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# Devonian antiarch placoderms from Belgium revisited

SÉBASTIEN OLIVE

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Anatomical, systematic, and paleobiogeographical data on the Devonian antiarchs from Belgium are reviewed, updated and completed thanks to new data from the field and re-examination of paleontological collections. The material of *Bothriolepis lohesti* is enhanced and the species redescribed in more detail. An undetermined species of *Bothriolepis* is recorded from the Famennian of Modave (Liège Province), one species of *Asterolepis* redescribed from the Givetian of Hingeon and another one described from the Givetian of Mazy (Namur Province). *Grossilepis rikiki* sp. nov. is recorded from the Famennian tetrapod-bearing locality of Strud (Namur Province) and from the Famennian of Moresnet (Liège Province). It is the first occurrence of *Grossilepis* after the Frasnian and on the central southern coast of the Euramerican continent. Its occurrence in the Famennian of Belgium may be the result of a late arrival from the Moscow Platform and the Baltic Depression, where the genus is known from Frasnian deposits. *Remigolepis durnalensis* sp. nov. is described from the Famennian of Spontin near Durnal (Namur Province). Except for the doubtful occurrence of *Remigolepis* sp. in Scotland, this is the first record of this genus in Western Europe. Its occurrence in Belgium reinforces the strong faunal affinities between Belgium and East Greenland and the hypothesis of a hydrographical link between the two areas during the Late Devonian.

Key words: Placodermi, *Asterolepis*, *Bothriolepis*, *Grossilepis*, *Remigolepis*, palaeobiogeography, Devonian, Belgium.

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## Introduction

Early studies assigned antiarchs to jawless ostracoderms (Woodward 1891; Patten 1912; Eastman 1917). Stensiö (1931) and Gross (1931) reinterpreted, independently, the antiarch remains as belonging to jawed vertebrates, to the class Placodermi, and this idea has since been widely accepted and confirmed (Moy-Thomas and Miles 1971; Denison 1975; Goujet and Young 1995). Johanson (2002) argued, based on the vascularisation of the pectoral fins, that antiarchs were not placoderms, but Young (2008) rejected that hypothesis.

Antiarchs are characterised by box-like dermal armour covering the head and thorax and by highly modified pectoral fins enclosed in interlocking dermal plates. Their geological range extends from the early Silurian (Wang 1991) to the Late Devonian (e.g., Johanson 1997a, b; Lukševičs 2001) and they include some genera with a worldwide distribution during the Late Devonian, e.g., *Remigolepis* and *Bothriolepis*.

There is no widely accepted classification of antiarchs, but the most consensual one (Janvier and Pan 1982; Young 1984; Zhu 1996; Lukševičs 2001) groups the asterolepidoids, bothriolepidoids, and sinolepids in the clade Euantiarcha (Janvier and Pan 1982). This clade, characterised by the presence of a brachial process, makes the bothriolepidoids sister group of the asterolepidoids or the sinolepids, according to different authors. The yunnanolepids are the sister group of the Euantiarcha. Lukševičs (2001) places the procondylolepids in the Euantiarcha but their position is still not resolved.

To date, Belgian antiarchs were poorly known and only few taxa have been published or mentioned in the literature. *Bothriolepis lohesti* Leriche, 1931 was the first described one but was partially known. Gross (1965) described a species of the genus *Asterolepis* from the Givetian of Belgium, and Clément and Prestianni (2009) misinterpreted the presence of *Bothriolepis* in the Belgian Famennian of two localities (i.e., Strud and Spontin).

During the Devonian, Belgium was located on the southeastern margin of Laurussia. This was a time of important sea level variations, but the progression of the sea towards the north never reached the north of Belgium. This is why Devonian strata in Belgium are located only in the south of the country, the source of the localities studied in this article (Fig. 1).



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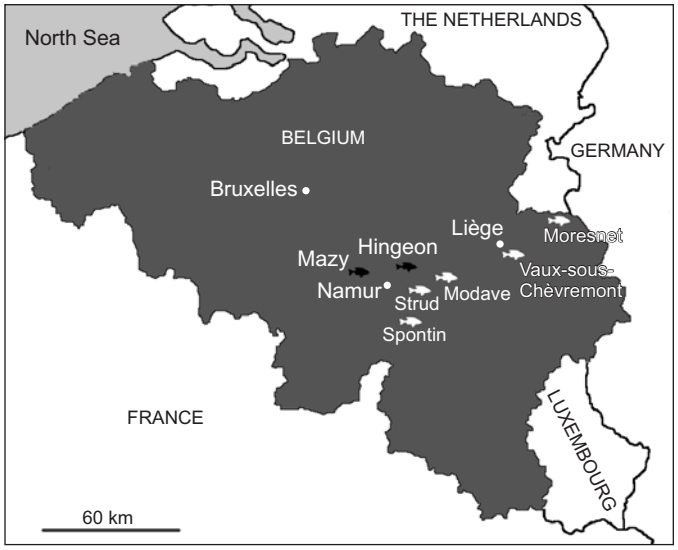



Fig. 1. Locality map of Belgian antiarch occurrences. Black fish symbols for Givetian finds; white for Famennian.

*Institutional abbreviations*.—IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; PALULG, Paleontological collections of the Université de Liège, Liège, Belgium; UCL, Université Catholique de Louvain-la-Neuve, Louvain-la-Neuve, Belgium.

*Anatomical abbreviations*.—ADL, anterior dorso-lateral plate; adlc, anterior dorso-lateral corner of PVL lateral lamina; AMD, anterior median dorsal plate; AVL, anterior ventro-lateral plate; CD1, dorsal central plate 1; CV1–4, ventral central plates; DM1–4, plates of the dorso-medial marginal series; La, lateral plate; ML1–5, plates of the lateral marginal series; MM1–4, plates of the medial marginal series; MV, median ventral plate; MxL, mixilateral plate; Nu, nuchal plate; PDL, posterior dorso-lateral plate; Pmg, postmarginal plate; Pn, paranuchal plate; Pp, postpineal plate; Prm, premedian plate; PVL, posterior ventro-lateral plate; Sm, semilunar plate; SM, submarginal plate; T, terminal plate; VM1–3, plates of the ventro-medial marginal series.

# Material and methods

All specimens have been mechanically prepared. Some have been whitened with ammonium chloride to make the observation of sensory line grooves easier. Some others have been photographed under immersion to enhance certain characters.

The limited number of samples for each taxon makes it unnecessary to use dermal plate measurement indices because they are more representative of individuals than of the taxon (Long and Werdelin 1986; Johanson 1998). Thus, the taxon descriptions are qualitative and not quantitative.

The ornament characterization (i.e., reticulate, nodose, and tuberculate) follows the definitions given by Young (1988).

The dermal skeleton of antiarchs is exemplified in Fig. 2, based on the four genera found in Belgium.

# Systematic palaeontology

Placodermi McCoy, 1848

Euantiarcha Janvier and Pan, 1982

Bothriolepidoidei Miles, 1968

Bothriolepididae Cope, 1886

Genus *Bothriolepis* Eichwald, 1840

*Type species*: *Bothriolepis ornata* Eichwald, 1840, subsequently designated by Woodward (1891); Priksha River, Russia, upper Famennian Lnyanka Beds, Devonian.

## *Bothriolepis lohesti* Leriche, 1931

Fig. 3.

1888 *Bothriolepis* or *Pterychtis* sp.; Lohest 1888: 60.
1889 *Bothriolepis*; Lohest 1889: 58.
1895 *Bothriolepis canadensis*; Lohest 1895: 39.
1931 *Bothriolepis*; Leriche 1931: 15, pl. 3.
1932 *Bothriolepis lohesti*; Gross 1932: 29.
1948 *Bothriolepis lohesti*; Stensiö 1948: 513.
1978 *Bothriolepis lohesti*; Denison 1978: 110.

*Type material*: No holotype was defined by Leriche (1931). Gross (1932) assigned as lectotype an AMD (Leriche 1931: pl. 3: 4), bearing now the number PALULG-2011.12.14.14A.

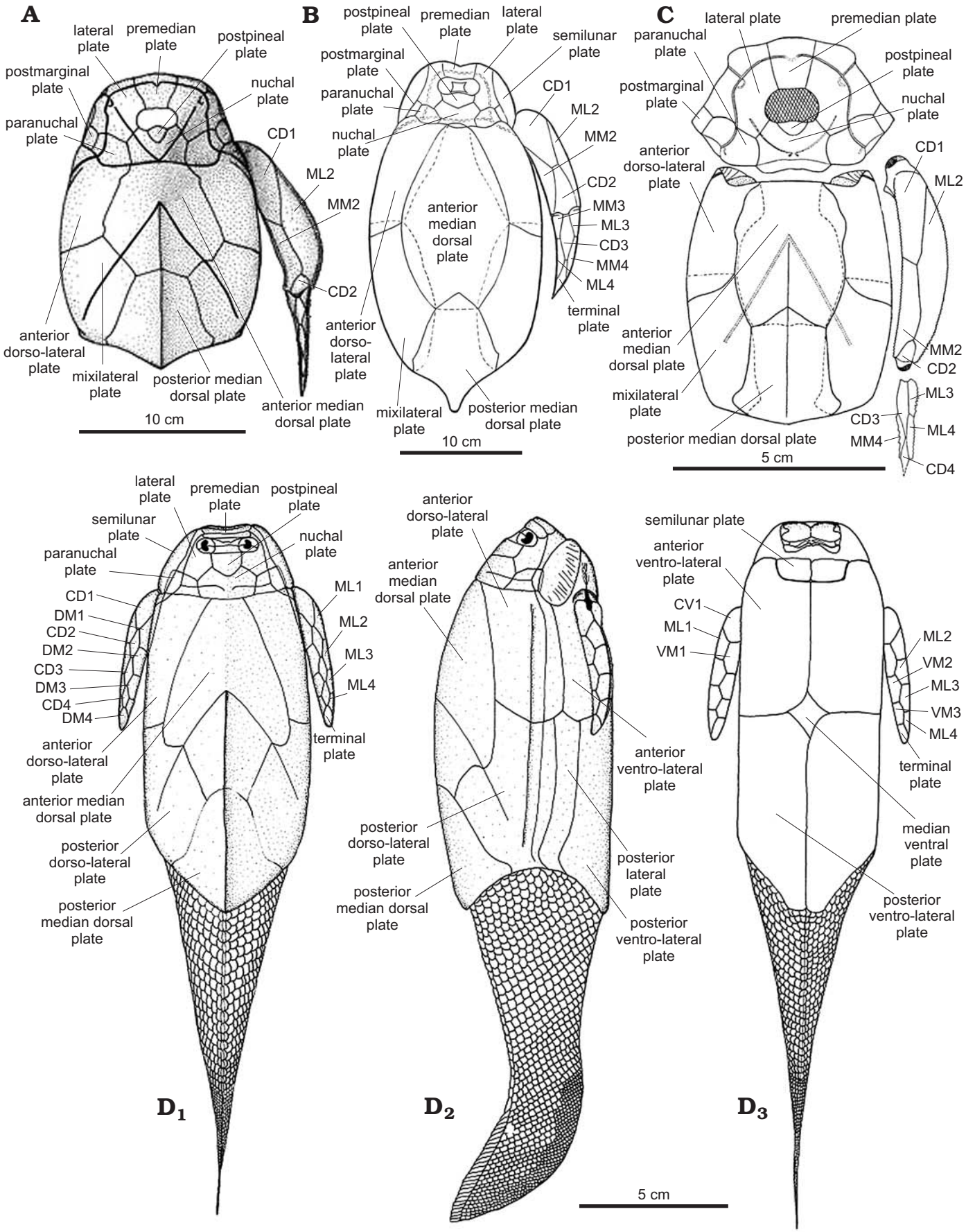
*Type locality*: Chèvremont, Liège Province, Belgium

*Type horizon*: Montfort/Evieux Formation, Famennian, Upper Devonian.

*Material*.—Partial headshield: UCL-P.V.L.10.621 (cast); AMD: PALULG-2011.12.14.15, PALULG-2011.12.14.16, PALULG-2011.12.14.17A; ADL: PALULG-2011.12.14.17B; ?ADL: IRSNB vert 5179-001; PMD: PALULG-2011.12.14.19, PALULG-2011.12.14.18; MxL: UCL-P.V.L.10.533, UCL-P.V.L.10.668; AVL: PALULG-2011.12.14.20; pectoral fin: PALULG-2011.12.14.14B, PALULG-2011.12.14.21, PALULG-2011.12.14.22; CV1: UCL-P.V.L. 10.656, PALULG-2011.12.14.23A, IRSNB vert 5179-002; ML2: PALULG-2011.12.15.9, PALULG-2011.12.15.10, PALULG-2011.12.15.11, PALULG-2011.12.15.12, PALULG--2011.12.15.13, PALULG-2011.12.14.23B. From Chèvremont and Vaux-sous-Chèvremont, both in Liège Province, Belgium, Montfort/Evieux Formation, Famennian, Upper Devonian. Chèvremont is the hill close to Vaux-sous-Chèvremont city. Old quarries and outcrops stretch between both localities. In old collections, there is often confusion between these two localities.

Fig. 2. Reconstructed dermal skeleton of the antiarch placoderm genera found in Belgium. **A**. *Bothriolepis canadensis*, dorsal view, after Werdelin and Long (1986: fig. 2). **B**. *Asterolepis maxima*, dorsal view, after Traquair (1914). **C**. *Grossilepis tuberculata*, dorsal view, after Gross (1941). **D**. *Remigolepis walkeri*, dorsal ($D_1$), lateral ($D_2$), and ventral ($D_3$) views, after Johanson (1997a). Abbreviations: CD1–4, plates of the dorsal central series; CV1, ventral central plate 1; DM1–4, plates of the dorso-medial marginal series; ML1–4, plates of the lateral marginal series; MM1–4, plates of the medial marginal series; VM1–3, plates of the ventro-medial marginal series. →

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*Description*

*Headshield.—Partial headshield* (Fig. 3A): UCL-P.V.L.10.621 displays a partial headshield with the nuchal, paranuchal, premedian, and lateral plates in connection. It is badly preserved and the plate margins are difficult to observe. However it seems that the nuchal plate is excluded from the orbital fenestra. The postpineal notch forms a strong angle posteriorly, i.e., almost 90°. The central sensory line grooves and the principal section of infraorbital sensory line are well observed.

*Trunkshield.—Anterior median dorsal plate, AMD* (Fig. 3B, C): This plate is as long as wide. Externally, it is almost flat, with only a slight bulge on the dorsal median ridge. The latter is only defined by a longitudinal row of fused tubercles on PALULG-2011.12.14.16. The tergal angle is well marked and situated between the anterior and middle thirds of the plate. It is roughly of 45°. The posterior oblique dorsal sensory line grooves are usually well defined. On PALULG-2011.12.14.14, the right posterior oblique dorsal sensory line groove is shortened or interrupted. The posterior oblique dorsal sensory line grooves run from the tergal angle and cut the posterior division of the lateral margin at the junction between its anterior and middle thirds. The anterior margin is fairly straight, except on PALULG-2011.12.14.14 where it is slightly concave and not convex as Stensiö (1948: 514) noticed. It is twice the length of the posterior margin. The antero-lateral and lateral corners are well defined. The posterior division of the lateral margin is as long as the anterior division except on the biggest AMD (PALULG-2011.12.14.14), where the posterior division is one third smaller than the anterior division. Only the right area overlapped by the mixilateral plate is observable (PALULG-2011.12.14.14). It is quite small. The posterior lateral margin displays a sigmoid shape, as observed in a specimen of *B. canadensis* (Stensiö 1948: fig. 182) and suggesting that the AMD both overlaps and is overlapped by the MxL. Internally, the AMD shows a triangular-shaped levator fossa stretching on all the anterior third length. It is limited laterally by fairly conspicuous postlevator thickenings, observable directly on PALULG-2011.12.14.16 and indirectly on impressions of the visceral surface (PALULG-2011.12.14.15 and PALULG-2011.12.14.17A). The postlevator cristae are quite sharp and high. Their confluence is located at the posterior edge of the anterior ventral pit . The median ventral ridge and ventral median groove are well marked.

*Posterior median dorsal plate, PMD* (Fig. 3D): The anterior margin is convex, with an obtuse median corner. The lateral process is well developed and extended. In fact, the margin between the lateral corner and postero-lateral corner is quite long compared to what is observed in *Bothriolepis canadensis* (Stensiö 1948: text-fig. 138A–R). The lateral margin situated in front of the lateral corner and running to the antero-lateral corner is straight. The posterior margin is convex, with an obtuse median angle. The plate is slightly arched with a low dorsal median ridge. The dorsal median ridge extends almost straight from the anterior angle to the posterior angle area.

*Anterior dorso-lateral plate, ADL* (Fig. 3E): Only the anterior part of a left ADL, in internal view, is preserved in the material. Both lateral and dorsal anterior laminae are present. The anteriormost part of the plate is hidden by a displaced AMD. The articulation area with the headshield is thus not observable. The ventral margin is convex on the preserved anterior part. The notch, for the external postlevator process of the AMD, is smooth and the postnuchal corner strongly developed. The dorso-medial margin is concave along all its preserved length. The anterior part of the lateral lamina is twice less wide than the median part. The dorso-lateral ridge is well pronounced, and the lateral lamina forms an angle of almost 150° with the dorsal lamina, but that value may be incorrect as a result of compression. The main lateral line groove is not directly observed, but suggested by a tiny edge running along the length of the lateral lamina that tends to join the dorso-lateral ridge anteriorly and to remain parallel to the dorso-lateral ridge posteriorly.

*Mixilateral plate, MxL* (Fig. 3F): As Stensiö (1948) noticed for *Bothriolepis canadensis*, the lateral lamina of MxL is often missing, crushed, compressed or damaged. It is the case in the available material of *Bothriolepis lohesti*, where the lateral lamina is crushed and damaged. Because of its bad preservation, it is difficult to evaluate the angle between the lateral and dorsal laminae. However, the specimen UCL-P.V.L.10.668 shows quite a well preserved area of transition between these two laminae and suggests that the angle is approximately 150°, as noticed for the ADL, with a sharp prominent dorso-lateral ridge. The crushed lateral lamina, in that specimen, presents a broad area overlapped by the PVL. The area overlapped by the posterior median dorsal plate is long and narrow. The posterior oblique dorsal sensory line groove crosses the anterior part of the dorso-medial margin and ends in the posterior third of the dorsal lamina.

*Anterior ventro-lateral plate, AVL* (Fig. 3G): This plate is badly preserved, with the anterior part and the lateral lamina damaged. The length of this plate is at least twice the width. The angle between the ventral and lateral laminae is roughly of 160°, and the ventro-lateral ridge is smooth. The subcephalic division is not well preserved. The posterior margin of the ventral lamina is straight and the posterior ventro-lateral corner well defined. The different portions of the medial margin seem straight but this is not obvious, because they are badly preserved. The brachial process is almost entirely damaged but the axillary foramen is observable and quite small. Internally, the crista transversalis interna anterior is well developed, as well as the transverse thickening on the visceral surface and the depression between the two cristae.

*Pectoral fin* (Fig. 3H).—PALULG-2011.12.14.22 and PALULG-2011.12.14.21 present only a part of the pectoral fin proximal segment, in ventral view. It is a long segment with the estimated width being approximately one quarter the length. It is quite incomplete because only the ventral central plate 1 and lateral marginal plate 2 are clearly preserved and connected. The margins of these plates are not well defined and the presence or absence of the ventral central plate 2

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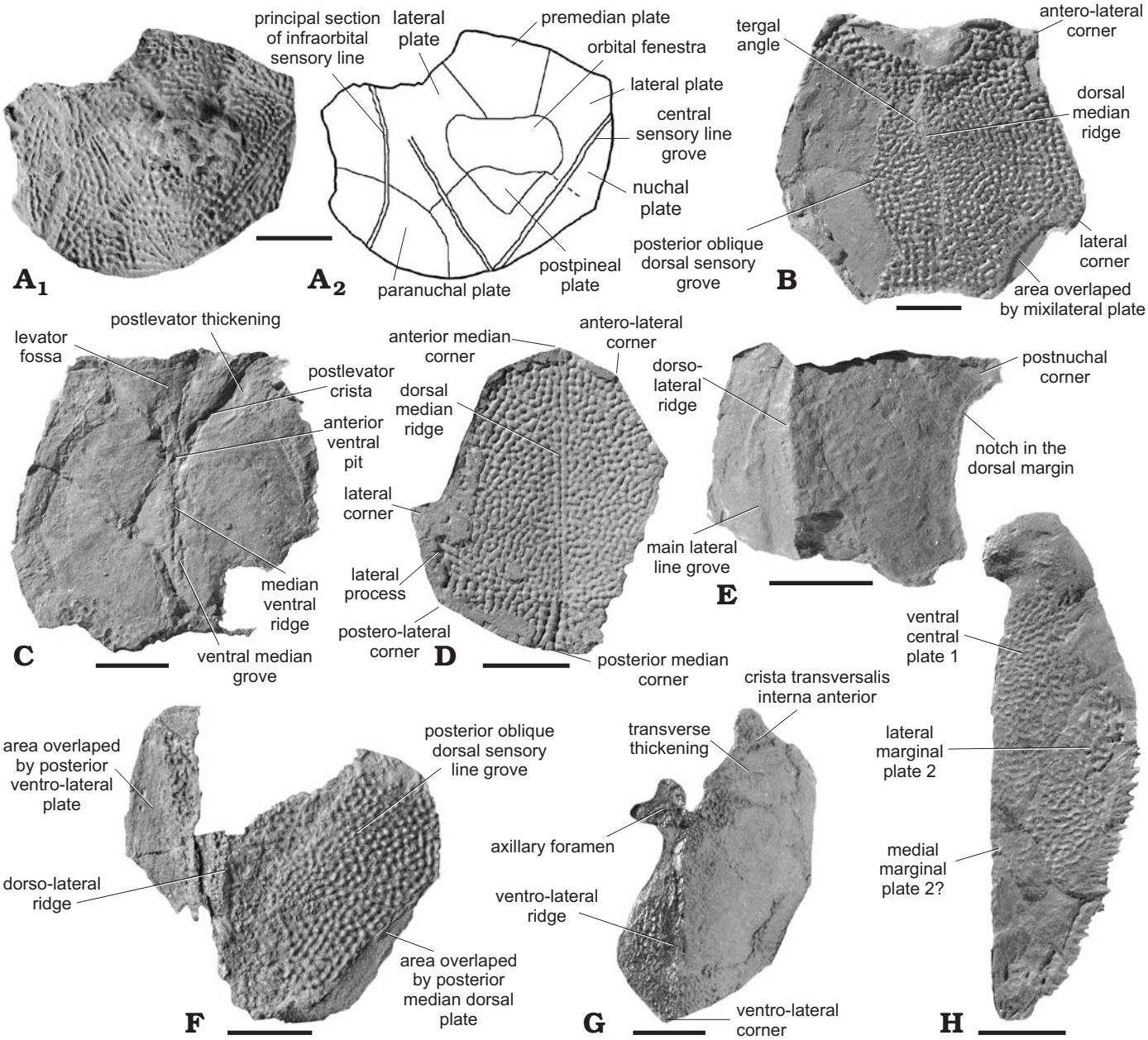



Fig. 3. Dermal plates of antiarch placoderm *Bothriolepis lohesti* Leriche, 1931, from Vaux-sous-Chèvremont and Chèvremont (Liège Province), Famennian, Devonian. **A**. UCL-P.V.L.10.621, partial headshield, external view. Photograph, whitened with ammonium chloride ($A_1$), explanatory drawing ($A_2$). **B**. PALULG-2011.12.14.14A, AMD, external view. **C**. PALULG-2011.12.14.17A, AMD, internal view. **D**. PALULG-2011.12.14.18, PMD, external view. **E**. PALULG-2011.12.14.17B, ADL, internal view. **F**. UCL-P.V.L.10.668, MxL, external view. **G**. PALULG-2011.12.14.20, AVL, external and internal views. **H**. PALULG-2011.12.14.22, pectoral fin, ventral view. Scale bars 10 mm.

cannot be checked. The mesial marginal plates 1 and 2 are not observable. The material also comprises isolated plates referred to CV1 and ML2. The ventral central plate 1 is more than twice longer than broad. The external ventral articular area is well developed. The ventro-medial margin is prominent on the largest specimen (UCL-P.V.L. 10.656). Lateral spines are numerous and closely set. These spines are not very elongated but strong and quite sharp. Basally all the spines are fused to a lamina, forming a tiny lateral crest.

*Ornament.*—On the dorsal elements, the ornament is coarse, with well-marked tubercles. "Short pieces of ridges with very few anastomoses" can also be observed on the material. "The pieces of ridges are clearly nodose and somewhat vermiculating" (Stensiö 1948: 515). The ornament is the same on all the plates. However, the ornament of the pectoral fin proximal segment, for specimens of the same size, can be either reticulate or nodose (PALULG-2011.12.14.21 and PALULG-2011.12.14.22), a retention of immature character already noticed by Stensiö (1948) for *B.canadensis*. The uniformity of the ornamentation and the equivalent size of all the plates suggest that all the material belongs to the same species.

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*Remarks.*—On the AMD, the strongly developed ventral median ridge, the slightly marked dorsal median ridge and the lack of anterior oblique dorsal sensory line, indicate that these plates belong to an adult specimens (Stensiö 1948). The relative breadth of the proximal segment of the pectoral fin and numerous few developed lateral spines argue for the same conclusion (Stensiö 1948).

The remains of this taxon were first noticed by Lohest (1888: 60), who referred them to the genera "*Bothriolepis* or *Pterychtis*", and then to the genus *Bothriolepis* (Lohest 1889: 58). Later, the same author (Lohest 1895: 39) assigned these remains to *Bothriolepis canadensis*. They consisted of "une tête complète, des organes natatoires et de nombreuses plaques dorsales et ventrales" (Lohest 1895: 39), i.e., a complete head, swimming appendages and numerous dorsal and ventral plates. Finally, Leriche (1931) studied this material and found only several anterior median dorsal plates, dorso-lateral plates and pectoral fins. In the present study, I have considered the historical material examined by Lohest (1888, 1889, 1895), Leriche (1931), and new material in the Université de Liège and in the Université Catholique de Louvain-la-Neuve collections. There is no trace of the complete head, never figured, and of the ventral plates studied by Lohest (1895). Leriche (1931) did not assign the historical material to *B. canadensis* because of (i) the more anastomosed ornamentation of *B. canadensis*, (ii) the different internal side of the anterior median dorsal plate, and (iii) the less developed lateral spines of the lateral marginal plate 2 of *B. canadensis*. He therefore assigned this material to a new species, *Bothriolepis lohesti,* and concluded that *B. lohesti* is a relative of *B. canadensis* and *Bothriolepis hydrophila*. According to Stensiö (1948), *B. lohesti* resembles *B. canadensis* by the development of the ornament, whereas it recalls *B. hydrophila* by the general shape of the AMD.

In the adult stage, *B. canadensis* could reach a total armour length of 18–19 cm (Stensiö 1948: 224), which corresponds approximately to a trunk armour length of 12–13 cm. This is different from *B. lohesti*, which reached a maximum trunk armour length of 8 cm. The shape of the anterior median dorsal plate of *B. lohesti* is quite similar to that of *B. canadensis* except that the dorsal median ridge is more pronounced in *B. canadensis*. Internally, and as noticed by Leriche (1931: 17), the postlevator cristae of *B. lohesti* are rather sharper than those of *B. canadensis*. Concerning the posterior median dorsal plate, both plates of both species are quite similar, except that the lateral process of *B. lohesti* is longer and more extended. On the anterior dorso-lateral plate of *B. canadensis*, the notch for the external postlevator process of AMD is pronounced. This is not the case for *B. lohesti*, where this notch is smooth. Leriche (1931: 18) argues that the spines of the pectoral fin lateral margin are more developed in *B. lohesti* than in *B. canadensis*. According to the variability shown by *B. canadensis* in this respect, it seems that several specimens of this species present spines that are similar to those observed in *B. lohesti* (i.e., Stensiö 1948: 355, fig. B). This criterion can consequently not discriminate the two species. Concerning the ornament, Stensiö (1948: 515) argued that the development of the ornament of *B. lohesti* "reminds mostly of large individuals of *B. canadensis*". In fact, in the adult stage, both can present a coarse ornament with tubercles and short pieces of ridges with very few anastomoses on the dorsal elements. Even if the adult ornament of *B. canadensis* can be more complicated, with frequent stellate tubercles at their bases, in general the ornament in both species is quite similar. Concerning the ornament on the proximal segment of the pectoral fin, *B. canadensis* often retains immature, reticular characters (Stensiö 1948). It is also observed for *B. lohesti*, with proximal segments showing a reticulate or nodose ornament (PALULG-5011 and PALULG-5012).

*Bothriolepis hydrophila* was certainly described on the basis of juvenile material (Stensiö 1948; Miles 1968). The comparison with other *Bothriolepis* species is therefore difficult. The trunk armour length of that species is maximally about 9 cm (Stensiö 1948). This corresponds to the trunk armour length of *B. lohesti*, which is of 8 cm. Contrary to the quite flat dorsal wall of *B. lohesti*, the dorsal wall of *B. hydrophila* is somewhat elevated, with a strongly developed dorsal median ridge. In both species, the anterior median dorsal plate is approximately as long as broad and the tergal angle is situated between the anterior and middle thirds of this plate. In both species, the postnuchal notch and external postlevator process are slightly developed or absent. The anterior median dorsal plate of *B. lohesti* overlaps the mixilateral plate but is also overlapped by that plate. This pattern is also observed in certain specimens of *B. hydrophila* (Stensiö 1948: 508, fig. 262B; Miles 1968: fig. 30). The posterior median dorsal plate of *B. lohesti* possesses stronger and more extended lateral processes than in *B. hydrophila*. The lateral spines of the pectoral fin proximal segment of both species are quite similar, i.e., broad and rather sharp. They are more numerous in *B. lohesti* than in *B. hydrophila*. Concerning the ornament, it is of a reticulate type and of uniform distribution in *B. hydrophila*. In one specimen (Miles 1968: pl. 19: 5) the ornament is both reticulate and tubercular. The ornament of *B. lohesti* is tuberculate but corresponds to the ornament of adult specimens, contrary to that of *B. hydrophila*.

Lukševičs (2001) noticed that *B. lohesti* and *Bothriolepis jani* Lukševičs, 1986 differ in that the AMD is less arched and the ornament consists of tubercles and nodose ridges in *B. lohesti*. He also noticed that the two species are similar in the shape and proportions of the AMD and in the sutural connections between AMD and MxL and concluded that they may be phylogenetically very close. The new material of *B. lohesti*, studied in this article, brings new insights in the comparison of the two species. *B. lohesti* differs also from *B. jani* by (i) the postpineal notch of the nuchal plate, which forms a strong angle posteriorly (rounded in *B. jani*), (ii) the well developed lateral processes of the PMD, (iii) the less arched dorsal median ridge (on the AMD and on the PMD), and (iv) the well developed postnuchal corner of the ADL. Therefore, the new material studied here slightly modifies Lukševičs'

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(2001) conclusion: both species seem phylogenetically less close than previously thought.

The material characterising *B. lohesti* has been completed with new specimens in collections. Even if this material is poor, and *B. lohesti* is only known by some elements of the trunk armour and pectoral fin, this species appears quite different from the other species of *Bothriolepis*, e.g., *B. canadensis*, *B. jani*, and *B. hydrophila*, and its status is not reconsidered. *B. hydrophila* is defined on juvenile material and, as noticed by Stensiö (1948) and Werdelin and Long (1986) for *B. canadensis*, ontogenetic changes are numerous from juvenile to adult. Therefore it is injudicious to use such material for morphological comparisons. However, *B. hydrophila* continues to be widely used for comparisons with other *Bothriolepis* species defined on adult characters and is included in phylogenetic analyses (Young 1988; Lukševičs 2001), whereas the data included in the matrix might reflect the growth stage. More data on adult material is necessary for comparisons with *B. lohesti*.

*Stratigraphic and geographic range*.—Famennian, Upper Devonian of Belgium.

## *Bothriolepis* sp.

Fig. 4.

*Material.*—AMD: PALULG-2011.12.15.13, PALULG-2011.12.15.14, PALULG-2011.12.15.15, UCL-P.V.L.10.646, UCL.P.V.L.10.697; MxL: UCL-P.V.L.10.624; AVL: PALULG-2011.12.15.16; ?CV1: PALULG-2011.12.15.17. From Modave quarry, also known as Pont-de-Bonne, Bonne Valley, Liège Province, Belgium, upper part of the Evieux Formation, Famennian, Upper Devonian.

### *Description*

*Trunkshield.—Anterior median dorsal plate, AMD* (Fig. 4A, B): This plate is as long as wide. Externally, it is smoothly arched. The tergal angle is situated slightly in front of the transition between the anterior and middle thirds of the plate. It is of roughly 45°. The posterior oblique dorsal sensory line grooves are clearly observed. The dorsal median ridge is weakly defined and runs from the tergal angle to the posterior margin. The anterior margin is concave and slightly longer than the posterior one. The external postlevator process is well defined and prominent. The lateral and the postero-lateral corners are clearly observable. The posterior median process is well defined. The maximal width of the plate is at the lateral corners. The width at the postlevator processes is slightly inferior. The anterior part of the lateral margin is twice the length of the posterior part. Internally, the postlevator thickenings are low but well denoted, the triangular-shaped levator fossa gently deep and the anterior ventral pit oval and tiny. The anterior part of the area overlapping ADL is well extended. These internal characters are only observable on the largest AMD (Fig. $3A_2$), which is the only one being preserved in internal view.

*Mixilateral plate, MxL* (Fig. 4C): The lateral lamina is not preserved and the dorsal lamina presents a damaged surface. The anterior part of the dorso-medial margin is straight and measures half the length of the posterior part. The dorso-medial corner, that separates them, is well defined. The length of the straight posterior margin equals the length of the slightly convex anterior margin. The posterior oblique dorsal sensory line groove is slightly marked and runs from the dorso-medial corner area to the limit between the anterior and middle thirds of the plate. Such a course is unusual for the posterior oblique dorsal sensory line. Thus, the identification of this plate could be misinterpreted.

*Anterior ventro-lateral plate, AVL* (Fig. 4D): This plate is only known in ventral view and is moderately well preserved. The ventral lamina is quite elongated and equals three times its width. The subcephalic division is roughly one third of the total plate length. The crista transversalis interna anterior is well developed, as is also the transverse thickening on the visceral surface and the depression between both cristae. The lateral lamina is so compressed that it is impossible to evaluate the angle made posteriorly by the ventro-lateral ridge. The pectoral joint area is observable but quite difficult to interpret because of the bad preservation. Nevertheless, quite a large axillary foramen is observable.

*Pectoral fin.*—Only one element of the pectoral fin is preserved. It is a fragment of the proximal segment, a ventral or a dorsal central plate 1 (Fig. 4E). The only element allowing this attribution is the rounded articular surface. An accurate attribution is impossible due to the very poor preservation.

*Ornament.*—The ornament is the same for all the plates described above, that is, a reticulate ornament composed of a smooth and regular network of interconnecting ridges.

*Remarks.*—The material described above is not sufficient to erect a new species, because there is not enough material, and because much of it is considered as belonging to half-mature individuals. This is the case of 5 out of 6 AMDs. Actually, they display several juvenile characters such as the presence of oblique transverse depressions and oblique transverse ridges, a developed posterior median process and a reticulate ornament. The length of these plates does not exceed 1.5 cm. However, they also display adult characters, such as a weak dorsal median ridge and the absence, at least not observable, of anterior oblique dorsal sensory line grooves. This mixture of juvenile and adult characters argues for half-mature individuals. AMD PALULG-2011.12.15.14 is bigger, roughly twice the width of the other AMDs, but its poor preservation does not provide much information. It could represent either adult material or belong to a different species. They are grouped here for convenience only.

The other trunk and pectoral plates are not in the same size range as the half mature AMDs. However they present exactly the same ornamentation, and this is why they are considered conspecific with the AMDs.

As Stensiö (1948: 211) noticed in the "Bothriolepinae", "certain formations were entirely reduced during the growth, whereas others appeared". The ornament is also modified during the growth. "In consequence of these changes young

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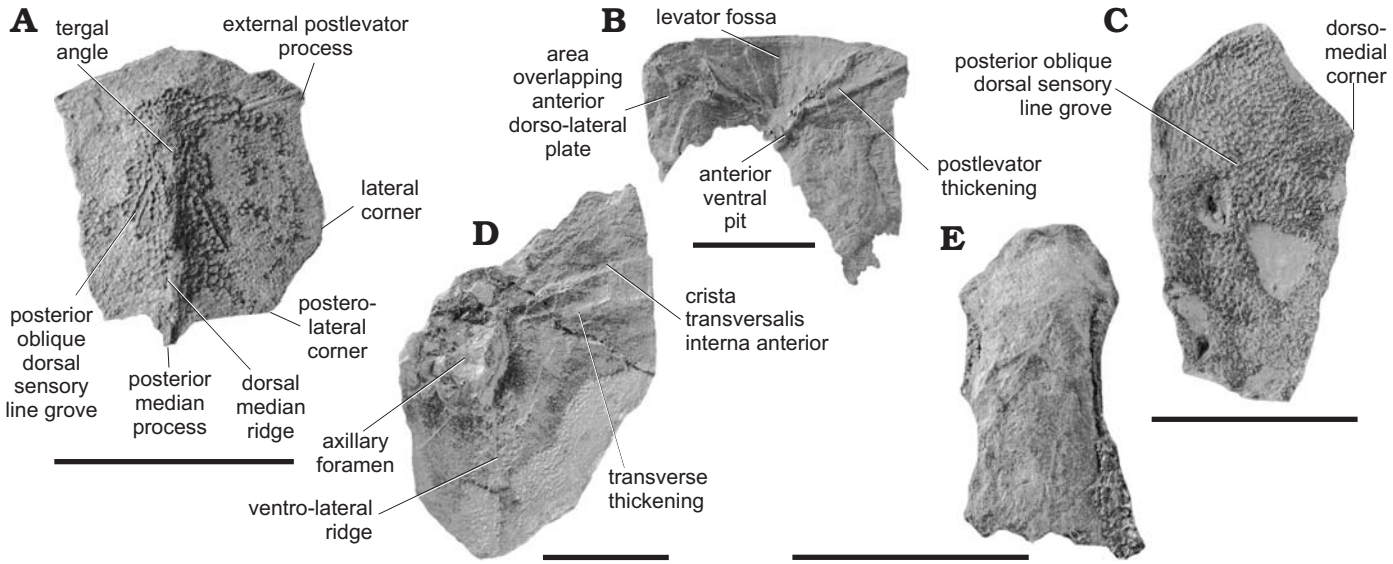



Fig. 4. Dermal plates of antiarch placoderm *Bothriolepis* sp., from Modave (Liège Province), Famennian, Devonian. **A**. UCL-P.V.L.10.646, AMD, external view. **B**. PALULG-2011.12.15.14, AMD, internal view. **C**. UCL-P.V.L.10.624, MxL, external view. **D**. PALULG-2011.12.15.16, AVL, internal view. **E**. ?CV1, PALULG-2011.12.15.17, internal view. Scale bars 10 mm.

and mature individuals always differ considerably from each other in several of their characters" (Stensiö 1948). Long and Werdelin (1986), Werdelin and Long (1986) and Johanson (1998) quantified these variations. Thus, it seems inappropriate to erect a new species of bothriolepid on the basis of juvenile or half-mature material. Therefore the *Bothriolepis* material from Modave, which is clearly half-mature (see below) and too fragmentary, is put in open nomenclature in this paper.

## Genus *Grossilepis* Stensiö, 1948

*Type species*: *Grossilepis tuberculata* (Gross, 1941); Bank of Pērse River near Koknese, Latvia, Lower Frasnian Pļaviņas Formation, Devonian.

## *Grossilepis rikiki* sp. nov.

Fig. 5.

2009 *Bothriolepis*; Clément and Prestianni 2009: 107: pl. 3: 2.

*Etymology*: From French colloquial language word *rikiki*, small; referring to the small size of the new species. According to article 31.2.3 of the International Code of Zoological Nomenclature, the name "rikiki" is to be treated as indeclinable because it is not a Latin or Latinized word.

*Type material*: Holotype: AMD: IRSNB P.9255a, b. Paratypes: Skull roof: IRSNB P.9253a, b; AMD: IRSNB P.9254; PMD: IRSNB P.9256a, b; CV1: IRSNB P.9258a, b; ML2: IRSNB P.9257.

*Type locality*: Strud, Namur Province, Belgium (IRSNB P.9255, IRSNB P.9254, IRSNB P.9258, IRSNB P.9257) and Moresnet, Liège Province, Belgium (IRSNB P.9253, IRSNB P.9256).

*Type horizon*: Evieux Formation, upper Famennian, Upper Devonian (IRSNB P.9255, IRSNB P.9254, IRSNB P.9258, IRSNB P.9257); Montfort/Evieux Formation, upper Famennian, Upper Devonian (IRSNB P.9253, IRSNB P.9256).

*Material*.—AMD: IRSNB vert 31594-001a, b; PMD: IRSNB vert 6845-001, PALULG-2011.12.15.18; CV1: IRSNB vert 31594-008a, b, IRSNB vert 32164-002a, b; ML2: IRSNB vert 31594-004a, b, IRSNB vert 31594-005a, b, IRSNB vert 31594-006a, b, IRSNB vert 31594-007a, b, IRSNB vert 31594-009a, b, IRSNB vert 31913-001a, b, IRSNB vert 31913-002a–c, IRSNB vert 32164-001. From Strud, Namur Province, Belgium, Evieux Formation, upper Famennian, Upper Devonian. IRSNB vert 15025-001a, b, from Moresnet, Liège Province, Belgium, Famennian, Upper Devonian.

*Diagnosis*.—Small bothriolepidoid with estimated length of dorsal wall of trunk-armour reaching about 4–5 cm. Headshield moderately vaulted, with a large orbital fenestra. Lateral plates elongated. Nuchal plate with an obtected nuchal area extending along the entire breadth of the plate, with a medial, complex posterior median process displaying several straight fingerings. Lateral division of the paranuchal plate almost as broad as the median division. Dorsal wall of trunk armour quite arched, with a well developed dorsal median ridge. Tergal angle situated between the anterior and middle thirds of the plate. Levator fossa well marked. Anterior margin of the anterior median dorsal plate sinusoidal and 1.5 times the length of the posterior margin. Area of the AMD overlapped by the posterior median dorsal plate quite extended, with a strong posterior median process. Area of the AMD overlapping the anterior dorso-lateral plate extended, and area overlapping the mixilateral plate elongated. Lateral processes of the posterior median dorsal plate quite extended. Lateral marginal plate 2 very elongate, up to six times longer than broad, with the mesial corner located very anterior. Ornament clearly nodose on the skull roof and anterior median dorsal plate and reticulate to nodose on the pectoral fin bones.

### *Description*

*Headshield* (Fig. 5A).—The anterior portion of the nuchal plate and the postpineal plate are not preserved, but it seems, however, that the orbital fenestra reaches a large size. Two

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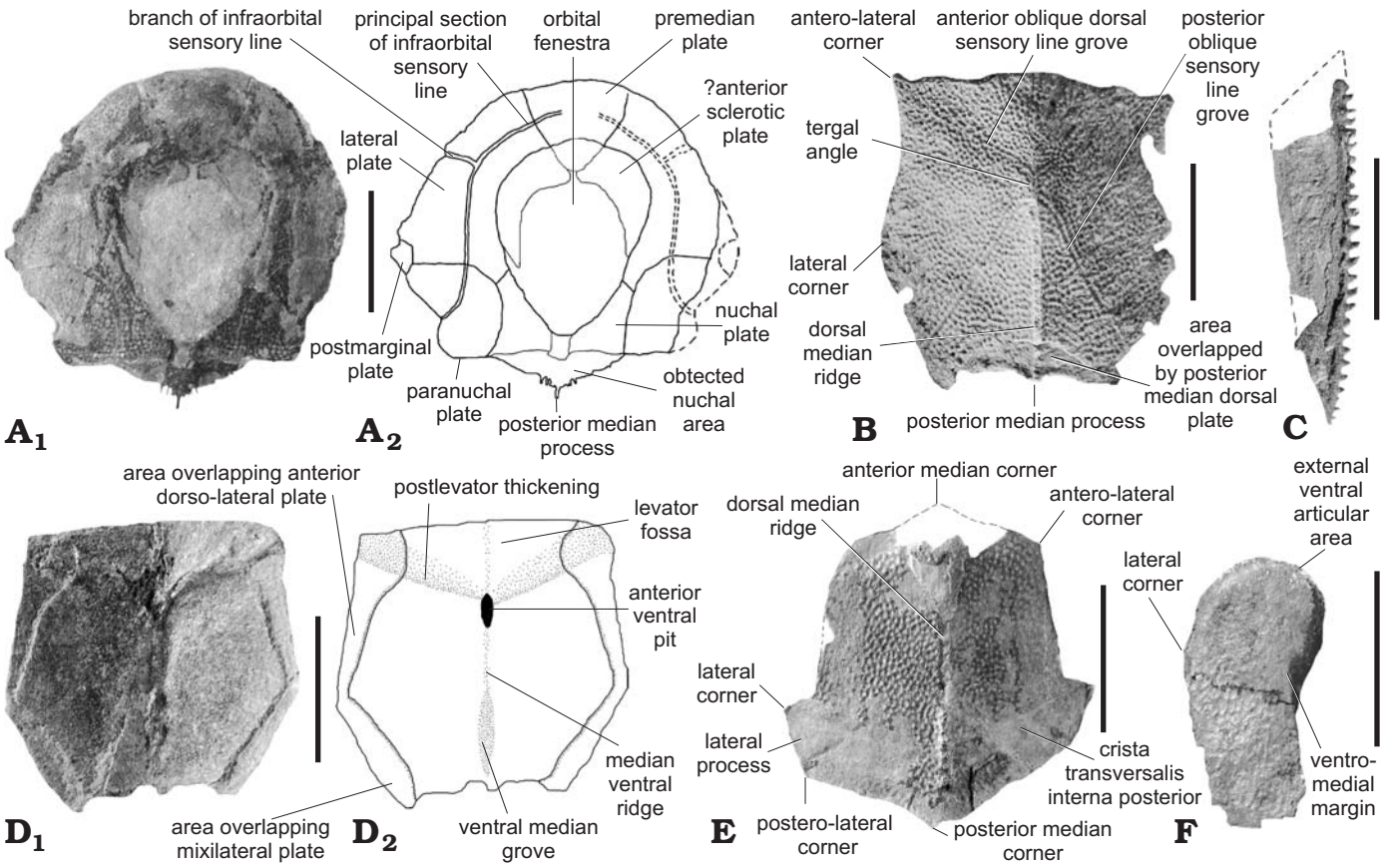



Fig. 5. Dermal plates of antiarch placoderm *Grossilepis rikiki* sp. nov., from Moresnet, Liège Province (A, E), Strud, Namur Province (B–D, F), Famennian, Devonian. **A**. IRSNB P.9253a, skull roof, external view; photograph ($A_1$), under water immersion; explanatory drawing ($A_2$), dotted line obtained by mirror image. **B**. IRSNB P.9254, AMD, external view, whitened with ammonium chloride. **C**. IRSNB P.9257, ML2, external and internal views, dotted line based on IRSNB vert 31594-007. **D**. IRSNB P.9255a, AMD, internal view; photograph ($D_1$), explanatory drawing ($D_2$). **E**. IRSNB P.9256a, PMD, external and internal views, dotted line based on the counterpart IRSNB P.9256b. **F**. IRSNB P.9258a, CV1, external view. Scale bars 10 mm.

symmetric elements are badly preserved in the fenestra. They could belong to the sclerotic ring and could be anterior sclerotic plates based on their position in the fenestra.

*Premedian plate, Prm*.—This plate is broader than long. The breadth is maximal at the anterior margin and gently decreases until it reaches half the value at the posterior margin. The principal section of infraorbital sensory line is not easily observed, because of the damaged bone.

*Lateral plate, La*.—This plate is rather long. It is narrow in its anterior part and broad in its posterior part. The orbital margin is concave, with the highest flexure at the middle length of the plate. The posterior portion of the plate, adjoining the nuchal and paranuchal plates, is quite narrow. The principal section of infraorbital sensory line (runs in the medial part of the plate. The branch of infraorbital sensory line is quite long. There is no trace of central sensory line grooves.

*Nuchal plate, Nu*.—The anterior part of the plate is not preserved. The posterior portion of the lateral margin is long and concave. The objected nuchal area extends along the entire breadth of the plate. It bears medially a posterior median process with several posterior straight fingerings. There is no observable trace of central sensory line grooves.

*Paranuchal plate, Pn*.—The principal section of the infraorbital sensory line crosses the plate in its middle. The lateral division of the plate is almost as broad as the median division. The postmarginal plate completes the lateral corner of the skull roof.

*Trunkshield*.—*Anterior median dorsal plate, AMD* (Fig. 5B, D): This plate is slightly longer than broad. Externally, the plate is arched with a salient and well-developed dorsal median ridge forming an obtuse angle, and running from the tergal angle backwards to the posterior margin. The tergal angle is situated between the anterior and middle thirds of the plate. The top of the dorsal median ridge forms a tiny flat strip on IRSNB P.9254, probably resulting from the post-mortem wear of a sharper dorsal median ridge. This strip is absent on the other AMDs. The anterior margin, 1.5 times the length of the posterior margin, is sinusoidal and the antero-lateral corners are well marked. The breadth at the level of the antero-lateral corners is slightly shorter than at that of the medio-lateral corners. The anterior part of the lateral margin, thus joining both corners, is concave. The posterior part of the same margin is quite straight and slightly shorter than the anterior part. The posterior margin is clearly concave. Underneath, the area overlapped by the posterior median dor-

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sal plate is quite extended and the posterior median process salient. On IRSNB P.9254, the slightly marked left anterior oblique dorsal sensory line groove runs in a smooth depression corresponding internally to the area between the levator fossa and postlevator thickening, from the tergal angle toward the lateral margin. It seems to stop gently before the lateral margin. The right anterior oblique dorsal sensory line groove is not observable. On IRSNB vert 15025-001, both anterior oblique dorsal sensory line grooves are present but very slightly marked, whereas the posterior oblique dorsal sensory line grooves are strongly marked. There is a slight bilateral asymmetry of the posterior oblique dorsal sensory line grooves of IRSNB P.9254. The right dlg2 forms a sharper angle with the median dorsal ridge than does the left one. Internally the levator fossa is well marked and the postlevator thickenings quite hilly. The anterior ventral pit (is oval and elongated, the median ventral ridge sharp and the ventral median groove (grm) elongated. The areas overlapping the anterior dorso-lateral plates (cf. ADL) and those overlapping the mixilateral plates are quite extended.

*Posterior median dorsal plate, PMD* (Fig. 5E): The PMD is slightly wider than long. The maximum width is across the lateral corners but the plate is quite uniform in breadth throughout its extent. The anterior margin is convex and the anterior median corner obtuse. The antero-lateral corner is located at the first anterior third of the plate. The lateral process is well marked with prominent lateral and postero-lateral corners. The postero-lateral corners are obtuse. The posterior margin is convex and the posterior median corner protruding. The plate is quite arched with a well-defined dorsal median ridge. The crista transversalis interna posterior is smooth and quite hilly.

*Pectoral fin.—Ventral central plate 1, CV1* (Fig. 5F): The posterior part is not preserved but this plate is at least twice longer than broad. The external ventral articular area is well preserved. The lateral corner is smooth. The ventro-medial margin is well marked.

*Lateral marginal plate 2, ML2* (Fig. 5C): This plate is at least six times longer than broad. This is a very elongate bone. The obtuse mesial corner, usually located at the middle length of the plate, occupies here a very anterior position (well observed on IRSNB vert 31594-007). The anterior part of the mesial margin is thus short. The slight incision on the posterior part of the mesial margin corresponds certainly to the anterior end of the notch for the dorsal central plate 2. The lateral margin is convex and bears spines that are numerous, slightly spaced out and mostly turned proximally.

*Ornament*.—The ornament on the anterior median dorsal plate is nodose; composed of a delicate and regular network of interconnecting ridges with tubercles developed at the junctions between ridges. On the ML2 plates, the ornament is reticulate (IRSNB vert 31913-002) or nodose (IRSNB vert 31594-009).

*Remarks*.—*Bothriolepis canadensis* is known for all its growth stages (Stensiö 1948). Referring to Stensiö's observations, and considering that the genus *Bothriolepis* is closely related to the genus *Grossilepis*, the material described here is certainly from half-mature individuals. In fact, the material presents a combination of (i) juvenile characters, i.e., ornament reticulate to nodose, large orbito-nasal fenestra (Werdelin and Long [1986] and Cloutier [2010] made the same observation), dorsal median ridge well developed, anterior oblique dorsal sensory line grooves present on several AMDs, anterior dorsal depression corresponding ventrally to the position of the postlevator thickening and posterior median process strongly developed; and (ii) mature characters, i.e., absence of central sensory line grooves on the skull roof, slightly-marked anterior oblique dorsal sensory line grooves, absence of the second anterior oblique dorsal sensory line groove on IRSNB P.9254 and presence of some tubercles in the ornament.

The bothriolepidid material from Strud and Moresnet is assigned to the genus *Grossilepis* based on the AMD overlap relations with the surrounding plates. Indeed, the AMD overlapping both the ADL and MxL is one of the diagnostic characters of the genus *Grossilepis*. Since no MxL or ADL of this taxon has been found, it is impossible to check the presence of the other diagnostic characters of this genus.

The genus *Grossilepis* includes three named species. *G. tuberculata*, from the Frasnian of Latvia, Lithuania and Russia (Gross 1941; Stensiö 1948; Lukševičs 2001), is the oldest described species of the genus, and the most complete one. It was described on the basis of numerous adult plates and its validity is not discussed here. *G. spinosa*, from the Middle Frasnian of Latvia (Gross 1942; Lukševičs 2001), was first described as *Bothriolepis spinosa* Gross, 1942. It was reassigned, with reservations, to the genus *Grossilepis* by Stensiö (1948: 615) in regard to "the shape of certain of its dermal bones, the sutural connection of the AMD and MxL plate, and the ornament". Lukševičs (2001) confidently assigned this species to the genus *Grossilepis*. *G. brandi* from the Frasnian of Scotland (Miles 1968) was described on the basis of very few remains. The AMD, ADL, and MxL are absent, so the diagnostic characters of the genus are impossible to check. The attribution of *G. brandi* to *Grossilepis* is therefore doubtful and it is proposed here to consider this species as a nomen dubium.

*Grossilepis rikiki* from Strud and Moresnet differs chiefly from *G. tuberculata* by (i) the shape of the lateral plate, which is larger in *G. tuberculata*, (ii) the shape of the orbital fenestra, larger in *G. rikiki*, (iii) the complex obtected nuchal area of the nuchal plate, (iv) the shape of the AMD, which is narrower in *G. tuberculata*, (v) the absence of central sensory line grooves on the nuchal and lateral plates, (vi) the overlapping areas of the AMD, which are clearly more developed in *G. rikiki*, (vii) the size of the dorsal wall of the trunk armour, *G. tuberculata* possesses a longer trunk armour roof, and (viii) by the ornament, tuberculate for *G. tuberculata* and mainly nodose for the *Grossilepis* species from Strud and Moresnet. It differs from *G. spinosa* in characters (iii), (v), (vi), (vii), (viii) and by the size and shape of the lateral

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spines of the proximal segment of the pectoral fin, which are strongly developed in *G. spinosa*.

Matukhin et al. (1980) described a species of *Grossilepis* (remaining in open nomenclature) from the Frasnian of Russia in the Marshrutninskaya locality, Krasnoyarsk region (northwestern Siberian Platform). Moloshnikov (2012) states that this species differs from the other species of *Grossilepis* by its narrow AMD and the short posterior margin of the AMD. It differs from *G. rikiki* by those characters too, but also by a more elongated levator fossa, less extended areas overlapping MxLs and ADLs, smoother lateral corners and the absence of antero-lateral corners.

Although the material from Moresnet and Strud seems to be half-mature nature, the differences with the few other species of *Grossilepis*, from a morphological and a stratigraphical point of views, are enough to justify the erection of a new species.

*Stratigraphic and geographic range*.—Type locality and horizon only.

## Asterolepidoidei Miles, 1968

## Asterolepidae Traquair, 1888

## Genus *Asterolepis* Eichwald, 1840

*Type species*: *Asterolepis ornata* Eichwald, 1840; Baltic States, Gauja Formation, Upper Givetian, Devonian.

### *Asterolepis* sp. 1

Figs. 6, 7.

1965 *Asterolepis*; Gross 1965: 3–5, fig. 1.

*Material*.—Nu: IRSNB P.1456; Pp: IRSNB P.1457; PMD: IRSNB P.1458; AVL: IRSNB P.1459a, b; CV1: IRSNB P.1460, IRSNB P.1461a, b; MM1: IRSNB P.1463; distal part of the pectoral fin: IRSNB P.1462a, b. From Hingeon, Namur Province, Belgium, Mazy Member, Bois de Bordeaux Formation, Upper Givetian, Middle Devonian.

#### *Description*

*Headshield*.—*Nuchal plate, Nu* (Fig. 6B, C).—Only the middle part of this plate is preserved. The posterior margin is convex with a small posterior median process on the objected nuchal area. A portion of the anterior margin is preserved. It constitutes a part of the postpineal notch. The middle pit-line groove is well marked and connected to the supratemporal pit-line groove, in turn linked to the external openings for the endolymphatic duct.

*Postpineal plate, Pp* (Fig. 6A, C): It is preserved almost entire, on the same block as the nuchal plate, but disconnected. It fits well with the shape of the preserved part of the postpineal notch of the nuchal plate. Thus, both plates certainly belonged to the same individual. The postpineal plate is broader than long. Anteriorly, it shows the limits of a smaller plate corresponding to a younger growth stage.

*Trunkshield*.—*Posterior median dorsal plate, PMD* (Fig. 6D): The PMD is relatively small compared to the rest of the material and might correspond to a juvenile individual. The dorsal median ridge and median ventral ridge are very sharp, forming an angle of about 90°. This plate tapers towards the anterior end. It displays an extended lateral process and a smooth posterior angle . The area overlapping the AMD (is extended, contrary to the narrow areas overlapping MxLs.

*Anterior ventro-lateral plate, AVL* (Fig. 6E, F): The subcephalic part is missing and the posterior part is badly preserved. The articular area with the pectoral girdle is missing too. Only the axillary foramen is present as a mold in the matrix. The ventral lamina is better preserved than the lateral one. The ventro-lateral ridge forms an angle of about 140°. The area overlapped by the right AVL is slightly observable medio-anterally. Concentric lines are present on the visceral surface of the ventral and lateral laminae.

*Pectoral fin*.—*Ventral central plate 1, CV1* (Fig. 7A, F): There are two specimens from Hingeon: a small one and a large one. They are both incomplete in the posterior portion. The ventro-medial margin is prominent and the external ventral articular area quite extended.

*Medial marginal plate 1, Mm1* (Fig. 7E): This plate is entirely preserved and relatively short. The proximal part is forked and unornamented whereas the distal part is ornamented. It is crossed proximo-distally by the pectoral pit-line groove. The posterior margin is slightly sinusoidal.

*Distal part of the pectoral fin* (Fig. 7B–D): A large part of the pectoral fin distal segment is preserved in ventral view. Neither the anteriormost part, nor the posteriormost part is preserved. The medial marginal plate 4 displays laterally short, spaced spines that are absent on the distal part of the plate. Gross (1965) noticed that a medial marginal plate 5 could be attached to the Mm4 but this is not observable. On the contrary, it is linked to the ventral central plate 4 (Cv4) by a strong edge. The posterior part of this plate is narrow, whereas the anterior part is large and flattened. It certainly corresponds to the insertion area of the pectoral fin proximal segment. Immersed in water or alcohol, the limit between the Cv4 and the lateral marginal 5 (ML5) is clearly observed. The ML5 is a long plate with a regular width. Its posterior limit is neither observable nor preserved. The terminal plate is not preserved, but a fragment of its impression might be present on the counterpart of the pectoral fin distal segment. However, its limits are not distinguishable.

*Ornament*.—The ornament is tuberculate on the nuchal plate. On the postpineal plate, some tubercles fuse to form small ridges. Some of them radiate from the centre of the plate. On the posterior median dorsal plate, Gross (1965: 4) defined the ornament as forming ramparts (“Wallbildung”). It is rather a reticulate ornament with some tubercles present. On the anterior ventro-lateral plate, the ornament is clearly tuberculate, with tubercles arranged in parallel rows. As for the ventral central plate 1, it bears few small, spaced tubercles, and the medial marginal plate bears huge, rough tubercles sometimes associated. The distal segment of the pectoral fin is devoid of ornament.

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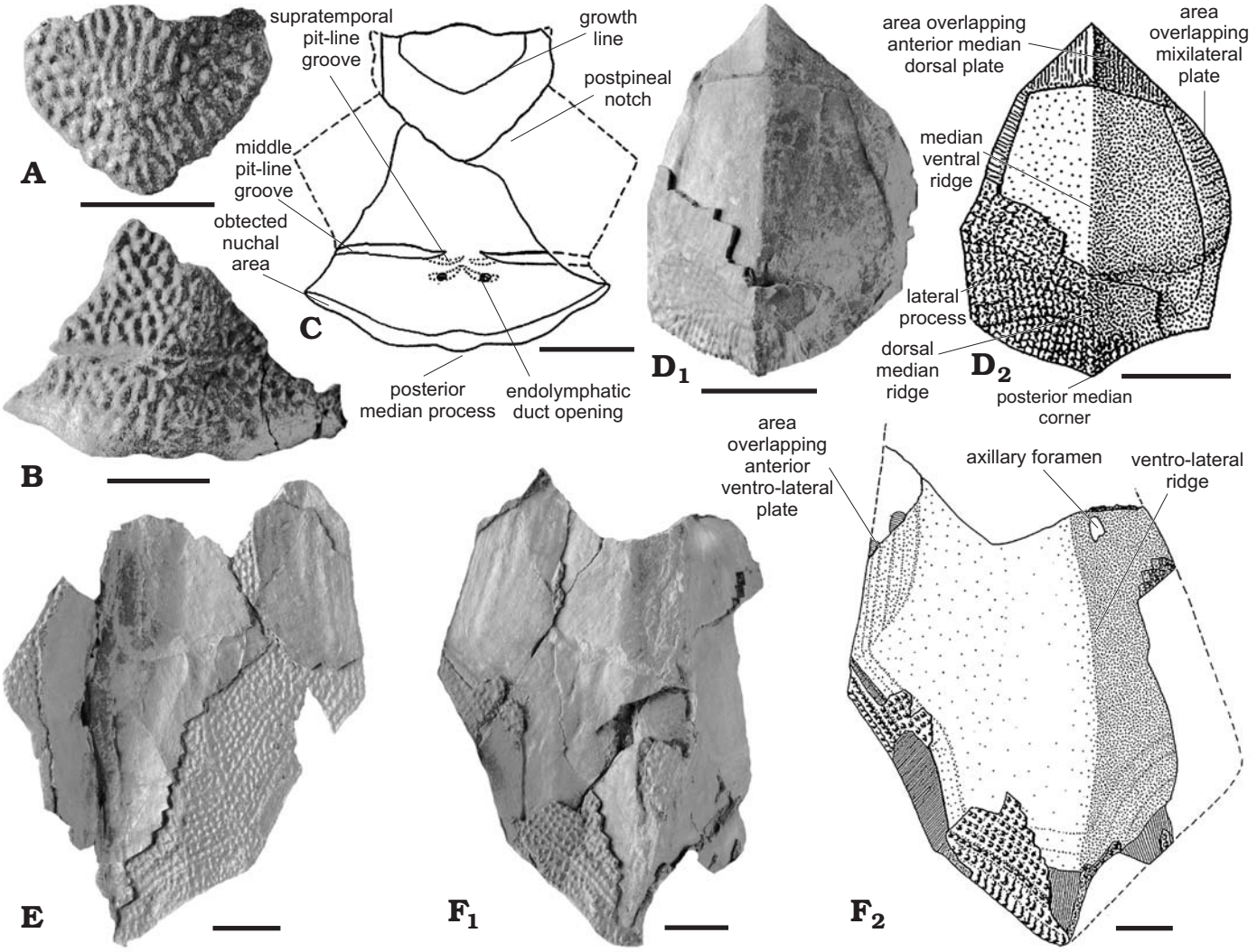



Fig. 6. Dermal plates of antiarch placoderm *Asterolepis* sp. 1, from Hingeon (Namur Province), Upper Givetian, Devonian. **A**. IRSNB P.1457, Pp, external view. **B**. IRSNB P.1456, Nu, external view. **C**. IRSNB P.1456 and 1457, Pp and Nu, external view. **D**. IRSNB P.1458, PMD, external and internal views; photograph ($D_1$), explanatory drawing ($D_2$). **E**. IRSNB P.1459b, AVL, external and internal views, counter-part of IRSNB P.1459a. **F**. IRSNB P.1459a, AVL, external and internal views; photograph ($F_1$), explanatory drawing ($F_2$). Drawings from Gross 1965. Scale bars 10 mm.

*Remarks*.—Compared to what Gross (1965) published the present work provides further details and the counterparts of some plates are figured here. The drawings made by Gross are very accurate and have been used here for the figures.

Gross (1965) described an indeterminate species of antiarch from the Givetian of Hingeon (*Asterolepis* sp. 1 in this paper). In spite of the small number of plates preserved, he assigned this form to *Asterolepis*, because all the bones matched that genus, and not those of other genera of antiarch. In fact, *Pterichthyodes* and *Byssacanthus* display shorter and wider postpineal plates. In *Gerdalepis*, the same plate bulges forward. The genus *Bothriolepis* is excluded because its medial marginal plate 1 is longer and narrower. The genus *Remigolepis* was not considered by Gross (1965), but the species from Hingeon clearly differs from that genus, notably by the organization of the pectoral fin plates. To date, and without supplementary material, the attribution of this material to *Asterolepis* by Gross (1965) is not reappraised and seems correct. He considered that the *Asterolepis* material from Hingeon resembles more *A. ornata* than any other species, but that the material was insufficient to assign it to any particular species of *Asterolepis*. His cautiousness is here followed.

## *Asterolepis* sp. 2

Fig. 8.

*Material*.—Unassigned plate of the trunk shield: IRSNB P.9260; Cd1: IRSNB P.9259. From Burtaux quarry, locality Alvaux, Mazy, Gembloux, Namur Province, Belgium. Alvaux Member, Bois de Bordeaux Formation, Givetian, Middle Devonian.

### *Description*

*Trunkshield*.—*Unassigned plate* (Fig. 8A): The assignment of that plate is not possible due to the very bad preservation. It is a lateral plate of the trunk shield as indicated by the presence of two laminae separated by a strong angle.

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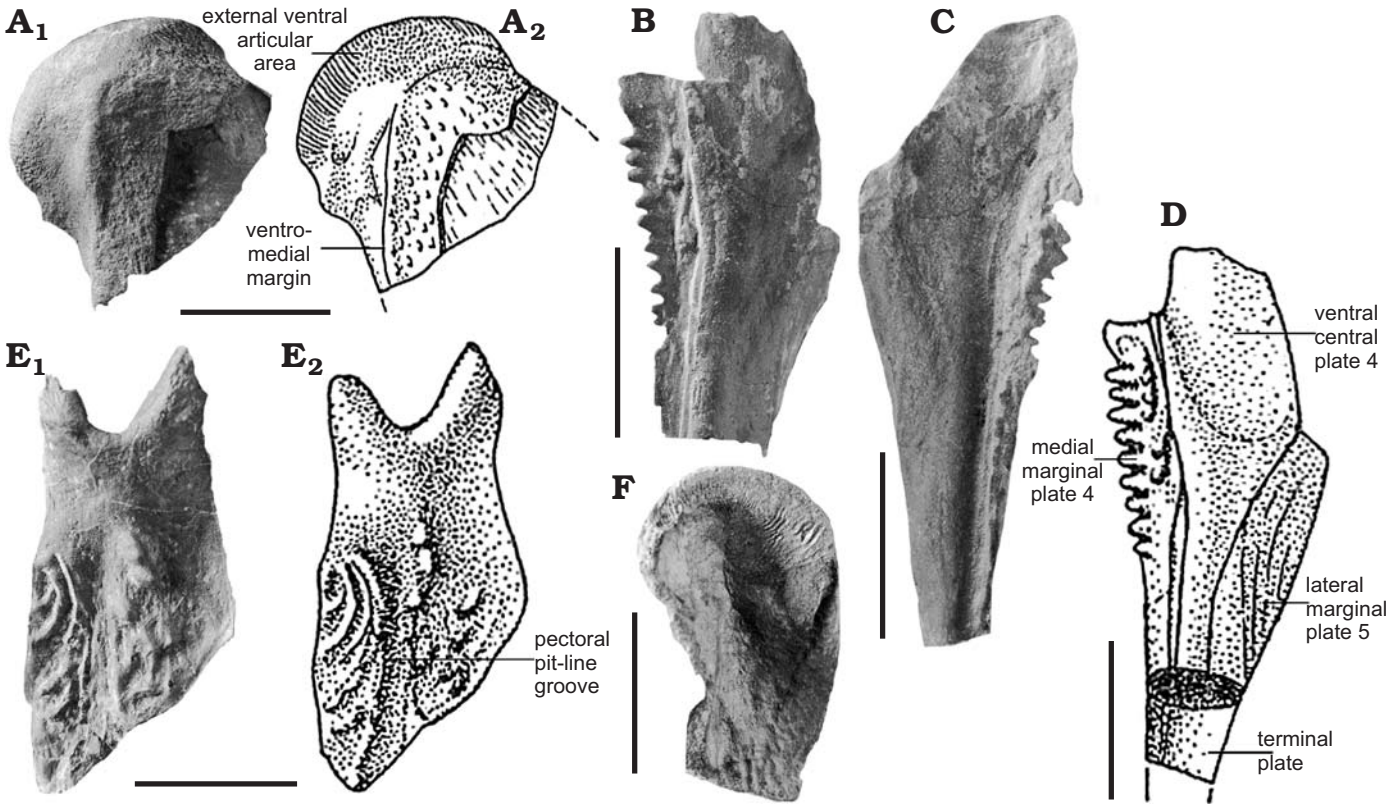



Fig. 7. Dermal plates of antiarch placoderm *Asterolepis* sp. 1, from Hingeon (Namur Province), Upper Givetian, Devonian. **A**. IRSNB P.1460, CV1, external view; photograph ($A_1$), explanatory drawing ($A_2$). **B**. IRSNB 1462a, distal part of the pectoral fin, external view. **C**. IRSNB 1462b, distal part of the pectoral fin, external view, counterpart of IRSNB 1462a. **D**. Drawing based on IRSNB 1462a and b, distal part of the pectoral fin, external view. **E**. IRSNB P.1463, MM1, external view; photograph ($E_1$), explanatory drawing ($E_2$). **F**. IRSNB P.1461a, CV1, internal view. Drawings from Gross 1965. Scale bars 10 mm.

*Pectoral fin.—Dorsal central plate 1, Cd1* (Fig. 8B): A well preserved specimen is available. It is rather long. The external dorsal articular area anterior to the unornamented area, is finely covered with tiny meshes. The posterior margin, articulating with the dorsal central plate 2, is concave. The margin, articulating with the medial marginal plate 2 is elongated and strongly concave, as in *Asterolepis ornata*. On the lateral margin, the lateral corner is quite prominent. The medial margin is slightly damaged but no spine is observable.

*Ornament.*—The ornament of *Asterolepis* sp. 2 is rather reticulate. On the unassigned plate, the ornament also consists of fine, rounded and flat tubercles arranged in a concentric and radiating pattern.

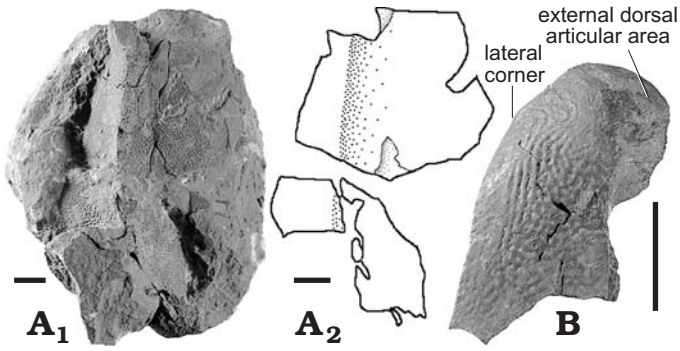



Fig. 8. Dermal plates of antiarch placoderm *Asterolepis* sp. 2., from Mazy (Namur Province), Givetian, Devonian. **A**. IRSNB P.9260, unassigned plate, external view; photograph ($A_1$); explanatory drawing ($A_2$). **B**. IRSNB P.9259, CD1, external view. Scale bars 10 mm.

*Remarks*.—The shape of the dorsal central plate and the rounded, flat tubercles of the ornamentation support the *Asterolepis* identification. The dorsal central plate strongly resembles the dorsal central plate of *A. ornata* (Gross 1931: pl. 5: 1a). Possibly, the specimens from Mazy could belong to the same form as the one from Hingeon. The amount and quality of the material in both localities is unfortunately not sufficient to confirm this conclusion.

## Remigolepidae Stensiö, 1931

## Genus *Remigolepis* Stensiö, 1931

*Type species*: *Remigolepis incisa* (Woodward, 1900); Ymer Island, south of the Dusen Fjord, East Greenland, Famennian, Devonian.

### *Remigolepis durnalensis* sp. nov.

Figs. 9–12.

2009 *Bothriolepis*; Clément and Prestianni 2009: 107.

*Etymology*: In reference to the locality, where the material has been found.

*Type material*: Holotype: AMD: IRSNB P.9266a, b. Paratypes: Prm: IRSNB P.9262; La: IRSNB P.9263a, b; Pp: IRSNB P.9264a, b; AMD: IRSNB P.9265a, b; PMD: IRSNB P.9267a, b; IRSNB P.9268a, b; ADL: IRSNB P.9269a, b; PDL: IRSNB P.9270a, b; IRSNB P.9271a, b;

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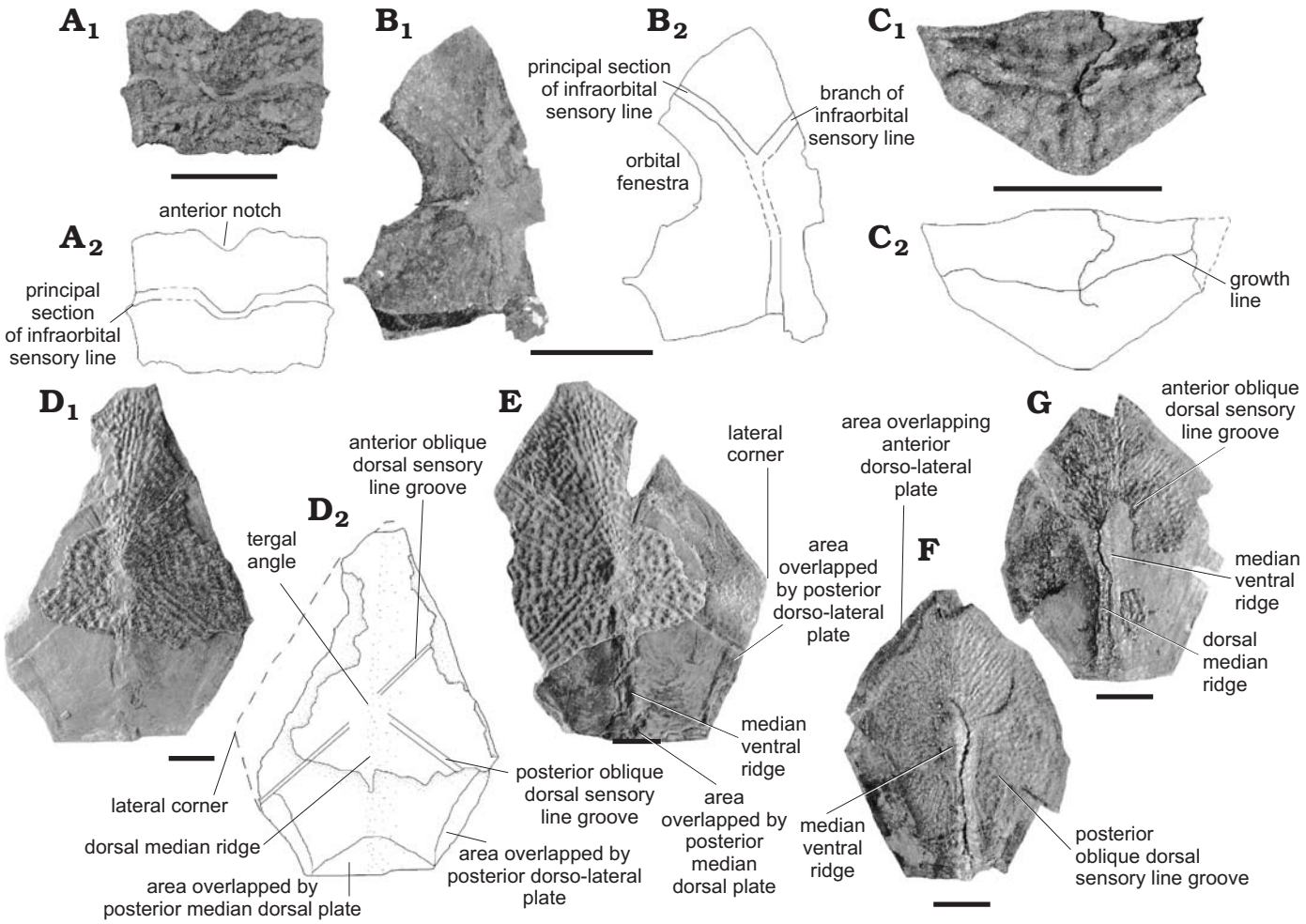



Fig. 9. Dermal plates of antiarch placoderm *Remigolepis durnalensis* sp. nov., from Spontin (Namur Province), Famennian, Devonian. **A**. IRSNB P.9262, Prm, external view, photographed under water immersion. **B**. IRSNB P.9263a, La, external view, photographed under water immersion. **C**. IRSNB P.9264a, Pp, external view, dotted line based on the counterpart IRSNB P.9264b, photographed under water immersion. **D**. IRSNB P.9265a, AMD, external and internal views, dotted line based on IRSNB P.9265b. **E**. IRSNB P.9265b, AMD, external and internal views. **F**. IRSNB P.9266b, AMD, external and internal views. **G**. IRSNB P.9266a, AMD, external and internal views. Photographs ($A_1$–$D_1$, E–G); explanatory drawings ($A_2$–$D_2$). Scale bars 10 mm.

PVL: IRSNB P.9272; PVL and PL: IRSNB P.9273a–d; CV1: IRSNB P.9261a, b; pectoral fin and AVL: IRSNB P.9274a, b.

*Type locality*: Tienne-des-Marteaux quarry also called Durnal 2, Bocq valley, Spontin, Namur Province, Belgium.

*Type horizon*: Montfort/Evieux Formation, Famennian, Upper Devonian.

*Material*.—PMD: IRSNB vert 32049-001a, b; ADL: IRSNB vert 32049-002 from the type locality.

*Diagnosis*.—Species of moderate size. Anterior edge of the Prm displaying a strong notch. Short postpineal plate. Dorsal wall of trunk-armour quite flat and reaching an estimated length of 15-16 cm. Tergal angle situated in the middle of the anterior median dorsal plate. Anterior margin of the anterior median dorsal plate narrow and representing one quarter of the posterior margin. Internal surface of the AMD displaying a median ventral ridge. Anterior and posterior oblique dorsal sensory line grooves well defined. Posterior median dorsal plate as long as broad. Anterior median angle of the posterior median dorsal plate prominent. Crista interna transversalis posterior slightly developed. Processus obstans well developed and articular fossa of the anterior dorso-lateral plate extended. Crista transversalis interna anterior oblique and high. Pectoral fin massive, almost three times as long as broad and stretching slightly less far than the posterior margin of the anterior ventro-lateral plate. Vermiculate ornament forming on several specimens a radiating and concentric network. Tuberculate ornament on the largest plates.

## *Description*

*Headshield*.—*Premedian plate, Prm* (Fig. 9A): It is almost as long as broad and crossed medially by the principal section of infraorbital canal. The anterior edge is marked in its middle by a not extended but well marked notch.

*Lateral plate, La* (Fig. 9B): According to its size, the only preserved lateral plate (IRSNB P.9263a, b) is most probably that of a juvenile. This plate is rather narrow with the posterior part broader than the anterior one. The principal and secondary sections of infraorbital sensory line are deeply incised. The orbit seems small.

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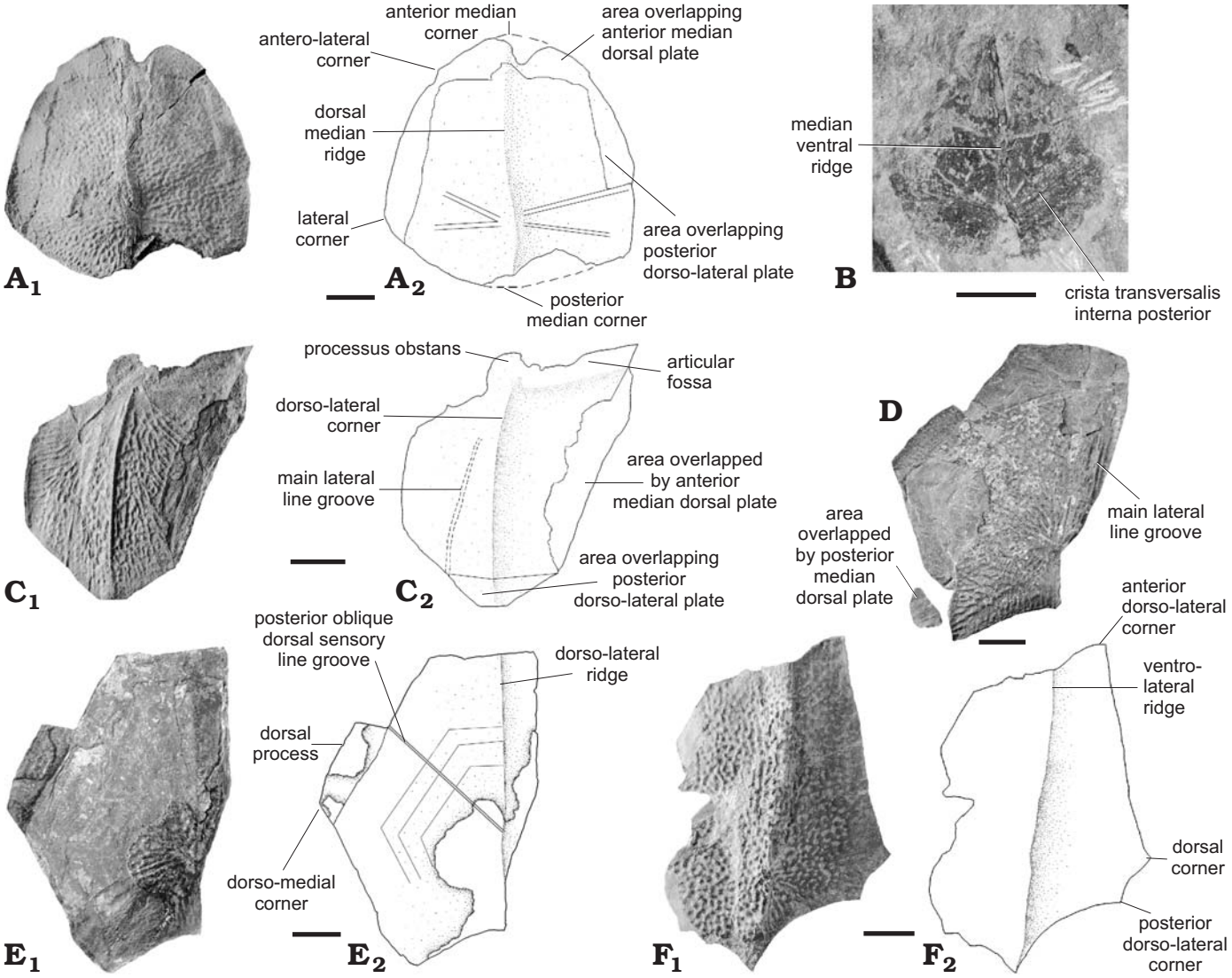



Fig. 10. Dermal plates of antiarch placoderm *Remigolepis durnalensis* sp. nov., from Spontin (Namur Province), Famennian, Devonian. **A**. IRSNB P.9267a, PMD, external view, dotted line based on IRSNB P.9268. **B**. IRSNB P.9268a, PMD, internal view, photographed under water immersion. **C**. IRSNB P.9269a, ADL, external view. **D**. IRSNB P.9271a, PDL, external and internal views. **E**. IRSNB P.9270a, PDL, external and internal views. **F**. IRSNB P.9272, PVL, external view. Photographs ($A_1$, B, $C_1$, D, $E_1$, $F_1$); explanatory drawings ($A_2$, $C_2$, $E_2$, $F_2$). Scale bars 10 mm.

*Postpineal plate, Pp* (Fig. 9C): The postpineal plate is wider than long. The anterior margin is slightly convex whereas the posterior margin is strongly convex. The antero-lateral margin forms a 160° angle with the postero-lateral margin. The postpineal plate shows anteriorly the limits of a smaller plate corresponding probably to a younger growth stage.

*Trunkshield.—Anterior median dorsal plate, AMD* (Fig. 9D–G): This plate is elongate. Externally, it is quite flat, with a slight arch constituted by the dorsal median ridge. The latter forms an obtuse angle and runs from the tergal angle, situated in the middle of the plate, backwards to the posterior margin. The dorsal median ridge is sharper on the smallest AMD (IRSNB P.9266) than on the largest one (IRSNB P.9265) where it is almost absent. The length of the anterior division of the plate is roughly the same as the posterior one. The anterior straight margin is narrow and represents one quarter of the straight posterior margin length. The lateral corners are more or less marked depending on the specimen considered. They are quite rounded on IRSNB P.9266 and more angular on IRSNB P.9265. The anterior part of the lateral margin is about twice longer than the posterior one. There is a dissymmetry of the lateral corners of IRSNB P.9266. The right lateral corner is situated more anteriorly than the left one and is therefore at half the length of the lateral margin. The posterior portion of the lateral margin has the typical sigmoid shape of the genus *Remigolepis*. It overlaps the posterior dorso-lateral plate anteriorly and is overlapped by the posterior dorso-lateral plate posteriorly. The posterior oblique dorsal sensory line grooves are well defined. They form an angle of about 45° with the dorsal median ridge. The posterior oblique dorsal sensory line grooves run from the tergal angle to the middle of the posterior part

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of the lateral margin. The anterior oblique dorsal sensory line grooves are less well defined but distinguishable. They form a right angle with the posterior oblique dorsal sensory line grooves, and run from the tergal angle to the middle of the anterior part of the lateral margin. A small anterior part of the visceral surface is observable. It shows a median ventral ridge, unusual for the genus *Remigolepis*, and a part of the area overlapping the anterior dorso-lateral plate on all its length. Otherwise, the rest of the visceral surface is quite smooth. On the internal surface of IRSNB P.9265, there are three areas corresponding to the compression of the right and left areas overlapped by the posterior dorso-lateral plates and to the compression of the area overlapped by the posterior median dorsal plate.

*Posterior median dorsal plate, PMD* (Fig. 10A, B): The plate is as broad as long. It is quite flat, with a smooth dorsal median ridge surmounting the plate and stretching from the posterior to the anterior angles. The anterior margin is strongly convex, with a strong median angle. The lateral corner is well pronounced whereas the antero-lateral corner is slightly marked. The posterior margin is also convex and the posterior angle rounded. The three overlapping areas are well indicated by prominent areas on the external surface, revealed by the fossilization. They are connected and well extended. IRSNB vert 32049-001 is an abnormal plate with the right side narrower than the left one. Ventrally (IRSNB P.9268), the crista transversalis interna posterior and the median ventral ridge are slightly developed but present.

*Anterior dorso-lateral plate, ADL* (Fig. 10C): The lateral and dorsal laminae are equivalent in width, even if the anterior part of the lateral lamina is much reduced, compared to the anterior part of the dorsal lamina. The processus obstans is well developed and the articular fossa is extended. The anterior part of the lateral lamina is very small, compared to the observable expanded posterior area. The dorso-lateral ridge is sharp, but the angle formed between the lateral and dorsal laminae is difficult to estimate because of the strong compression of the plate during fossilization (about 170° on IRSNB P.9269). The main lateral line groove is not clearly visible. It probably runs from the posterior margin of the lateral lamina to the anterior third of the same lamina, along the dorso-lateral ridge. The area overlapping the posterior dorso-lateral plate is indirectly observable in the form of a prominent area on the external surface due to the compression during fossilization. The area overlapped by the anterior median dorsal plate is clearly visible.

*Posterior dorso-lateral plate, PDL* (Fig. 10D, E): The dorsal lamina bulges slightly in its middle. The angle formed by the two laminae is approximately 150°, with a quite strong dorsal median ridge. The dorsal lamina is about twice as long as broad. The dorso-medial corner is well pronounced. The anterior margin is straight, contrary to the concave posterior margin. The dorso-medial margin displays a sigmoid anterior part due to an elongated process. The posterior part of the dorso-medial margin is straight and about as long as the anterior part. A little part of the area overlapped by the PMD is observed on IRSNB P.9271. The lateral lamina is four times longer than wide. It is less developed than the dorsal lamina, with a width about four times less than that of the latter. This lamina extends over the anterior two-thirds of the plate. The main lateral line groove is not clearly visible. It may run alongside the convex ventral margin of the lateral lamina. The posterior oblique dorsal sensory line groove runs from the posterior area of the dorsal median ridge to the anterior end of the dorsal process. On IRSNB P.9270, the visceral surface shows several growth lines that have their ossification centre on the posterior part of the dorsal median ridge.

*Posterior ventro-lateral plate, PVL* (Figs. 10F, 11A): The ventro-lateral ridge is strongly pronounced. The top of the ridge is widened in the middle on IRSNB P.9272. IRSNB P.9273 displays a less marked ventral lateral ridge because of the compression. The anterior margin of the ventral lamina is straight, and the margin, corresponding to the border with the median ventral plate, is straight and quite long. The lateral lamina is elongated and wider through its dorsal corner. The margin running from the dorsal corner to the anterior dorso-lateral corner is concave. The margin, joining the dorsal corner to the posterior dorso-lateral corner, is also concave and quite extended. The lateral process itself is well developed. The posterior margin of the lateral lamina is concave. The subanal division is relatively large because it occupies about one fourth of the PVL total length. The area overlapped by the left PVL is elongated and narrow. The area overlapped by the AVL is quite narrow too.

*Posterior lateral plate, PL* (Fig. 11A): The only preserved posterior lateral plate (IRSNB P.9273) is in connection with a posterior ventro-lateral plate. It is very low relatively to its length and higher anteriorly than posteriorly. The anterior margin forms a rather acute angle with the anterior portion of the dorsal margin. The posterior dorsal angle is rounded and the height at this level reaches one third of the anterior height. The ventral margin displays posteriorly a re-entrant angle, into which the PVL inserts. The area overlapped by the AVL is thin.

*Anterior ventro-lateral plate, AVL* (Fig. 11C): Only one specimen of AVL is available (IRSNB P.9274). The anterior portion, and thus the anterodorsal process rising to overlap the ADL, is not preserved. The joint with the pectoral fin is masked by the pectoral fin, which is connected to the AVL. The ventro-lateral ridge is strongly compressed, and the lateral lamina rather damaged but extended. The margin shared with the median ventral plate is long and concave. The median ventral plate should occupy a large place in the ventral shield. Internally, the crista transversalis interna anterior is oblique. It seems high but is partly broken.

*Pectoral fin* (Fig. 11B, C).—The ventral side of the pectoral fin is entirely visible. This fin extends posteriorly slightly less than the posterior margin of the anterior ventro-lateral plate. It is quite broad, giving it a stout shape. It is about three times as long as broad. It is divided into two rows of plates with unique proximal and distal plates. The ventral central plate 1 (CV1) is as long as broad. The ventro-medial marginal plate series

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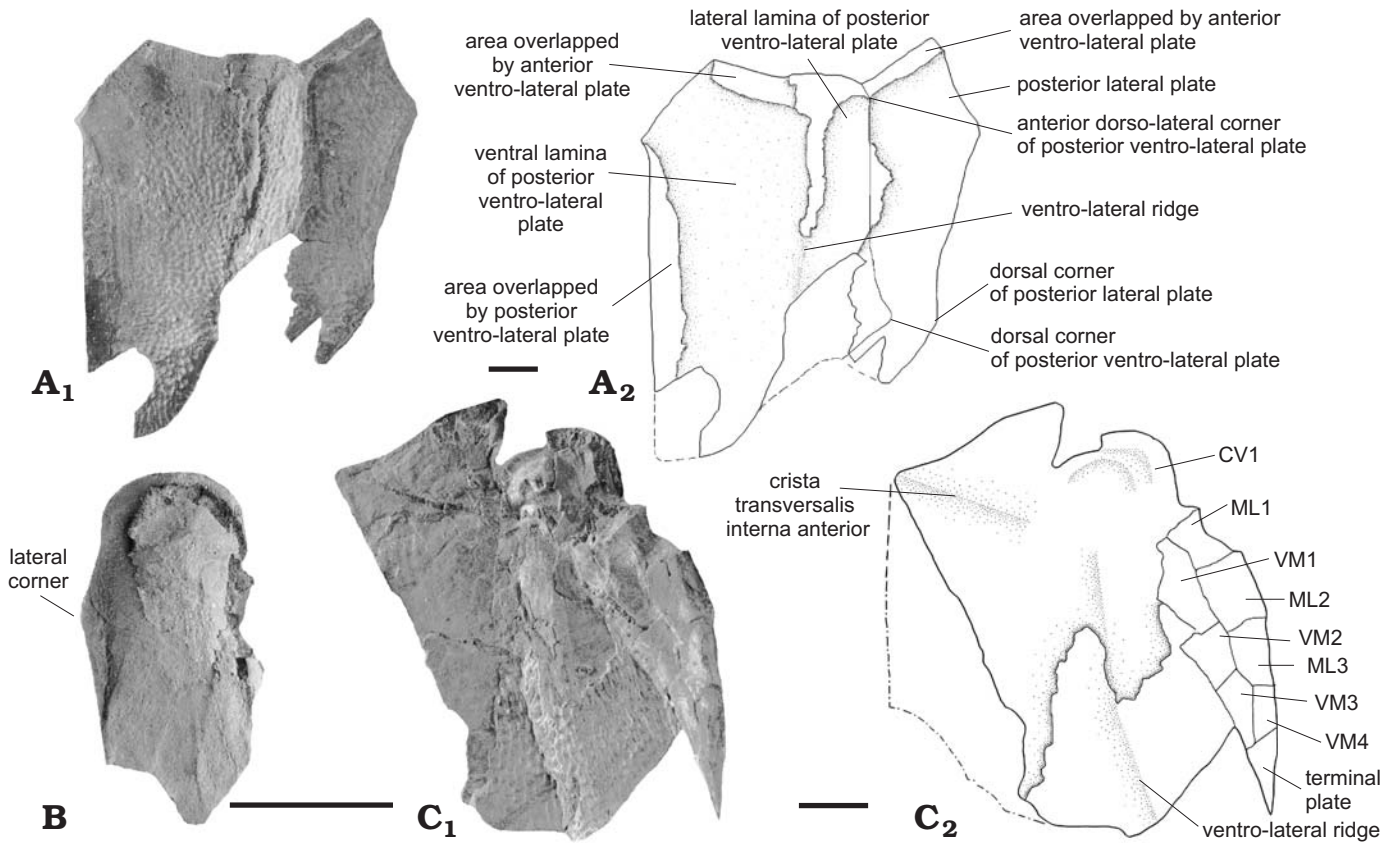



Fig. 11. Dermal plates of antiarch placoderm *Remigolepis durnalensis* sp. nov., from Spontin (Namur Province), Famennian, Devonian. **A**. IRSNB P.9273a, PVL + PL, external view; photograph of natural cast ($A_1$), explanatory drawing ($A_2$), dotted line based on PVL and PL of other *Remigolepis* species. **B**. IRSNB P.9261a, CV1, internal and external views. **C**. IRSNB P.9274a, pectoral fin + AVL, ventral view; photograph ($C_1$); explanatory drawing ($C_2$), dotted line based on IRSNB P.9274b. Abbreviations: CV, ventral central plate; ML, lateral marginal plate; VM, ventro-medial marginal plate. Scale bars 10 mm.

(VM1–VM3) displays three polygonal plates with the VM1 badly preserved. The lateral marginal plate series (ML1–ML4) displays four polygonal plates. The ML1 is preserved as an impression, and its shape is not clearly distinguishable. The terminal plate (T) is posteriorly sharp.

The dorsal central plate 1 (CD1) is at least twice longer than broad (IRSNB P.9261), with a well-defined lateral corner.

*Ornament*.—The ornament of the trunk elements is made of vermiculating, coarse, short pieces of ridges. It can form a radiating network, on the smallest AMD (IRSNB P.9266), and a radiating and concentric network, according to the area of the plate, on the largest AMD (IRSNB P.9265). On the largest plates, it is made of individual or anastomosed tubercles (IRSNB P.9273). On IRSNB P.9267, some tubercles are organized in sensory groove-like structures and form a cross-like structure extending over all the posterior part of the PMD. Except for the lateral plate, which seems unornamented, the other cephalic plates display the same ornament than the trunk plates, i.e., vermiculating, coarse, short pieces of ridges.

*Remarks*.—Even on the largest AMD (IRSNB P.9265), the anterior oblique dorsal sensory line grooves are present. This character is typical of juvenile individuals in *Bothriolepis* (Stensiö 1948) but seems to be retained in adults of *R. durnalense*.

It seems that *R. durnalense*, at least its trunk armour, becomes more dorso-ventrally compressed during its growth. In fact, the lateral lamina of the PVL is deeper in smaller individuals (IRSNB P.9272) than in larger ones (IRSNB P.9273). However, this lower plate is perhaps compensated by a higher posterior lateral plate and/or a higher lateral lamina of the posterior dorso-lateral plate. There is currently not enough material to test such a hypothesis.

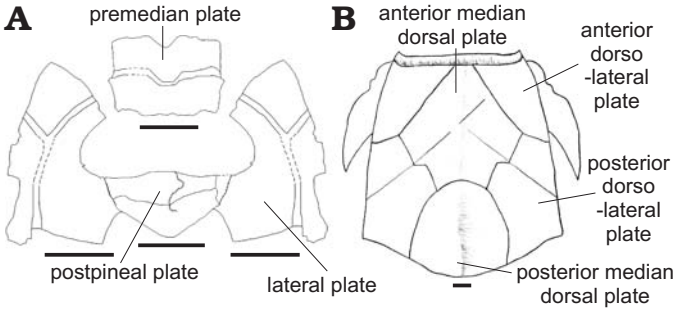



Fig. 12. Reconstructions of the dermal shield of antiarch placoderm *Remigolepis durnalensis* sp. nov., from Spontin (Namur Province), Famennian, Devonian. **A**. Reconstruction of the incomplete head shield (the left lateral plate is the mirror image of the right one), dorsal view. **B**. Trunk reconstruction, dorsal view. Scale bars 10 mm.

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The antiarch from Spontin belongs to *Remigolepis* because of the absence of the joint in the pectoral appendages, the short and broad premedian plate notched anteriorly, the AMD overlapping PDLs anteriorly but overlapped by them posteriorly, and the PDLs and PLs not fused.

Stensiö (1931) erected the genus *Remigolepis* and named several species from the Upper Devonian of East Greenland. The material referable to the type species, *R. incisa* (Woodward, 1900), consists only, and with certainty, of two AMDs (Stensiö 1931). They resemble the AMD of *R. durnalense* by the shape and the ornament consisting of coarse, rounded or slightly elongated tubercles arranged in rather distinct rows that radiate from the dorsal angle. However, the anterior oblique dorsal sensory line grooves, observable in *R. durnalense*, are absent in *R. incisa*, and further comparisons are impossible because of the small amount of material.

*R. cristata* Stensiö, 1931 differs from *R. durnalense* by the longer anterior margin of the AMD and by the spine-like process on the dorsal median ridge. *R. kochi* Stensiö, 1931 differs from *R. durnalense* by its ornament, which forms low striae radiating from the tergal angle on the AMD. The ornament of *R. durnalense* is more vermiculating. *R. kochi* also differs from *R. durnalense* by a more elongated PMD, by a strong dorsal process on the PVL (Stensiö 1931: pl. 26: 5) and by a smaller overall length of the trunk shield. *R. kullingi* Stensiö, 1931 differs from *R. durnalense* notably by a more elongated PMD and by a more delicate ornament (concentric arrangement on the AMD). *R. acuta* Stensiö, 1931 differs from *R. durnalense* by its larger size (about twice longer than *R. durnalense*) and by a narrower PMD.

Of the two Australian species, *R. redcliffensis* Johanson, 1997b differs from *R. durnalense* by a stronger dorsal median ridge, by the absence of oblique dorsal sensory line grooves and by a reduced processus obstans. *R. walkeri* Johanson, 1997a differs from *R. durnalense* by narrower Prm and Pp plates, by the shape of the Pp plate, by a stronger dorsal median ridge and by a lower crista transversalis interna anterior.

The Kirgizian *R. suusamyrensis* Panteleyev, 1992 and *R. karakoliensis* Panteleyev, 1992 are small species, very different from *R. durnalense*. The total length of their trunk armour equals the length of the sole AMD of *R. durnalense*. Moreover, the shape of their AMDs does not match with that one of *R. durnalense*; i.e. more rounded in *R. suusamyrensis* and more elongated in *R. karakoliensis*.

Among the Chinese species, *R. major* Pan, 1987 (in Pan et al. 1987) and *R. xixiaensis* Pan, 1987 (in Pan et al. 1987) are large species that differ radically from *R. durnalense*. The first one could reach a head and trunkshield length of 45 cm, and the latter of 30 cm, whereas in *R. durnalense* it is nearly 20 cm. They also differ from *R. durnalense* by a smooth ventral surface of the AMD. Moreover, the AMD of *R. major* is anteriorly pointed, whereas the AMD of *R. durnalense* presents a short anterior margin. By contrast, *R. xiangshanensis* Pan, 1987 (in Pan et al. 1987) differs from *R. durnalense* by its small size. Moreover, the angle between the posterior oblique dorsal sensory line grooves on the AMD is more obtuse in *R. xiangshanensis* and the ventral surface of the AMD smooth. *R. zhongweiensis* Pan, 1987 (in Pan et al. 1987) and *R. zhongningensis* Pan, Wang, Liu, Gu, and Hang, 1980 are in the size range of *R. durnalense*. However the first one differs from the Belgian species by narrower Pp and PMD and by a more elongated AMD without oblique dorsal sensory line grooves. The latter differs from *R. durnalense* by the shape of the AMD, which displays almost parallel lateral margins, by a tergal angle located anteriorly, by a slender PMD with well-developed cristae transversalis interna posterior and by a slender pectoral fin. Finally, *R. microcephala* Pan, 1987 (in Pan et al. 1987) differs from *R. durnalense* by a Prm anterior notch slightly defined, by a massive Pp and by wider AMD and PMD.

The material defining the Scottish species ?*Remigolepis* sp. only consists of an isolated AMD (Andrews 1978). It comes from a large species because the AMD alone is 15 cm in length. It differs from *R. durnalense* by the size and by coarse tubercles arranged in rows parallel to the margins. *R. armata* Lukševičs, 1991 from Russia differs notably from *R. durnalense* by the spine on the dorsal surface of the PMD plate and by the AMD, which does not taper anteriorly.

The material of *Remigolepis* from Belgium is sufficient and diagnostic enough to erect a new species. This discovery enlarges the spatial distribution of the genus to Western Europe and confirms its cosmopolitan distribution during the Late Devonian.

*Stratigraphic and geographic range*.—Type locality and horizon only.

# Discussion

**Belgium through Devonian times and the palaeoenvironment of the studied localities**.—In Belgium, as well as in the entire Rhenohercynian basin, the Middle Devonian corresponds to a transgressive system. The Early Devonian coast was overstepped northward on the London-Brabant Massif (Ziegler 1990). The Givetian deposits on the southern margin of Belgium display Old Red Sandstone facies represented by the Bois de Bordeaux Formation (= "Roches rouges de Mazy") that crop out between the Senne Valley (Soignies, Feluy, Lens, etc.) and the Mehaigne Valley (Huccorgne, Lavoir). The Formation is subdivided into three members by Lacroix (1991): the Mautienne Member begins with a conglomerate overlying the disconformity on the Silurian rocks, and is mainly made of reddish siliciclastics; the Alvaux Member is composed of limestone (oolitic, bioclastic, sometimes dolomitic) interbedded with shale; and the Mazy Member consists of red sandstone, siltstone, and shale, with few intercalations of reddish limestone.

The Givetian locality of Mazy (south of Gembloux), which yielded some remains of *Asterolepis* (see above, *Asterolepis* sp. 2), belongs to the Alvaux Member, and corre-

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sponds to a shallow marine environment (Lacroix 1974). Hingeon (north of Namur) also yielded remains of *Asterolepis* (*Asterolepis* sp. 1) from the Mazy Member, whose composition is strongly heterogeneous, as noted by Asselberghs (1936). It mainly consists of two red rock units separated by a limestone horizon. *Asterolepis* sp. 1 probably comes from the limestone horizon, as suggested by the blue-green matrix of the fossils from old collections. The Mazy Member certainly corresponds to a more continental environment.

The Late Devonian transgression pushed back the seashore northward on the London-Brabant Massif (Ziegler 1990). The entire Brabant Massif, and thus Southern Belgium, was covered by the sea. To date, no antiarchs have been found in the Frasnian deposits of Belgium. This could be explained by (i) a lack of extensive fieldwork in the considered deposits, or (ii) an unsuitable (more marine) environment. The transgressive phase reached its acme during the late Frasnian and from this time to almost the end of the Late Devonian, the Namur-Dinant Basin, situated south of the London-Brabant Massif, shows evidence of a regression and the re-appearence of siliciclastic deposits (Thorez and Dreesden 1986; Thorez et al. 2006). The lower Famennian rocks (Famenne shale) were mainly deposited offshore, on a shallow epicontinental platform in relatively open marine conditions (Thorez et al. 2006), as indicated by evidence from conodont biofacies (Dreesen and Thorez 1980). Sediments of the middle and upper Famennian (Condroz Group) indicate an important progradation of deltaic complexes (Thorez et al. 2006). The environment during this time changed from open marine to restricted marine (Dreesen and Thorez 1994; Thorez et al. 2006) during the marine regression initiated at the end of the middle Famennian (Johnson et al. 1985). All the Famennian localities studied in this paper belong to the Montfort-Evieux Group. According to Thorez et al. (2006), they all correspond to a lagoonal environment behind a sand barrier. Locally, as in the Strud quarry (south-east of Namur), the facies indicates a more continental (fluvial) environment, i.e., "palaeosoils-channels complexes" (Garrouste et al. 2012: supplementary material) indicating a braided-channel system in an alluvial plain.

**Hydrographical link with East Greenland**.—Clément and Boisvert (2006) noted in the Famennian of Belgium *Soederberghia* and ?*Jarvikia*, two long-snouted dipnoans known from the Famennian of East Greenland. They claimed that these taxa provide evidence for a geographical link between East Greenland and Belgium during the Late Devonian. This link is now further supported by the presence of *Remigolepis* and other fish taxa in the Famennian of Belgium. In fact, taxa common to East Greenland and Belgium include an *Ichthyostega*-like tetrapod (Clément et al. 2004), arthrodires such as *Groenlandaspis* (Janvier and Clément 2005), *Phyllolepis* (Lohest 1888; Leriche 1931), and the cosmopolitan antiarch *Bothriolepis* (Leriche 1931; this paper), osteolepiforms such as *Eusthenodon*, and porolepiforms such as *Holoptychius* (Lohest 1888; Leriche 1931). This argues for strong hydrographic links between East Greenland and the southern coast of the Euramerican continent during the Late Devonian. No shallow marine, continental, deep marine or oceanic basins connected East Greenland to Belgium in the Famennian (Ziegler 1990). The East Greenland basin was surrounded by cratonic highs at that time. Therefore, it may have been a connection between the two areas via a fluviatile system. Such a hypothesis entails a large, about 1700 km, fluviatile network connecting the two areas by the end of the Devonian.

**Palaeogeographic considerations for the genus *Grossilepis***.—*Grossilepis* was previously known from the Frasnian deposits of Latvia, Lithuania, and Russia only. The occurrence of *G. brandi* in the Frasnian of Scotland is not discussed here because of the invalidity of this species. The occurrence of this genus in the Famennian of Belgium enlarges its distribution, spatially because it now occupies the southern margin of Euramerica, and temporally because its stratigraphic range is now extended into the Famennian. During the Late Devonian, the Moscow Platform, Baltic Depression and Belgium were connected by shallow marine to continental basins (Ziegler 1990). The occurrence of *Grossilepis* in the Famennian of Belgium may be the result of a late arrival or it has not yet been found in the Frasnian deposits of Belgium.

# Conclusions

Before this study, only *Bothriolepis* and *Asterolepis* were known from the Devonian of Belgium. A reappraisal of material in Belgian institutions, and extensive field expeditions in the Devonian of Belgium, allowed more detailed descriptions of the already known species (i.e., *Bothriolepis lohesti* and *Asterolepis* sp. 1) and to document new occurrences of other genera such as *Remigolepis* and *Grossilepis*. The full list of valid antiarch taxa from Belgium is: *Bothriolepis lohesti* Leriche, 1931, *Bothriolepis* sp., *Grossilepis rikiki* sp. nov., *Asterolepis* sp. 1, *Asterolepis* sp. 2, and *Remigolepis durnalensis* sp. nov. The new occurrences of *Remigolepis* and *Grossilepis* in the Devonian of Belgium have important palaeobiogeographical implications. The occurrence of *Remigolepis* reinforces the strong faunal affinities between Belgium and East Greenland during the Famennian and the hypothesis of a hydrographic link between the two areas. The occurrence of *Grossilepis* in the Famennian of Belgium suggests a late arrival of that genus from the Moscow Platform and the Baltic Depression, where it occurs in Frasnian deposits.

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