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A NEW GROENLANDASPIDID ARTHRODIRE (VERTEBRATA: PLACODERMI) FROM THE FAMENNIAN OF BELGIUM

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(9 figures, 1 table and 2 plates)

ABSTRACT. A new species of the arthrodire genus *Groenlandaspis* is described from the upper part of the Evieux Formation (Upper Famennian), based on several specimens collected from quarries at Modave and Villers-le-Temple, Liège Province, Belgium. It is the first occurrence of this widespread genus in continental Europe. This new species is characterized by an almost smooth dermal armour, except for some scattered tubercles on its skull roof, median dorsal and spinal plates. Its median dorsal plate is triangular in shape and almost perfectly equilateral in lateral aspect and bears large, spiniform denticles on its posterior edge. All these *Groenlandaspis* remains occur in micaceous, dolomitic claystones or siltstones probably deposited in a subtidal environment. Outcrops of the same area have yielded other vertebrate remains, such as the placoderms *Phyllolepis* and *Bothriolepis*, acanthodians, various piscine sarcopterygians (*Holoptychius*, dipnoans, a rhizodontid, *Megalichthys*, *Eusthenodon* and a large tristichopterid), and a tetrapod that is probably close to *Ichthyostega*. The biogeographical history of the genus *Groenlandaspis* is briefly outlined, and the late Frasnian-Famennian interchange of vertebrate taxa between Gondwana and Euramerica is discussed.

Keywords : Vertebrata, Placodermi, *Groenlandaspis*, Famennian, Belgium, Palaeobiogeography**.**

RESUME. Un nouvel Arthrodire Groenlandaspididé (Vertebrata: Placodermi) du Famennien de Belgique. Une nouvelle espèce du genre d'Arthrodire *Groenlandaspis* est décrite sur la base de plusieurs spécimens récoltés dans la partie supérieure de la Formation d'Evieux (Famennien supérieur), dans les carrières de Modave et Villers-le-Temple, Province de Liège, Belgique. Il s'agit de la première mention de ce genre en Europe continentale, par ailleurs largement répandu. Cette nouvelle espèce est caractérisée par une cuirasse dermique pratiquement dépourvue d'ornementation, sauf sur les plaques du toit crânien et les plaques médiane dorsale et spinale. Sa plaque médiane dorsale est triangulaire et presque parfaitement équilatérale en vue latérale et porte de grands denticules spiniformes sur son bord postérieur. Ces restes de *Groenlandaspis* sont conservés dans un claystone ou siltstone dolomitique légèrement micacé probablement déposé dans un environnement sub-tidal. Dans la même région, les affleurements de la Formation d'Evieux ont livré d'autres restes de Vertébrés, tels que les Placodermes *Phyllolepis* et *Bothriolepis*, des acanthodiens et divers poissons Sarcoptérygiens (*Holoptychius*, des Dipneustes, un Rhizodontide, *Megalichthys*, *Eusthenodon*, et un grand Tristichoptéridé) et un tétrapode probablement proche d'*Ichthyostega*. L'histoire biogéographie du genre *Groenlandaspis* est brièvement évoquée et l'échange des taxons de Vertébrés entre le Gondwana et l'Euramérique au Frasnien-Famennien est discuté.

Mots-clés : Vertebrata, Placodermi, *Groenlandaspis*, Famennien, Belgique, Paléobiogéographie**.**

1. Introduction

The late Famennian vertebrates of the Famenne area (Ardennes, Belgium) are relatively rare, and most reported occurrences date back to the time when the numerous quarries were exploited for sandstone in the region, which extends from the Namur to Liège areas. Only a few articles deal with vertebrate records from this area, most of them are from the late nineteenth and early twentieth centuries (Malaise *in* Mourlon, 1875; Malaise, 1887; Lohest, 1882, 1888a, b, 1889; Destinez, 1904; Leriche, 1931). Additional specimens have been either described, or re-described, in the twentieth century (Gross, 1965; Lelièvre, 1982; Blieck & Lelièvre, 1995; Cloutier & Candilier, 1995; Taverne, 1997). Recently, new vertebrate occurrences have turned up, in the wake of the extensive sedimentological field studies carried out by Jacques Thorez (Liège University; Thorez & Dreesen, 1986; Thorez *et al.*, 1988), and some hitherto unrecorded taxa have been described (Clément, 2002; Clément *et al.*, 2004). To date, the Famennian of the Famenne area has yielded placoderms (*Bothriolepis*, *Phyllolepis*, *Ardennosteus*),

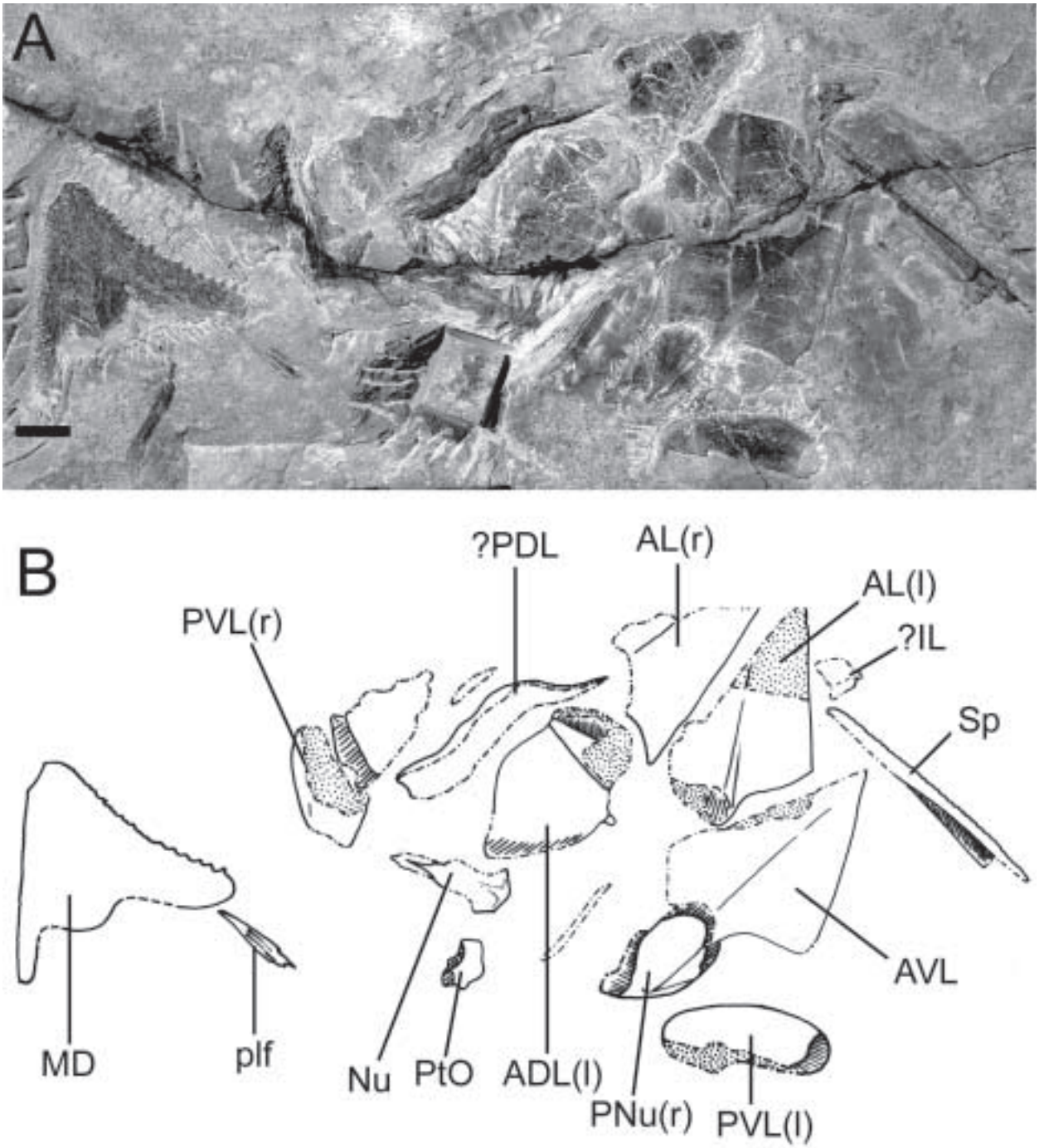

Plate 1. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Modave, Liège Province, Belgium. Ensemble of plates in block Nr 35 (holotype), Palaeontological collection, University of Liège, Belgium. A, photograph in immersion in water, before removal of the PtO plate. B, explanatory sketch. Scale bar = 10mm. Alternating dash and dots = broken limits. Areas preserved as impressions stippled. Abbreviations: ADL(l), anterior dorsolateral plate of the left side; AL, anterolateral plate [(l), left side; (r), right side)]; AVL, anterior ventrolateral plate; ?IL, fragmentary interolateral plate; MD, median dorsal plate (holotype); Nu, nuchal plate; ?PDL, probable posterior dorsolateral plate; plf, plant fragment; PNu(r), paranuchal plate of the right side; PtO, postorbital plate of the left side; PVL, posterior ventrolateral plate [(l), left side; (r), right side]; Sp, spinal plate, probably of the left side.

acanthodians, actinopterygians (*Osorioichthys*), piscine sarcopterygians (*Holoptychius*, dipnoans, a *Strepsodus*-like rhizodontid, ?*Glyptopomus*, *Megalichthys*, *Eusthenodon,* and a large, unnamed tristichopterid possibly close to *Platycephalichthys*), and an ichthyostegid tetrapod (Clément *et al.*, 2004).

Here we report the first occurrence of the placoderm genus *Groenlandaspis* in the Famennian of Belgium, which is also the first occurrence of this taxon in continental Europe. *Groenlandaspis* is a classical placoderm of the late Famennian vertebrate assemblages in North America, Greenland and Britain; it occurs as early as the Eifelian in Gondwanan regions and is widespread there in the Givetian and Frasnian, but its distribution extends into Euramerica (or Laurentia-Baltica) only in the Famennian.

This *Groenlandaspis* material from the Hoyoux Valley, Liège Province, Belgium, is referred here to a new species and is deposited in the palaeontological collection of the University of Liège, Belgium. It consists of two blocks of dark, dolomitic claystone from the Modave quarry (also known as Pont-de-Bonne quarry), which bear assemblages of head and trunk armour plates, some of which most probably belong to the same individual and, at any rate, are obviously derived from the same outcrop and much the same bed (Pls.1, 2A, B). In addition, an isolated spinal plate of *Groenlandaspis* from the Famennian of Villers-le-Temple, Liège Province, is identical to that of the specimen from Modave, yet of larger size (Pl. 2D, Fig. 7I).

The only groenlandaspidid arthrodire previously recorded from the Famennian of the Famenne area is represented by an incomplete, high-crested median dorsal plate fragment (Pl. 2C), also from Modave, which was referred to the late Pragian-Emsian genus *Tiaraspis* by Gross (1965, fig. 4A; pl. 2: 2, 3; Pl. 2C). At a time when the similarly high-crested median dorsal plate of *Groenlandaspis* was still unknown, Gross (1965) considered that this specimen could only belong to *Tiaraspis* and thus could not be Famennian in age, but rather early Devonian. Gross (1965) invoked a labelling mistake in order to make it agree with its identification as *Tiaraspis*, and thus regarded it as coming from the Lower Devonian of the neighbouring area of Hingeon. However, this specimen bears much resemblance to the median dorsal plate of the new species described here and there is no reason to doubt its Famennian age, as it is preserved in the typical, black dolomitic claystone of the upper part of the Evieux Formation. Long *et al.* (1997) compared this specimen to the median dorsal plate of the groenlandaspidid *Africanaspis doryssa* (Fig. 4M), from the Upper Famennian of South Africa, which possesses an extremely high and slender median dorsal plate, and a similar, posterior series of large and sharp denticles. It also resembles, yet to a lesser extent, the median dorsal plate of *Turrisaspis elektor* (Fig. 4N), from the Upper Famennian of Pennsylvania (Daeschler *et al.*, 2003). However, a close examination of the specimen described by Gross (1965), which is very small, made us doubt that it is complete. Curiously, it would match almost perfectly the size of the broken tip of the median dorsal plate in the new material described here and diplays the same, large and sometimes bifid posterior denticles as the latter. There is, however no evidence that the two specimens are derived from the median dorsal plate of the same individual.

2. Material and methods

The two blocks in which the specimens are preserved (University of Liège, Palaeontological collection, referred to below as Nr 35 and 38) probably come from the same outcrop, as their lithology is exactly similar, with dark grey dolomitic claystone, showing exactly the same superficial weathering. These numbers may not be the original one, as there is some confusion in the old numbering of the specimens in the Liège University Palaeontological collection. Notably, the fragmentary median dorsal plate from Modave figured by Gross (1965) is glued on a piece of cardboard that bears the collection number A/2005 and the specimen itself bears, in addition a small green label on which is written "18". The same green labels, with "35" and "38" were stuck on the blocks we describe here, and we suspect they may all belonged to the same lot of specimens from Modave, possibly from the same lens. Unfortunately the original catalogues made by P. Destinez in the late nineteenth and early twentieth centuries are uninformative in this respect, and this cannot be checked (E. Poty, Liège, pers. com. 2003). Therefore we retain here this provisional numbering as "block Nr 35" and "block Nr 38", until a new catalogue of the collection is made.

Judging from the style of the locality information written directly on the blocks, these specimens were almost certainly been discovered and registered in the late nineteenth century. They are both labelled as coming from the Modave quarry (in fact, a series of several small quarries along the Hoyoux river), in the Dinant synclinorium, which is known for having yielded many other vertebrate remains in the late nineteenth century (Lohest, 1888a). Both blocks contain only *Groenlandaspis* remains, and we presume that all the remains from each block belong to the same individual, since none of the dermal plates of the same side are found in more than one exemplar in each block. Slight differences in the proportions of the paranuchal plates (Fig. 1B, C) in the respective blocks also suggest the presence of two individuals. The isolated spinal plate from Villers-le-Temple, which is much larger than those in the other two blocks, is also preserved in the same kind of dark grey dolomitic claystone or siltstone.

The specimens have been prepared with a needle, and the paranuchal and anterior median ventral and right posterolateral plates of block Nr 38, as well as the postorbital plate of block Nr 35 (PL (r), PNu, AMV, PtO, Pls 1B, 2A2) have been removed from the blocks to be transferred in resin and prepared from the other side.

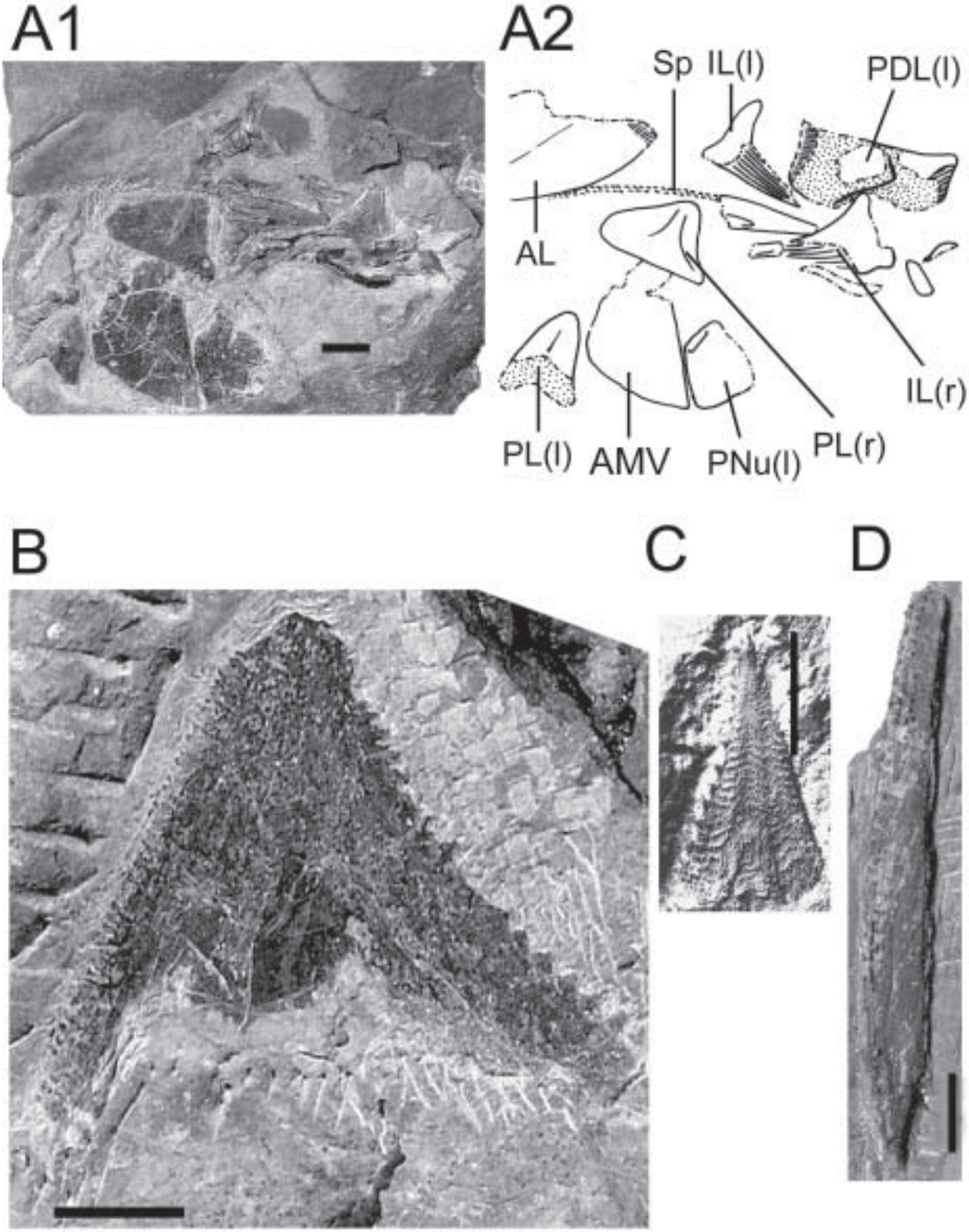

Plate 2. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Liège Province, Belgium. A-C, from Modave; D, from Villers-le-Temple. Palaeontological collection, University of Liège, Belgium. A, block Nr 38, photographed in immersion in water (A1), before removal of the PL, AMV, PNu and PL(r) plates, and explanatory scheme (A2). B, Median dorsal plate (belonging to the holotype in block Nr 35) in lateral view. C, tip of a median dorsal plate (Nr A/2005) in lateral view, referred to by Gross (1965) as *Tiaraspis* sp. D, isolated spinal plate of the left side in dorsal view (Nr 5924). Scale bar = 10 mm. Alternating dash and dots = broken limits. Areas preserved as impressions stippled. Abbreviations: AL, anterolateral plate; AMV, anterior median ventral plate; IL, interolateral plate [(l), left side; (r), right side]; PDL(l), posterior dorsolateral plate of the left side; PL, posterolateral plate [(l), left side; (r), right side]; PNu(l), paranuchal plate of the left side; Sp, spinal plate.

3. Geological setting

The lithostratigraphy of the Evieux Formation mainly consists of straticulated (micaceous) siltstones and claystones, and the depositional environment is considered as subtidal, dominated by waves and storms (Thorez *et al.*, 1988). The matrix of the all these *Groenlandaspis* specimens consists of weakly micaceous claystone and siltstone, with poor feldspar and quartz grain sorting and corresponds to the classical sediments in the Famennian of Belgium, particularly in the upper part of the Evieux Formation.

4. Systematic study

Phylum Vertebrata Linnaeus, 1758
Subphylum Gnathostomata Gegenbaur, 1877
Class Placodermi McCoy, 1848
Subclass Arthrodira Woodward, 1891
Order Phlyctaenioidei Miles, 1973
Suborder Phlyctaenii Miles, 1973
Family Groenlandaspididae Obruchev, 1964

Remarks : The phlyctaeniid family Groenlandaspididae includes the genera *Groenlandaspis*, *Tiaraspis*, *Boomeraspis*, *Turrisaspis*, *Africanaspis*, *Mithakaspis*, and *Mulgaspis* (see Table 1). It is defined by a number of unique characters, namely the preorbital plates entirely separated by the pineal plate, the closely-set condyles of the dermal neck joint, the midline contact between the anterior and posterior dorsolateral plates of each side, the very deep trunk armour with a narrow and high-crested median dorsal plate, and the inverted V-shaped pattern of the main lateral-line groove on the posterior dorsolateral plate (Long *et al.*, 1997; Young & Goujet, 2003).
The Groenlandaspididae is almost certainly a monophyletic taxon. Although they have once been regarded as a possible relative of the brachythoracid arthrodire family Holonematidae by Denison (1978), there is now clear evidence that they belong to the Phlyctaenii (Goujet, 1984; Young & Goujet, 2003) among the Arthrodira.

Genus *Groenlandaspis* Heintz, 1932

Type species. *Groenlandaspis mirabilis* Heintz, 1932; Upper Devonian (Upper Famennian), East Greenland.

Remarks : The material of the type species of the genus *Groenlandaspis*, *G. mirabilis* from the Upper Famennian of Greenland, includes posterior dorsolateral plates (PDL, Fig. 8D, E), but its characteristically high-crested median dorsal plate was (and still is) unknown. *G. mirabilis* and all other species referred to this genus share the characteristic inverted V-shaped dorsal flexure of the main lateral-line groove (llg, Fig. 8), and the median suture between the anterior and posterior dorsolateral plates of each side (sutPDL, Fig. 4B). The high-crested median dorsal plate of the Groenlandaspididae was first described in *Tiaraspis*, from the Upper Pragian-Emsian of Germany (Gross, 1933, 1962; Schultze, 1984; Fig. 7A) but, at that time, no relation was suggested between this genus and *Groenlandaspis mirabilis*. The discovery of *Groenlandaspis* in the Middle Devonian of Antarctica by Ritchie (1974, 1975) came as a surprise, firstly because this genus was previously unknown outside Greenland, and, second, because it yielded the first evidence for its peculiar, high-crested median dorsal plate (Figs 7C-L). Once the morphology of the armour of *Groenlandaspis* was understood, this genus and other closely related groenlandaspidid genera turned up in many Devonian localities all over the world, sometimes as specimens collected long ago and referred to other placoderm genera. *Groenlandaspis* is now known from Australia and Antarctica (Ritchie, 1974, 1975, 2004; Young, 1993), Turkey (Janvier & Ritchie, 1977; Janvier, 1983; Janvier *et al.*, 1984), Iran (Janvier & Ritchie, 1977; Blieck *et al.*, 1980), Ireland (Woodward, 1891; Ritchie, 1974, 1975), South Africa (Chaloner *et al.*, 1980; Long *et al.*, 1997; Anderson *et al.*, 1999), the Falkland Islands (Maisey *et al.*, 2002), and North America (Daeschler *et al.*, 2003). In addition, the « primitive brachythoracid » described from the Frasnian Cuche Formation of Colombia by Janvier & Villarroel (2000) is likely to be in fact a *Groenlandaspis* species with coarsely tuberculate ornamentation (G. Young, pers. com., 2001). *Groenlandaspis* appears thus as quite a common taxon as early as the Emsian (Young, 1993) and even earlier, as suggested by the several unnamed species from the ?late Pragian-Eifelian Dulcie Sandstone and Cravens Peak Beds of Australia (Young & Goujet, 2003), but it is unknown in North America, Europe, and possibly eastern Asia before the Famennian. The only possible exception is the a spinal plate from the Uppermost Frasnian of Scaat Craig, Scotland, referred to as *Cosmacanthus malcolmsoni* by Agassiz (1844), and long regarded as an acanthodian spine. Denison (1979, p. 56) pointed out that this unique specimen was the spinal plate of an arthrodire and recent examination suggest that it is a spinal plate of a Groenlandaspidid (S. Ivanov, pers. com. 2004). If Scaat Craig is correctly dated, this would be the only evidence for this genus before the Famennian in Euramerica. Moreover, if *Cosmacanthus malcolmsoni* can be proved to be a plate of *Groenlandaspis* (by the discovery of more diagnostic plates, such as the anterior or posterior dorsolateral plates), then the name *Groenlandaspis* would become a junior synonym of *Cosmacanthus*.
To date, the genus *Groenlandaspis* is represented by seven named species (including the new species described herein), and a number of other, still undescribed species, referred to in the literature as *Groenlandaspis* sp., in particular from Antarctica and Australia (Tab.1). However, the recent erection of several other groenlandaspidid genera, namely *Africanaspis* (Long *et al.*, 1997), *Turrisaspis* (Daeschler *et al.*, 2003) and *Mithakaspis* (Young & Goujet, 2003), has made the genus *Groenlandaspis* difficult to

Taxa	Locality	Age	References
Tiaraspis subtilis (Gross, 1933)	Rhineland, Germany	Emsian	Gross, 1933, 1962; Schultze, 1984
T. (Dichotiaraspis) barbarae (Bardenheuer, 1990)	Rhineland, Germany	Emsian	Bardenheuer, 1990
?*Tiaraspis* sp.	Spitsbergen	Wood Bay Formation, Pragian	Gross, 1965
Tiaraspis sp.	"Hingeon"	"Lower Devonian"	Gross, 1965 (in error; see *G. thorezi*)
Boomeraspis goujeti Long, 1995	Antarctica	Basal Aztec Siltstone, Upper Givetian	Long, 1995
Mithakaspis lyentye Young & Goujet, 2003	Australia	Cravens Peak beds, ?Upper Pragian-Eifelian	Young & Goujet, 2003
Africanaspis doryssa Long, Anderson, Gess & Hiller, 1997	South Africa	Witpoort Formation, Famennian	Long *et al*., 1997
Turrisaspis elektor Daeschler, Frumes & Mullison, 2003	Pennsylvania, USA	Catskill Formation, Famennian	Daeschler *et al*., 2003
Mulgaspis evansorum Ritchie, 2004; *M. altus* Ritchie, 2004	Australia	Merrimerriwa Formations, Mulga Downs Group, ?Eifelian	Ritchie, 1969, 1975, 1987, 2004.
Groenlandaspis mirabilis Heintz, 1932	East Greenland	Upper Famennian	Heintz, 1932; Stensiö, 1934,1936, 1939
G. antarctica (Ritchie, 1975)	Antarctica	Aztec Siltstone *B. karawaka*-zone, Upper Givetian	Ritchie, 1975
G. disjectus (Woodward, 1891)	Kilkenny, Ireland	Kiltorcan Beds, Upper Famennian	Woodward, 1891; Ritchie, 1974, 1975
G. seni Janvier & Ritchie, 1977	Kemer, Turkey	Upper Antalya Nappe, Frasnian	Janvier & Ritchie, 1977; Janvier, 1983
G. theroni (Chaloner, Forey, Gardiner, Hill & Young, 1980)	South Africa	Bokkeveld Group, Givetian	Chaloner *et al*., 1980 Anderson *et al*., 1999
G. riniensis Long, Anderson, Gess & Hiller, 1997	South Africa	Witpoort Formation, Upper Famennian	Long *et al*., 1997
G. pennsylvanica Daeschler, Frumes & Mullison, 2003	Pennsylvania, USA	Catskill Formation, Famennian	Daeschler *et al*., 2003
G. thorezi n. sp.	Ardennes, Belgium	Evieux Formation, Upper Famennian	This article. *Tiaraspis* sp., Gross, 1965; ?*Africanaspis* sp., Long *et al*., 1997
Groenlandaspis sp.	Khush-Yeilagh, Eastern Alborz, Iran	Emsian	Janvier & Ritchie, 1977; Blieck *et al*., 1980
Groenlandaspis sp.	Kemer, Turkey	Upper Antalya Nappe, Frasnian	Janvier *et al*., in prep.
Groenlandaspis sp.	Portishead, England	Famennian	Ritchie, 1975
Groenlandaspis sp.1	Australia	Cravens Peak beds, ?Upper Pragian-Eifelian	Young & Goujet 2003
cf. *Groenlandaspis* sp. 2	Australia	Cravens Peak beds, ?Upper Pragian-Eifelian	Young & Goujet 2003
Groenlandaspis sp.	Antarctica	Aztec Siltstone, Givetian	Young, 1993
Groenlandaspis sp.	Australia	Avon River Group Howitt fauna, ?Upper Givetian-Lower Frasnian	Young, 1993
Groenlandaspis sp.	Australia	Freestone Creek Fauna, Lower Frasnian	Young, 1993
Groenlandaspis sp.	Australia	Twofold Bay Formation, Lower Famennian	Young, 1993
Groenlandaspis sp.	Australia	Jemalong-Canowindra Fauna, Upper Famennian	Ritchie, 1975; Young, 1993
Groenlandaspis sp.	Australia	Worange Point Formation, Upper Famennian	Young, 1993
Groenlandaspis sp.	Australia	Hervey Group, Grenfell fauna, Upper Famennian- ? Lower Carboniferous	Ritchie, 1975; Young, 1993
Groenlandaspis sp.	Hakkari, Turkey	Köprülü Formation, Uppermost Famennian	Janvier *et al*., 1984
?*Groenlandaspis* sp.	Falkland Islands	Port Philomel Formation, Givetian	Maisey *et al*., 2002
?*Groenlandaspis* sp.	Colombia	Cuche Formation, Frasnian	Janvier & Villarroel, 2000

Table 1. Geographical and stratigraphical distribution of the species of Groenlandaspididae recorded up to 2004.

define on the basis of uniquely derived characters. In fact, when considering Young & Goujet's (2003) amended definition of the Groenlandaspididae, *Groenlandaspis* would merely appear as an ensemble of generalized species of this family. Long *et al*. (1997) considered that *Groenlandaspis* should be characterized by the loss of the ridges which, in the other Groenlandaspididae and most Phlyctaenii, mark the external surface of the anterior and posterior dorsolateral plates, in particular the longitudinal, dorsolateral ridge. Nevertheless such ridges, yet faint, sometimes occur in some species referred to *Groenlandaspis*, as it is the case in the new species described below (lr, Fig. 4A, C, D). A more reliable definition of the genus would now require a better knowledge of its type species, *G. mirabilis*, and an extensive phylogenetic analysis of the Groenlandaspididae in general, as soon as the many undescribed groenlandaspidid species are published. It is not ruled out, for example, that such genera as *Africanaspis* or *Turrisaspis* will turn out to be nested within *Groenlandaspis*.

Groenlandaspis thorezi sp. nov.
(Pl. 1, 2; Figs 1-6, 7I, 8L)

Designation of name. A species named in honour of Dr. Jacques Thorez (Liège), who devoted most of his career to the study of the sedimentology and stratigraphy of the Famennian in its type area, the Famenne Valley and the Ardenne Massif.

Diagnosis. A medium-sized *Groenlandaspis* whose median dorsal plate is almost perfectly equilateral and triangular in shape, with a slightly concave posterior margin bearing a series of large, sometimes bifid denticles. The ornamentation is weakly developed, as tubercles on the head plates and the leading edge of the spinal plate, but these are completely lacking on the other lateral and ventral thoracic plates.

Holotype. An ensemble of plates (left ADL, left and right AL, AVL, ?IL, MD, Nu, right PNu, left PtO, right and left PVL, and left Sp) assumed to belong to the same individual, and preserved in a single block. University of Liège, Belgium, Palaeontological collection Nr 35 (Pls 1A, 2B).

Referred material. All plates on blocks Nr 38 (Pls. 1A, 2A1; University of Liège, Belgium, Palaeontological collection). An Isolated spinal plate from Villers-le-Temple, Liège Province, Belgium (University of Liège, Palaeontological collection, Nr 5924 (Pl. 2D). Probably the dorsal tip of a median dorsal plate from Modave (University of Liège, Palaeontological collection, Nr A/2005; Pl. 2C; Gross, 1965, fig. 4A; pl. 2: 2, 3).

Type locality and age. Modave quarry, also known as Pont-de-Bonne, Hoyoux Valley, Liège Province, Belgium; Upper part of the Evieux Formation, Famennian, Upper Devonian.

Remarks. The virtual lack of ornamentation on most dermal plates of *G. thorezi* could be thought to be evidence stage, but this is ruled out, because the few growth series known in arthrodires show the contrary; that is, juvenile individuals have a more extensive ornamentation than adult ones (Trinajstic & McNamara, 1999, p. 88). Moreover, the spinal plate from Villers-le-Temple (Pl. 2D, Fig. 5I), which is about 30% larger than those in blocks Nr 35 and 38 (and presumably belongs to an older individual), is also devoid of ornamentation on its dorsal surface and only bears a few series of very large, spiniform tubercles on its leading edge and on the lateral edge of its free portion.

4.1. Description

4.1.1. Skull roof

a) Nuchal (Nu) plate: The Nu plate (Nu, Pl. 1B, Fig. 1A) displays the same arrowhead shape as that of other groenlandaspidids. Compared to the few nuchal plates described from other *Groenlandaspis* species, it resembles most closely that of *G. antarctica* (Ritchie, 1975). It also displays a distinctive transverse ridge along its posterior margin and a prominent median boss at a short distance from the posterior margin (b, Fig. 1A2). Its external surface is evenly ornamented with medium-sized, low and rounded tubercles.

b) Paranuchal (PNu) plate: A complete PNu plate of the right side is preserved on block Nr 35 (PNu(r), Pl. 1B, Fig. 1C), and a less complete one, of the left side, has been prepared from block Nr 38 (PNu(l), Pl. 2A2, Fig. 1B). It displays some ornamentation of medium-sized, scattered tubercles, as on the Nu plate, but these become sparser anterolaterally. These two PNu plates display some differences, which suggest that they do not belong to the same individual. In particular, the PNu plate of the right side displays, in addition to the main lateral-line groove (llg, Fig. 1B, C), an anteromedially directed groove (ppl?, Fig. 1C) which resembles the similarly placed groove on the PNu of *Turrisaspis elektor* (Daeschler *et al*., 2003, figs 6C, 11F). Daeschler *et al*. (2003) considered this supernumerary groove as unique to *Turrisaspis*, and possibly a posterior prolongation of the supraorbital groove on the central and paranuchal plates, but it is better interpreted as an anterior extension of the posterior pit-line towards the central plate. Another possible difference is the smooth zone medially to this goove in the PNu plate of the right side (Fig. 1C) and its more extended pararticular process (pap, Fig. 1C). These differences are likely to be individual variations in the same species. The external opening of the endolymphatic duct cannot be clearly observed in any of these two PNu plates.
The ventral surface of the PNu plate of the left side shows the articular fossa (artf, Fig. 1B). Using the

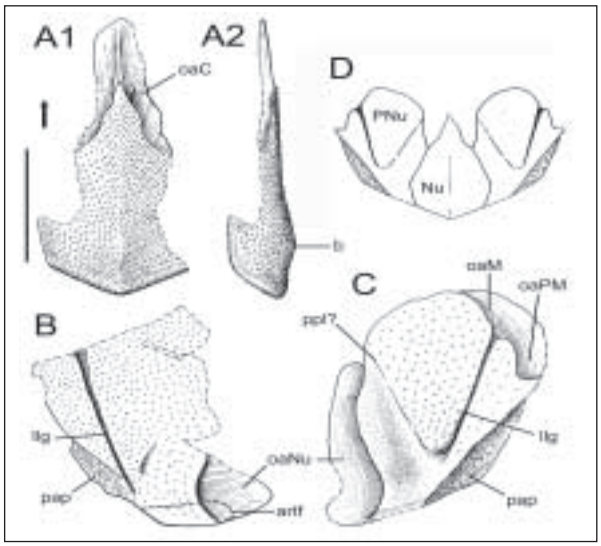

Figure 1. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Modave, Liège Province, Belgium. Palaeontological collection, University of Liège, Belgium. A, nuchal plate in dorsal (A1) and lateral (A2) view (from block Nr 35); B, incomplete paranuchal plate of the left side in dorsal view (from block Nr 38; outline of the articular fossa in dashed line); C, paranuchal plate of the right side in dorsal view (from block Nr 35); D, attempted reconstruction of the posterior part of the skull roof, obtained by assembly of the nuchal plate in A and the paranuchal plate in C. Scale bar = 10 mm. Alternating dash and dots = broken limits. Arrow points forward. Abbreviations: artf, outline of the articular fossa; b, median boss of nuchal plate; llg, main lateral-line groove; Nu, nuchal plate; oaC, overlap area for the central plate; oaM, overlap area for the marginal plate; oaNu, overlap area for the nuchal plate; oaPM, overlap area for the postmarginal plate; pap, pararticular process; PNu, paranuchal plate; ppl?, possible anterior extension of the posterior pit-line.

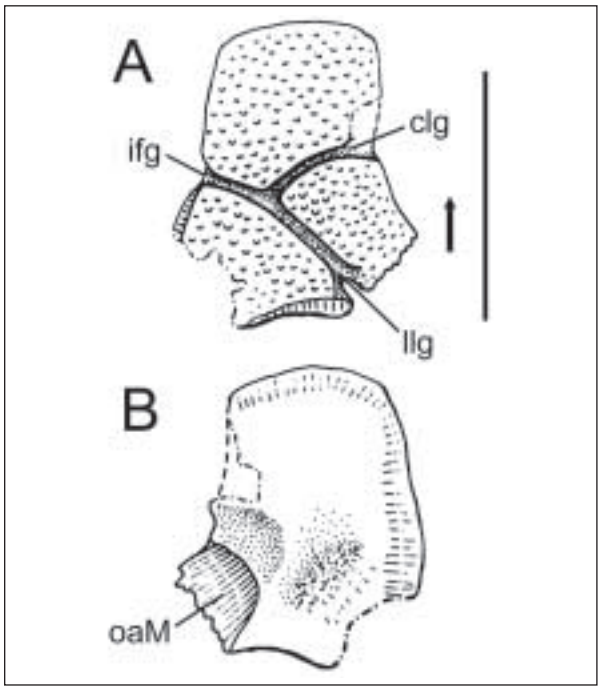

Figure 2. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Modave, Liège Province, Belgium. Palaeontological collection, University of Liège, Belgium, block Nr 35. Postorbital plate of the left side in dorsal (A) and ventral (B) view. Scale bar = 10 mm. Alternating dash and dots = broken limits; dash = reconstructed limits. Arrow points forward. Abbreviations: ifg, infraorbital sensory-line groove; clg, central sensory-line groove; llg, main lateral-line groove; oaM, overlap area for the marginal plate.

Nu-PNu overlap areas (oaNu, Fig. 1B, C), and the orientation of the articular fossa, a reconstruction of the posterior part of the skull roof has been attempted. This shows a moderately acute posterior angle (Fig. 1D), which resembles most closely that of *G. antarctica* (Ritchie, 1975, fig. 2a). In addition, this reconstruction suggests that the central plate (unknown) projected a narrow posterior process between the Nu and PNu plates, as in *G. antarctica* (Ritchie, 1975, fig. 2a). The pararticular process, the surface of which is made up by spongiose bone, is broad and extends farther anteriorly than in all other *Groenlandaspis* species where it has been described (pap, Fig. 1B, C).

c) Postorbital (PtO) plate: An isolated left PtO plate has been prepared from block Nr 35 (PtO, Pl. 1B; Fig. 2). It provides little information, except for its unusually long anterior portion, but the outline of its orbital margin is unclear.

4.1.2. Thoracic armour

a) Median dorsal (MD) plate: The MD plate is triangular in shape in lateral view and almost equilateral (Pl. 2B, Fig. 3). Its ventral margin, which bounds its overlap areas for the ADL and PDL plates is markedly bilobate. Although its apex is broken, its H/L ratio may be estimated as about 0.87. Its ornamentation consists of small, scattered tubercles, which are best visible on its leading edge, where they are arranged in parallel, horizontal and more or less sinusoidal, rows (Pl. 2B, Fig. 3A). A few large, spiniform, sometimes bifid tubercles also occur along its posterior edge, which is slightly concave. The apex of the plate is somewhat angular, and most likely broken. No other fragment of this plate has been found nearby, and it may be assumed that the break occurred pre-mortem or pre-deposition. It is worthy noticing that the MD plate from Modave referred by Gross (1965) to *Tiaraspis* (Pl. 2C) almost perfectly matches the missing tip of the MD plate of *G. thorezi* (Fig. 3B), and displays the same horizontal and slightly sinusoidal rows of scattered tubercles (visible mainly in immersion on the MD of the holotype) on

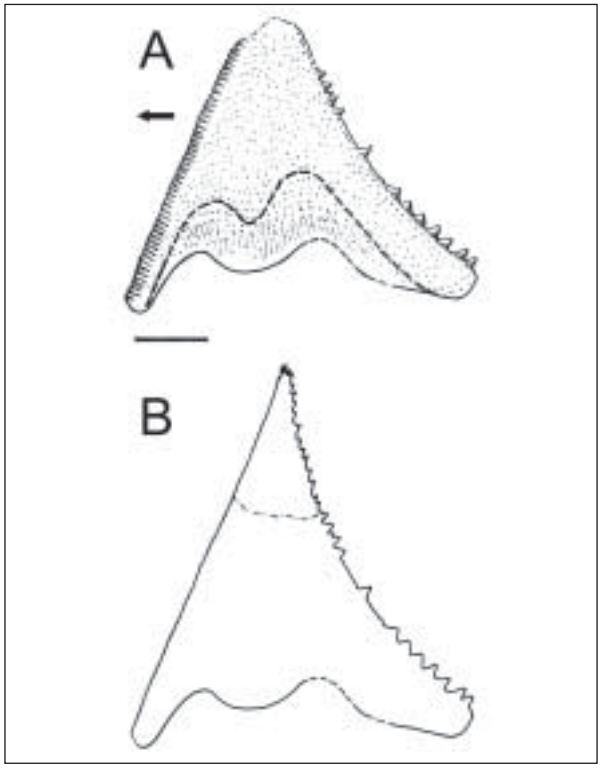

Figure 3. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Modave, Liège Province, Belgium. Palaeontological collection, University of Liège, Belgium, block Nr 35. Median dorsal plate in lateral view. A, reconstruction based on the median dorsal plate of the holotype, bold dash = median limit of the internal surface; B, reconstruction combining the outline of the median dorsal plate of the holotype and specimen A/2005. Scale bar = 10 mm. Arrow points forward. Alternating dash and dots = broken limits. Reconstructed limits dashed.

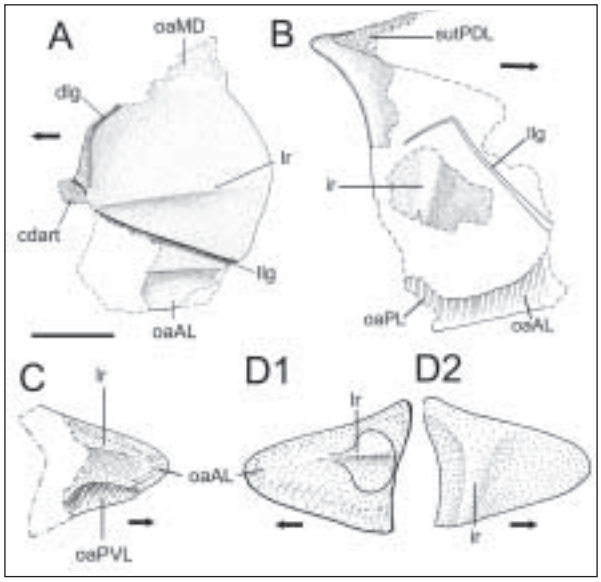

Figure 4. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Modave, Liège Province, Belgium. Palaeontological collection, University of Liège, Belgium. A, incomplete anterior dorsolateral plate of the left side in lateral view (from block Nr 35); B, incomplete posterior dorsolateral plate of the left side in medial view (from block Nr 38; combining the impression of the external surface and main lateral-line groove with actual plate fragments seen in medial view); C, incomplete posterolateral plate of the right side in lateral view (from block Nr 38); D, posterolateral plate of the left side in lateral (D1) and medial (D2) view (from block Nr 38). Scale bar = 10 mm. Arrows points forward. Alternating dash and dots = broken limits. Unstippled areas are only preserved as impressions. Abbreviations: cdart, articular condyle; dlg, dorsolateral groove; ir, internal ridge; llg, main lateral-line groove; lr, lateral ridge; oaAL, overlap area for the anterolateral plate; oaMD, overlap area for the median dorsal plate; oaPL, overlap area for the posterolateral plate; oaPVL, overlap area for the posterior ventrolateral plate; sutPDL, suture with the contralateral posterior dorsolateral plate.

its lateral surfaces, and the same enlarged and sharp tubercles along its posterior edge. At any rate, the ventral margin of the specimen described by Gross (1965) is certainly not an overlap area, as he suggested, but a broken and somewhat abraded zone of spongiose bone. The attempted reconstruction of the MD plate in Figures 3B and 6 is a combination of the outline of the MD plate of the holotype and that of Gross' "*Tiaraspis*" specimen, brought to the same scale. There is thus a strong probability that the MD plate of *G. thorezi* was in fact very sharp and pointed.

The ventrolateral part of the MD plate on the left side has collapsed against that of the right side, showing somewhat the outline of the median dorsal margin of its internal surface (dashed line in Figure 3A).

b) Anterior dorsolateral (ADL) plate: The ADL plate of the left side is partly preserved (Fig. 4A). It shows part of the articular condyle (artcd, Fig. 4A) and part of the overlap areas for the MD and anterolateral (AL) plates (oaMD, oaAL, Fig. 4A). The main lateral-line groove runs posteroventrally from the articular area, as in other *Groenlandaspis* species (llg, Fig. 4A). The posterior margin of the plate, which overlaps the posterior dorsolateral (PDL) plate, is somewhat lobate in shape. The ornamentation is practically lacking, except for some barely visible, scattered tubercles in its dorsal part. A straight and almost horizontal ridge marks its lateral surface (lr, Fig. 4A). Dorsally to the articular condyle, the surface of the plate margin is spongious, and further dorsally it turns into a relatively broad, dorsolateral groove (dlg, Fig. 4A), which probably accommodated the anterior tip of the MD plate.

c) Posterior dorsolateral (PDL) plate: Neither of the two PDL plates is well preserved; unfortunately so, because the characters of this plate are widely used to differentiate the *Groenlandaspis* species. However, part of the left PDL plate is visible on block Nr 38 (PDL(l), Pl. 2A2;

Fig. 4B), and the impression of its missing part shows the pattern of the main lateral-line groove (llg, Fig. 4B). The latter displays the characteristic dorsal flexure, which occurs relatively far from the posterior margin of the plate. This plate also shows the large area for the suture with the contralateral PDL plate (sutPDL, Fig. 4B), a character of the Groenlandaspididae. Judging from its impression, the surface of the PDL plate seems to be entirely devoid of ornamentation. The overlap areas for the posterolateral and anterolateral plates are barely visible in impression (oaPL, oaAL, Fig. 4B). That for the ADL plate is not preserved. Small preserved portions of the middle part of the plate show a prominent internal ridge (ir, Fig. 4B), also known in *G. pennsylvanica* (Daeschler *et al.*, 2003, fig. 2E) and probably present in all groenlandaspidids, as it seems to be linked to the extensive dorsal suture between the two PDL plates of each side (sutPDL, Fig. 4B). A probable PDL plate is buried vertically in the sediment of block Nr 35, and broken along its vertical axis (?PDL, Pl. 1B). Thanks to this position, its section shows the double curvature of this plate, which is also characteristic for the Groenlandaspididae.

d) Posterolateral (PL) plate: Both PL plates are preserved (PL(l), PL(r), Pl. 2A2; Fig. 4C, D). They show the internal surface (partly in impression for the PL of the right side) and the well-marked internal posterior thickening (ir, Fig. 4D2). The PL plate of the right side is partly exposed in external view and its preserved surface is unornamented (Fig. 4C). The preparation of part of the external surface of the PL plate of the left side shows that only a small, heart-shaped area is covered with a layer of compact bone (Fig. 4D1), the remaining surface being spongiose or marked with parallel ridges where overlapped. Considering the position of the well-marked longitudinal ridge on the external surface (lr, Fig. 4C, D1) and the posterior thickening of their internal surface, we propose to orient the PL plates as shown in Figures 4D and 6. Like in other *Groenlandaspis* species, this plate is roughly tri-radiate in shape. Its anterior expansion, which is overlapped by the AL plate, is comparatively large (oaAL, Fig. 4C, D1), and its dorsal process, which overlaps the PDL plate is relatively long. Its ventral process, which is overlapped by the posterior ventrolateral plate, is slightly shorter and displays a well-marked overlap area (oaPVL, Fig. 4C). The anterior expansion of the PL plate of *G. thorezi* is much deeper and extends much farther anteriorly than in all other hitherto described *Groenlandaspis* species in which it is known (Ritchie, 1975, fig. 2C; Long *et al.*, 1997, fig. 3). The external surface of the plate bears a well-marked longitudinal ridge (lr, Fig. 4C, D1), a character that Long (1995) regarded as typically absent in *Groenlandaspis*, though retained by other Groenlandaspididae [e.g., *Boomeraspis* (Long, 1995, fig. 6B) and *Turrisaspis* (Daeschler *et al.*, 2003, fig. 9J, K)]. Since a longitudinal ridge is also present on the PL plate of other phlyctaeniid arthrodires (Goujet, 1984, fig. 63; Long, 1995, fig. 6C, D) the lack of any ridge on the PL plate was regarded by Long (1995) as unique to *Groenlandaspis*. The presence of this ridge in *G. thorezi* suggests that this character was nevertheless retained by some *Groenlandaspis* species, and that *G. thorezi*, despite its young age, may be less derived than other species of this genus in this respect.

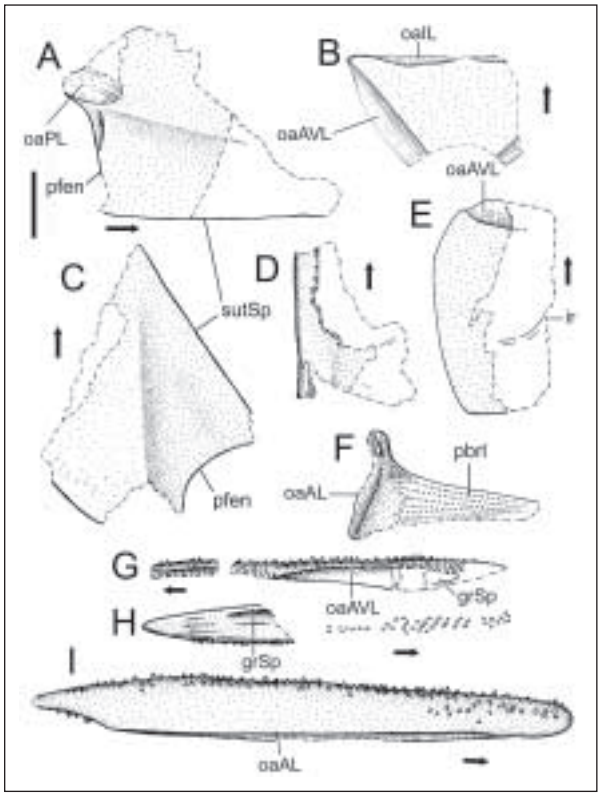

Figure 5. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Liège Province, Belgium (A-H from Modave; I, from Villers-le-Temple). Palaeontological collection, University of Liège, Belgium. A, incomplete anterolateral plate of the left side in internal view (from block Nr 35); B, incomplete anterior median ventral plate in ventral view (from block Nr 38); C, incomplete anterior ventrolateral plate of the left side in ventral view (from block Nr 35); D, E, incomplete posterior ventrolateral plates of the right (D) and left (E) sides in ventral view (from block Nr 35); F, incomplete interolateral plate of the left side in posterior view (from block Nr 38); G, incomplete spinal plate in ventral view (from block Nr 35), H, incomplete spinal plate in probably ventral view (from block Nr 38); I, almost complete spinal plate of the left side in dorsal view (Nr 5924). Scale bar = 10 mm. Alternating dash and dots = broken limits. Unstippled areas are only preserved as impressions. Arrows points forward. Abbreviations: grSp, ventro-medial groove in the free portion of the spinal plate; ir, internal ridge; oaAL, overlap area for the anterolateral plate; oaAVL, overlap area for the anterior ventrolateral plate; oaIL, overlap area for the interolateral plate; oaPL, overlap area for the posterolateral plate; pbrl, postbranchial lamina; pfen, margin of the pectoral fenestra; sutSp, suture with the spinal plate.

e) Anterolateral (AL) plate: Neither AL plate is complete (AL(r), AL(l), Pls. 1B, 2A2; Fig. 5A). Nevertheless, they display the characteristic longitudinal ridge, which overhangs a concave ventral surface. The AL plate of the left side (AL(l), Pl.1B, Fig. 5A) is exposed in internal view, and shows the overlap area for the anterior end of the PL plate (oaPL, Fig 5A). It is probable that its longitudinal external ridge was prolonged posteriorly by the ridge on the PL plate (lr, Fig. 4C, D1). The external surface of the AL plate is practically smooth, and only bears here and there very small, much-scattered tubercles, which are only visible on the AL impression in block Nr 38 (AL, Pl. 2A2).

f) Anterior median ventral (AMV) plate: An incomplete AMV plate has been prepared from block Nr 38 (AMV, Pl. 2A2; Fig. 5B) and shows part of the overlap areas for the interolateral and anterior ventrolateral plates (oaIL, oaAVL, Fig. 5B). Judging from its preserved limits, it seems to have been slightly broader and shorter than the AMV of *Groenlandaspis antarctica* (Ritchie, 1975, fig. 2B).

g) Anterior ventrolateral (AVL) plate: Only part of the AVL plate of the left side is preserved in ventral view (AVL, Pl. 1B; Fig. 5C). Like in other groenlandaspidids, it shows a well-defined, depressed triangular area, limited by the spinal plate laterally (sutSp, Fig. 5C), the margin of the pectoral fenestra posteriorly (pfen, Fig. 5C), and a straight oblique ridge medially. Its surface is completely devoid of ornamentation.

h) Posterior ventrolateral (PVL) plate : Only parts of the PVL plates are preserved in block Nr 35 (PVL(r), PVL(l), Pl. 1B; Figs 5D, E). Judging from that of the left side in external view (Fig. 5E), it seems to have been relatively elongated yet shorter than the AVL plate; that is, with the same proportions as in *G. antarctica* (Ritchie, 1975, fig. 2B). It shows a distinct overlap area for the AVL plate anteriorly (oaAVL, Fig. 5E), and its internal impression displays a well-marked internal ridge (ir, Fig. 5E), which prolonged ventrally the internal ridge of the PL plate (ir, Fig. 4D2; see also Miles, 1964, fig. 9B). Like the AVL plate, it is entirely smooth.

i) Interolateral (IL) plate: Both IL plates are partly preserved in block Nr 38 (IL(r),IL(l), Pl. 2A2; Fig 5F), and probably a small fragment of IL plate occurs in block Nr 35 (?IL, Pl. 1B). Their anterior surface is typically ornamented with the parallel, curved ridges of the postbranchial lamina (pbrl, Fig. 5F), and their posterolateral surface shows the overlap area for the AL plate (oaAL, Fig. 5F).

j) Spinal (Sp) plate: Both Sp plates from blocks Nr 35 and 38 (Sp, Pls. 1B, 2A2) are poorly preserved, but one, mainly preserved as an impression, provides information about its total length (Sp, Pl. 2A2; Fig. 5H). Their leading edge, or lateral margin, is ornamented with large, scattered tubercles, which become spiniform posteriorly. One of them (on block Nr 38) displays small portions of the overlap areas for the AVL plates (oaAVL, Fig. 5G). The free portion that extends posteriorly beyond the level of the pectoral fenestra is relatively short and bears the trace of a medioventral groove (grSp, Fig. 5G, H).
The isolated Sp plate from Villers-le-Temple is notably larger than those in blocks Nr 35 and 38, though embedded in the same, black dolomitic matrix (Pl. 2D; Fig. 5I). It shows much the same proportions as the latter and is thus likely to belong to *G. thorezi* as well, since its dorsal surface is almost completely smooth. It only bears large, scattered tubercles along its lateral margin and on the foremost portion of its dorsal margin. Its free portion is also very short and bears a few, spiniform tubercles along its medial margin.
On the basis of the plates preserved in blocks Nr 35 and 38, which belong to individuals of about the same size, a reconstruction of the dermal armour of *Groenlandaspis thorezi* can be proposed (Fig. 6). Considering the available plate limits, the thoracic armour appears significantly deeper and shorter than in the two *Groenlandaspis* species reconstructed to date: *G. antarctica* (Ritchie, 1975) and *G. riniensis* (Long *et al.*, 1997). This implies a probably steeper position of the skull roof, which agrees with the shape of the posterior skull-roof margin (Fig. 1D).

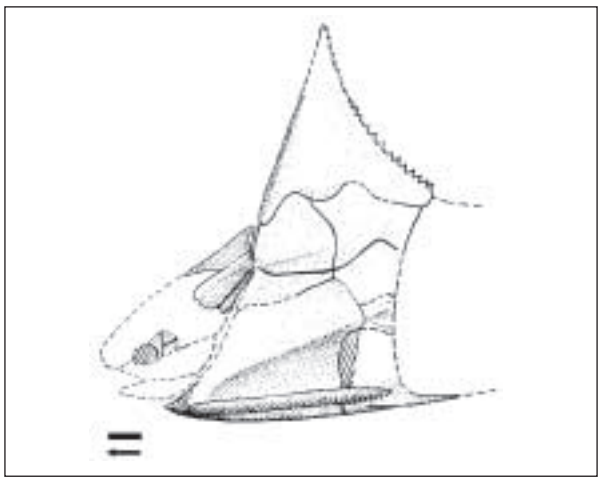

Figure 6. *Groenlandaspis thorezi* n. sp., upper part of the Evieux Formation, Upper Famennian, Upper Devonian, Liège Province, Belgium. Attempted reconstruction of the dermal armour, based on the plates preserved in blocks Nr 35 and 38 of the Palaeontological collection, University of Liège, Belgium. Orbit and pectoral fenestra obliquely hatched. Scale bar = 10 mm. Arrow points forward. Dashed line = hypothetical plate limits.

4.2. Comparison

Groenlandaspis thorezi differs from most other *Groenlandaspis* species named to date by the shape of its MD plate (Fig. 7I). The MD plate is unknown in the type species of the genus, *G. mirabilis*, but *G. thorezi* clearly differs from the latter by its extremely reduced ornamentation. Out of the numerous *Groenlandaspis* species (some being still unnamed but succinctly described), the MD plate of *G. thorezi* most closely resembles in outline that of *Mulgaspis altus* Ritchie 2004, from the ?Eifelian Mulga Downs Group of western New South Wales (NSW), Australia (Fig. 7H; Ritchie, 1975, fig 3f; 2004, fig. 9B). It resem-

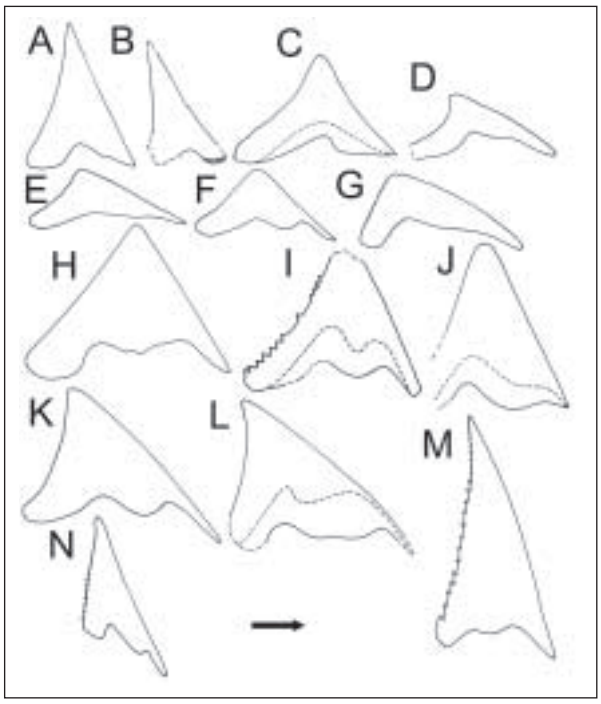

Figure 7. Median dorsal plates of Groenlandaspididae in right lateral view. Not to scale. Arrow points forward. The dashed line in C, I, J, L indicates the median outline of the internal surface of the plate. A, *Tiaraspis subtilis* (Gross, 1933), late Pragian-Emsian of Rhineland; B, *Mithakaspis lyentye* Young & Goujet, 2003, ?late Pragian-early Eifelian of Australia; C, *Groenlandaspis* sp., Emsian of Iran; D, *Groenlandaspis disjectus* (Woodward, 1891), Upper Famennian of Ireland ; E, *G. antarctica* Ritchie, 1975, Upper Givetian of Antarctica; F, *G. pennsylvanica* Daeschler, Frumes & Mullison, 2003, Upper Famennian of Pennsylvania, USA; G, *G. riniensis* Long, Anderson, Gess & Hiller, 1997, Upper Famennian of South Africa; H, *Mulgaspis altus* Ritchie, 2004, ?Eifelian, Mulga Downs Group, Australia; I, *G. thorezi*, n. sp., Upper Famennian of Belgium; J, *G. seni*, Frasnian of Turkey; K, *Groenlandaspis* sp., Upper Famennian of Grenfell, Australia; L, *Groenlandaspis* sp., Frasnian of Turkey; M, *Africanaspis doryssa* Long, Anderson, Gess & Hiller, 1997, Upper Famennian of South Africa; N; *Turrisaspis elektor* Daeschler, Frumes & Mullison, 2003, Upper Famennian of Pennsylvania, USA. (A, from Schultze, 1984; B, from Young & Goujet, 2003; C, from Blieck *et al*. 1980; D, E, K, from Ritchie, 1975; H, from Ritchie, 2004; J, from Janvier & Ritchie, 1977; Janvier, 1983; F, N, from Daeschler *et al*., 2003; G, M, from Long *et al*., 1997).

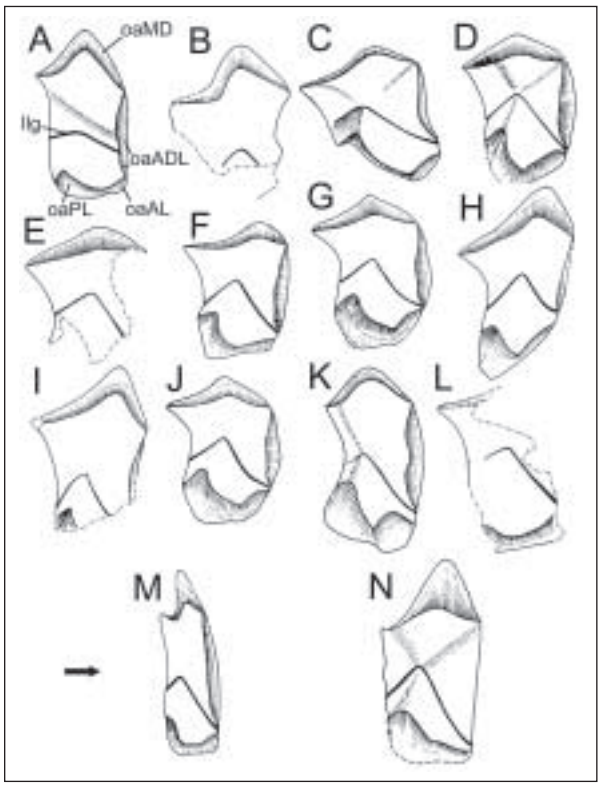

Figure 8. Posterior dorsolateral plates of the right side of Groenlandaspididae in lateral view. Not to scale. Arrow points forward. A, *Tiaraspis subtilis* (Gross, 1933), late Pragian-Emsian of Rhineland; B, *Groenlandaspis* sp., Emsian of Iran; D, *Boomeraspis goujeti* Long, 1995, Givetian of Antarctica; D, *Groenlandaspis mirabilis* Heintz, 1932, Upper Famennian of Greenland; E, *Groenlandaspis* cf. *G. mirabilis*, Upper Famennian of Greenland; F, *Groenlandaspis disjectus* (Woodward, 1891), Upper Famennian of Ireland; G, *G. antarctica* Ritchie, 1975, Upper Givetian of Antarctica; H, *Groenlandaspis* sp., Upper Famennian of Grenfell, Australia; I, *G. seni* Janvier & Ritchie, 1977, Frasnian of Turkey; J, *G. pennsylvanica* Daeschler, Frumes & Mullison, 2003, Upper Famennian of Pennsylvania, USA; K, *G. riniensis* Long, Anderson, Gess & Hiller, 1997, Upper Famennian of South Africa; L, *G. thorezi*, n. sp., Upper Famennian of Belgium; M, *Turrisaspis elektor* Daeschler, Frumes & Mullison, 2003, Upper Famennian of Pennsylvania, USA; N, *Africanaspis doryssa* Long, Anderson, Gess & Hiller, 1997, Upper Famennian of South Africa. (A, from Gross 1962; B, from Janvier &Ritchie, 1977; Blieck *et al*., 1980; C, from Long, 1995; D, from Stensiö, 1936; E, from Stensiö, 1939; F, based on Ritchie, 1974; G, from Ritchie, 1975; H, based on Ritchie, 1974; I, from Janvier & Ritchie, 1977; J, from Daeschler *et al*., 2003; K, from Long *et al*., 1997; M, from Daeschler *et al*., 2003; N, from Long *et al*., 1997). Abbreviations: llg, main lateral-line groove; oaADL, overlap area for the anterior dorsolateral plate; oaAL, overlap area for the anterolateral plate; oaMD, overlap area for the median dorsal plate; oaPL, overlap area for the posterolateral plate.

bles more remotely that of an unnamed species from the Upper Famennian of Grenfell, NSW, Australia (Fig. 7K; Ritchie, 1975, fig. 3e), as well as that of a still unnamed species from the Frasnian of Turkey (Fig. 7L; Janvier *et al*., in preparation), which, however, differs from *G. thorezi* in having an extensive, vermiculate ornamentation and a posteriorly tapering apex. The MD plate of *G. thorezi* is much deeper than that of *G. disjectus* (Fig. 7D; Ritchie, 1975, fig. 3b*), G. antarctica* (Fig. 7E; Ritchie, 1975, fig. 3a), *G. riniensis* (Fig. 7G; Long *et al*., 1997, fig. 11), and *G. pennsylvanica* (Fig. 7F; Daeschler *et al.*, 2003, fig. 4a), but significantly lower than that of *G. seni* (Fig. 7J; Janvier & Ritchie, 1977, fig.1a).

The PDL plate of *G. thorezi* (Fig. 8L) most closely resembles that of *G. mirabilis* (Fig. 8D), *G. disjectus* (Fig. 8F), *G. antarctica* (Fig. 8G), and to some extent *G. pennsylvanica* (Fig. 8J). As pointed out by Long (1995), the widely open angle of the flexure of the main lateral-line groove and its relatively low and anterior position is probably plesiomorphous for *Groenlandaspis*, as it is also the condition met with in *Boomeraspis* (Fig. 8C) and *Tiaraspis* (Fig. 8A), and, to some extent the unnamed species from the Emsian of Khush-Yeilagh, Iran (Fig. 8B) (Janvier & Ritchie, 1977; Blieck *et al*., 1980; Schultze, 1984; Long, 1995). Yet it is probable that this character shows much intraspecific variation, as suggested by the slightly different patterns described in PDL plates from Greenland (Heintz, 1932; Stensiö, 1936; Fig. 8D, E).

The free portion of Sp plate of *G. thorezi* is short relative to the total length of this plate, and compares to the Sp plate of *G. antarctica* (Ritchie, 1975, fig. 2B). It is significantly shorter than that of *G. riniensis* (Long *et al*., 1997, fig. 7C), *G. seni* and the *Groenlandaspis* sp. from the Upper Famennian of eastern Turkey (Janvier *et al*., 1984, pl. 2:1).

G. thorezi also differs from all other described and named *Groenlandaspis* species by its very weakly developed ornamentation on most of the dorsal head and trunk plates, and its lack of ornamentation on the lateral and ventral plates of the thoracic armour. A similar lack of ornamentation, however, also occurs in one or two unnamed *Groenlandaspis* species from the Upper Famennian Worange Point and Grenfell faunas in Australia (Young, 1993; Young *et al.*, 1993), as well as in one unnamed species from the ?Upper Pragian-Eifelian Cravens Peak Beds of Australia (Young & Goujet, 2003).

4.3. Discussion

To date, most *Groenlandaspis* species, apart from *G. riniensis* and, to some extent, *G. antarctica*, are known from a few plates, though sometimes represented by a relatively abundant material. In addition, a number of undescribed species are only mentioned in the literature (see Table 1). The comparison of *G. thorezi* to other species of the same genus, and the Groenlandaspididae in general, will be limited here to mere overall resemblance or dissemblance, pending a detailed phylogenetic analysis of the entire family. Judging from the number of unnamed species, or «forms», mentioned in the literature, in particular from the Middle and Upper Devonian of Australia and Antarctica (Young, 1993, 2002; Young & Goujet, 2003; Young *et al*., 1993; Long, 1995; Ritchie, 1975, 2004), one may foresee that the Groenlandaspididae, and especially *Groenlandaspis*, may soon turn out to show the same range of specific diversity (and perhaps intraspecific variability) as the bothriolepidid antiarchs, with which they are often associated. Therefore, an outline of groenlandaspidid phylogeny is badly needed before too many generic names are erected on the basis of autapomorphies of a single species.

Several « smooth forms » (i.e., with no, or little ornamentation) of undescribed *Groenlandaspis* species have been recorded from the Devonian of Australia and Antarctica (Young , 1993; Young & Goujet , 2003). For want of other morphological data, it is not possible to tell whether these «smooth forms» constitute a group, or this character arose independently in several late Famennian *Groenlandaspis* lineages. Other characters are widely used in groenlandaspidid taxonomy, such as the shape of the PDL and MD plates or the pattern of the main lateral-line flexure on the PDL plate, and are assumed to be reliable, for want of a detailed account of their individual variation. Young & Goujet (2003), however, warned against the possibly wide range of individual variation in the shape of the MD plate within populations of the same *Groenlandaspis* species. The taxonomic significance of the general shape of the MD plate is still uncertain and Young & Goujet (2003) warned against a wide range of individual raviation for this plate. Yet available metric data made on admittedly small samples show little variation (Daeschler *et al.* 2003), except for the MD plates referred to *Mulgaspis evansorum* (Ritchie 2004, Fig. 5A, C-F).

The late Pragian-Early Emsian genus *Tiaraspis* might be regarded as the sister-group of all other groenlandaspidids, because it retains several general phlyctaeniid characters, apparently lost or strongly modified in other taxa of this family; in particular, it lacks the marked inflection of the main lateral-line groove on the PDL plate (Young & Goujet, 2003). The Givetian *Boomeraspis* could also be a generalised groenlandaspidid, possibly more so than *Tiaraspis*, as it retains elongate PDL and PL plates, but it is unclear whether or not it shows the median suture of the ADL and PDL plates, which characterizes the family (Long, 1995; Young & Goujet, 2003). When considering *Tiaraspis* as an outgroup, the general groenlandaspidid condition for the MD plate could be very high, straight and pointed in shape. Yet groenlandaspidids display a wide range of diversity as to this character as early as the Emsian or Eifelian, with both high-crested and low-crested forms (Blieck *et al*.; 1980; Ritchie, 1975; Young & Goujet, 2003). Such a diversity is also observed throughout the Middle and Upper Devonian and it is possible that the shape of the MD plate is strongly homoplastic.

5. Remarks on the distribution of the Groenlandaspididae

The earliest known well-dated groenlandaspidids include *Tiaraspis*, from the late Pragian-early Emsian of Rhineland, Germany, and the unnamed *Groenlandaspis* species from the Emsian of Iran (Tab.1). In addition, several unnamed groenlandaspidids have been described, alongside *Mithakaspis lyentye*, from the Cravens Peak Beds of Australia, assumed to be ?late Pragian to early Eifelian in age (Young & Goujet, 2003). The groenlandaspidids are also widely known from the Middle and Upper Devonian (see Table 1), but seem to gain a nearly global distribution only in the Famennian (Fig. 9A), when they occur in North America (*Groenlandaspis pennsylvanica* and *Turrisaspis elektor*), Greenland (*G. mirabilis*) and western Europe (*G. disjectus*, *G. thorezi*). Apart from *Tiaraspis* from Rhineland, all pre-Famennian groenlandaspidids known to date are from areas that are derived from the Devonian Gondwana (including Iran and Turkey), with the possible exception of *Cosmacanthus malcolmsoni* (if the latter actually is a groenlandaspidid), from the supposedly late Frasnian of Scaat Craig, Scotland. This occurrence, however, remains to be confirmed by more diagnostic material.

Young (1993) and Long *et al*. (1997) considered that the entire family Groenlandaspididae was originally endemic to Gondwana, and explained the occurrence of *Tiaraspis* in Rhineland by the fact that this area was part of the Gondwanan margin, a theory advocated by some geophysics-based models, but for which there is, to date, no clear evidence. At any rate, the occurrence of certain, exclusively Euramerican taxa, such as heterostracans and osteostracans, in the Emsian of Rhineland throws doubts on this theory. More likely, groenlandaspidids were widespread in the Early Devonian, then became endemic to Gondwana. An alternative explanation is that there has been a brief incursion of Gondwanan vertebrate taxa into Euramerica in the Emsian, as suggested by other data, such as the sudden occurrence of gyracanthid acanthodians and antarctilamnid-like chondrichthyans in the late Pragian and Emsian of Rhineland and eastern Canada (Schultze, 1984; Miller *et al*., 2003; S. Desbiens, pers. com. 2002), two groups which have subsequently disappeared from Euramerica, until the gyracanthids came back here in the late Famennian.

The Famennian now appears as a time of major interchange between Gondwana and Euramerica. Beside the gyracanthid acanthodians, two placoderm (phyllolepids and groenlandaspidids) and two sarcopterygian taxa (rhizodontids and megalichthyids), only known in Gondwana prior the Famennian, progressively occur in Euramerica during the Famennian. The phyllolepid and groenlandaspidid placoderms are widely known in Gondwana since the Givetian and Emsian, respectively (the groenlandaspidids being fairly abundant in most Middle-Upper Devonian vertebrate localities of the Gondwanan regions). Among sarcopterygians, the rhizodontids and megalichthyids are known from Gondwanan regions since the Givetian and Frasnian, respectively. Conversely, some taxa known in Euramerica since the Middle Devonian, such as the antiarch *Asterolepis* (Janvier & Villarroel, 2000) and the tetrapods seem to pass into Gondwana (and China for the tetrapods; Zhu *et al*., 2002) in about the same time (as early as the Late Frasnian for *Asterolepis*). All these organisms were strictly bound to either marine marginal, or fresh water environments, and most probably unable to cross major oceanic barriers. Their biogeographical pattern is thus comparable to that of continental organisms. This remarkable faunal interchange is thus assumed to be a consequence of a collision between Euramerica-Gondwana in the late Frasnian or early Famennian (Fig. 9B; Dalziel *et al*., 1994; Janvier & Villarroel, 2000; Young *et al*., 2000; Young & Moody, 2002; Young *et al.* 2003). The impact of this biogeographical event on the ecology of the Famennian vertebrate faunas in general is difficult to evaluate, but it

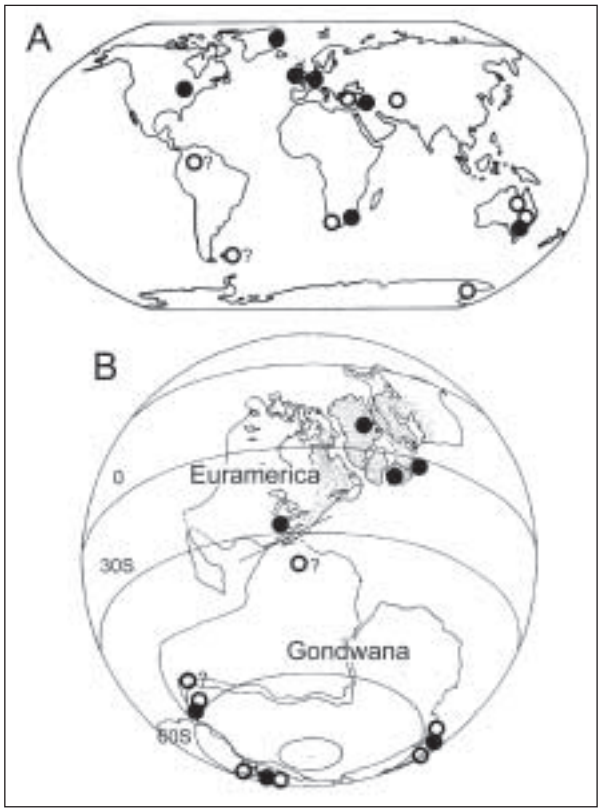

Figure 9. A, Present-day geographical distribution of the occurrences of the genus *Groenlandaspis*. Open circles are pre-Famennian occurrences, closed circles are Famennian occurrences (the occurrence of *Cosmaspis malcolmsoni*, thought to be possibly *Groenlandaspis*, in the late Frasnian of Scotland is not indicated here, as it awaits confirmation). B, same occurrences plotted on the palaeogeographical reconstruction proposed by Dalziel *et al*. (1994) for the late Devonian (ca. 370 Myr). The stippled area represents the extension of the Old Red Sandstone. (B, modified from Dalziel *et al*., 1994, fig.4).

is possible that the large rhizodontid and megalichthyid sarcopterygians may have been competitors for the early tetrapods and may be the cause of the virtual disappearance of this group by the latest Famennian (Clément *et al*. 2004).

6. Conclusions

Groenlandaspis thorezi is a new species of the phlyctaeniid arthrodire genus *Groenlandaspis*, which is characterized by the strongly developed, sometimes bifid, denticles along the posterior edge of the median dorsal plate, and by the lack of ornamentation of most of the lateral and ventral plates of the thoracic armour. It is the first occurrence of the genus *Groenlandaspis* in western continental Europe and, alongside phyllolepid placoderms, gyracanthid acanthodians, and megalichthyid and rhizodontid sarcopterygians, belongs to the pageant of migrants from Gondwana, which progressively invaded Euramerica in Famennian times. In addition, this arthrodiran genus is the classical component of the tetrapod-bearing faunal assemblages known to date, be it in Greenland, Pennsylvania, or Australia. Its occurrence in the Evieux Formation of Belgium is consistent with with this rule, considering the recent discovery of a tetrapod in Strud, Liège Province (Clément *et al*., 2004).

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