

NEW PTERASPIDIFORM HETEROSTRACANS (VERTEBRATA) FROM THE LOWER DEVONIAN OF LA GILEPPE AND NONCEVEUX, BELGIUM

François THIRION & Alain BLIECK*

(7 figures and 2 plates)

Université de Lille 1, Sciences de la Terre, UMR 8157 du CNRS "Géosystèmes", Equipe de Paléontologie et Paléogéographie du Paléozoïque, F-59655 Villeneuve d'Ascq cedex (France). E-mail: francois.thirion@live.fr, Alain.Blieck@univ-lille1.fr
* corresponding author

ABSTRACT. Original material of vertebrates from two Lower Devonian localities of the Belgian Ardenne Massif is described. The material from La Gileppe includes *Rhinopteraspis crouchi* (Vertebrata, Heterostraci, Pteraspidiformes) and is the first confirmation of vertebrate for this late Lochkovian locality belonging to the Z Spore Zone, and correlated to the lower part of the *Althaspis leachi* Fish Zone. This confirms the overlapping range of *R. crouchi* and *A. leachi* in the siliciclastic Lower Devonian of Western Europe. An orbital plate and two other elements of an undetermined pteraspidiform from Nonceveux are added to the material already known from this locality. The Nonceveux locality is late Lochkovian in age and belongs to the G Spore Zone, which is correlated to the base of the *A. leachi* Fish Zone. The La Gileppe material is composed of small specimens which are interpreted as either of juvenile individuals or of small adults. It is consistent with previous results on French-Belgian localities among the Early Devonian siliciclastic deposits of Western Europe (Old Red Sandstones and allied facies) which have been interpreted as confined, restricted marine environments.

KEYWORDS: *Rhinopteraspis crouchi*, post-oral cover, juvenile specimens, Spore Zones G and Z, *Althaspis leachi* Zone, upper Lochkovian.

RESUME. De nouveaux Hétérostracés Ptéraspidiformes (Vertebrata) du Dévonien inférieur de La Gileppe et de Nonceveux, en Belgique. Du matériel inédit de Vertébrés provenant de deux localités du Dévonien inférieur du massif ardennais belge est décrit. Le matériel de La Gileppe révèle la présence de *Rhinopteraspis crouchi* (Vertebrata, Heterostraci, Pteraspidiformes) et constitue la première confirmation de Vertébrés pour cette localité qui est datée de la palynozone Z, corrélée à la partie inférieure de l'ichthyozone à *Althaspis leachi* (Lochkovien supérieur). Ceci confirme le recouvrement des extensions stratigraphiques de *R. crouchi* et *A. leachi* dans le Dévonien inférieur siliciclastique d'Europe occidentale. Une plaque orbitaire et deux autres éléments osseux d'un Ptéraspidiforme indéterminé de Nonceveux sont ajoutés au matériel déjà connu pour ce site qui est daté de la palynozone G, corrélée à la base de l'ichthyozone à *A. leachi* (Lochkovien supérieur). Le matériel de La Gileppe se compose de spécimens de petite taille qui peuvent être interprétés soit comme des individus juvéniles soit comme des adultes de petite taille. Ceci est en accord avec les résultats précédemment obtenus sur les localités de France-Belgique au sein des dépôts siliciclastiques éodévoniens d'Europe occidentale (Vieux Grès Rouges et faciès associés) ; les localités franco-belges ont été interprétées comme des environnements confinés en milieu marin restreint.

MOTS-CLES : *Rhinopteraspis crouchi*, couvercle post-oral, spécimens juvéniles, palynozones G et Z, Zone à *Althaspis leachi*, Lochkovien supérieur.

1. Introduction

The inventory of the Lower Devonian heterostracan-bearing localities in the Artois-Ardenne region was drawn up by Blieck (1982). Of the 35 localities listed at that time, 14 yielded identifiable remains of heterostracans, that enabled the biostratigraphic scale already suggested by White (1956) to be completed. The revision of the biozonation of the standard scale of the Old Red Sandstone series of England and its correlation with the scale from Artois and the Ardenne (Blieck & Janvier, 1989), the discovery of new localities in Belgium and in the Grand Duchy of Luxemburg (Blieck *et al.*, 1996a-b, 1998;

Delsate *et al.*, 2003, 2004), as well as restudy of localities already present in the inventory (Blieck & Goujet, 1991; Blieck *et al.*, 1995; Pille, 2004) have completed and expanded geographically the data on the Lower Devonian of the region.

The two localities studied in this work belong to the Lower Devonian of the Belgian Ardenne Massif (Fig. 1). For both localities, the vertebrate material is composed of pteraspidiform remains. Nonceveux has already yielded heterostracan material (Raynaud, 1942; Asselbergs, 1946; Blieck, 1982: loc. n° 19; Blieck & Goujet, 1991). Here, new specimens are described from this locality. The



Figure 1: Location of the La Gileppe (1) and Nonceveux (2) fossiliferous sites (modified after Pille, 2004).

Figure 1: Localisation des sites fossilifères de La Gileppe (1) et Nonceveux (2) (modifié d'après Pille, 2004).

material of La Gileppe includes pteraspidiiform specimens that are described for the first time for this locality. The material has been collected in the field in the late 1990s and early 2000s by P. Steemans, E. Poty and students of the University of Liège, and recently by E. Goemaere of the Belgian Geological Survey. It is housed in the collections of Palaeontology of the University of Liège, designated under the reference ULg-P followed by the number of each specimen; and in the collections of the Royal Institute of Natural Sciences of Belgium, in Brussels, designated under the reference IRSNB followed by the number of each specimen. It has been prepared mechanically from its siliciclastic, non calcareous matrix.

2. Geographical and stratigraphical setting

The two localities are in the Lower Devonian of the NE part of the Ardenne Massif (Fig. 1), and belong to the Bois d'Ausse Formation. They are situated in the Province of Liège (Belgium).

2.1. La Gileppe (Map I.G.N.: 1/10000 n°43/5; Lambert coordinates: 143.340 N, 263.900 E)

The locality is along a gravel road suitable for motored vehicles which pass alongside the north-western bank of the La Gileppe dam lake, Province of Liège, Belgium (Fig. 2). The fossiliferous layers of the outcrop are constituted of alternating blue shales, sandstones and quartzites with nodules. The vertebrate remains were collected during different field sessions from 1999 to 2004 by P. Steemans and his students, and comes from a bed of a grey to bluish, partly micaceous, dark siltstone, where the palynological sample n° 10 of the section B of La Gileppe (Steemans & Gerrienne, 1984, fig. 2) come from (Fig. 3). It is "Gedinnian" (late Lochkovian) in age, and located in the lower Bois d'Ausse Formation (*sensu* Steemans & Gerrienne, 1984; Godefroid *et al.*, 1994). This outcrop belongs to the southern border of the Vesdre Synclinorium.

Asselberghs (1920 ; cited by Leriche, 1924 and Asselberghs, 1946) has mentioned « des restes de poissons Ostracodermes [...] dans le vallon de la Borchêne, affluent de la Gileppe ». Nevertheless, no discovery of additional vertebrate material has come to confirm this mention. Steemans & Gerrienne (1984) proceeded with a palynological study of the outcrop, which allowed to assign the upper part of the section to the Bois d'Ausse Formation (formerly "Grès du Bois d'Ausse"), which is now dated here as "Gedinnian" (late Lochkovian to earliest Pragian), and not as "Siegenian" as Asselberghs (1946) suggested. The pteraspid material, which comes from the bed of sample n° 10 of Steemans & Gerrienne (1984) (Fig. 3) is thus dated of the Spore Zone Z (*Emphanisporites zavallatus* var. *zavallatus* interval biozone), late Lochkovian in age (Streel *et al.*, 1987; Steemans, 1989). This material is attributed to *Rhinopteraspis crouchi*.

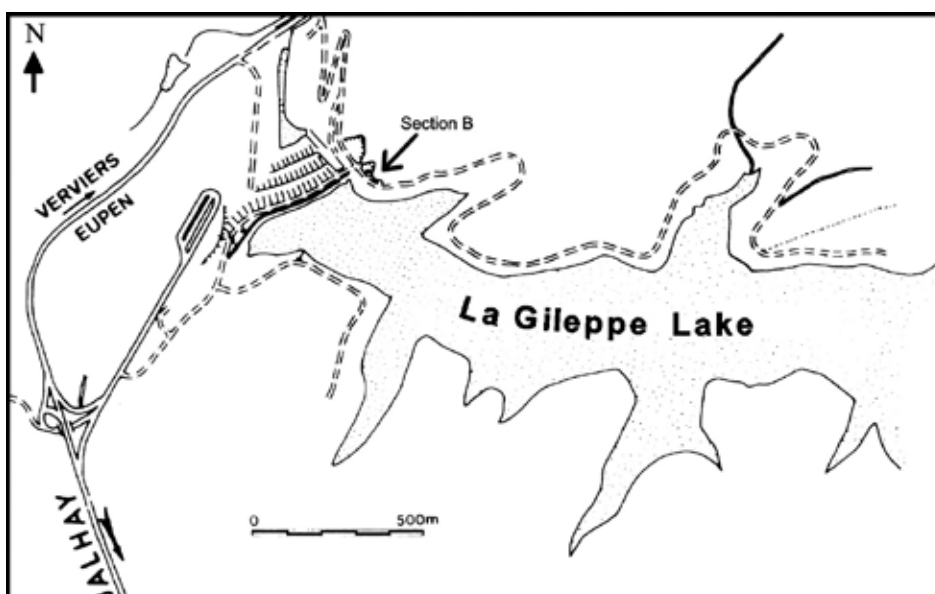


Figure 2: Location of section B on the north-western bank of the dam lake of La Gileppe (modified after Steemans & Gerrienne, 1984).

Figure 2: Emplacement de la coupe B à l'extrémité nord-ouest du lac de barrage de La Gileppe (modifié d'après Steemans & Gerrienne, 1984).

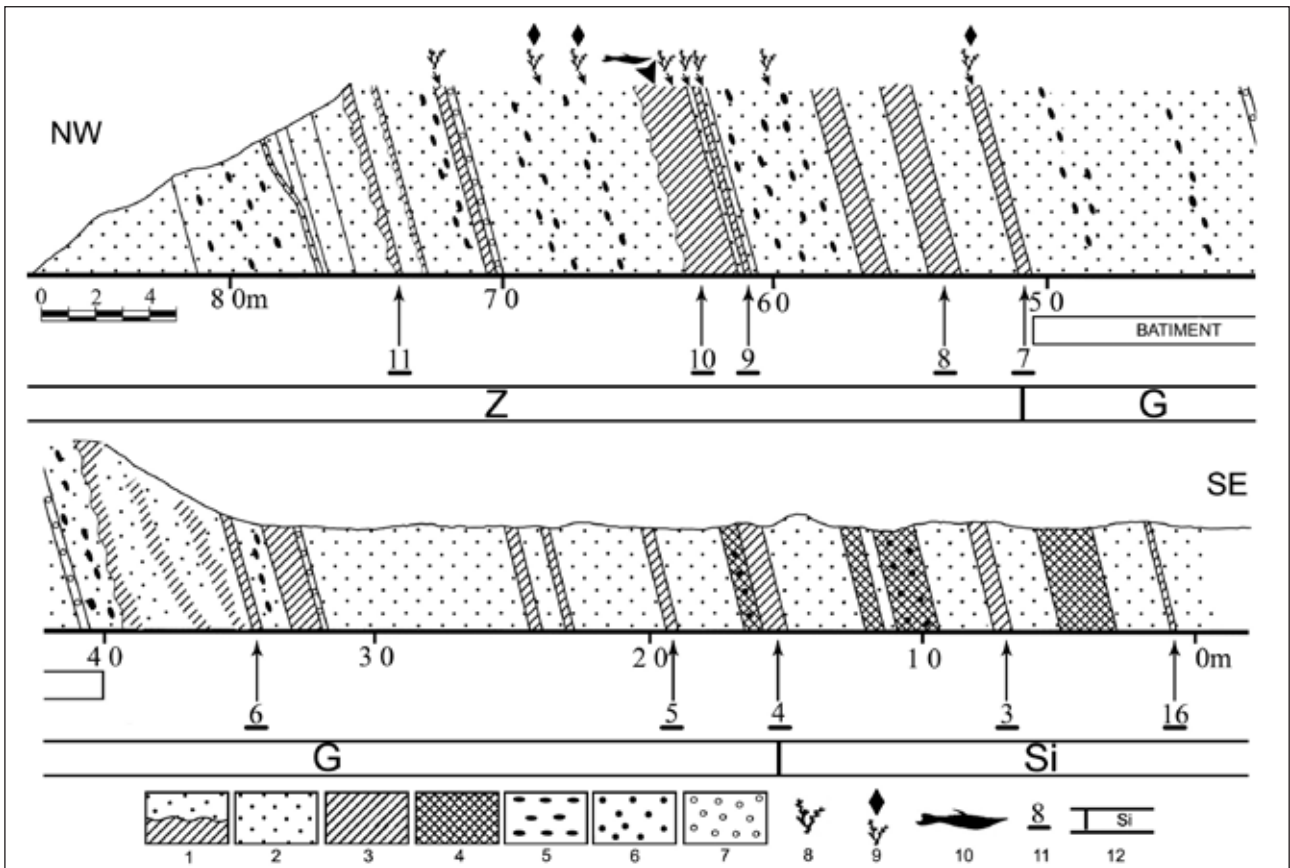


Figure 3: Stratigraphical section B of La Gileppe (after Steemans & Gerrienne, 1984), with indication of the *R. crouchi* horizon, the range of spore zones Z, G and Si (after Steemans in Steemans & Gerrienne, 1984), and the macroflora horizons studied by Gerrienne (in Steemans & Gerrienne, 1984). Captions: 1- eroding surface; 2- sandstones and quartzites; 3- blue shales; 4- red and variegated shales; 5- shaly nodules; 6- calcareous nodules; 7- conglomeratic layers; 8- macroflora; 9- macroflora assemblages studied by P. Gerrienne; 10- *R. crouchi* horizon; 11- palynological samples of P. Steemans; 12- range of spore zones.

Figure 3: Coupe stratigraphique B de La Gileppe (d'après Steemans & Gerrienne, 1984), avec indication du niveau à *R. crouchi*, extension des palynozones Z, G et Si (d'après Steemans in Steemans & Gerrienne, 1984), et niveaux à macroflore étudiés par Gerrienne (in Steemans & Gerrienne, 1984). Légendes: 1- contact ravinant, 2- grès et quartzites, 3- schistes bleus, 4- schistes rouges et bigarrés, 5- nodules schisteux, 6- nodules carbonatés, 7- roches poudinguiiformes, 8- macroflore, 9- assemblages de plantes étudiés par P. Gerrienne; 10- niveau à *R. crouchi*; 11- échantillons palynologiques de P. Steemans; 12- extension des palynozones.

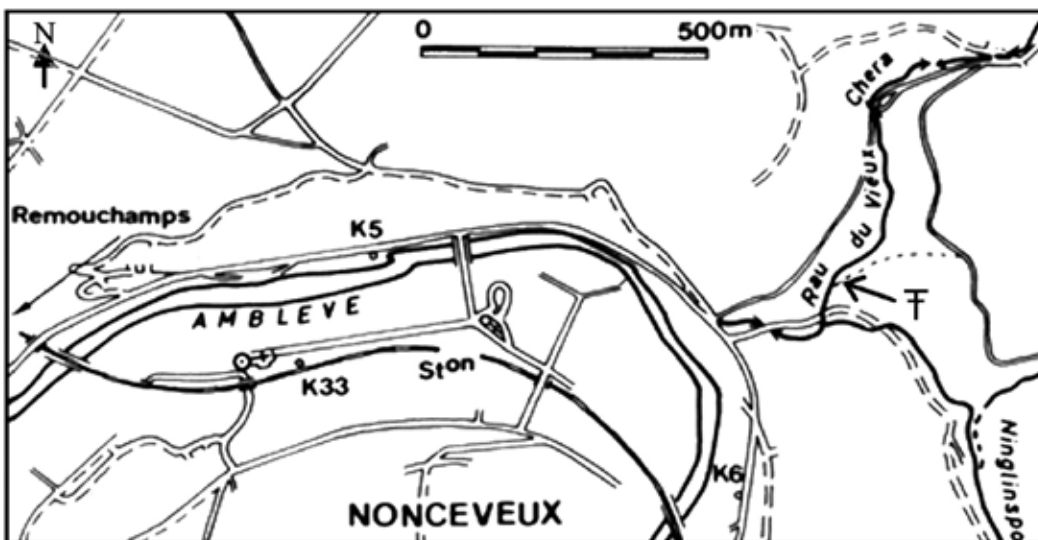


Figure 4: Location of the Nonceveux fossiliferous site, indicated by "F" (modified after Gerrienne, 1991).

Figure 4: Emplacement du site fossilifère de Nonceveux, indiqué par le signe "F" (modifié d'après Gerrienne, 1991).

2.2. Nonceveux (Map I.G.N.: 1/10000 n°49/3; Lambert coordinates: 129.610 N, 247.780 E)

The Nonceveux locality is situated along a footpath which runs upward the valley of the “Vieux Chéra” (aka. “Vieille Chéra”) brook, near to the confluence with the Ninglinspo brook, a tributary of the Amblève river, NE of Nonceveux, Province of Liège (Fig. 4). It corresponds to the locality of Raynaud (1942, p. 85) which has been redescribed and studied by Steemans (1981, fig. 2; 1989, p. 54 and fig. 12: sample Zo), Gerrienne (1991, fig. 1, loc. A) and Blicck & Goujet (1991). It consists of a series of quartzites, coarse sandstones and blue shales from the base of the Bois d’Ausse Formation (*sensu* Godefroid *et al.*, 1994; also Hance *et al.*, 1992; not Fooz Formation as erroneously written in Blicck, 1982). It belongs to the south-eastern border of the Dinant Synclinorium.

Raynaud (1942, p. 85) mentioned remains of *Pteraspis dunensis* Roemer and *Pteraspis rotunda* Gross, but for White (1956, p. 4) “all the specimens that [he has] seen belong to either *R. leachi* or to *Protaspis* sp.” However, the only registered specimens from Nonceveux which are housed in the collections of Palaeontology of the University of Liège were attributed to *Belgicaspis crouchi* by Blicck & Jahnke (1980, p. 374; also Steemans, 1981), then re-determined as *Rhinopteraspis crouchi* by Blicck (1982), and finally as *R. crouchi?* by Blicck & Goujet (1991, fig. 3).

The Nonceveux locality had first been dated as “lower Siegenian” (Asselberghs, 1946; also Goujet & Blicck, 1979; Blicck, 1980); however, *R. crouchi* is the index species of the *R. crouchi* Zone which is correlated to the middle-late Lochkovian and the “Dittonian” (see refs. in Blicck & Janvier, 1989). So, the occurrence of *R. crouchi?* in Nonceveux would suggest that this species persisted into the Pragian (“Siegenian”) (Goujet & Blicck, 1979; Blicck, 1984). However, the palynological study of Steemans (1981, 1989) attributes the fossiliferous site (sample Zo of Steemans, 1989, fig. 91) to the Spore Zone G (*Emphanisporites zavallatus* var. *gedinniensis* interval biozone), which is dated as late Lochkovian (“late Gedinnian”) (Streel *et al.*, 1987). This datation had already been suggested by S. Leclercq (in Gerrienne, 1991).

Here we report the discovery of a fragmentary orbital plate by P. Steemans in 1996, and of two additional fragmentary specimens by E. Goemaere this year. They are included in a dark shaly siltstone. No orbital plate has been described by Blicck & Goujet (1991, fig. 3) who attributed the material known at that time (two dorsal discs, one ventral disc, and a rostral plate) to *Rhinopteraspis crouchi?*. The new material adds to the knowledge of the pteraspid material of Nonceveux, but its lack of diagnostic features does not allow to attribute it to *R. crouchi?*. It is attributed to an undetermined pteraspidiform, even if we hypothesize that it belongs to the same taxon as that described by Blicck & Goujet (1991).

3. Systematic palaeontology

Phylum Craniata Linnaeus 1758
 Sub-phylum Vertebrata Linnaeus 1758
 Class Pteraspodomorphi Goodrich 1909
 Subclass Heterostraci Lankester 1868
 Order Pteraspidoformes Berg 1940
 Sub-order Pteraspidoidei *sensu* Pteraspidina
 in Janvier 1996
 Family Pteraspidae Claypole 1885
 Genus *Rhinopteraspis* Jaekel 1919
Rhinopteraspis crouchi (Lankester 1868)

Diagnosis (translated from Blicck, 1980): Species of medium size. Rostral plate longer than larger ($laR/LoR = 0,22-0,75$), with a posterior suture which is convex backward. The anterior extremity of the rostrum is often rolled up. About 6 dentine ridges per mm on the plates and the scales. The preoral plate is well individualized, it is triangular in shape and has a ventral preoral field ornamented with small, transversally aligned tubercles.

Locality and horizon: North-western bank of the La Gileppe lake, Province of Liège, Belgium; bed of palynological sample n° 10 of the section B of Steemans & Gerrienne (1984, fig. 2); lower Bois d’Ausse Formation; upper Lochkovian (“Gedinnian”); Spore Zone Z (*Emphanisporites zavallatus* var. *zavallatus* interval biozone) [see section 2.1].

Material: Among the plates of the cephalic carapace of *R. crouchi*, only the oral plates, the cornual plates and the dorsal spine are missing in the material of La Gileppe. However, it is noteworthy that a post-oral cover has been discovered. The material which has been mechanically prepared is composed of the following specimens: ULg-P n° 2008.02.17.2 a-b (part and counterpart), disarticulated dorsal shield; 2008.02.17.3, a 3D preserved, but tectonically flattened cephalic carapace; 2008.02.17.4 a-b, rostral plate and dorsal disc; 2008.02.17.5, ventral disc; 2008.02.17.6, ventral disc; 2008.02.17.7 a-b, dorsal and ventral discs; plus a series of fragmentary bony elements.

Description

Dorsal disc

Most of the preserved specimens are distorted and partly crushed (Pl. I: B, F; Pl. II: C). The best preserved one is the specimen ULg-P n° 2008.02.17.7 which is a small disc, ca. 34-35 mm long and 24 mm wide. The dorsal disc is longer than larger and has an ovoid form. The dentine ridges are concentric on the disc and ca. 7 per mm. The anterior edge is convex on both sides of a median line which corresponds to the suture of the pineal plate. The lateral sides are convex to the outside and are slightly converging to the back side, so that the disc is wider in its anterior part. The posterior side bears a several mm deep notch that corresponds to the emplacement of the dorsal spine, homologous to a first dorsal ridge scale.

Pineal plate

This plate is only present on the specimen ULg-P n° 2008.02.17.3 (Pl. I: B, D). It is wider than longer. Its posterior side is convex rearward, its anterior side is concave forward, so that this plate has a V-shape, very open forward. Its lateral sides are short and in contact with the orbital plates, so that the orbito-pineal belt is continuous (*sensu* Blicek, 1984). The ornamentation is composed of concentric dentine ridges that are 6-7 per mm.

Orbital plate

Preserved on the specimens ULg-P n° 2008.02.17.3 (Pl. I: A, B) and 2008.02.17.2 (Pl. II: C), the orbital plates are lozenge-shaped and arched. Their anterior process is short, their posterior process is long and pointed, and their median process is short. The orbit is near to the outer side

at the widest part of the plate, and is orientated forward. The dentine ridges are centred around the orbit. On specimen 2008.02.17.3, the median process is in contact with the pineal plate, making a continuous orbito-pineal belt (Pl. I: D).

Rostral plate

Three rostral plates have been prepared (Pl. I: E; Pl. II: B, C; Fig. 5 d-e). They are small and longer than wider (27 x 9 mm for the specimen ULg-P n° 2008.02.17.4; Fig. 5e and Pl. II: B). The anterior side is sharp because the lateral sides are converging to the front side. The posterior edge is convex rearward. On its ventral face, the rostral plate shows an ornamentation of dentine ridges that are V-shaped to the front and 6-7 per mm. On its dorsal face, the V-shaped ridges are directed to the rear (Fig. 5 d-e).

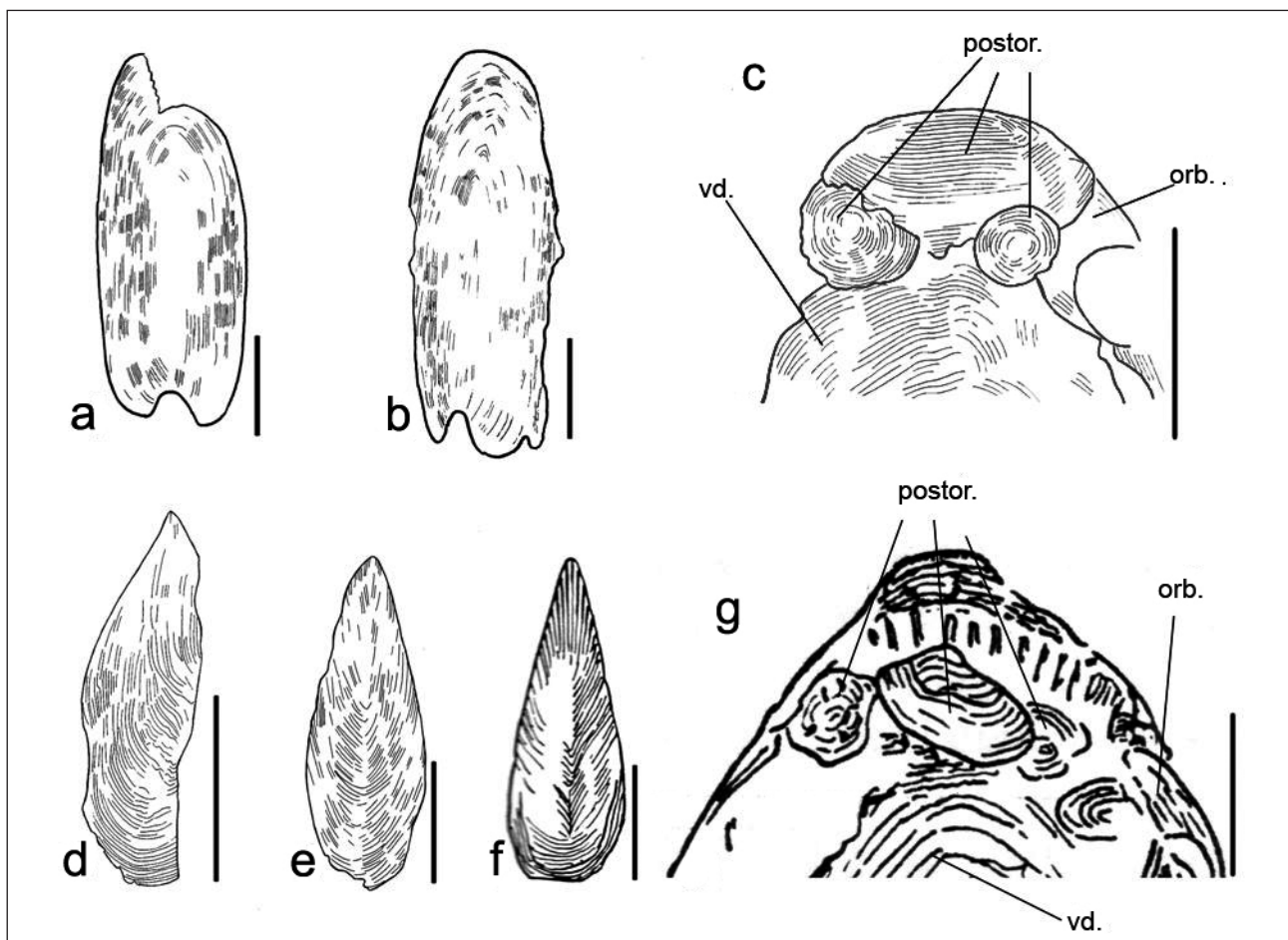


Figure 5: Camera lucida drawings of dermal plates of *R. crouchi* from La Gileppe and comparison with specimens of *R. crouchi* figured by White (1973). **a-** ventral disc, specimen ULg-P n° 2008.02.17. 5 ; **b-** ventral disc, specimen 2008.02.17.6, same as Pl. II: D; **c-** post-oral cover, specimen 2008.02.17.3, same as Pl. I: A, C; **d-** natural external mould of the dorsal face of a rostral plate, specimen 2008.02.17.3, same as Pl. I: E; **e-** rostral plate in dorsal view, specimen 2008.02.17.4, same as Pl. II: B; **f-** juvenile rostral plate in dorsal view, specimen BMNH-P25167 (White, 1973, text-fig. 27); **g-** post-oral cover of a half-grown individual, specimen BMNH-P25176 (White, 1973, text-fig. 15). Abbreviations: postor.- postoral plates; orb.- orbital plate; vd.- ventral disc. Scale bars : 1cm.

Figure 5: Dessins à la chambre claire de plaques dermiques de *R. crouchi* de La Gileppe et comparaison à des spécimens de *R. crouchi* figurés par White (1973). **a-** disque ventral, spécimen ULg-P n° 2008.02.17. 5 ; **b-** disque ventral, spécimen 2008.02.17.6, le même que Pl. II: D; **c-** couvercle post-oral, spécimen 2008.02.17.3, le même que Pl. I: A, C; **d-** empreinte naturelle externe de la face dorsale d'un rostre, spécimen 2008.02.17.3, le même que Pl. I: E; **e-** plaque rostrale en vue dorsale, spécimen 2008.02.17.4, le même que Pl. II: B; **f-** plaque rostrale juvénile en vue dorsale, spécimen BMNH-P25167 (White, 1973, text-fig. 27); **g-** couvercle post-oral d'un individu n'ayant atteint que la moitié de la taille adulte, spécimen BMNH-P25176 (White, 1973, text-fig. 15). Abréviations: postor.- plaques post-orales; orb.- plaque orbitaire; vd.- disque ventral. Barres d'échelle: 1 cm.

Branchial plate

The branchial plates are present on the specimens ULg-P n° 2008.02.17.2 and 2008.02.17.3 (Pl. I and II: C). They are fragmentary. Their ornamentation is longitudinal as for all the pteraspidiiforms (Blieck, 1984). We count 6-7 dentine ridges per millimeter.

Ventral disc

Several small ventral discs have been prepared (Pl. I: A; Pl. II: D; Fig. 5 a-b). They are narrow and have an ovoid shape. Their maximal width is approximately in the middle of their length. The anterior side is curved, the lateral sides are convex to the outside, and the posterior side presents a median notch of several millimeters which corresponds to the emplacement of the first ventral ridge scale. The dentine ridges are concentric from a median primordium in a posterior position (Fig. 5 a-b). We count 7 dentine ridges per millimeter.

Post-oral plates

These plates are rarely preserved; they are only visible on the specimen ULg-P n° 2008.02.17.3 (Pl. I: A, C; Fig. 5c). These plates are in an anterior position and in contact with the ventral disc. They are made of a cluster of three platelets: a median one and two lateral ones. The median platelet has a pentagonal shape and is wider than longer. Its ornamentation is composed of concentric dentine ridges from a primordium on its anterior part. These ridges are well spaced out on the posterior part of the platelet and are more narrowly patterned on its anterior part. The two other platelets are in a posterolateral position in relation to the median one. They also show an ornamentation of concentric dentine ridges. Even if the edges of these platelets are worn out, their ornamentation suggests a circular shape for them (Fig 5c). They are probably homologous to the “anterior lateral plates” of the post-oral series of plates of White (1973, text-fig. 12 and 15).

Discussion: taphonomy vs. environment

All the dermal plates which are described here seem to correspond to a single species because of many morphological similarities between the isolated plates and the almost completely articulated specimens ULg-P n° 2008.02.17.2 and 2008.02.17.3 (respectively Pl. II : C and Pl. I). It is the shape of the rostral plate and of the orbito-pineal belt which settles the taxonomic attribution to *Rhinopteraspis crouchi*. The specimen 2008.02.17.3 is one of the rare pteraspidiiforms to present a preserved post-oral zone. It differs from the specimen BMNH-P25176 figured by White (1973, text-fig. 14-15) by the arrangement of the lateral plates in relation to the median plate. They are in a lateral position to the median plate on BMNH-P25176 whereas they are in a posterolateral position on 2008.02.17.3 (compare Fig. 5 c and g). This difference may have been caused either by a tectonic or by a diagenetic deformation, suffered both by the specimens of La Gileppe and of Cwm Mill, Monmouthshire, England (White, 1973).

All the specimens of La Gileppe are small. The rostral plates are similar to the rostral plates that have been figured by White (1973) for young individuals of the species *R. crouchi* (Fig. 5f; see White, 1973, text-fig. 21 and 27). The ventral discs of La Gileppe are also similar to the juvenile individuals of *R. crouchi* described by White (1973, text-fig. 16-19). This would suggest that the material of La Gileppe is only composed either of young individuals, or of small adults. This point has already been discussed by Blieck & Janvier (1999, p. 84 and fig. 9.5). These authors have indeed noticed in ichthyofacies IIA of the Upper Silurian-Lower Devonian siliciclastic series of the North Atlantic regions a statistical difference in the size and shape of the rostrum of *Pteraspis rostrata*, *Rhinopteraspis crouchi* and *Althaspis leachi* from Great Britain and the French-Belgian localities (Blieck & Janvier, 1999, fig. 9.5). “There are smaller individuals of the same species in France and Belgium. This could be due to locally less abundant food, connected with more confined conditions (“lagoonal dwarfing” in Guélorget & Perthuisot, 1983, p. 85-86)” (Blieck & Janvier, 1999, p. 84). Such confined, supposedly restricted marine conditions in Artois, N. France, are not in disagreement with the results of the tectonostratigraphic analysis of Meilliez (1989). To be eventually congruent with this schematical proposal, we need an analysis of the palaeoenvironmental conditions which were present in Lochkovian time at La Gileppe.

Pteraspidiiformes gen. et sp. indet.

Locality and horizon: Locality NE of Nonceveux, Province of Liège, Belgium; base of the Bois d’Ausse Formation; Spore Zone G (*Emphanisporites zavallatus* var. *gedinniensis* interval biozone); upper Lochkovian (“upper Gedinnian”) [see section 2.2].

Material: The material which has been mechanically prepared is composed of the following specimens: ULg-P n° 2008.02.17.1, fragmentary right orbital plate; IRSNB n° P. 8454, fragment of a dermal plate; IRSNB n° P 8455, small dorsal disc.

Description and discussion

Only the posterior process and the anterior/median edge of the orbit are preserved on the specimen ULg-P n° 2008.02.17.1 (Fig. 6 and Pl. II: A). The specimen shows an ornamentation of concentric dentine ridges (5-6/mm). In some places, the underlying tissue appears and shows an alveolar structure, typical for the cancellous layer (middle layer) of heterostracans. However, the lack of diagnostic characters only allows us to assign this specimen to Pteraspidiiformes indet.. A direct comparison of this specimen (an orbital plate) to the material described by Blieck & Goujet (1991: two dorsal discs, one ventral disc, and one rostral plate) is impossible. However, owing to the fact that all these specimens come from the same locality and have similar preservation, we may eventually hypothesize that they belong to the same taxon as Blieck & Goujet’s (1991) one, viz., *R. crouchi*?



Figure 6: Pteraspidiformes gen. et sp. indet., camera lucida drawing of orbital plate ULg-P n° 2008.02.17.1 from Nonceveux; same specimen as Pl. II: A. Scale bar: 1cm.

Figure 6: Pteraspidiformes gen. et sp. indet., dessin à la chambre claire de la plaque orbitaire ULg-P n° 2008.02.17.1 de Nonceveux; même spécimen que Pl. II: A. Barre d'échelle: 1 cm.

The specimen IRSNB n° P 8454 corresponds to a fragmentary dermal plate with a series of fine, longitudinal dentine ridges, and might be of either a ventral or a dorsal disc. The specimen IRSNB n° P 8455 represents a slightly more than half of a small dorsal disc whose external layer of dentine is worn and shows both the middle cancellous layer and the inner natural mould of the plate in several places. These two specimens are no more diagnostic than the orbital plate and are also attributed to Pteraspidiformes indet. Nevertheless, these new discoveries show that the Nonceveux locality has been delivering material of pteraspids for more than half a century since Raynaud (1942). It can be considered as a rather rich locality and we may expect to find more and better preserved specimens.

4. Biostratigraphical comments

As concerned with vertebrates, both localities of La Gileppe and Nonceveux are monospecific: *R. crouchi* in La Gileppe, *R. crouchi?* in Nonceveux (to which may probably be attributed the Pteraspidiformes gen. et sp. indet. described here). So this would attribute both localities to the *R. crouchi* Biozone (*sensu* Blicek & Janvier, 1989).

However, both localities are dated of the late Lochkovian G (Nonceveux) and Z (La Gileppe) spore interval zones, that is at the transition between the MN and BZ spore assemblage zones (*sensu* Streele *et al.*, 1987 and Steemans, 1989 a.o.). They are thus correlated to the lower part of the range of *Althaspis leachi* (Fig. 7 after Steemans, 1989, fig. 135; Blicek & Goujet, 1991, fig. 5; Godefroid *et al.*, 1994, fig. 14). This datation implies an overlapping range of *R. crouchi* and *A. leachi*, as well as other results show an overlapping range of *A. leachi* and *R. dunensis*, an hypothesis first proposed by Steemans (in Streele *et al.*, 1987, fig. 4: “*leachi* + *crouchi* zone” and “*dunensis* + *leachi* zone”; also Steemans, 1989, fig. 135).

This hypothesis has been questioned by Blicek & Janvier (1989, p. 147 *et seq.*) because in Artois, after a careful revision of the stratigraphical range of all the material of vertebrates, such an overlapping is never observed (also Blicek & Goujet, 1991, p. 75). This means

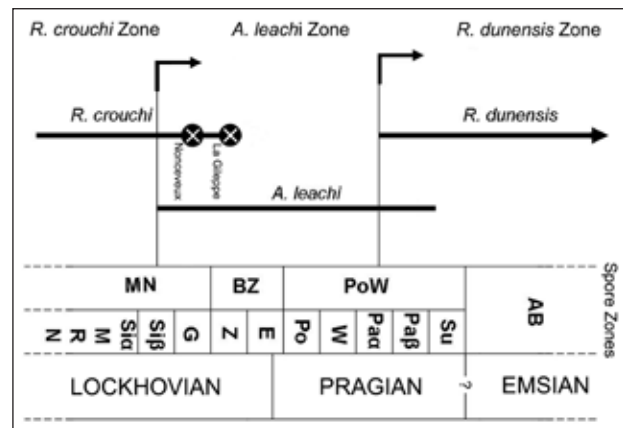


Figure 7: Stratigraphical location of the Nonceveux and La Gileppe fossiliferous sites, plotted against the spore zonation of Steemans (1989), and the fish (agnathan) biozones of Blicek & Janvier (1989) as defined by Blicek in Godefroid *et al.* (1994, fig. 14) for the Ardenne-Rhenish Slate Massif. Note that (1) the material of La Gileppe is attributed here to *R. crouchi*, (2) the material of Nonceveux has been attributed to *R. crouchi?* by Blicek & Goujet (1991), and (3) the new material of Nonceveux is attributed here to Pteraspidiformes gen. et sp. indet. The stage boundaries are after Streele *et al.* (1987, fig. 14).

Figure 7: Position stratigraphique des sites fossilifères de Nonceveux et La Gileppe, par rapport à la palynozonation de Steemans (1989) et aux biozones de vertébrés (agnathes) de Blicek & Janvier (1989) telles qu'elles ont été définies par Blicek in Godefroid *et al.* (1994, fig. 14) pour le massif ardennes-rhénan. Notez que (1) le matériel de La Gileppe est attribué ici à *R. crouchi*, (2) le matériel de Nonceveux a été attribué par Blicek & Goujet (1991) à *R. crouchi?*, et (3) le nouveau matériel de Nonceveux est attribué ici aux Pteraspidiformes gen. et sp. indet. Les limites d'étages sont celles de Streele *et al.* (1987, fig. 14).

that no sample has ever yielded *R. crouchi* and *A. leachi* both together (conditionally that the fossil material has been correctly described and revised). This is also the case in the Ardenne. So, based upon correlations to the standard spore zonation for the Ardenne-Rhenish region, Nonceveux and La Gileppe correspond to the two latest datations of *R. crouchi* and are late Lochkovian in age (Fig. 7).

5. Conclusion

The new pteraspid material of both La Gileppe and Nonceveux brings interesting results in the anatomy, stratigraphical range and palaeoenvironment of *Rhinopteraspis crouchi*. For La Gileppe, it is the first confirmation of pteraspidiform heterostracans. The whole material is assigned to *R. crouchi*. Two almost complete specimens have been prepared, one of which is preserved in 3D and presents the morphology of the post-oral zone which is rarely preserved in pteraspids. For Nonceveux, if the new material does not allow any specific determination to be made, it is the first time that an orbital plate is found there; it is attributed to Pteraspidiformes indet., but may be attributed to *R. crouchi?* *sensu* Blicek & Goujet (1991).

Both localities, Nonceveux and La Gileppe, correspond to the latest datations of *R. crouchi*, being dated of the G and Z spore zones respectively, and thus correlated to the lower *Althaspis leachi* Fish Zone (late Lochkovian). The fossil material of La Gileppe includes only small specimens interpreted as either juveniles or small adults. This is in agreement with previous observations in Artois where the Early Devonian heterostracan-bearing localities have been interpreted as confined, restricted marine environments.

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Plate I

Rhinopteraspis crouchi, La Gileppe, section B, Bois d'Ausse Formation, upper Lochkovian. Specimen ULg-P n° 2008.02.17.3: tectonically flattened, 3D preserved cephalic carapace.

A- Ventral view.

B- Dorsal view.

C- Detail of the anterior part of the ventral shield with the post-oral cover; same specimen as Fig. 5c.

D- Detail of the anterior part of the dorsal shield with the orbito-pineal belt.

E- External mould of part of the dorsal face of the rostral plate; same specimen as Fig. 5d.

F- Detail of the ornamentation of the dorsal disc.

Planche I

Rhinopteraspis crouchi, La Gileppe, coupe B, Formation du Bois d'Ausse, Lochkovien supérieur. Spécimen ULg-P n° 2008.02.17.3: carapace céphalique conservée en 3D, écrasée tectoniquement.

A- Vue ventrale.

B- Vue dorsale.

C- Détail de la partie antérieure du bouclier ventral avec son couvercle postoral; même spécimen que Fig. 5c.

D- Détail de la partie antérieure du bouclier dorsal avec sa ceinture orbitopinéale.

E- Empreinte naturelle externe d'une partie de la face dorsale de la plaque rostrale; même spécimen que Fig. 5d.

F- Détail de l'ornementation du disque dorsal.

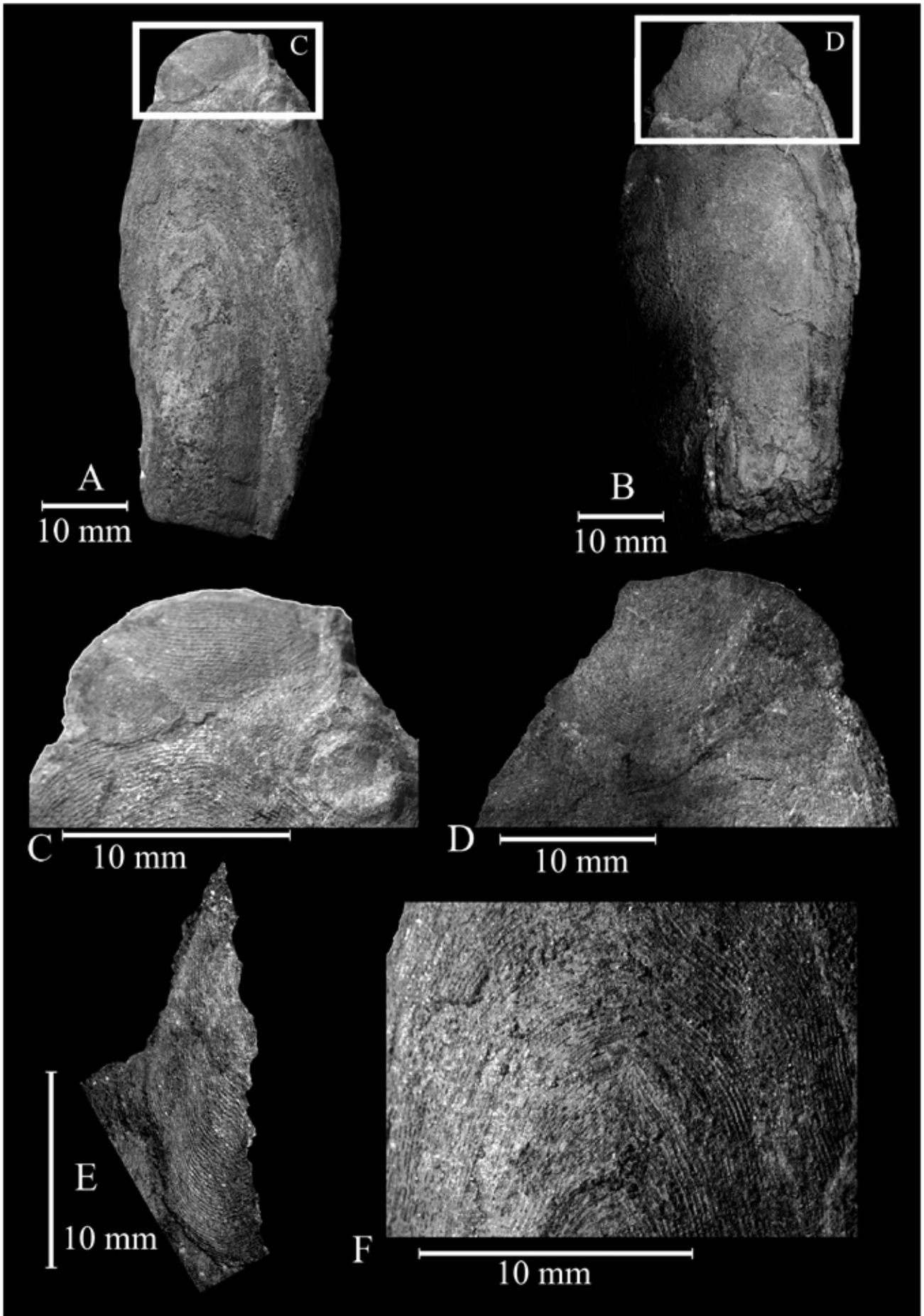


Plate II

A- Pteraspidiiformes gen. et sp. indet., Nonceveux, lowermost Bois d'Ausse Formation, upper Lochkovian. Specimen ULg-P n° 2008.02.17.1: uncomplete right orbital plate; same specimen as Fig. 6.

B-D- *Rhinopteraspis crouchi*, La Gileppe, section B, Bois d'Ausse Formation, upper Lochkovian.

B- Specimen ULg-P n° 2008.02.17.4, dorsal view of a rostral plate; same specimen as Fig. 5e.

C- Specimen ULg-P n° 2008.02.17.2, almost complete disarticulated dorsal shield.

D- Specimen ULg-P n° 2008.02.17.6, ventral disc; same specimen as Fig. 5b.

Planche II

A- Pteraspidiiformes gen. et sp. indet., Nonceveux, partie basale de la Formation du Bois d'Ausse, Lochkovien supérieur. Spécimen ULg-P n° 2008.02.17.1: plaque orbitaire droite incomplète; même spécimen que Fig. 6.

B-D- *Rhinopteraspis crouchi*, La Gileppe, coupe B, Formation du Bois d'Ausse, Lochkovien supérieur.

B- Spécimen ULg-P n° 2008.02.17.4, vue dorsale d'une plaque rostrale; même spécimen que Fig. 5e.

C- Spécimen ULg-P n° 2008.02.17.2, bouclier dorsal désarticulé mais presque complet.

D- Spécimen ULg-P n° 2008.02.17.6, disque ventral; même spécimen que Fig. 5b.

