

Early Devonian heterostracans of Wihéries and Paliseul, with notes on pteraspids of La Gileppe and an acanthodian of Paliseul (Belgium)

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ABSTRACT. The Lower Devonian siliciclastic series of Paliseul and Wihéries, in the Ardenne Massif, have delivered vertebrate remains. Paliseul rests on an equivalent of the St Hubert Formation, late Lochkovian in age; Wihéries rests on an equivalent of the Bois d'Ausse Formation, late Pragian in age. The vertebrates collected in these localities are mainly pteraspidiiform heterostracans. The revision of the specimens collected in the Racheneur quarry, NW of Wihéries, allows the redescription of *Europrotaspis? wiheriesiensis*. It is characterized, *inter alia*, by the morphology of its dorsal shield with two long arched branchial plates. However, its cornual plates are unknown. It is endemic to the Ardenne area. Recently collected specimens from quarries north of Paliseul are attributed to *Althaspis leachi*, as well as the older specimens collected in the 1950s; they all correspond to badly preserved internal moulds of mostly dorsal shields. *A. leachi* is also known from Wihéries; it seems that the latter material is of not fully grown individuals. Additionally, an interesting dorsal shield with apparently a small multi-element cornual plate has been collected in one of the Paliseul quarries (cf. *Europrotaspis? wiheriesiensis*), as well as a partially articulated acanthodian. The occurrence of *Rhinopteraspis dunensis* in both an ancient quarry east of Wihéries, and in the upper levels of the Racheneur quarry, NW of Wihéries, is confirmed.

KEYWORDS: *Althaspis leachi*, *Europrotaspis? wiheriesiensis*, *Rhinopteraspis dunensis*, Acanthodii indet., Lochkovian, Pragian, Ardenne massif.

RÉSUMÉ. Les Hétérostracés du Dévonien inférieur de Wihéries et de Paliseul, avec des notes sur des Ptéraspidés de La Gileppe et un Acanthodien de Paliseul (Belgique). La séquence siliciclastique du Dévonien inférieur de Paliseul et de Wihéries, dans le Massif ardennais, renferme des restes de Vertébrés. Paliseul repose sur un équivalent de la Formation de St Hubert, d'âge lochkovien supérieur; Wihéries repose sur un équivalent de la Formation du Bois d'Ausse, d'âge praguien supérieur. Les Vertébrés récoltés dans ces localités sont essentiellement des Hétérostracés Ptéraspidiformes. La révision des spécimens qui ont été récoltés dans la carrière Racheneur, au NW de Wihéries, permet de redécrire *Europrotaspis? wiheriesiensis*. Cette espèce est caractérisée, entre autres, par la morphologie de son bouclier dorsal avec deux plaques branchiales longues et arquées. Cependant ses plaques cornuales sont inconnues. Elle est endémique à l'Ardenne. D'autres spécimens, récoltés récemment en carrière au nord de Paliseul, ainsi que les anciens spécimens qui avaient été récoltés dans les années 1950, sont attribués à *Althaspis leachi*; ils correspondent tous à des moulages internes naturels mal conservés, principalement de boucliers dorsaux. *A. leachi* est également connu à Wihéries; ce matériel semble être celui d'individus dont la croissance fut incomplète. Un bouclier dorsal intéressant, récolté dans l'une des carrières de Paliseul, présente une petite plaque cornuale constituée apparemment de plusieurs éléments (cf. *Europrotaspis? wiheriesiensis*). Un spécimen partiellement en connexion d'un Acanthodien a également été récolté à Paliseul. Enfin, la présence de *Rhinopteraspis dunensis* à la fois dans une ancienne carrière à l'est de Wihéries et dans les niveaux supérieurs de la carrière Racheneur, au NW de Wihéries, est confirmée.

MOTS CLÉS : *Althaspis leachi*, *Europrotaspis? wiheriesiensis*, *Rhinopteraspis dunensis*, Acanthodii indet., Lochkovien, Praguien, Massif de l'Ardenne.

1. Introduction

The Early Devonian period corresponds to adaptive radiations of early vertebrates in relation to the setting of Old Red Sandstones and their new ecological niches during the late Caledonian – early Variscan orogeny (e.g. Friend et al., 2000; Blicek, 2011). Heterostracans, and in particular pteraspidiiform heterostracans, are typical elements of these Early Devonian vertebrate faunas. This group of agnathans has been extensively used in biostratigraphical correlations, and provides markers for the interpretation of the sedimentary environments of the Lower Old Red Sandstone facies, which is still controversial (see discussion in Blicek, 2011). The material presented here comes from a series of quarries in the vicinity of Wihéries, Paliseul and La Gileppe in Wallonia, south Belgium (Fig. 1), and has been the subject of a Master's thesis (Pille, 2004). Pteraspids have been known from all three localities since the beginning of the 20th century: Leriche (1912) for Wihéries, Asselberghs (1920) for La Gileppe, and Asselberghs (1955) for Paliseul (see the review of Blicek, 1982).

The specimens of Wihéries come from two different localities:

— the original material of Leriche (1912) has been collected in the “Grès de Wihéries” from “l'une des carrières ouvertes à l'Est du village de Wihéries” (one of the quarries, east of the Wihéries village; Leriche, 1912, p. 50) that has yielded few specimens of the pteraspidiiform *Rhinopteraspis dunensis*; they are curated in the collections of the Royal Belgian Institute of Natural Sciences, Brussels;

— all other specimens come from the Racheneur quarry where two fossiliferous levels have been defined: an upper level (f1, Leriche, 1948) corresponding to the *Rhinopteraspis dunensis* Biozone (*Dunensis* zone in Blicek & Jahnke, 1980, p. 373), and a lower level (f2, Leriche, 1948) corresponding to the *Althaspis leachi* Biozone (*Leachi* zone in Blicek & Jahnke,

1980, p. 373-374; *Althaspis leachi* Biozone in Blicek & Janvier, 1989, p. 154). The latter has yielded a vertebrate assemblage with the pteraspidiiforms *Europrotaspis? wiheriesiensis* and *Althaspis leachi*, the placoderm *Prosphymaspis? corneti*, as well as various invertebrates: eurypterid, bivalve, and lingulid remains (Leriche, 1948; Denison, 1978; Blicek, 1982), and plant remains (Gerrienne, 1991). In 1978 when I visited the locality with Dr. Hervé Lelièvre (Muséum National d'Histoire Naturelle, Paris), the lower level only was accessible along the Vivrœux brook near the quarry; but it was inaccessible in 1979, due to abundant vegetation. Most of the material studied here comes from this lower level. It is curated in the collection of the Polytechnical Faculty of Mons University, Belgium (now called Polytech'Mons) from which it has been borrowed (see the detail of studied specimens in Appendix 1). *Europrotaspis? wiheriesiensis* (Brotzen, 1936) in particular was in need of a revision. During the study of the material borrowed from Polytech'Mons, it appeared that one specimen had been collected in a “middle level” (FPMS specimen 7156 a-b – Appendix 1).

The specimens of Paliseul originally come from a series of old quarries located between 1 km and 1.5 km north of Paliseul, on both edges of the Eutrope-Fontaine brook (Asselberghs, 1955). They correspond to the pteraspidiiforms *Althaspis leachi* and *Europrotaspis? sp.* (White, 1956; Blicek & Jahnke, 1980; Blicek, 1982). This material is curated in the geological collections of the Catholic University of Leuven, Belgium (Katholieke Universiteit Leuven - Afdeling Geologie) from which it has been borrowed (see the detail of studied specimens in Appendix 1). The Paliseul quarries were visited in 1978: the northern quarries n° 1 and 2 (*sensu* Asselberghs, 1955) had already been merged into a single large quarry; the western quarries n° 3, 4 and 8 (*ibid.*) had also been merged into a single large one. No pteraspidiiform material was seen in 1978. However, new fossil material has recently

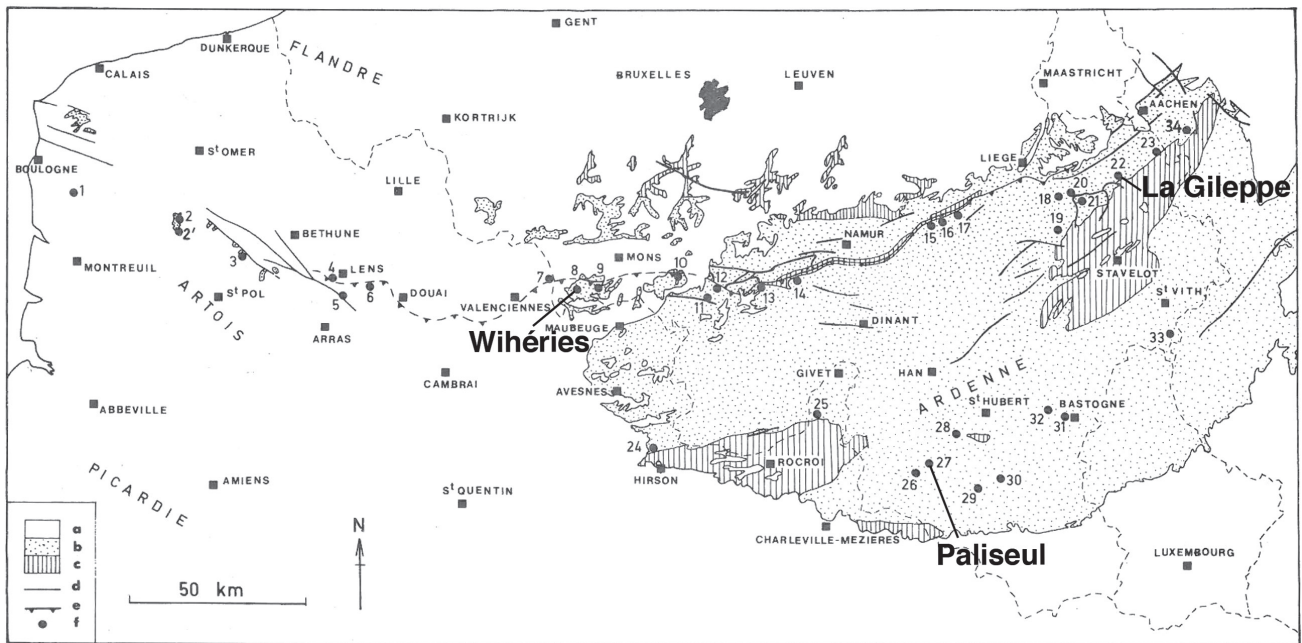


Figure 1. Location of Wihéries (n° 8), Paliseul (n° 27) and La Gileppe (n° 22) fossiliferous sites on Blicek's (1982, fig. 1) geological scheme of northern France and southern Belgium. Captions: a, Post-Palaeozoic; b, Upper Palaeozoic; c, Lower Palaeozoic; d, faults; e, Midi Fault; f, heterostracan-bearing localities.

Figure 1. Emplacement des sites fossilifères de Wihéries (n° 8), Paliseul (n° 27) et La Gileppe (n° 22) sur le schéma géologique du nord de la France et du sud de la Belgique de Blicek (1982, fig. 1). Légende : a, Post-Paléozoïque ; b, Paléozoïque supérieure ; c, Paléozoïque inférieure ; d, failles ; e, Faille du Midi ; f, gisements à hétérostracés.

been collected in this locality: first during a visit made in 2004 with L. Pille (Lille 1 University), Prof. E. Poty, C. Hendrickx and S. Van de Walle (Liège University) in the Château-du-Loup quarry (corresponding to quarry n° 4 of Asselberghs, 1955) (*A. leachi*, undetermined pteraspids and a fragment of an acanthodian); second by an amateur in La Périère (or La Pélire) quarry (corresponding to quarry n° 2 of Asselberghs, 1955) (cf. *Europrotaspis? wihériesiensis*) [photographs of this material having been provided by S. Van de Walle]. This material is curated in the geological collections of the University of Liège from which it has been borrowed (see the detail of studied specimens in Appendix 1).

The aim of this paper is to publish a revision of part of the original Wihéries and Paliseul material as well as a description of the newly collected material. All the studied fossils correspond to heterostracan vertebrate remains, except one specimen of an undetermined acanthodian. The heterostracan remains correspond mostly to internal moulds of dorsal and ventral discs, orbital plates, rostral plates, dorsal shields and scales. Many specimens are incomplete, and eventually partly distorted. In some cases, small elements are attributed to juvenile individuals (see Appendix 1). This paper is based upon the Master's thesis work of Pille (2004) to which additional observations and interpretations have been made (including undetermined pteraspid material from La Gileppe Dam section).

Abbreviations: FPMS – Faculté Polytechnique de Mons (now Université de Mons, Polytech'Mons, Département Mines-Géologie: Géologie fondamentale et appliquée); RBINS – Royal Belgian Institute of Natural Sciences (IRSNB – Institut royal des Sciences naturelles de Belgique); KBIN – Koninklijk Belgisch Instituut voor Natuurwetenschappen); KUL – Katholieke Universiteit Leuven (Afdeling Geologie); ULg – Université de Liège (Département de Géologie).

2. Geological setting

2.1. Wihéries

Wihéries is located in the province of Hainaut (for geographical location, see the I.G.N. maps n° 45/5 and 6 at 1:10 000; Belgian Lambert 1972 coordinates (m): $x = 106900, y = 120000$; longitude:

$3^{\circ} 45' 03.75''$ E, latitude: $50^{\circ} 23' 50.38''$ N) (Fig. 1). The material was collected in two different quarries:

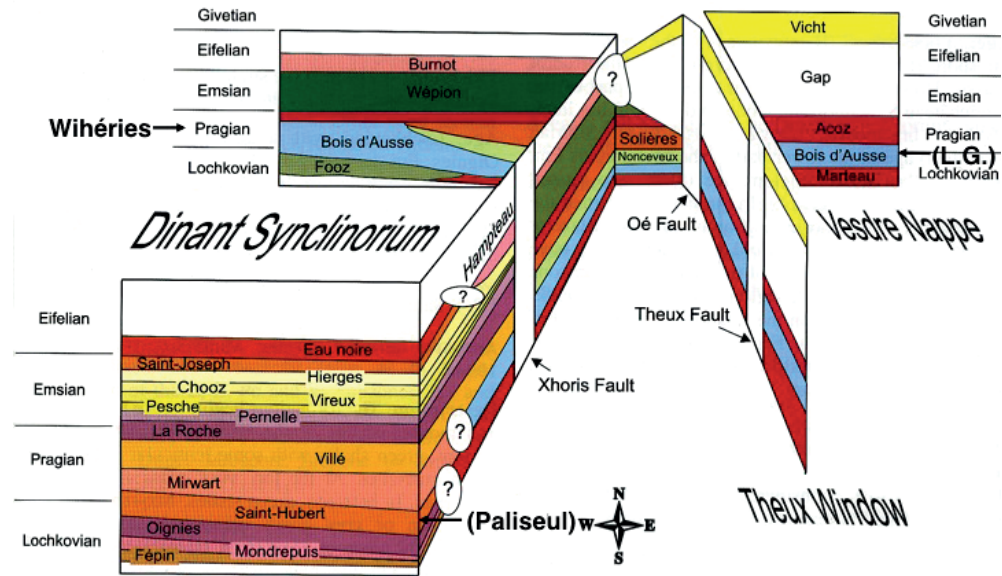
1) in one of the quarries east of Wihéries, in the “Grès de Wihéries” lithofacies (see here below for modern nomenclature and geological age); the three original specimens were collected by C. Malaise who gave them for study to M. Leriche (Leriche, 1912, p. 50); they have been attributed to *Rhinopteraspis dunensis* (“*Pteraspis dunensis*, Roemer, 1854” in Leriche, 1912, Pl. E: 1-3); those quarries east of Wihéries had been opened in the 19th century, but were closed in 1948 (Leriche, 1948, p. 284);

2) all other material comes from the Racheneur quarry where sandstones and quartzites of the “Grès de Wihéries” were exploited for the manufacture of aggregates and building stones (Blicek, 1982). Quarrying activity has totally ceased, and the quarry was being filled up in the early 1990s (after Gerrienne, 1991). This quarry is located just NW of Wihéries (Leriche, 1948, fig. 1), at the northern edge of the Dinant Synclinorium (previously named “Dinant Basin”, e. g., Lecompte, 1968) in the Ardenne Allochthon (Meilliez et al., 1992; Mansy et al., 1999; Bélanger et al., 2012), within an inlier called “Massif de Dour” which is included in the thrust massifs in the southern part of the “Bassin Houiller du Borinage” (Borinage Coal Measures) (Asselberghs, 1922). The latter is shown on both geological maps n° 150 Quiévrain-St. Ghislain (Belgium) at 1:40 000 and Le Quesnoy (France) at 1:50 000.

Asselberghs (1922; also Leriche, 1948) considered the characteristics of the “Grès de Wihéries” as similar to those of the Bois d'Ausse sandstones that he assigned to the “Taunusian” (“Siegenian”). The “Grès de Wihéries” are laterally correlated with the type locality of the Bois d'Ausse Formation. This quartzitic-sandy-dominated formation is divided into massive thick beds, themselves subdivided into beds with oblique stratifications containing middle-sized interstratified grey shales (“grey bluish schist interstratification” in Leriche, 1924; review in Dejonghe et al., 1994). According to White (1956; following Leriche, 1948), there were two fossiliferous horizons in the Racheneur quarry, thirty metres apart from each other; the fossils come from small shaly layers intercalated in the sandstones. The upper level (f1) consists of bluish black shales whereas the lower level (f2) is characterized by brownish shales. According to Blicek & Jahnke (1980), the upper level f1 corresponds to the *Rhinopteraspis dunensis* Biozone (*Dunensis* zone in Blicek

Figure 2. Location of Wihéries, Paliseul and La Gileppe fossiliferous sites on Godefroid et al.'s (1994, fig. 3) stratigraphical chart of Lower Devonian formations of the Ardenne massif. Note that Paliseul is not located in the Dinant Synclinorium, but more southerly in the Neufchâteau-Eifel Synclinorium, in an equivalent of the Saint-Hubert Formation; and that La Gileppe (L.G.) is located just NE of the Vesdre Nappe, in the Bois d'Ausse Formation.

Figure 2. Emplacement des sites fossilifères de Wihéries, Paliseul et La Gileppe sur la charte stratigraphique des formations du Dévonien inférieur du massif ardennais par Godefroid et al. (1994, fig. 3). Notez que Paliseul n'est pas situé dans le Synclinorium de Dinant, mais plus au sud dans le Synclinorium de Neufchâteau-Eifel, dans un équivalent de la Formation de Saint-Hubert; et que La Gileppe (L.G.) est situé juste au NE de la Nappe de la Vesdre, dans la Formation du Bois d'Ausse.



& Jahnke, 1980, p. 373), and the lower level f2 to the *Althaspis leachi* Biozone (*Leachi* zone in Blicek & Jahnke, 1980, p. 373-374; *Althaspis leachi* Biozone in Blicek & Janvier, 1989, p. 154). The specimens studied here come mostly from the lower level f2, but it appears that one specimen (FPMS 7156 a-b, chosen here as the lectotype of *Europrotaspis? wiheriesiensis*) comes from a third level (here noted f2') which lies in an intermediate location (see detail in Appendix 1).

Blicek (1982) placed the Lochkovian-Pragian ("Gedinnian-Siegenian") boundary between both fossiliferous levels f1 and f2. This seems to be confirmed by a palynological study which shows that the Bois d'Ausse Formation is dated from the Lochkovian Siß spore Zone to the late Pragian Su spore Zone (Stemans in Dejonghe et al., 1994). However, the palynological study produced by Stemans (1989) and Gerrienne (1991) on the heterostracan-bearing samples from the Racheneur quarry, shows that these samples may be attributed to the late Pragian Su spore Zone (Stemans, 1989), not the Lochkovian (see Blicek in Godefroid et al., 1994, fig. 14) (Fig. 2).

According to various authors (including Asselberghs, 1946; Leriche, 1948; White, 1956; Denison, 1978; Blicek, 1982 and pers. obs., 1978; Strel et al., 1987; Stemans, 1989; Gerrienne, 1991), the faunal and floristic lists are as follows:

- upper level f1 (late Pragian): *Rhinopteraspis dunensis* (see Leriche, 1924, pl. IV: ventral disc; 1948, fig. 3, pl. I: 2-2a: branchial plate) + *Althaspis leachi* (FPMS specimen 7144, fragment of a juvenile ventral disc – Appendix 1; thus extending the stratigraphical distribution of *A. leachi* above the f2 level); plus the placoderms *Prosphythaspis? corneti*, *Prosphythaspis? sp.*, and the "invertebrates" *Modiolopsis corneti* and *Lingula racheneuri*;

- middle level f2' (late Pragian): *Europrotaspis? wiheriesiensis* (FPMS specimen 7156 a-b, nearly complete dorsal shield, lectotype of the species – Appendix 1);

- lower level f2 (late Pragian): all other fossil material, that is, "invertebrates": *Spirorbis sp.*, *Estheria stockmansi*, *Pterygotus sp.*; vertebrates: *Althaspis leachi*, *Europrotaspis? wiheriesiensis*, and Pteraspidae gen. et sp. indet. 1 [*Drepanaspis* has been mentioned by Maillieux, 1932, p. 8; and *Drepanaspis schrieli* by Asselberghs, 1946, p. 118, but disputed by Leriche, 1948, p. 286-287; no drepanaspid remains have been observed in the

studied material]; and plants: *Pachytheca sp.*, *Prototaxites sp.*, *Prototaxites forfarensis*, *Taeniocrada dubia*, *Aphyllopteris cf. robusta*, *Dawsonites arcuatus*, *Drepanophycus spinaeformis*, *Gosslingia breconensis* (formerly *Hostimella racheneuri*).

2.2. Paliseul

Paliseul is in the Belgian province of Luxembourg (Belgian Lambert 1972 coordinates (m): $x = 205000$, $y = 66000$. longitude: $5^{\circ}10' 04.88''$ E, latitude: $49^{\circ}50' 06.00''$ N). The fossil material originally comes from a series of old quarries located between 1 km and 1.5 km north of Paliseul, on both edges of the Eutrope-Fontaine brook (Asselberghs, 1955). Those quarries are still partly active. They were visited in 1978 and 2004, and now correspond to two main groups of quarries: (A) the northern quarries n° 1 and 2 (*sensu* Asselberghs, 1955) have been merged into a single large quarry, east of the Eutrope-Fontaine brook, along the road to Opont; some fossil material collected by an amateur (cf. *Europrotaspis? wiheriesiensis*; photos kindly provided by S. Van de Walle) comes from La Pèrre (or La Pèrre) quarry, corresponding to quarry n° 2 of Asselberghs (1955), and now transformed into a rubbish dump; (B) the western quarries n° 3, 4 and 8 (*ibid.*) have also been merged into a single large one (with a ca. 200 m long quarried face), west of the Eutrope-Fontaine brook; the fossil material collected in 2004 with L. Pille (Lille 1 University), Prof. E. Poty, C. Hendrickx and S. Van de Walle (Liège University), comes from the Château-du-Loup quarry, corresponding to quarry n° 4 of Asselberghs (1955) that is still active.

The quarries of Paliseul are located in the Synclinorium of Neufchâteau-Eifel, also called synclinorium of Charleville (Blicek & Jahnke, 1980) as part of the Ardenne Allochthon (geological map n° 207: Vivy-Paliseul at 1:40 000; see Meilliez et al., 1992; Mansy et al., 1999; Bélanger et al., 2012). The local lithofacies called "schistes aimantifères de Paliseul" (Lecompte, 1968) corresponds to thick beds of a sandy, grey and blue set of quartzites with sericitic cement and micaceous joints, as well as psammitic sandstones and psammites in thin beds (Asselberghs, 1955). It is an equivalent to the "Assise de Saint-Hubert", now called Saint-Hubert Formation (Stainier, 1994). It is dated as late Lochkovian: *Leachi* Zone, upper "Gedinnian" in Blicek (1982, fig. 3; in Godefroid et al., 1994, fig. 14), late Lochkovian Siß to

Z spore zones in Steemans (1989, fig. 88; also Stainier, 1994), *Althaspis leachi* Biozone of Blicek & Janvier (1989) (Fig. 2). The faunal list includes (Asselberghs, 1955; Blicek, 1982, and Appendix 1 here):

- in the Château-du-Loup quarry (quarry n° 4 of Asselberghs, 1955): *Althaspis leachi*, Pteraspidae gen. et sp. indet. 1, and part of an acanthodian squamation (*Acanthodii* indet.);

- in La Périère (or La Pélire) quarry (quarry n° 2 of Asselberghs, 1955): cf. *Europrotaspis? wiheriesiensis*;

- in former quarries 5 and 7, south of quarries 1-2 of Asselberghs (1955): *A. leachi*, cf. *E.? wiheriesiensis* (*Europrotaspis?* sp. indet. in Blicek, 1982).

In all localities, *Modiolopsis* remains have been collected with the fish (Asselberghs, 1955). However, the stratigraphical relationships of those various vertebrate-bearing layers are unknown.

2.3. La Gileppe

This locality has only delivered a few undetermined pteraspid specimens that are mentioned here below in the corresponding section. The most recent account on La Gileppe pteraspids was by Thirion & Blicek (2009) who give all details on the stratigraphy and age of the locality.

3. Systematic study

Nomenclatural notes.

As explained by Nielsen (2012), many authors attribute Vertebrata to Linnaeus (1758) who, however, did not recognize this group of organisms. In the rules of the International Code of Zoological Nomenclature, “vernacular forms are not excluded” for family-group names (ICZN, 1999, article 11.7.2; Nielsen, 2012, p. 435). “Such names are accepted in their Latin form when subsequently Latinized, and they are attributed to the author (and date) of the vernacular form” (Nielsen, 2012), “only if it has been latinized by later authors and has been generally accepted as valid by authors interested in the group concerned” (ICZN, 1999, article 11.7.2). This is applied by Nielsen (2012) to Vertebrata whose name was introduced by Lamarck (1801, p. 7 and table 8) as “animaux à vertèbres”, that is, for the four classes of the time, “Mammaux [*sic*], Oiseaux, Reptiles, Poissons” (Lamarck, 1801, p. 8). The authorship of the name Vertebrata is thus corrected here as Vertebrata Lamarck, 1801 (see also Blicek & Styza, 2014).

The authorship of the taxon Pteraspiformes is often attributed to Berg (1940, p. 108: Pteraspiformes) [e.g. Voichyshyn, 2011, p. 83]. However, this taxon name was introduced first by Berg (1937, p. 1277: Pteraspiformes — with the other order names Astraspiformes, Psammosteiformes, Cythaspiformes, Amphispaspiformes, etc.) in a paper presented as “a short extract from the complete account which contains characteristics of all classes, orders, and suborders of fish-like vertebrates”, that is, Berg (1940).

The classification of pteraspid taxa used here is based upon Pernègre & Elliott’s (2008) cladistic analysis. However, the genus *Althaspis* has not been integrated in Pernègre & Elliott’s analysis which selected taxa belonging to the morphologically best-known Pteraspiformes, in which the dorsal shield, as well as its lateral sensory line system, are completely known (Pernègre & Elliott, 2008, Appendix 1). *Althaspis* is here considered as sister-group to *Rhinopteraspis* as in Blicek’s (1984) preliminary analysis, the latter genus being included in the family Pteraspidae *sensu* Pernègre & Elliott (2008, fig. 4). To confirm the close relationships of *Althaspis* and *Rhinopteraspis*, it must be noted that both genera were classified in the family Rhinopteraspididae NOVITSKAYA (1983, p. 164-165 and figs 75-76; cf. Voichyshyn, 2011, p. 122) on the basis of “a markedly elongated cigar-shaped carapace”, “a long rostrum”, “a stout, backwardly inclined dorsal spine” and a ‘contacting’ orbitopineal zone – all characters that are more pronounced than in other pteraspids (Novitskaya, 1983, p. 164).

Open nomenclature and synonymy lists follow Matthews’ (1973) recommendations.

Subphylum Vertebrata LAMARCK, 1801

†Class Pteraspidomorpha GOODRICH, 1909

Subclass Heterostraci LANKESTER, 1868

Order Pteraspidoformes BERG, 1937

Clade Pteraspidoidei [*sensu* Pernègre & Elliott, 2008;

Pteraspida *sensu* Janvier, 1996]

Family Protaspidae BRYANT, 1933

Genus *Europrotaspis* WHITE, 1961

Europrotaspis? wiheriesiensis (BROTZEN, 1936) [*sensu* Blicek, 1984]

(Figs 3-4; Pl. I: A-F; Pl. II: A, C; Pl. III: A-E)

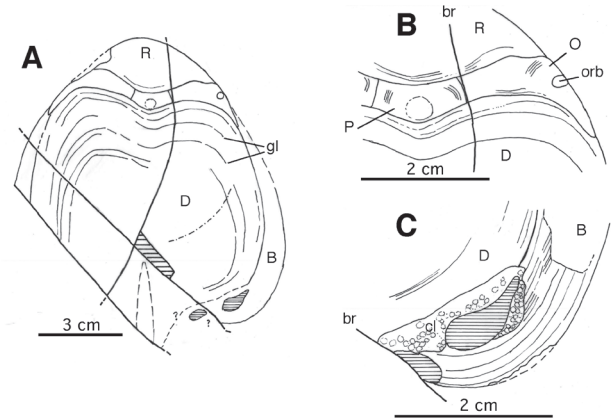


Figure 3. *Europrotaspis? wiheriesiensis* from the Racheneur quarry, Wihéries, middle level f2’; equivalent of the Bois d’Ausse Formation, late Pragian. Camera lucida drawings of specimen FPMS 7156a, lectotype, external natural mould of a nearly complete dorsal shield. A - general view; B - left anterior part of the shield with detail of the orbito-pineal belt; C - left posterior part of the shield with detail of the posterior branchial area. Captions: br - breaks, B - branchial plate, cl - cancellous layer of bone, D - dorsal disc, gl - growth lines, O - orbital plate, orb - left orbit, P - pineal plate, R - rostral plate; horizontally hatched areas correspond to lacunae (gaps) in the specimen. Same specimen as on Plate I A-C.

Figure 3. *Europrotaspis? wiheriesiensis*, carrière Racheneur, Wihéries, niveau moyen f2’; équivalent de la Formation du Bois d’Ausse, Praguien supérieur. Dessins à la chambre claire du spécimen FPMS 7156a, lectotype, moule naturel externe d’un bouclier dorsal presque complet. A - vue d’ensemble; B - partie antérieure gauche du bouclier avec détail de la ceinture orbito-pinéale; C - partie postérieure gauche du bouclier avec détail de la région branchiale postérieure. Légendes: br - cassures, B - plaque branchiale, cl - couche cancellaire de l’os, D - disque dorsal, gl - lignes de croissance, O - plaque orbitaire, orb - orbite gauche, P - plaque pinéale, R - plaque rostrale; les zones hachurées horizontalement correspondent à des lacunes dans le spécimen. Même spécimen que sur la Planche I A-C.

?1924 *Pteraspis*.— Racheneur, p. B 90, B 117, B 159.

v.1925 *Pteraspis dunensis* F. Roemer.— Leriche, fig. 4.

v.1926 *Pteraspis dunensis* F. Roemer.— Leriche, pl. I, II: 1-4.

1933 *Pteraspis rotunda* n. sp.— Gross, p. 53 [the material of *P. rotunda* figured in this paper concerns the locality of Overath, Germany]

*1936 *Protaspis wiheriesiensis* n. sp.— Brotzen, p. 20.

1938 *Protaspis wiheriensis* [*sic*].— White, p. 99.

1946 *Protaspis wiheriensis* Brotzen [*sic*].— Asselberghs, p. 118 [*vide* White, 1938].

1948 *Pteraspis (Cyrtaspis) wiheriensis* Brotzen [*sic*].— Leriche, p. 287.

1956 *Protaspis*.— White, p. 4.

1957 *Protaspis wiheriesiensis* Brotzen.— Fahlbusch, p. 45, 50.

1968 *Pt. rotunda* [*sic*].— Lecompte, p. 30.

1980 *Europrotaspis wiheriesiensis* (Brotzen).— Blicek & Jahnke, p. 373.

1982 *Europrotaspis? wiheriesiensis*.— Blicek, p. 13.

.1984 *E.? wiheriesiensis* (Brotzen, 1936).— Blicek, p. 64, 70; fig. 47D.

v.2004 nov. gen. 1 *wiheriesiensis*.— Pille et al., p. 121; fig. 1 A-B.

2006 nov. gen. 1 *wiheriesiensis*.— Blicek et al., p. 23-24.

N.B.— Several other papers have either simply mentioned, or described and figured heterostracan remains that have often been preliminarily attributed to “*Pteraspis*” or “*Pteraspis dunensis*”

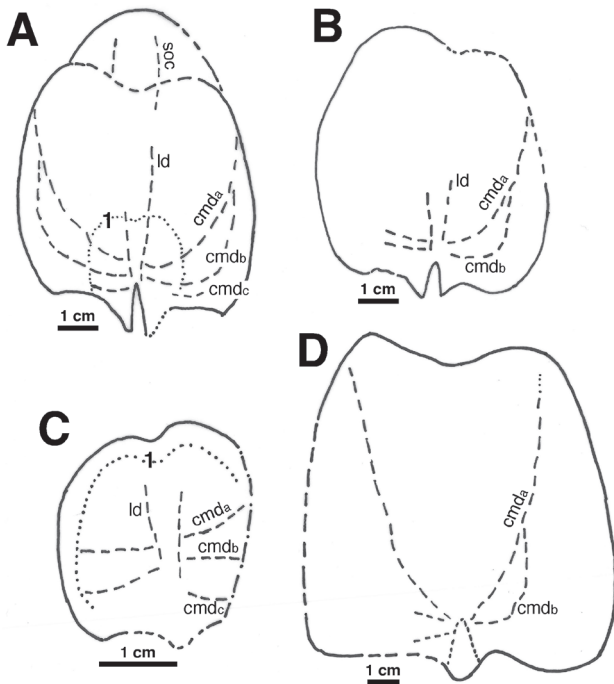


Figure 4. *Europrotaspis? wiheriesiensis* from the Racheneur quarry, Wihéries, lower level f2; equivalent of the Bois d'Ausse Formation, late Pragian. Sketches made after black-and-white photographs of the sensory line system of the dorsal disc (A-D) and the rostral plate (A). Nomenclature of the sensory canals is after Blicek (1984, fig. 1). A- elastomere mould of specimen FPMS 7149b, paralectotype, visceral face of part of an adult dorsal shield (same as Pl. I D); B- specimen FPMS 7143a, external mould of a dorsal disc with part of visceral surface of bone (same as Pl. I F); C- specimen FPMS 7154, very small dorsal disc (same as Pl. II C); D- specimen FPMS 7164, large dorsal disc in visceral view (same as Pl. III A). Captions: cmdb-cmdbc- transverse commissures of the dorsal disc, ld- medio-dorsal canal, soc-supra-orbital canal, 1- first (?) growth stage of the dorsal disc.

Figure 4. *Europrotaspis? wiheriesiensis*, carrière Racheneur, Wihéries, niveau inférieur f2 ; équivalent de la Formation du Bois d'Ausse, Praguien supérieur. Schémas réalisés à partir de photos noir-et-blanc du système des lignes sensorielles du disque dorsal (A-D) et de la plaque rostrale (A). Nomenclature des canaux sensoriels d'après Blicek (1984, fig. 1). A- moulage élastomère du spécimen FPMS 7149b, paralectotype, face viscérale d'un bouclier dorsal adulte (même spécimen que Pl. I D) ; B- spécimen FPMS 7143a, moule externe d'un disque dorsal avec une partie de la surface viscérale de l'os (même spécimen que Pl. I F) ; C- spécimen FPMS 7154, très petit disque dorsal (même spécimen que Pl. II C) ; D- spécimen FPMS 7164, grand disque dorsal en vue viscérale (même spécimen que Pl. III A). Légendes : cmdb-cmdbc- commissures transversales du disque dorsal, ld- canal médio-dorsal, soc- canal supra-orbitaire, 1- premier (?) stade de croissance du disque dorsal.

in the Racheneur quarry of Wihéries (see the synonymy list of Pille, 2004, p. 7-8); after a careful checking, it appears that these remains do not correspond to *E.? wiheriesiensis*, but to either *Althaspis leachi* or *Rhinopteraspis dunensis* [see here below, the corresponding sections] (Leriche, 1912, 1924, 1925 [fig. 3, pl. II-IV], 1926 [fig. 1-3, pl. III-IV]; Asselberghs, 1922; Racheneur, 1923; Maillieux, 1936, p. 29; 1940, p. 5; Gerrienne, 1991, p. 288). They may have eventually been attributed to *Drepanaspis* (Maillieux, 1932, p. 8; Gross, 1933, p. 56); however, Gross (1937, p. 7) re-attributed the scales figured by Leriche (1926, Pl. I: 2, III and IV: 1-2) to *P. dunensis* — see here above, section 2.1.

Preliminary remark. Since Leriche's (1925, 1926) descriptions and illustrations, this taxon has never been properly defined. Brotzen (1936) recognized it as a separate species, and named it *wiheriesiensis* after its original locality. Its generic attribution has been quite uncertain although several authors considered that it has to be included within what is now understood as family Protaspididae (*sensu* Pernègre & Elliott, 2008; see the synonymy list here above). A detailed reappraisal of the species, with description of each known element of its cephalic armour, is thus given here.

Lectotype. Specimen FPMS 7156 a-b, a nearly complete dorsal shield: a) external natural mould, and b) counterpart (Fig. 3; Pl. I: A-C; Pille et al., 2004, fig. 1 A-B).

Type locality and horizon. Racheneur quarry, NW of Wihéries, west of the Vivroëux brook, province of Hainaut, Belgium (Leriche, 1948, fig. 1). FPMS 7156 a-b comes from a level most probably laying between both fossiliferous horizons called f1 and f2 by Leriche (1948, fig. 2): "Wihéries, niveau moyen" on the original label of the fossil, here named level f2'. "Grès de Wihéries", a lateral equivalent of the Bois d'Ausse Formation (Dejonghe et al., 1994). Late Pragian Su spore Zone (Stemans, 1989, p. 67-69 and 230-231; also Gerrienne, 1991). Corresponding probably to the late *Althaspis leachi* Biozone, because f2' lies above the lower level f2 which corresponds to the *Althaspis leachi* Biozone (*Leachi* zone in Blicek & Jahnke, 1980, p. 373-374; *Althaspis leachi* Biozone in Blicek & Janvier, 1989, p. 154).

Paralectotype. Specimen FPMS 7149 a-b, part of an adult dorsal shield: a) internal natural mould, b) visceral face of the shield (Leriche, 1926, Pl. II: 1; Pille, 2004, Pl. I: D-E) (Fig. 4A; Pl. I: D-E). From the Racheneur quarry, Wihéries, lower level f2 (Leriche, 1948, fig. 2). "Grès de Wihéries", a lateral equivalent of the Bois d'Ausse Formation; late Pragian Su spore Zone (Stemans, 1989, p. 67-69 and 230-231); *Althaspis leachi* Biozone (*Leachi* zone in Blicek & Jahnke, 1980, p. 373-374).

Other material. [A] 22 other specimens from Wihéries are referred to *Europrotaspis? wiheriesiensis*. They mostly include partially preserved dorsal shields and ventral discs, several of them being fragmentary. Two of them, FPMS 7170 (internal natural mould of a very incomplete dorsal disc) and 7182 (fragment of a large ventral disc) are attributed to *E.? wiheriesiensis?*. See detail in Appendix 1. All come from the lower level f2, equivalent to the Bois d'Ausse Formation, late Pragian Su spore Zone, *Althaspis leachi* Biozone (*ibid.*). [B] A single specimen, KUL n° 6, a fragment of a dorsal disc connected to a fragmentary branchial plate, comes from Paliseul quarry 7 (*sensu* Asselberghs, 1955); it is attributed to cf. *E.? wiheriesiensis* (*Europrotaspis?* sp. indet. in Blicek, 1982). « Schistes aimantifères de Paliseul », an equivalent of the "Assise de Saint-Hubert", now called Saint-Hubert Formation (Stainier, 1994). It is dated as late Lochkovian: *Leachi* Zone, upper "Gedinnian" in Blicek (1982, fig. 3; in Godefroid et al., 1994, fig. 14), late Lochkovian Siß to Z spore zones in Stemans (1989, fig. 88; also Stainier, 1994), *Althaspis leachi* Biozone of Blicek & Janvier (1989).

Diagnosis. Rostral plate broader than long. Quadrangular pineal plate. Continuous orbito-pineal belt with a slightly convex suture between pineal and orbital plates. Pineal canal in the pineal plate. Transverse sensory canals posteriorly distributed on the dorsal disc. Branchial plates very long and very arched. Apparent absence of cornual plates. Very broad dorsal disc. Orbital plates with short post-orbital process, short anterior process and moderate median process.

Description. Neither the cornual plates, nor the dorsal spine or the plates of the oral cover were observed on the preserved specimens.

Rostral plate. The rostral plate is partially present on both type specimens, FPMS 7149 a-b and 7156 a-b. No rostral plate is entirely preserved on the studied specimens where the ventral face of the rostrum is not visible. The dorsal part of the plate is broader than long (laR 38-50 mm x LoR ca. 21 mm; Table 1). Its general shape can be compared to an isosceles triangle with a broad base and smooth basal angles. On specimen FPMS 7156a, the posterior suture of the rostral plate is 4.8 cm long. The posterior limit of the rostrum follows the layout of the anterior edge of the dorsal disc (Fig. 3 A-B; Pl. I: C). It is sinuous. On specimen FPMS 7149 a, the rostral plate is in direct, abnormal contact with the dorsal disc (Pl. I: D). This is due to the absence of the pineal plate and anterior parts of both orbital plates, with overlapping of the anterior edge of the dorsal disc upon the rostral plate. The ornamentation of the rostral plate is only partially

Dorsal shield	FPMS 7143b	FPMS 7147	FPMS 7149a paralectotype	FPMS 7150	FPMS 7154 juv.	FPMS 7156a lectotype	FPMS 7164
laT			ca. 2 x 38			ca. 2 x 49	
LoT			88+			105+	
laT/LoT			86,3 %			93,3 %	
laR			ca. 2 x 19			2 x 25	
LoR			21+			~ 21	
laR/LoR			180 %			238 %	
LoR/LoT			23,8 %			20 %	
laP						~ 15	
laD	ca. 2 x 36	92	ca. 2 x 33	ca. 2 x 49	2 x 16	ca. 2 x 39	105
LoD	79	?	~ 70	110 (?)	~ 31	?	110 / 115
laD/LoD	91,1 %		94,2 %	89 %	103,2 %		91,3 - 95,4 %
LoO						16 (?)	
LoB			68+			~ 70	
LoB/LoT			77,2 %			66,6 %	

Ventral disc	FPMS 7142b	FPMS 7148a	FPMS 7150	FPMS 7151a juv.	FPMS 7163	FPMS 7167 juv.
laV	66	80	ca. 2 x 44	25	ca. 2 x 25	21
LoV	67	97	115	28	61	24+
laV/LoV	98,5 %	82,4 %	76,5 %	89,2 %	81,9 %	87,5 %

Table 1. Measurements and ratios of the dorsal shield and ventral disc of *Europrotaspis? wiheriesiensis* after the collections of Polytech'Mons, Belgium, following Blicek's (1984, fig. 1) definitions. Measurements are in mm. Captions: laT- total width of dorsal shield, LoT- total length of dorsal shield, laR- rostral width, LoR- rostral length, laP- pineal width, laD- width of dorsal disc, LoD- length of dorsal disc, LoO- orbital length, LoB- branchial length, laV- width of ventral disc, LoV- length of ventral disc. Abbreviation: juv.- juvenile.

Tableau 1. Mesures et rapports du bouclier dorsal et du disque ventral d'*Europrotaspis? wiheriesiensis* d'après les collections de Polytech'Mons, Belgique, suivant les définitions de Blicek (1984, fig. 1). Les mesures sont en mm. Légendes : laT- largeur totale du bouclier dorsal, LoT- longueur totale du bouclier dorsal, laR- largeur rostrale, LoR- longueur rostrale, laP- largeur pinéale, laD- largeur du disque dorsal, LoD- longueur du disque dorsal, LoO- longueur orbitaire, LoB- longueur branchiale, laV- largeur du disque ventral, LoV- longueur du disque ventral. Abréviation : juv.- juvénile.

preserved. It is composed of traces of fine dentine ridges (7 ridges per mm on FPMS 7156a; 8/mm on FPMS 7149a, Pl. I: E) that are parallel to the posterior boundary of the plate.

Pineal plate. The pineal plate is quadrangular in shape (Fig. 3 B) and ca. 15 mm wide (Table 1). The occurrence of two small infilled pores on the right half of specimen FPMS 7156a seems to indicate that the pineal plate is crossed by the pineal canal. Laterally, the pineal plate comes into contact with the orbital plates on a length of 4.7 mm; this suture is slightly convex. The orbito-pineal belt is continuous (Fig. 3 B; Pl. I: B).

Orbital plates. The orbital plate has a moderately long median process which joins the edge of the pineal plate and completely separates the rostral plate from the dorsal disc. Its anterior and posterior processes are short (Fig. 3 A-B; Pl. I: C), so that the orbital plate is only ca. 16 mm long on the lectotype (Table 1).

Dorsal disc. Present on many specimens, this disc is rarely connected with other plates except on both the lectotype and paralectotype. It is affected by deformations of tectonic origin such as lengthening, crushing and/or distortion (e.g. on Pl. I: F). It is heart-shaped and almost as broad as long (Fig. 3A; Pl. I: C, D, F; Pl. III: A, D). Its size is variable: from 70 to 115 mm in length, and from 66 to 105 in width (Table 1). One very small specimen, FPMS 7154 (Pl. II: C), is attributed to a juvenile individual (width 32 mm, length ca. 31 mm). Its width/length ratio (laD/LoD 103.2 %, Table 1) shows that it is a bit wider than long, which is unusual for this species. The degree of curvature of the dorsal disc is difficult to estimate when the specimens are crushed (flattened) or broken.

Dorsal spine. It is not preserved, but the lectotype FPMS 7156b (Fig. 3A) shows a notch at the posterior median part of the dorsal disc; this notch is 3 mm wide, and 15 mm long. The ornamentation is not visible here, most probably because of the crushing of the spine (see Leriche, 1925). The specimen FPMS 7164, a large dorsal disc in visceral view (Pl. III: A), shows the base of the dorsal spine that is fused to the dorsal disc and is 19 mm long and 8 mm wide.

Branchial plates. The branchial plates are very long and arcuate (Fig. 3A; Pl. I: C-D); narrow in their anterior part,

they widen backwards. They correspond to more than a third of the total length of the dorsal shield (LoB/LoT 66.6 – 77.2 %, Table 1), which is rare among pteraspids (see, e.g. Blicek, 1984). They follow the posterior edge of the dorsal disc and continue rearwards while bending towards the median part of the shield. Their posterior termination is never well preserved, and the pattern of their relationships to the cornual plate and branchial openings is undefined (Fig. 3C, Pl. I: A). Their ridges of dentine are longitudinal, and 7/mm on FPMS 7156a.

Branchio-cornual region. As said here above, in absence of a preserved cornual plate, the branchial-cornual region is unknown. Detail of the left posterior part of specimen FPMS 7156a (Fig. 3 A, C, and Pl. I: A, C) shows two areas corresponding to holes within the specimen. If there was a small cornual plate on this species, it may have been located along the most posterior part of the dorsal disc, where the branchial plate has turned towards the median plane of the specimen, as in *Europrotaspis* itself (Blicek, 1984, fig. 47 A, C); alternatively there was no cornual plate, and the branchial opening was located at the tip of the branchial plate as in *Protaspis* (Blicek, 1984, fig. 49).

Ventral disc. The ventral disc is mostly oval, with a posterior median bulge (Pl. III: C-D). This bulge corresponds to the ventral outer-directed convex part of the carapace, that was continued by the ventral ridge scales of the trunk on the living animal. This bulge is relatively more pronounced on the specimen FPMS 7148a (Pl. III: C) than on the specimen FPMS 7150 (Pl. III: D). This difference may be due to differential growth or to deformations of tectonic origin. Larger ventral discs are 50 to 88 mm wide (laV, Table 1), and 61 to 115 mm long (LoV, Table 1). Smaller ventral discs, as e.g. FPMS 7151a (Pl. II: A) or 7167, interpreted as being from juvenile individuals, have a rounder shape, with a bigger width/length ratio (Table 1: laV/LoV 87.5 to 89.2 %) than larger discs, interpreted as being from adult individuals (Table 1: laV/LoV 76.5 to 82.4 %). This is probably the result of positive allometry in growth of the ventral disc. Exceptionally, the specimen FPMS 7142 is a medium-sized ventral disc with a nearly circular shape (Pl. III: B; Table 1: laV/LoV 98.5 %); however, even if partially fractured, it does not seem to have been tectonically distorted.

Figure 5. cf. *Europrotaspis?* *wiheriesiensis* from La Pérère quarry, Paliseul (quarry n° 2 of Asselberghs, 1955), province of Luxembourg, Belgium; “Schistes aimantifères de Paliseul”, equivalent of the Saint-Hubert Formation; late Lochkovian Siß to Z spore zones; *Althaspis leachi* Biozone. Partially preserved dorsal shield with its dorsal disc (D), right branchial plate (B), possible cornual platelets (C?) and right branchial opening (bro), with a detail of the branchio-cornual region on the right.

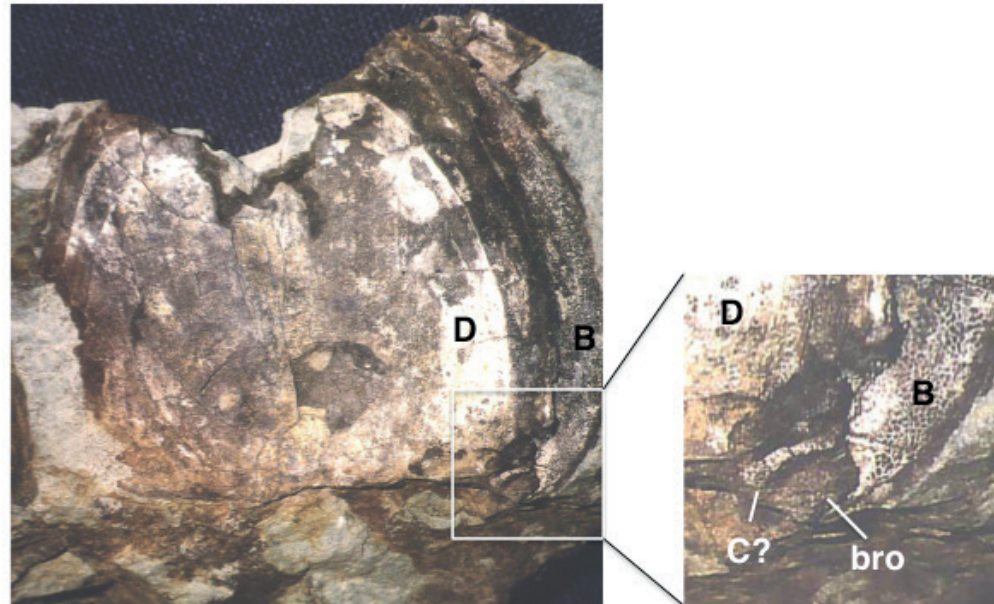


Figure 5. cf. *Europrotaspis?* *wiheriesiensis* de la carrière de La Pérère à Paliseul (carrière n° 2 d'Asselberghs, 1955), province de Luxembourg, Belgique; « Schistes aimantifères de Paliseul », équivalent de la Formation de Saint-Hubert; zones de spores Siß à Z, Lochkovien supérieur; Biozone à *Althaspis leachi*. Bouclier dorsal partiellement conservé avec son disque dorsal (D), sa plaque branchiale droite (B), ses plaquettes cornuales possibles (C?) et son ouverture branchiale droite. Détail de la région branchio-cornuale sur la droite.

Sensory line system. Only part of the sensory line system has been observed, mostly after the traces of the canals within the bone, left by crushing of the cancellous layer of the bone around the fine-sandstone-filled sensory canals (e.g. Pl. I: F), or after their outer natural moulds left on the sandstone matrix. The supra-orbital canals, on the dorsal lamina of the rostral plate, are subparallel (soc, Fig. 4A). On the dorsal disc, part of the median dorsal longitudinal canals (ld, Fig. 4) has been observed: they diverge from the rear part of the disc, towards the supra-orbital canals (Fig. 4A). The three pairs of transverse commissures are very posteriorly located on the dorsal disc (cmd_{a-c}, Fig. 4); the most anterior ones (cmd_a) diverge and end at the contact with the dorsal lamina of the branchial plates (Fig. 4 A-B) or more anteriorly on the larger disc (Fig. 4D). The second transverse commissure (cmd_b) has a very curved course and joins the first one (Fig. 4A, B, C). The third pair of transverse canals has not been fully reconstructed (cmd_c, Fig. 4C). Ontogenic variations of the pattern of the sensory canals are visible (Fig. 4). On the juvenile individuals (Fig. 4C), the transverse commissures are nearly straight and diverge slightly towards the side edges of the plate. On the adult individuals (Fig. 4 A, B, D), they have curved courses and diverge strongly towards the front part of the dorsal disc. Several dorsal discs show growth stages (e.g. Pl. I: C, D, F; Pl. III: A, D). The smallest one, tentatively interpreted here as the first one (1 on Fig. 4A), shows the same simple pattern of sensory canals as a small disc interpreted as a juvenile specimen (FPMS 7154, Fig. 4 C and Pl. II: C). This thus identifies allometric growth of the dorsal disc, where the course of the canals is redirected frontwards during addition of successive growth zones to the front and the lateral edges of the disc.

Ornamentation. There are 7 ridges of dentine per mm on nearly all measured plates. Ridges appear to be very worn.

Squamation. Only few scales are preserved among the studied material. A series of 6 disarticulated flank scales is preserved on side of the ventral disc of the specimen FPMS 7150 (Pl. III: D). The best preserved one (Pl. III: E) is rhombic, a classical shape for pteraspid heterostracans. Its convex external face is covered of rows of small transverse dentine elements,

parallel to the anterior edge of the scale. This scale is 1 cm long and 1.2 cm wide; its original location upon the flank of the animal is unknown.

Discussion. An important problem to solve is the assignment of the species *wiheriesiensis* to a genus. Some characters such as the pineal plate (quadrangular and in contact with both orbital plates), the sensory canal system (with transverse commissures being located in the rear part of the dorsal disc) and the long branchial plates, are characteristic of both genera *Europrotaspis* and *Protaspis* (see references in the review of Blicek, 1984, fig. 47, 49 — however, the location of transverse commissures in the rear part of the disc is a general character of pteraspids due to the forward growth of the dorsal disc that leaves the first formed canals behind, and it cannot be used as a diagnostic feature). However, the pineal plate of the lectotype FPMS 7156 a-b (Fig. 3 A-B, Pl. I: B-C) is V-shaped, with both anterior and posterior sutures curved (convex) rearward, contrary to the pineal plate of *Europrotaspis crenulata* and *E. arnelli* whose anterior suture is not curved rearward (Blicek, 1984, fig. 47 A, C), and to *Protaspis bucheri*, *P. dorfi* and *P. macgrewi* whose posterior suture is more arched rearward (*ibid.*, fig. 49 A-C). *Europrotaspis* being a European genus (discovered in both Great Britain and Ukraine [Podolia]), it seems more likely to compare, at a first glance, the material of Wihéries to *Europrotaspis* than to *Protaspis*, which is endemic to western USA. However, the cornual plate of *wiheriesiensis*, if it existed, is unknown, and cannot be compared to the pattern of the branchio-cornual region of *Europrotaspis* which, according to White (1961, fig. 16 and 20), presents a branchial opening being limited laterally by a narrow cornual plate located at the posterior-side corner of the dorsal disc. In the Master's thesis work of Pille (2004; see also Pille et al., 2004, fig. 1), the morphology of the posterior part of the left branchial plate of FPMS 7156 was interpreted with an enclosed branchial opening between the dorsal disc and the branchial plate; however, discussion with Prof. D.K. Elliott (Northern Arizona University, USA), during a visit to Villeneuve d'Ascq in June 2013, lead to the conclusion that the drop-shaped area located between the dorsal disc and the branchial plate (Fig. 3 C, and Pl. I: A) does not correspond to the branchial opening, but to a gap (hole) in the specimen. So, the generic attribution of *Protaspis wiheriesiensis* BROTZEN 1936 remains uncertain, and I keep it inside *Europrotaspis* with a question mark.

cf. *Europrotaspis?* *wiheriesiensis*
(Fig. 5)

Material. This taxon is represented by two specimens, that is, a partial dorsal shield and a partial ventral disc. They come from

La Pérère quarry of Paliseul (quarry n° 2 of Asselberghs, 1955; same age as the *Althaspis leachi* material from Paliseul – see the corresponding section here below). They have been collected by an amateur and their photographs transmitted by Stephan Van de Walle, a former student of the University of Liège in 2004. This material has been deposited in the collections of this university [However, S. Van de Walle is no more in contact]. Due to its morphology, it is worth being described.

Description and comparison. Both specimens fit the size and shape of the dorsal shield and ventral disc of *Europrotaspis? wiheriesiensis*. The most interesting specimen is the dorsal shield. It is incomplete but shows most of its posterior part, including the dorsal disc, right branchial plate, and what seems to be a multi-element cornual plate (Fig. 5). The dorsal disc is very large and heart-shaped as in the dorsal disc of *E.? wiheriesiensis* (Fig. 4). The right branchial plate is very similar to the branchial plate of *E.? wiheriesiensis* (Fig. 3A), that is, very long and arched. It goes down to the posterior lateral corner of the dorsal disc, where it turns mediad and bears the external branchial opening (bro, Fig. 5). This opening is bounded antero-medially by a series of three small bony elements (C?, Fig. 5). This is very similar to the morphology of the branchio-cornual region of *Rodenaspis brevispina* (Denison, 1970, fig. 11: “*Protaspis (Protaspis) brevispina* n. sp.”; see Blicek, 1984, fig. 50 C) which also shows a series of three small platelets at the posterior lateral corner of the dorsal disc. These platelets “line the medial side of the branchial duct” and have been interpreted as a possible cornual plate system by Denison (1970, p. 17). If it can be confirmed that the specimen from La Pérère quarry is of *Europrotaspis? wiheriesiensis*, it would bring a solution to the question of the branchio-cornual region of this species (see the corresponding section here above). Additionally, if it is confirmed that it is related to the protaspidid *Rodenaspis*, it would bring both a solution for the phylogenetic relationship of *E.? wiheriesiensis*, and an indication of palaeobiogeographic relationships between the Ardenne and Wyoming (USA) in the Early Devonian.

Family Pteraspidae CLAYPOLE, 1885 [*sensu* Pernègre & Elliott, 2008]

Genus *Althaspis* ZYCH, 1931

Althaspis leachi (WHITE, 1938)

(Pl. II: B, D-H; Pl. IV: A-G)

Preliminary remark. A full list of synonyms for this species has not yet been produced. The name *leachi* was introduced for the first time by White (1938, p. 87) as a ‘variety’ of *Pteraspis (Rhinopteraspis) dunensis* (Roemer) for new material from the Lower Devonian of Swanlake Bay, Pembrokeshire, in South Wales. It is now accepted as a separate species of the genus *Althaspis*, and the correct binomen is ‘*Althaspis leachi* (WHITE, 1938)’ [see Blicek & Jahnke, 1980, table 1; Blicek, 1984, p. 68; Blicek & Goujet, 1991, p. 69]. However, the Web site of the Paleobiology Database introduced a mistake in the nomenclature of this species. This online database did indeed display the following binomen: “†*Althaspis leachi* White 1934” (PDB, 2013a) according to informations gathered from the book of Dineley & Metcalf (1999, Chapter 4: Early Devonian fossil fishes sites of the Welsh Borders; PDB, 2013b). However, there are two different citations of *Althaspis leachi* in that chapter of Dineley & Metcalf (1999): ‘*Althaspis leachi* (White, 1938)’ (*ibid.*, p. 113) and ‘*Althaspis leachi* White, 1934’ (*ibid.*, p. 139), but the reference ‘White, 1934’ is not given in the reference list, contrary to ‘White, 1938’. As said here above, the correct binomen of the species is ‘*Althaspis leachi* (WHITE, 1938)’. So, the citation ‘*Althaspis leachi* White, 1934’ is totally incorrect. Finally, it appears that the Paleobiology Database has been partly corrected, as concerned with the year of authorship, as it now cites the species as follows : ‘†*Althaspis leachi* White 1938’ (PDB, 2014). The lists of synonyms here below take only into account the material from Wihéries and Paliseul.

Althaspis leachi from Wihéries.

- v.1925 *Pteraspis dunensis* F. Roemer.- Leriche, fig. 3, pl. II: 1-1a, 2-2a, pl. III: 1-3, pl. IV: 2.
- v.1926 *Pteraspis dunensis* F. Roemer.- Leriche, figs 1, 2 and 3, pl. III: 1-3, pl. IV: 1-2.
- 1932 *Drepanaspis*.- Maillieux, p. 8. [*vide* Gross, pers.comm.]
- 1933 *Drepanaspis schrieli*.- Gross, p. 56. [for specimen FPMS 183: Leriche, 1926, pl. III: 3, and pl. IV: 1-1a; after pers. obs. in the FPMS collection]
- ?1936 *Pteraspis dunensis*.- Maillieux, p. 29.
- 1937 *Pteraspis dunensis* (Roemer).- Gross, p. 7-9. [for specimen FPMS 183, *ibid.*]
- 1938 *Pteraspis dunensis* (Roemer) var. *leachi* nov. - White, p. 98-99.
- ?1940 *Pteraspis dunensis* F. Roemer.- Maillieux, p. 5.
- 1946 *Pteraspis dunensis*.- Asselberghs, p. 118.
- v.1948 *Pteraspis dunensis* F. Roemer.- Leriche, pl I: 1.
- .1956 *R. leachi*.- White, p. 4.
- 1965 *Drepanaspis schrieli* Gross.- Tarlo, p. 34. [*vide* Gross, 1933]
- 1968 *Pteraspis dunensis*.- Lecompte, p. 30.
- .1980 *Althaspis leachi* (White).- Blicek & Jahnke, p. 373-374.
- v.1982 *Althaspis leachi*.- Blicek, p. 13 and fig. 2c.
- v.1984 *A. leachi*.- Blicek, p. 33 and fig. 9c.
- 1991 *Pteraspis leachi*.- Gerrienne, p. 288.

Material. One specimen comes from Wihéries, Racheneur quarry, upper level f1: FPMS n° 7144 (fragment of a juvenile ventral disc). This level is dated of the late Pragian Su spore Zone (Stemans, 1989, p. 67-69 and 230-231) and corresponds to the *Rhinopteraspis dunensis* Biozone (*Dunensis* zone in Blicek & Jahnke, 1980, p. 373).

All the other specimens come from Wihéries, Racheneur quarry, lower level f2 — “Grés de Wihéries”, a lateral equivalent of the Bois d’Ausse Formation; late Pragian Su spore Zone (Stemans, 1989, p. 67-69 and 230-231); *Althaspis leachi* Biozone (*Leachi* zone in Blicek & Jahnke, 1980, p. 373-374):

a) *A. leachi* : FPMS n° 7145 (dorsal lamina in external natural mould of a rostral plate with the orbito-pineal region; Pl. II: E-F), 7152 a-b [anterior part of a dorsal disc and right orbital plate (part and counterpart); Leriche (1925, Pl. IV: 3-3a); Pl. II: G-H], 7157 (adult? dorsal disc, mostly preserved as internal mould, with preserved bone on lateral edges; Pl. II: B), 7161 (left anterior part of a ventral disc, mostly in internal mould), 7172 (anterior part of a juvenile ventral disc), 7173 (part of a dorsal disc), 7174 (part of an adult ventral disc), 7175 (posterior part of a rostral plate), 7177 (internal mould of an incomplete, adult dorsal disc), and 7185 a-b (ventral disc: a) mostly internal mould with the rear part lacking, b) external mould);

b) *A. leachi* ? : FPMS n° 7155 a-b [small ventral disc (part and counterpart); Leriche (1926, Pl. II: 3); Pl. II: D], 7162 (crushed anterior part of an adult ventral disc), and 7180 (fragment of dorsal? disc).

All the other specimens of *A. leachi* from the Racheneur quarry have been described and figured in the papers of Leriche (1925, 1926, 1948 — see the synonymy list) and measured by Blicek (1982, 1984 — *idem*). They are curated in the ‘Faculté Polytechnique de Mons’ (Belgium).

Description and comparison. All the preserved specimens are isolated elements, and often in internal or external natural moulds. The rostral plate of *Althaspis leachi* is shaped as a lengthened isosceles triangle (White, 1938; Leriche, 1925). In the present material from Wihéries, it is represented by two specimens. FPMS 7145 is the natural mould of the dorsal face of a rostrum with part of the orbito-pineal region attached (Pl. II: E-F). Its size (35 mm wide x 66 mm long) is one of the smallest for *Althaspis* (see Blicek, 1984, fig. 9). The posterior suture of the rostral plate is regularly convex rearward. The pineal plate, although incomplete, is a V-shaped quadrangle with both anterior and posterior sutures convex rearward, and it bears 5 traces of the external pores of the pineal canal (Pl. II: F). FPMS 7175 corresponds to the posterior part of a rostral plate of a size and shape similar to FPMS 7145.

A single specimen, FPMS 7152 a-b, shows the right orbital area connected to the anterior part of a dorsal disc (Leriche, 1925, Pl. IV: 3-3a; here Pl. II: G-H). However, the orbital plate is incomplete (the anterior process being absent) and displaced onto the dorsal disc. The preserved part is 34 mm long, and the total length of the plate may be evaluated at 40-45 mm (Pl. II: H). All other specimens are isolated dorsal or ventral discs. The best preserved one is FPMS 7157, a dorsal disc, mostly preserved as internal mould, with preserved bone on its lateral edges (Pl. II: B). It is 40 mm wide and 68 mm long, thus nearly twice as short as the original *leachi* material of White (1938, fig. 1, a 125 mm long x 80 mm wide dorsal disc). This feature, combined with the size of the rostral plate FPMS 7145 (Pl. II: E), seems to indicate that this *A. leachi* material from Wihéries is of not fully grown individuals. FPMS 7157 shows 5 worn dentine ridges per mm (ri/mm) on its lateral edges. FPMS 7173 corresponds to another incomplete dorsal disc of a bigger size (ca. 60 mm wide x more than 110 mm long) with 7 ri/mm. FPMS 7185 a-b is a ventral disc, mostly preserved in internal mould with the rear part lacking (part and counterpart). It is ca. 40 mm wide (being a bit distorted transversally) and it is more than 80 mm long. FPMS n° 7155 a-b is a small ventral disc (part and counterpart, 23 mm wide x 29 mm long), doubtedly attributed to *A. leachi* (Pl. II: D), that Leriche (1926, Pl. II: 3, FPMS former specimen number 193-194) already recognized as a "bouclier ventral, légèrement écrasé, d'un très jeune individu".

Althaspis leachi from Paliseul.

- v.1955 *Pteraspis dunensis* Roemer.- Asselberghs, figs 2-3.
- .1956 *P. (Rhinopteraspis) leachi*.- White, p. 3.
- 1962 *Pteraspis leachi*.- Wo. Schmidt in Lecompte, p. 150.
- 1968 *Pteraspis leachi*.- Lecompte, p. 29.
- .1980 *Althaspis leachi* (White).- Blicek & Jahnke, p. 375.
- v.1982 *Althaspis leachi*.- Blicek, p. 15 and fig. 2d.
- v.1984 *A. leachi*.- Blicek, p. 33 and fig. 9d.

Material. The studied material of *A. leachi* from Paliseul is curated in two different collections, i.e. the Katholieke Universiteit Leuven (Afdeling Geologie) [KUL] and the Université de Liège (Département de Géologie) [ULg].

The material of *A. leachi* of the Katholieke Universiteit Leuven includes a series of 5 specimens partly figured by Asselberghs (1955). They all correspond to badly preserved internal moulds in a quartzitic sandstone: KUL n° 1 (part of a dorsal shield in internal mould; Paliseul quarry 5; Asselberghs, 1955, fig. 2), n° 2 (part of a dorsal shield in internal mould; Paliseul quarry 7; Asselberghs, 1955, fig. 3), n° 3-3a (part and counterpart of posterior part of a dorsal disc; Paliseul quarry 7), n° 4 (fragment of a dorsal disc with anterior part of dorsal spine; Paliseul quarry 7), and n° 5-5a (part of a dorsal shield in internal mould; Paliseul quarry 7). [A sixth specimen, KUL n° 6, also from Paliseul quarry 7, is attributed to cf. *E. ? wiheriesiensis* (*Europrotaspis*? sp. indet. in Blicek, 1982) — see section *Europrotaspis* here above].

The material of *A. leachi* of the Université de Liège (Département de Géologie) includes a series of three specimens collected in 2004 in the Château-du-Loup quarry, corresponding to quarry n° 4 of Asselberghs (1955). As for the specimens of Leuven, they correspond to badly preserved internal moulds of shields, embedded in a quartzitic medium-grained sandstone, with a brownish-orange alteration of the fossils: ULg Pali2004-01-1 (part of a dorsal shield mostly in internal mould; Pl. IV: D-F), ULg Pali2004-01-2 a-b (part of a large dorsal shield in external (a) and internal (b) mould; Pl. IV: A-C), and ULg Pali2004-01-3 a-b (large (adult) ventral disc in external (a) and internal (b) mould; Pl. IV: G).

Both collections are from the local lithofacies called "schistes aimantifères de Paliseul" (Asselberghs, 1955; Lecompte, 1968), that is equivalent to the "Assise de Saint-Hubert", now called Saint-Hubert Formation (Stainier, 1994). It is dated as late Lochkovian: *Leachi* Zone, upper "Gedinnian" in Blicek (1982, fig. 3; in Godefroid et al., 1994, fig. 14), late Lochkovian Siß to Z spore zones in Steemans (1989, fig. 88; also Stainier, 1994), *Althaspis leachi* Biozone of Blicek & Janvier (1989).

It must be noted that another small collection of pteraspid material from Paliseul has been observed by the author, while on visit on February 1980, in the Institut für Geowissenschaften (former Institut für Geologie und Paläontologie, Fachbereich Geowissenschaften) der Philipps-Universität, Marburg a/Lahn (Germany). It has been collected by Prof. Wo. Schmidt during a field trip in the Ardenne massif on the 24th May 1966, and it is labelled as "Stbr. Paliseul, Ob. Gedinne, mit *Pteraspis leachi*". It includes ca. 10 internal, badly preserved moulds of various ventral and dorsal discs, that may be attributed to *A. leachi* ?

Description and comparison. After the specimens KUL n° 1, 2 (Asselberghs, 1955, figs 2-3), and 5, the dorsal shield of *A. leachi* is rather large: dorsal width of the shield (laT *sensu* Blicek, 1984, fig. 1) ca. 70 mm (the specimens are partly crushed laterally); dorsal length of the shield (LoT) ca. 200 mm; width of the rostral plate (laR) 34 – 45 mm; length of the rostral plate (LoR) ca. 81 mm. This is in agreement with the original *leachi* material from South Wales where the best preserved specimens show that "we may estimate the total length of the whole dorsal shield, without the dorsal spine, at 22.8 cm" (White, 1938, p. 89), and that "the best rostrum ... is 10.3 cm long and 4.2 cm between the orbits" (White, 1938, p. 87) [see Blicek, 1982, fig. 2; 1984, fig. 9]. On specimen KUL n° 3-3a, the posterior part of a dorsal disc shows a 95 mm long dorsal spine (already noted by Asselberghs, 1955, p. 942). On specimens n° 1 and 2, the orbito-pineal belt, between the rostral plate and the dorsal disc, is V-shaped, but the sutures between the pineal and the orbital plates are hardly seen because those specimens correspond to internal moulds.

The ULg specimens of *A. leachi* from Paliseul give informations on the rostral, pineal, orbital, and median dorsal plates. Both specimens ULg Pali-2004-01-1 and Pali-2004-01-2 show a partial rostral plate. Their size is similar to the specimens in the Leuven collection. But their dorsal face only is observable. The bone has been partly removed and shows its cancellous layer (Pl. IV: A, B, F). In both specimens, the distal and the posterior right parts of the rostrum are missing. Their general shape is triangular. The side view of Pali-2004-01-1 (Pl. IV: D) makes it possible to observe the posterior depression of the rostral plate, in front of the dorsal disc. The pineal plate is preserved in the same specimens ULg Pali-2004-01-1 and Pali-2004-01-2. This plate is a V-shaped quadrangle with a rearward convex anterior and posterior suture (Pl. IV: B, F). Its external (lateral) edges are nearly parallel to each other, rectilinear, and in contact with the median processes of the orbital plates. The orbito-pineal belt is thus continuous as in all *A. leachi* specimens (e.g. White, 1938; Blicek, 1984).

The orbital plates are also visible on the specimens ULg Pali-2004-01-1 and Pali-2004-01-2. They appear to be nearly complete, but, as for the rest of both specimens, the bone is worn and shows its cancellous layer. They are in contact both with the rostral plate and the dorsal disc by mean of long median processes (Pl. IV: A, B, F), and join the median pineal plate. The visible left orbit of Pali-2004-01-1 has a diameter of 2.5 mm. The plate in front of the orbit is short and tapering. Behind the orbit, the plate is longer and its size decreases regularly. The dorsal disc is elongate (Pl. IV: E). The posterior part of the disc is more arcuate transversely than the anterior. It shows a notch for the branchio-cornual region at one third of its posterior edge, but neither the branchial nor the cornual plates are preserved. The partly preserved dorsal spine of Pali-2004-01-2b (Pl. IV: C) is slightly curved, due to probable diagenetic and/or tectonic deformation. No measurements have been made on these altered specimens of *A. leachi* of the Liège collection.

Genus *Rhinopteraspis* JAEKEL, 1919
Rhinopteraspis dunensis (ROEMER, 1855)
 (Fig. 6)

Preliminary remark. A full list of synonyms for this species has not yet been produced. The species was originally named as *Palaeoteuthis Dunensis* by Roemer (1855, p. 72-74, pl. XIII), the genus name coming from the fact that the original specimen was thought to be of a cephalopod, and orientated upside down

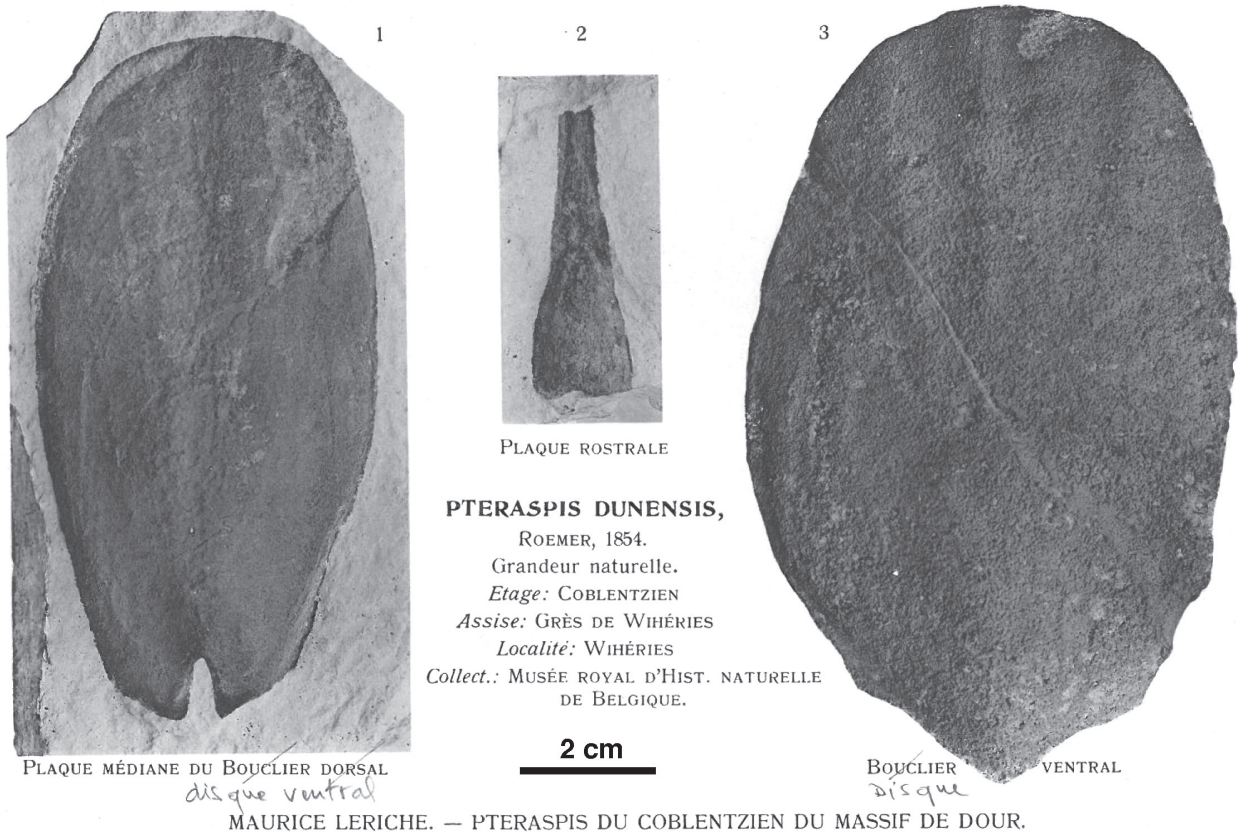


Figure 6. Facsimile of Plate E of Leriche (1912), showing the three original specimens of *Rhinopteraspis dunensis* from a quarry east of Wihéries; equivalent of the Bois d'Ausse Formation, late Pragian. 1- specimen RBINS P1322 (formerly EFP 1322), internal mould of a ventral disc; 2- specimen RBINS P1323 (formerly EFP 1323), internal mould of an incomplete rostral plate; 3- specimen RBINS P1324 (formerly EFP 1324), internal mould of a ventral disc. Annotated on the original separate of the author. Metric scale added.

Figure 6. Fac-similé de la Planche E de Leriche (1912), montrant les trois spécimens originaux de *Rhinopteraspis dunensis* provenant d'une carrière à l'est de Wihéries; équivalent de la Formation du Bois d'Ausse, Praguien supérieur. 1- spécimen IRSNB P1322 (originellement EFP 1322), moule interne d'un disque ventral; 2- spécimen IRSNB P1323 (originellement EFP 1323), moule interne d'une plaque rostrale incomplète; 3- spécimen IRSNB P1324 (originellement EFP 1324), moule interne d'un disque ventral. Annoté sur le tirage-à-part d'origine de l'auteur. L'échelle métrique a été ajoutée.

by Roemer (1855, pl. XIII; in fact a partly preserved pteraspid ventral disc). For synonyms, see in particular Jaekel (1919), White (1956, 1960), Fahlbusch (1957), Tarlo (1961, *pro parte*), Blicek (1980), Blicek & Jahnke (1980), and Friman (1986). The following list of synonyms takes only into account the material from Wihéries.

- 1912 *Hylolithes* and *Stricklandia* [sic].- Malaise in Leriche, p. 50.
v.1912 *Pteraspis dunensis*, Roemer, 1854.- Leriche, pl. E: 1-3.
1922 *Pteraspis dunensis* F. Roemer.- Asselberghs, p. B 267. [fide Leriche, 1912]
?1923 *Pteraspis*.- Racheneur, p. B 209.
?1924 *Pteraspis*.- Racheneur, p. B 90, 117, and 159.
v.1924 *Pteraspis dunensis* F. Roemer.- Leriche, p. 150; pl. IV: 1-3.
.1948 *Pteraspis dunensis* F. Roemer.- Leriche, fig. 3 and pl. I: 2-2a.
.1956 *R. dunensis*.- White, p. 4.
.1980 *Rhinopteraspis dunensis* (F.A. Roemer).- Blicek & Jahnke, p. 373.
.1982 *Rhinopteraspis dunensis*.- Blicek, p. 13.
1991 *Pteraspis dunensis*.- Gerrienne, p. 288.

Comments on the specimens from a quarry east of Wihéries.
As explained in section 2.1, the first specimens of pteraspids found in the vicinity of Wihéries came from one of the quarries, east of Wihéries, not from the Racheneur quarry (Leriche, 1912, 1948). Those three specimens were determined as a dorsal disc ("plaque médiane du bouclier dorsal", Leriche, 1912, pl. E: 1), a rostral plate ("plaque rostrale", *ibid.*, pl. E: 2) and a ventral shield ("bouclier ventral", *ibid.*, pl. E:3) of "*Pteraspis dunensis* Roemer, 1854". They are curated in the collections of the Royal Belgian Institute of Natural Sciences, Brussels (RBINS), under

the numbers P1322, P1323 and P1324 (formerly EFP 1322, 1323 and 1324). P1322 is in fact the internal mould of a ventral disc, not a dorsal disc, because of the forward-curved shape of its front suture without indentation for the pineal plate (Fig. 6: 1; Leriche, 1912, pl. E: 1); the posterior median notch observed on the specimen is not for the dorsal spine (as thought by Leriche, 1912, p. 51) but for the most anterior ventral ridge scale; this specimen was redetermined as "*Rhinopteraspis leachi*" by E.I. White who visited the RBINS collections in 1955. P1323, corresponding to the internal mould of a rostral plate (Fig. 6: 2; Leriche, 1912, pl. E: 2), was redetermined as "*Pteraspis indet.*" by E.I. White. P1324 (Fig. 6: 3; Leriche, 1912, pl. E: 3) is not a ventral shield but just the internal mould of a ventral disc, that is wider than P1322; it was redetermined as "*Protaspis wiheriesiensis*" by E.I. White (see White, 1956, 1960). In fact, all three specimens may actually correspond to *Rhinopteraspis dunensis*. The rostral plate has slightly concave lateral edges, and is tapering forward; it is longer than wide and slender (Fig. 6: 2); its shape is "très allongée et très élancée; elle s'atténue régulièrement vers l'avant" (Leriche, 1912, p. 51), and fits the shape of *R. dunensis* rostral plates (see, e.g., Fahlbusch, 1957, fig. 4). The preserved part of the plate is 44 mm long, and the complete plate was probably ca. 70 to 75 mm long. This length corresponds to the small specimens of *R. dunensis* as shown by Blicek (1980, fig. 10 B). Concerning the ventral discs, P1322 (Fig. 6: 1) is 52 mm wide (laV) and 103 mm long (LoV), with a laV/LoV ratio of 0.50; P1324 (Fig. 6: 3) is 74 mm wide (laV) and 117 mm long (LoV), with a laV/LoV ratio of 0.63. Both ventral discs have a shape and size which fit the variability of measured *R. dunensis* ventral discs (Blicek, 1980, table I), P1324 having a relatively high laV/LoV ratio. So, I propose here to maintain the original taxonomic determination of Leriche (1912) for this material from a quarry east of Wihéries, that is *Rhinopteraspis dunensis*.

Comments on the specimens from the Racheneur quarry, Wihéries. Racheneur (1923, 1924) presented to the Société Géologique de Belgique samples of arenaceous shales intercalated in the Wihéries sandstones, with “*Pteraspis*”. The quarry where the material comes from is not precisely given; but, it is most probably the quarry where Mr Racheneur was working, which has since been known as the “Racheneur quarry”. Leriche (1924, pl. IV: 1-3) described and figured a large ventral disc, attributed to *Pteraspis dunensis*, and coming from the same quarry as Racheneur’s (1923, 1924) specimens, that is the Racheneur quarry (pers. obs. in the collection of Polytech’Mons). It has been collected in the upper fossiliferous level of the quarry, i.e. level f1. It has been considered by White (1956, p. 4) as the only true *dunensis* specimen from the Racheneur quarry. This ventral disc (formerly n° 184 in the Polytech’Mons collection) is 80 mm wide (laV) and more than 165 mm long (LoV), thus having a laV/LoV ratio of ca. 0.48, and 5-6 dentine ridges per mm. These measurements fit the variability of *R. dunensis*, but this specimen corresponds to the biggest ventral discs of the species (in Blieck, 1980, table I). A second specimen comes from the upper level f1, it is a fragmentary branchial plate (Leriche, 1948, fig. 3 and pl. I: 2-2a) that can be attributed to *R. dunensis* (Blieck & Jahnke, 1980, p. 373; also Blieck, 1982, p. 13). [However, this specimen was not observed in the Polytech’Mons collection when I visited it in 1978.] The upper level f1 corresponds to the *Rhinopteraspis dunensis* Biozone (*Dunensis* zone in Blieck & Jahnke, 1980, p. 373), and to the late Pragian Su spore Zone (Stemans, 1989, p. 67-69 and 230-231). The material of *R. dunensis* from a quarry east of Wihéries (see the section here above) does probably correspond to the same biostratigraphic level. However, apart from *R. dunensis* itself, formal correlation arguments are missing.

Pteraspidae gen. et sp. indet. 1
(Pl. III: F)

Material. Specimens FPMS 7171 (fragments of a disc), 7178 (fragments of dermal plates showing the structure of the middle layer), 7179 (an incomplete, rhombic flank scale), 7181 (very worn fragments of dermal plates), 7184 (fragment of a dermal plate and mould of a ridge scale), and 7186 a-b (part of a dorsal shield: a) internal mould, b) external mould), all from Wihéries, Racheneur quarry, lower level f2 (*Althaspis leachi* Biozone, late Pragian Su spore Zone). Specimens ULg Pali2004-01-5 (ventral disc; Pl. III: F), and ULg Pali2004-01-6 a-b (fragments of dermal plates in internal (a) or external (b) mould), both from Paliseul, Château-du-Loup quarry (*Althaspis leachi* Biozone, late Lochkovian Sif to Z spore zones).

Description. All these specimens are fragmentary pteraspidae remains of mostly internal moulds of various plates and scales. A single one is figured here (ULg Pali2004-01-5, Pl. III: F) and represents the worn visceral face of a ventral disc, showing part of the lamellar basal layer and part of the cancellous layer of the bone; it is 64 mm wide and more than 80 mm long. It cannot be attributed with certainty to any of the three pteraspidae species recognized in both Wihéries and Paliseul.

Pteraspidae gen. et sp. indet. 2

Other undetermined pteraspidae material has been collected by C. Hendrickx, a former student of the University of Liège. This material comes neither from Wihéries nor from Paliseul, but from the La Gileppe Dam section in eastern Belgium (see, e.g., Stemans, 1989, p. 70-72). It has been collected during a field-trip guided by Ph. Stemans, and comes from the Lochkovian-Pragian transitional beds of the Bois d’Ausse Formation (pers. comm. Ph. Stemans to Prof. E. Poty – e-mail dated 20 Nov. 2014) [see Stemans, 1989, fig. 25; Dejonghe et al., in Godefroid et al., 1994, p. 107-111]. It includes fragments of various plates and two internal moulds of ventral discs that have been deposited in the collection of the University of Liège under numbers 2014.11.201 to 2014.11.20n.

Superclass Gnathostomata GEGENBAUR, 1874
Clade Eugnathostomata [*sensu* Turner et al., 2010]

†Class Acanthodii OWEN, 1846
Acanthodii indet.
(Pl. III: G)

Material. Specimen ULg Pali2004-01-4: fragments of squamation and spines; Paliseul, Château-du-Loup quarry (Pl. III: G).

Description and comparison. This is a large fragment of a squamation composed of small (ca. 1 mm²) square scales seen from their base. This base is globular as in all acanthodian scales (e.g. Denison, 1979). The fragment is 140 mm long x 88 mm wide, with a few fragments of spines. Both the scales and spines are worn in a white matter that contrasts well with the dark brown colour of the sandy matrix. Other isolated altered scales are dispersed all over the block of sandstone where the squamation comes from. It is similar to the ischnacanthiform acanthodian *Nerepisacanthus denisoni* Burrow (2011, figs 2 A-D and 3 A-B) represented by a partially articulated specimen. However, on specimen ULg Pali2004-01-4, the scales are grouped into concentric rows. Owing to the occurrence of fragmentary spines, it may represent the mid-region of the fish between the pectoral and pelvic fin spines, as on *Nerepisacanthus*. Nevertheless, the specimen ULg Pali2004-01-4 would need more preparation in order to go further in its taxonomic determination.

4. Conclusion

This monographic paper redescibes the pteraspidae fauna of two Early Devonian localities of the Ardenne in Belgium, viz. Wihéries (late Pragian, both *Althaspis leachi* and *Rhinopteraspis dunensis* biozones) and Paliseul (late Lochkovian, *A. leachi* Biozone), with addition of new material collected in the field from Paliseul, and La Gileppe in eastern Belgium. This fauna has been described in a series of papers in the early 20th Century, under various species names (where all large bony plates, either rostral, ventral or dorsal, were attributed to *Pteraspis dunensis* F. Roemer), which did not help to clearly understand what species are really present. The present paper thus aims at clarifying the taxonomy through a review of all papers and published specimens. It confirms that the *A. leachi* Biozone spans the Lochkovian-Pragian boundary because it is late Lochkovian in age in Paliseul, and late Pragian in Wihéries. The fauna of the lower fossiliferous level (f2) of Wihéries (Racheneur quarry) includes a protaspidae pteraspidae, *Europrotaspis? wiheriesiensis*, which needed to be properly redescibes. However, a problem remains unsolved, i.e. the morphology of its branchio-cornual region. A single specimen collected by an amateur in La Périere quarry of Paliseul, here determined as cf. *Europrotaspis? wiheriesiensis*, shows such a branchio-cornual region with a series of three cornual platelets that seem similar to the cornual region of *Rodenaspis brevispina* from the USA. Finally, the pteraspidae from the upper level (f1) of Wihéries (Racheneur quarry) and from an ancient quarry east of Wihéries is confirmed as *Rhinopteraspis dunensis* (*Pteraspis dunensis* F. Roemer in the original determination of M. Leriche). It also confirms that the Racheneur quarry of Wihéries is one of the rare places where the *A. leachi* and *R. dunensis* biozones are present. The few additional specimens collected in La Gileppe are attributed to undetermined pteraspidae.

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Appendix 1 – Annexe 1

Catalogue of studied specimens – *Catalogue des spécimens étudiés*

We list here the specimens that have been studied for this paper, giving 1) the collection number, 2) the taxon name, 3) a short description, 4) the origin, and 5) eventual illustrations of each specimen. *Liste des spécimens qui ont été étudiés pour ce travail avec 1) le numéro de collection, 2) le nom de taxon, 3) une description courte, 4) l'origine, et 5) les éventuelles illustrations de chaque spécimen.*

Abbreviations – *Abréviations* : FPMS – Faculté Polytechnique de Mons (now Université de Mons, Polytech'Mons, Département Mines-Géologie : Géologie fondamentale et appliquée) ; KUL – Katholieke Universiteit Leuven (Afdeling Geologie) ; ULG – Université de Liège (Département de Géologie).

FPMS 7141, *Europrotaspis? wiheriesiensis*; anterior part of a small dorsal disc (external natural mould); Wihéries, Racheneur quarry, lower level f2.

FPMS 7142 a-b, *E.? wiheriesiensis*; nearly circular ventral disc: a) external mould, b) counterpart (ventral disc with partly preserved bone); Wihéries, Racheneur quarry, lower level f2; Pille (2004, Pl. III: B); Pl. III: B.

FPMS 7143 a-b, *E.? wiheriesiensis*; dorsal disc: a) external mould with part of visceral surface of bone, b) counterpart in internal mould; Wihéries, Racheneur quarry, lower level f2; Pille (2004, Pl. I: F); Pl. I: F.

FPMS 7144, *Althaspis leachi*; fragment of a juvenile ventral disc; Wihéries, Racheneur quarry, upper level f1.

FPMS 7145, *A. leachi*; dorsal lamina in external natural mould of a rostral plate with the orbito-pineal region; Wihéries, Racheneur quarry, lower level f2; Pille (2004, Pl. II: E-F); Pl. II: E-F.

FPMS 7146, *E.? wiheriesiensis*; left part of a dorsal disc in internal mould; Wihéries, Racheneur quarry, lower level f2.

FPMS 7147, *E.? wiheriesiensis*; large and very wide dorsal disc with branchial plates, incomplete on front and rear parts; Wihéries, Racheneur quarry, lower level f2.

FPMS 7148 a-b, *E.? wiheriesiensis*; ventral disc: a) internal natural mould, b) counterpart as external mould; Wihéries, Racheneur quarry, lower level f2; Leriche (1925, fig. 4), Pille (2004, Pl. III: C); Pl. III: C.

FPMS 7149 a-b, *E.? wiheriesiensis*; paralectotype, part of an adult dorsal shield: a) internal natural mould, b) visceral face of the shield; Wihéries, Racheneur quarry, lower level f2; Leriche (1926, Pl. II: 1), Pille (2004, Pl. I: D-E); Pl. I: D-E.

FPMS 7150, *E.? wiheriesiensis*; ventral disc in external view, partly overlapping a dorsal disc in visceral view, with a series of flank scales on side of the ventral disc; Wihéries, Racheneur quarry, lower level f2; Leriche (1926, Pl. I: 1-2), Pille (2004, Pl. III: D-E); Pl. III: D-E.

FPMS 7151 a-b, *E.? wiheriesiensis*; juvenile ventral disc: a) external mould, b) counterpart; Wihéries, Racheneur quarry, lower level f2; Leriche (1926, Pl. II: 4), Pille (2004, Pl. II: A); Pl. II: A.

FPMS 7152 a-b, *A. leachi*; anterior part of a dorsal disc and right orbital plate (part and counterpart); Wihéries, Racheneur quarry, lower level f2; Leriche (1925, Pl. IV: 3-3a), Pille (2004, Pl. II: G-H); Pl. II: G-H.

FPMS 7153, *E.? wiheriesiensis*; anterior part of a large ventral disc; Wihéries, Racheneur quarry, lower level f2.

FPMS 7154, *E.? wiheriesiensis*; very small, juvenile dorsal disc; Wihéries, Racheneur quarry, lower level f2; Leriche (1926, Pl. II: 2), Pille (2004, Pl. II: C); Pl. II: C.

FPMS 7155 a-b, *A. leachi?*; small ventral disc (part and counterpart); Wihéries, Racheneur quarry, lower level f2; Leriche (1926, Pl. II: 3), Pille (2004, Pl. II: D); Pl. II: D.

FPMS 7156 a-b, *E.? wiheriesiensis*; lectotype, nearly complete dorsal shield: a) external natural mould, b) counterpart; Wihéries, Racheneur quarry, middle level f2; Pille (2004, Pl. I: A-C); Pl. I: A-C.

- FPMS 7157, *A. leachi*; adult? dorsal disc, mostly preserved as internal mould, with preserved bone on lateral edges; Wihéries, Racheneur quarry, lower level f2; Pille (2004, Pl. II: B); Pl. II: B.
- FPMS 7158, *E.? wiheriesiensis*; anterior part of a rather large ventral disc with parallel growth zones; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7159, *E.? wiheriesiensis*; left anterior part of a large ventral disc in internal mould; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7160, *E.? wiheriesiensis*; distorted and fractured juvenile ventral disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7161, *A. leachi*; left anterior part of a ventral disc, mostly in internal mould; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7162, *A. leachi?*; crushed anterior part of an adult ventral disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7163, *E.? wiheriesiensis*; medium-sized ventral disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7164, *E.? wiheriesiensis*; large dorsal disc in visceral view; Wihéries, Racheneur quarry, lower level f2; Pille (2004, Pl. III: A); Pl. III: A.
- FPMS 7165, *E.? wiheriesiensis*; anterior part of a small dorsal disc in internal natural mould; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7166, *E.? wiheriesiensis*; external moulds of two small, incomplete dorsal discs; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7167, *E.? wiheriesiensis*; juvenile ventral disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7168, *E.? wiheriesiensis*; anterior part of a juvenile dorsal disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7169, *E.? wiheriesiensis*; anterior part of a large (adult) dorsal disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7170, *E.? wiheriesiensis?*; internal natural mould of a very incomplete dorsal disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7171, Pteraspidae gen. et sp. indet. 1; fragment of a disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7172, *A. leachi*; anterior part of a juvenile ventral disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7173, *A. leachi*; part of a dorsal disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7174, *A. leachi*; part of an adult ventral disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7175, *A. leachi*; posterior part of a rostral plate; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7176, *E.? wiheriesiensis*; external natural mould of a small dorsal disc whose right part is lacking; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7177, *A. leachi*; internal mould of an incomplete, adult dorsal disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7178, Pteraspidae gen. et sp. indet. 1; fragments of dermal plates showing the structure of the middle layer; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7179, Pteraspidae gen. et sp. indet. 1; an incomplete, rhombic flank scale; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7180, *A. leachi?*; fragment of dorsal? disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7181, Pteraspidae gen. et sp. indet. 1; very worn fragments of dermal plates; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7182, *E.? wiheriesiensis?*; fragment of a large ventral disc; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7184, Pteraspidae gen. et sp. indet. 1; fragment of a dermal plate and mould of a ridge scale; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7185 a-b, *A. leachi*; ventral disc: a) mostly internal mould with the rear part lacking, b) external mould; Wihéries, Racheneur quarry, lower level f2.
- FPMS 7186 a-b, Pteraspidae gen. et sp. indet. 1; part of a dorsal shield: a) internal mould, b) external mould; Wihéries, Racheneur quarry, lower level f2.
- ULg Pali2004-01-1, *A. leachi*; part of a dorsal shield mostly in internal mould; Paliseul, Château-du-Loup quarry; Pille (2004, Pl. IV: D-F); Pl. IV: D-F.
- ULg Pali2004-01-2 a-b, *A. leachi*; part of a large dorsal shield: a) external mould, b) internal mould; Paliseul, Château-du-Loup quarry; Pille (2004, Pl. IV: A-C); Pl. IV: A-C.
- ULg Pali2004-01-3 a-b, *A. leachi*; large (adult) ventral disc: a) external mould, b) internal mould; Paliseul, Château-du-Loup quarry; Pille (2004, Pl. IV: G); Pl. IV: G.
- ULg Pali2004-01-4, Acanthodii indet.; fragments of squamation and spines; Paliseul, Château-du-Loup quarry; Pille (2004, Pl. III: G); Pl. III: G.
- ULg Pali2004-01-5, Pteraspidae gen. et sp. indet. 1; ventral disc; Paliseul, Château-du-Loup quarry; Pille (2004, Pl. III: F); Pl. III: F.
- ULg Pali2004-01-6 a-b, Pteraspidae gen. et sp. indet. 1; fragments of dermal plates in internal (a) or external (b) mould; Paliseul, Château-du-Loup quarry.
- KUL n° 1, *A. leachi*; part of a dorsal shield in internal mould; Paliseul quarry 5; Asselberghs (1955, fig. 2).
- KUL n° 2, *A. leachi*; part of a dorsal shield in internal mould; Paliseul quarry 7; Asselberghs (1955, fig. 3).
- KUL n° 3-3a, *A. leachi*; part and counterpart of posterior part of a dorsal disc; Paliseul quarry 7.
- KUL n° 4, *A. leachi*; fragment of a dorsal disc with anterior part of dorsal spine; Paliseul quarry 7.
- KUL n° 5-5a, *A. leachi*; part of a dorsal shield in internal mould; Paliseul quarry 7.
- KUL n° 6, cf. *E.? wiheriesiensis*; fragment of a dorsal disc connected to a fragmentary branchial plate; Paliseul quarry 7.

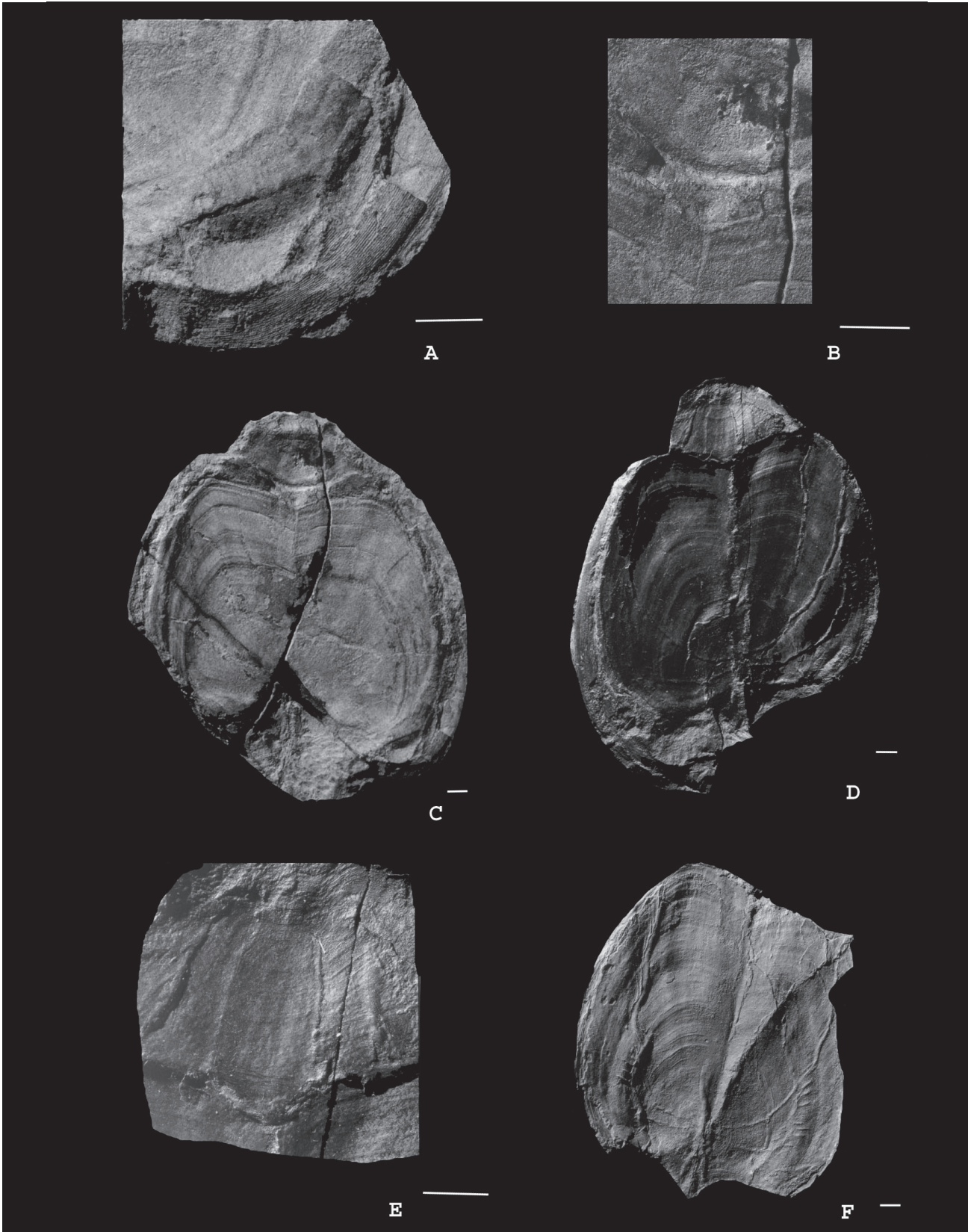


Plate I. *Europrotaspis? wiheriesiensis*, Racheneur quarry, Wihéries, province of Hainaut, Belgium; “Grès de Wihéries”, lateral equivalent of the Bois d’Ausse Formation; late Pragian Su spore Zone; *Althaspis leachi* Biozone. A-C- specimen FPMS 7156a, lectotype (from the middle level f2’); A- posterior part of the left dorsal-branchial region, B- pineal area, C- general view of the dorsal shield in external natural mould. D-E- specimen FPMS 7149b, paralectotype (from the lower level f2); D- general view of the visceral face of the dorsal shield, E- detail of the rostral plate. F- specimen FPMS 7143a (from the lower level f2), dorsal disc in external mould with part of visceral surface of bone, showing the pattern of sensory line system by crushing of the bone around the fine-sandstone-filled sensory canals. All white metric scales represent 5 mm.

Planche I. *Europrotaspis? wiheriesiensis*, carrière Racheneur, Wihéries, province du Hainaut, Belgique ; « Grès de Wihéries », équivalent latéral de la Formation du Bois d’Ausse ; Zone de spore Su, Praguien supérieur ; Biozone à *Althaspis leachi*. A-C- spécimen FPMS 7156a, lectotype (du niveau moyen f2’) ; A- partie postérieure de la région dorso-branchiale gauche, B- région pinéale, C- vue générale du bouclier dorsal en moulage naturel externe. D-E- spécimen FPMS 7149b, paralectotype (du niveau inférieur f2) ; D- vue générale de la face viscérale du bouclier dorsal, E- détail de la plaque rostrale. F- spécimen FPMS 7143a (du niveau inférieur f2), disque dorsal en moulage externe avec une partie de la surface viscérale de l’os, montrant le tracé du système des lignes sensorielles par écrasement de l’os autour des canaux sensoriels emplis de grès fin. Toutes les échelles métriques blanches représentent 5 mm.

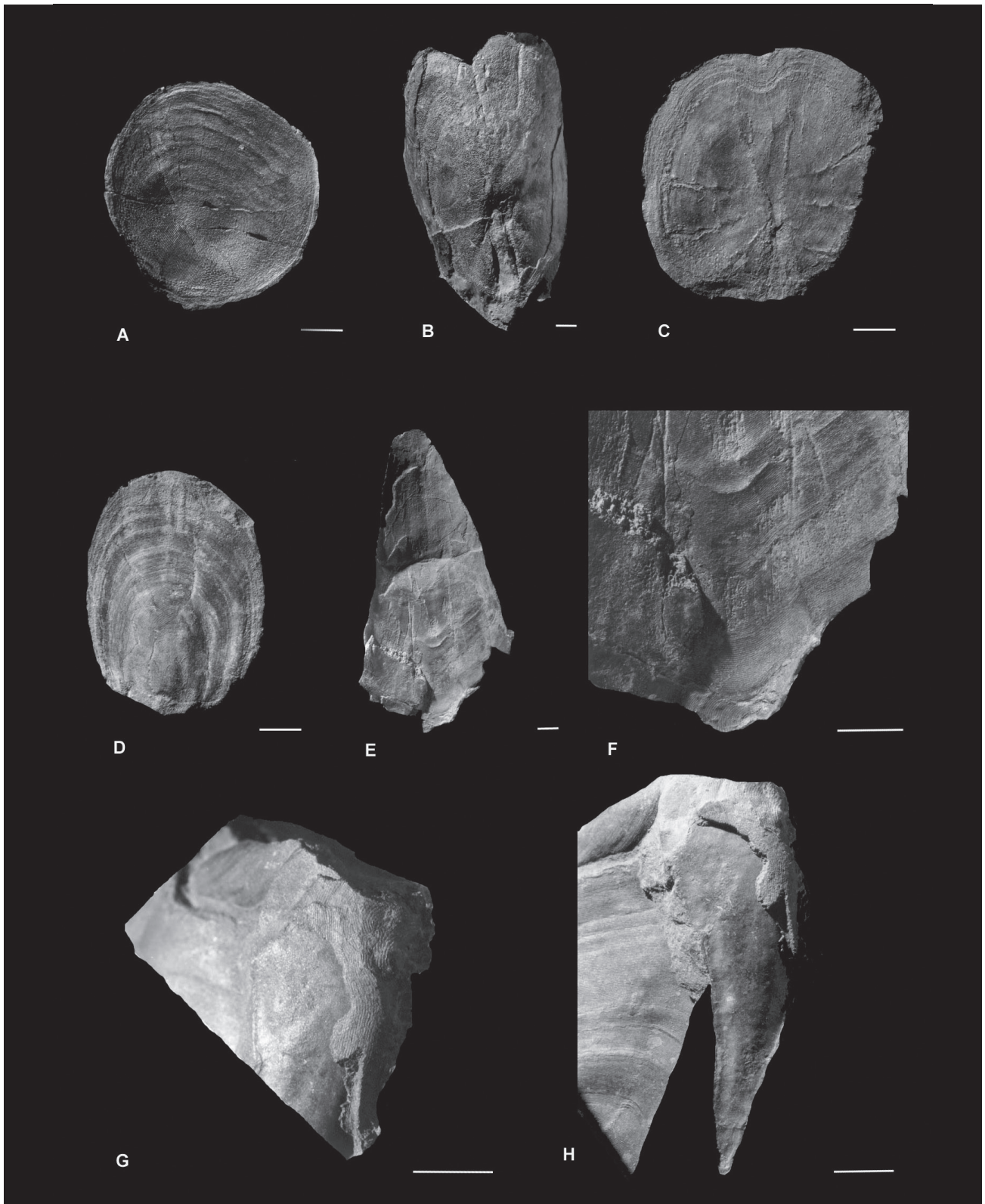


Plate II. Heterostracans from the lower level f2 of Racheneur quarry, Wihéries, province of Hainaut, Belgium; “Grès de Wihéries”, lateral equivalent of the Bois d’Ausse Formation; late Pragian Su spore Zone; *Althaspis leachi* Biozone. A- *Europrotaspis?* *wiheriesiensis*, specimen FPMS 7151a, external natural mould of a juvenile ventral disc; B- *Althaspis leachi*, specimen FPMS 7157, adult? dorsal disc, mostly preserved as internal mould, with preserved bone on lateral edges; C- *E.?* *wiheriesiensis*, specimen FPMS 7154, very small, juvenile dorsal disc, internal mould; D- *A. leachi?*, specimen FPMS 7155a, small ventral disc, internal mould. E-F- *A. leachi*, specimen FPMS 7145, dorsal lamina in external natural mould of a rostral plate with the orbito-pineal region; E- general view, F- detail of the posterior part of the rostrum with the orbito-pineal region. G-H- *A. leachi*, specimen FPMS 7152b, anterior part of a dorsal disc and right orbital plate; G- detail with the bone preserved around the orbit (on right), H- general view. All white metric scales represent 5 mm.

Planche II. Hétérostracés du niveau inférieur f2 de la carrière Racheneur, Wihéries, province du Hainaut, Belgique ; « Grès de Wihéries », équivalent latéral de la Formation du Bois d’Ausse ; Zone de spore Su, Praguien supérieur ; Biozone à *Althaspis leachi*. A- *Europrotaspis?* *wiheriesiensis*, spécimen FPMS 7151a, moulage naturel externe d’un disque ventral jeune ; B- *Althaspis leachi*, spécimen FPMS 7157, disque dorsal adulte?, conservé surtout en moule interne, avec de l’os conservé le long des bords latéraux ; C- *E.?* *wiheriesiensis*, spécimen FPMS 7154, très petit disque dorsal (jeune) en moule interne ; D- *A. leachi?*, spécimen FPMS 7155a, petit disque ventral en moule interne. E-F- *A. leachi*, spécimen FPMS 7145, lamelle dorsale d’une plaque rostrale en moule naturel externe, avec la région orbito-pinéale ; E- vue générale, F- détail de la partie postérieure du rostre et de la région orbito-pinéale. G-H- *A. leachi*, spécimen FPMS 7152b, partie antérieure d’un disque dorsal et plaque orbitaire droite ; G- détail avec l’os conservé autour de l’orbite (à droite), H- vue générale. Toutes les échelles métriques blanches représentent 5 mm.

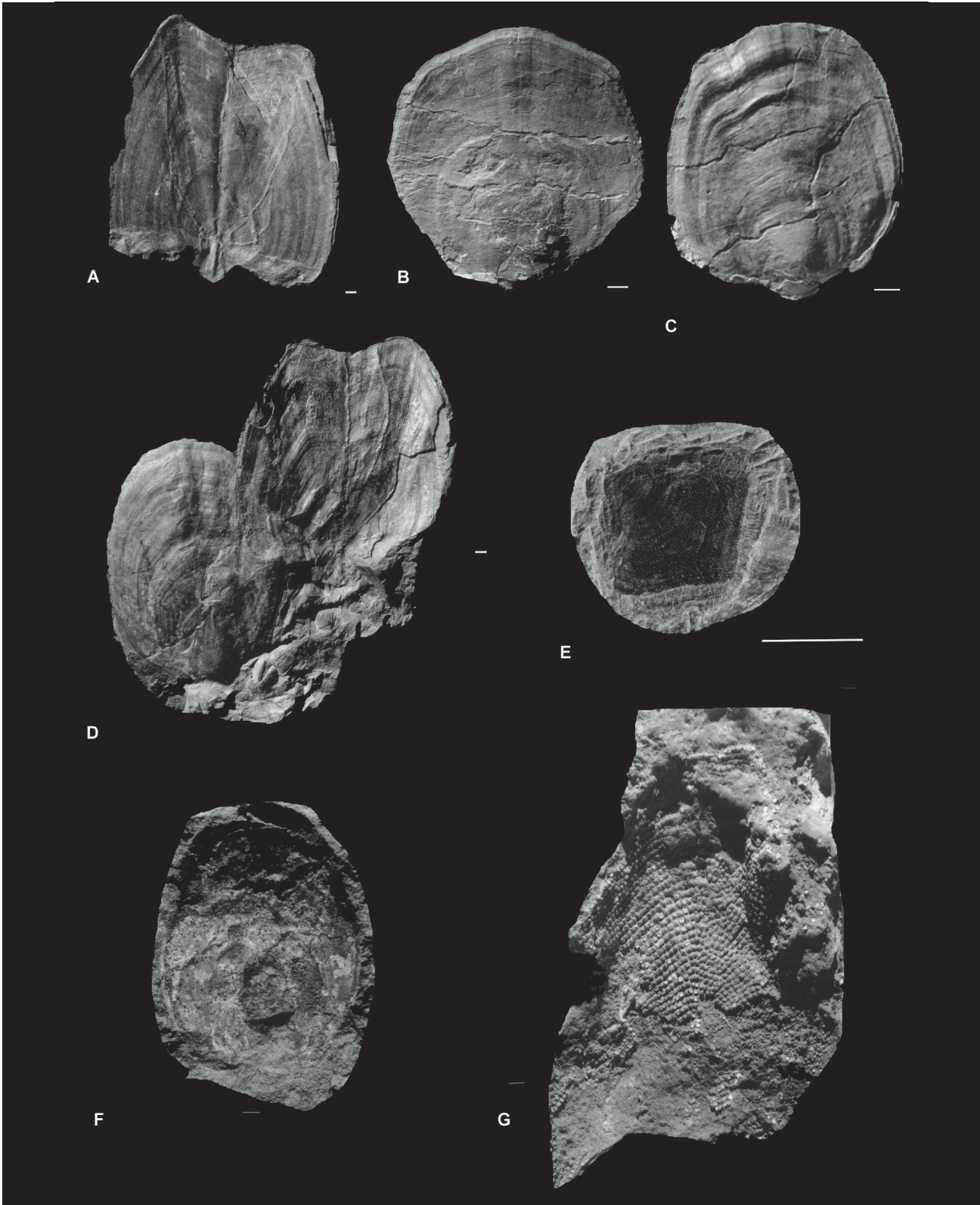


Plate III. A-E- *Europrotaspis? wiheriesiensis*, from the lower level f2 of Racheneur quarry, Wihéries, province of Hainaut, Belgium; “Grès de Wihéries”, lateral equivalent of the Bois d’Ausse Formation; late Pragian Su spore Zone; *Althaspis leachi* Biozone. A- specimen FPMS 7164, large dorsal disc in visceral view; B- specimen FPMS 7142b, nearly circular ventral disc, external surface with partly preserved bone; C- specimen 7148a, ventral disc, internal natural mould. D-E- specimen FPMS 7150, partly overlapping ventral disc, dorsal disc and scales; D- general view, E- detail of flank scale, with anterior tip at right. F-G- Vertebrates from the Château-du-Loup quarry (quarry n° 4 of Asselberghs, 1955), Paliseul, province of Luxembourg, Belgium; « Schistes aimantifères de Paliseul », equivalent of the Saint-Hubert Formation; late Lochkovian Siß to Z spore zones; *Althaspis leachi* Biozone. F- Pteraspidae gen. et sp. indet. 1, specimen ULg Pali2004-01-5, ventral disc, worn visceral face; G- Acanthodii indet., specimen ULg Pali2004-01-4, fragment of squamation. All white metric scales represent 5 mm.

Planche III. A-E- *Europrotaspis? wiheriesiensis*, du niveau inférieur f2 de la carrière Racheneur, Wihéries, province du Hainaut, Belgique; « Grès de Wihéries », équivalent latéral de la Formation du Bois d’Ausse; Zone de spore Su, Praguien supérieur; Biozone à *Althaspis leachi*. A- spécimen FPMS 7164, grand disque dorsal, face viscérale; B- spécimen FPMS 7142b, petit disque ventral quasi-circulaire, face externe avec l’os en partie conservé; C- spécimen 7148a, moule interne naturel d’un disque ventral. D-E- spécimen FPMS 7150, disques ventral et dorsal se chevauchant en partie et écailles; D- vue d’ensemble, E- détail d’une écaille des flancs. F-G- Vertébrés de la carrière du Château-du-Loup (carrière n° 4 d’Asselberghs, 1955), Paliseul, province du Luxembourg, Belgique; « Schistes aimantifères de Paliseul », équivalent de la Formation de Saint-Hubert; zones de spores Siß à Z, Lochkovien supérieur; Biozone à *Althaspis leachi*. F- Pteraspidae gen. et sp. indet. 1, spécimen ULg Pali2004-01-5, disque ventral, face viscérale altérée; G- Acanthodii indet., spécimen ULg Pali2004-01-4, fragment de squamation. Toutes les échelles métriques blanches représentent 5 mm.

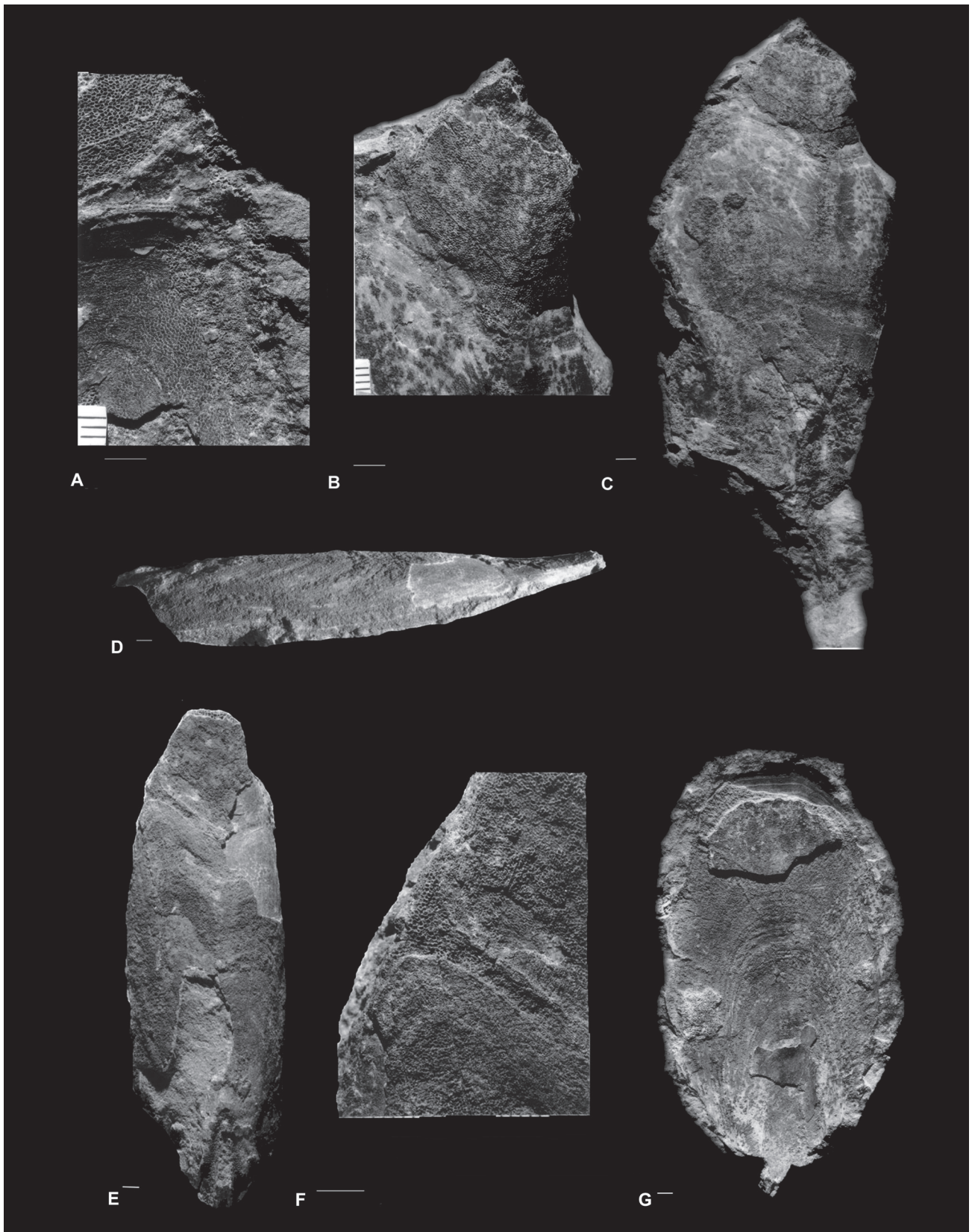


Plate IV. *Althaspis leachi* from the Château-du-Loup quarry (quarry n° 4 of Asselberghs, 1955), Paliseul, province of Luxembourg, Belgium; “Schistes aimantifères de Paliseul”, equivalent of the Saint-Hubert Formation; late Lochkovian Sifß to Z spore zones; *Althaspis leachi* Biozone. A-C- specimen ULg Pali2004-01-2 a-b, part of a large dorsal shield; A- Pali2004-01-2a, detail of left orbital region of the external mould, B- Pali2004-01-2b, detail of orbito-pineal region of the internal mould, C- Pali2004-01-2b, internal mould, general view. D-F- specimen ULg Pali2004-01-1, part of a dorsal shield mostly in internal mould; D- right lateral view, E- external dorsal view, F- detail of left orbital region. G- specimen ULg Pali2004-01-3a, large ventral disc in external mould, with pieces of bone preserved in front and rear parts. All white metric scales represent 5 mm.

Planche IV. *Althaspis leachi* de la carrière du Château-du-Loup (carrière n° 4 d’Asselberghs, 1955), Paliseul, province du Luxembourg, Belgique ; « Schistes aimantifères de Paliseul », équivalent de la Formation de Saint-Hubert ; zones de spores Sifß à Z, Lochkovien supérieur ; Biozone à *Althaspis leachi*. A-C- spécimen ULg Pali2004-01-2 a-b, partie d’un grand bouclier dorsal ; A- Pali2004-01-2a, détail de la région orbitaire gauche du moule externe, B- Pali2004-01-2b, détail de la région orbito-pinéale du moule interne, C- Pali2004-01-2b, moule interne, vue d’ensemble. D-F- spécimen ULg Pali2004-01-1, partie d’un bouclier dorsal essentiellement en moule interne ; D- vue latérale droite, E- vue externe dorsale, F- détail de la région orbitaire gauche. G- spécimen ULg Pali2004-01-3a, grand disque ventral en moule externe, avec des portions d’os conservées à l’avant et à l’arrière. Toutes les échelles métriques blanches représentent 5 mm.