persisted into the Upper Carboniferous (basal Stephanian).

Euproops mariae n. sp. (Figs. 2,3).

Derivation of name: the name refers to M^{rs} Maria Ménard, discoverer of the specimen.

Holotype: Carapace USTL-CC026 (Figs. 2,3).

Type locality: in the rubble of a coal tip at Graissesac locality, southern Massif Central (France); Stephanian B–C, Upper Carboniferous.

Diagnosis: species of *Euproops* with the following characteristics: Elongated (tr.) prosoma; massive, trapezoidal cardiac lobe, delimited by deep dorsal furrows;

narrow and well-defined opisthosomal axis, with five inflated lobes posteriorly followed by a terminal enlarged portion, and narrowest at the level of the fourth and fifth lobes; lateral lobes with faint traces of segmentation; opisthosomal rim with short and massive marginal spines.

Description: the smooth carapace is horseshoe-shaped, elongated (tr.) and dorsoventrally compressed, reaching 2 cm in length and 2,5 cm in width. As it is moderately compressed, its dorsal features are distinct.

The prosoma, semicircular in outline, is three times wider (tr.) than long (sag.), evenly convex, and larger than opisthosoma. The well-defined massive cardiac lobe, trapezoidal in shape, globose, is relatively long (sag.) and wide (tr.). The dorsal or cardiac furrows are deep. The interopthalmic areas do not show any furrows. The paired ophthalmic ridges extend forward and outward (concave inwards) from the posterior margin. The ophthalmic spines at the posterior ends of the ridges are narrow. The anterior section of the paired ophthalmic ridges appears to lie very close to the anterior margin of the carapace. The lateral eyes are not distinct. The eyes may be far forward, where the ophthalmic ridges turn inward. The relatively long, inward facing and narrow genal spines (reaching the fourth node), are prolongations of the lateral margin of the prosoma.

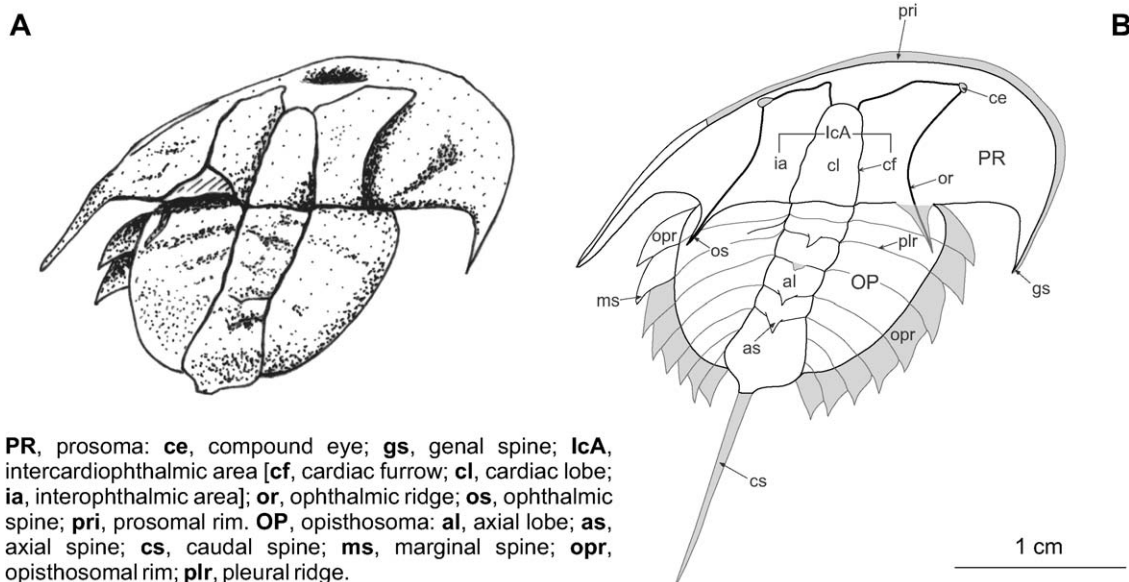


Fig. 2. Scheme of the carapace of *Euproops mariae* n. sp. (A) and interpretation (B). Reconstructed elements appear in grey.
Fig. 2. Schéma de la carapace de *Euproops mariae* n. sp. (A) et interprétation (B). Les régions reconstituées sont grisées.

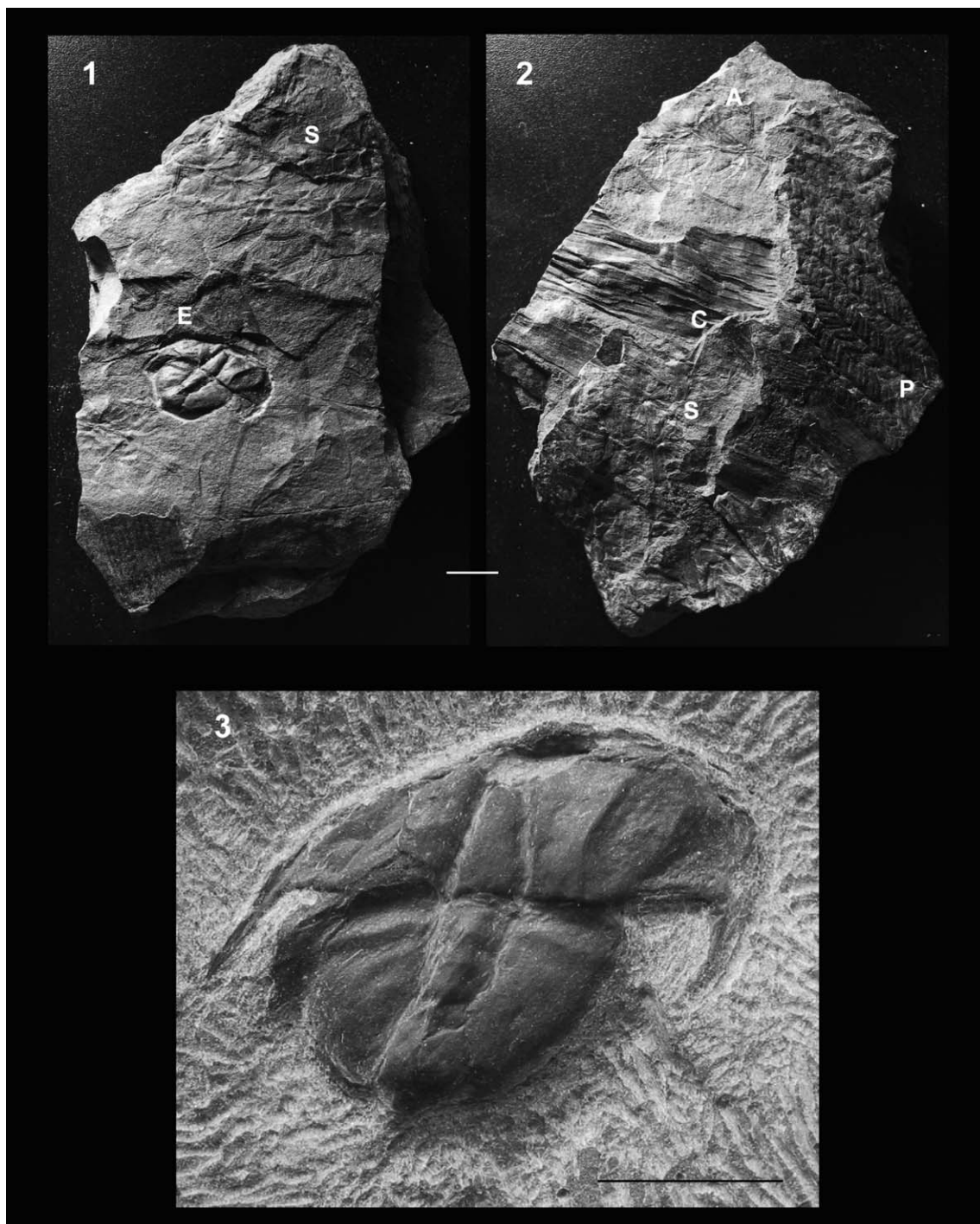


Fig. 3. Details of sample USTL-CC026. **1**, *Euproops mariae* n. sp. (dorsal view), and associated macroflora (S: *Sphenophyllum oblongifolium*); **2**, Macroflora from the reverse side of the block (A: *Asterophyllites equisetiformis*; C: *Calamites* sp.; P: *Pecopteris* sp.; S: *Sphenophyllum oblongifolium*); **3**, *Euproops mariae* n. sp., detail of the dorsal view of the carapace. Scale : 10 mm.

The sub-elliptic opisthosoma is fully fused to form a thoracetrone. It is broader (tr.) than it is axially long (sag.). It is nearly twice as long (sag.) as the prosoma. The axial lobe of the opisthosoma is clearly defined and narrow. It is composed of five axial nodes, ending posteriorly in a terminal enlarged boss. It is narrowest at the level of the fourth and fifth lobes. Lateral lobes show faint traces of segmentation. On the left side, the carapace shows a partial opisthosomal flange, with massive lateral fixed opisthosomal spines. The tail spine appears to be broken.

Remarks on systematics: *Euproops* is an extremely conservative and constant genus in terms of its shape, throughout its range. Euproopid species are characterized by long, narrow and slightly incurved genal spines; the first opisthosomal segment reduced to a microtergite, lacking adjacent lateral tergal (pleural) fields; the fusion of the bases of the fixed lateral spines, which form an opisthosomal flange; the presence of the lateral fixed opisthosomal spines and the absence of movable opisthosomal spines; the concave course of ophthalmic ridges to the cardiac lobe; a posterior triangular axial lobe which tapers posteriorly [3].

Other typical characters are: the carinate ophthalmic spines, the lateral opisthosomal flange, and the slight lateral prosomal flange. The latter characters are not always obviously visible on all species.

The related genus *Liomesaspis* Raymond, 1944, is characterized by the same ophthalmic ridge-configuration as *Euproops*; it differs in having minute and slightly incurved genal spines, highly inflated ophthalmic spines, and in secondarily losing the fixed lateral opisthosomal spines [3].

The related genus *Alanops* Racheboeuf et al., 2002, is characterized by the absence of ophthalmic ridges, ophthalmic spines and genal spines in adult specimens [25].

All the main features of the genus *Euproops* are found in the specimen we have examined, except for the number of opisthosomal lobes. Indeed, the recognition of nine segments on the opisthosomal axis is difficult in our species: (1) the microtergite is generally obscured by the posterior margin of the prosoma, as in all specimens which are not in an enrolled posture; (2)

the opisthosomal rim, partially preserved, does not permit the number of terminal fused segments to be precisely determined.

Only three species have been previously recorded from the Late Carboniferous/Early Permian, and ascribed to this genus. Hitherto most euproopids have been described from North America, Great Britain, Poland and Czech Republic; a few are known from France and Belgium : *Euproops danae* (Meek and Worthen, 1865), from the Westphalian D of the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek (Illinois), and from the Westphalian of England, the northern France and Belgium; *E. anthrax* Prestwich, 1840, from the Westphalian A–B of Belgium; *E. rotundatus* (Prestwich, 1840) from the Westphalian A of the West Lancashire Coalfield (England), from the Westphalian B of the Upper Silesia Coal Basin of Sosnowiec (Poland), from the Westphalian D of the South Wales Coalfield, and from the Westphalian of the northern France and adjacent portions of Belgium. After revision by Anderson [1], 13 previously recorded species (from the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek; Illinois) were grouped in *Euproops danae*. Consequently, and in contrast with to previous reports [15], the diversity within the Carboniferous euproopids is apparently low.

Euproops mariae n. sp. differs from *E. danae* in having a more pronounced cardiac lobe, not constricted posteriorly and without a median tubercle, deep axial furrows, a broad opisthosomal rim with short and massive marginal spines, and a lateral lobed thoracetrone with ill-defined traces of interpleural ribs. *E. danae* has a narrow opisthosomal rim formed by the widened bases of relatively long marginal spines [1].

The new species differs from *E. rotundatus*, by its better-defined cardiac lobe, without any narrow raised median ridge, its longer genal spines and its lateral lobed thoracetrone with traces of interpleural ribs. As in *E. rotundatus*, *E. anthrax* possesses a median ridge on the cardiac lobe too, prolonged into an opisthosomal axis that tapers posteriorly; it differs from *E. mariae* n. sp. by its relatively long marginal spines.

In Anderson's view [1], a poorly defined segmentation, a smooth lateral lobed thoracetrone with only faint

Fig. 3. Détails de l'échantillon USTL-CC026. 1, *Euproops mariae* n. sp. (vue dorsale) et macroflore associée (S: *Sphenophyllum oblongifolium*) ; 2, Macroflore visible de l'autre côté (A: *Asterophyllites equisetiformis* ; C: *Calamites* sp. ; P: *Pecopteris* sp. ; S: *Sphenophyllum oblongifolium*) ; 3, *Euproops mariae* n. sp., détail de la carapace en vue dorsale. Échelle : 10 mm.

traces of interpleural ribs, or ill-developed nodes on the axial rings, are not considered to be valid specific features. According to Anderson [1], specimens preserved in the roof shale of a coal are likely to be distorted by compression, e.g. showing an exaggerated width of the prosoma and a tectonic anterior–posterior shortening. Surface details as tuberculation may be poorly preserved or lost during fossilization. In addition, a flattening of the anterior prosomal arch would produce a relatively narrow and straight anterior border. These are considered to be taphonomically induced features. In sideritic nodular preservation, carapaces would not have been shielded from the worst effects of tectonic deformation.

According to the observable features on our carapace, the deformation may only be related to sediment compaction, and likewise the surface-preservation seems good enough for precise observations. Thus, Anderson's remarks are not confirmed by the material preserved in sideritic-nodules from Poland [14], in which fine details can be observed on a fragmentary specimen, though they are not on whole but deformed ones.

5. Conclusions

According to the new data from Graissessac, we draw the following conclusions:

- *Euproops mariae* n. sp. gives an additional dimension to the study of Carboniferous diversity amongst Xiphosura.
- *E. mariae* n. sp., is Stephanian B–C in age according to the floral data; it is the most recent *Euproops* so far known.
- The newly described euproopid has not been encountered at other localities or stratigraphic levels. Closely allied species have been collected from northern France, Belgium, England, Poland, Czech Republic, and USA. Such faunal differences cannot depend on taphonomic/preservation artefacts, as explained by Anderson [1]: all taxa occur in nodules as well as in argillites, in which they can be either badly or perfectly preserved. Thus, it cannot be proved that some of the observed differences in diversity are anything but an artefact, due to the scarcity of the fossil Xiphosura.
- As far as the general Carboniferous environmental context is known at Graissessac, *Euproops mariae*

n. sp. inhabited a freshwater environment; it has been collected in association with continental plant remains, and was fossilized in a flood plain facies.

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