The rise and fall of Late Devonian (Frasnian) trilobites from Belgium: taxonomy, biostratigraphy and events

Allart P. VAN VIERSEN* & Willy VANHERLE1

1Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht, The Netherlands; apvanviersen@gmail.com.
2Bosstraat 173, 3582 Koersel, Belgium; willem.vanherle1@telenet.be.

*corresponding author.

ABSTRACT. Trilobites are recorded from Frasnian strata in Belgium on the basis of old museum collections and contemporary fieldwork. Of the four third-order Transgressive-Regressive (T-R) cycles recognised here in the latest Givetian to late Frasnian, the last three are each associated with a version of a largely coherent, acastid–scutelluid dominated trilobite fauna. Accents of this “base” fauna encompassed probably primarily allochthonous elements. The timing and effects of the late Frasnian Kellwasser Event in Belgium differ according to fossil group and their position along the ramp. The new data from this study are suggestive of distinct extinction patterns for the trilobite associations of the reefal environments and lateral facies. No evidence was identified for a direct impact of the Kellwasser levels on the Belgian trilobite fauna, although not a single trilobite is known with certainty from strata above the base of the Lower Kellwasser level. Comparisons to trilobite faunas from other countries are suggestive of open, shallow-water migration routes between southern Laurussia and peri-Gondwana during most of the Frasnian. New taxa are Bradocryphaeus echinatus sp. nov., Magreanops renatae gen. & sp. nov. (both Moulin Liénaux Formation), Bradocryphaeus laomedeaia sp. nov., Bradocryphaeus neptuni hotonensis sp. nov., Cyphaspis koiometeriensis sp. nov. (all Grands Breux Formation), Magreanops monachus gen. & sp. nov., Quadratispina excelsa sp. nov. (both Bovesse Formation) and Pterocoryphe platymarginata sp. nov. (Champ Broquet Formation). Magreanops gen. nov. represents the first and only known big-eyed phacopid from Frasnian strata worldwide, breaching the established latest Givetian to late Famennian gap of this group.

KEYWORDS: Trilobites, systematic palaeontology, palaeoecology, palaeobiogeography, extinctions.

1. Introduction

The Frasnian was a period of recurrent global eustatic perturbations that had already commenced in the Middle Devonian and led to major faunal crises. Frasnian trilobites, encompassing exclusively benthic and endobenthic inhabitants of the continental shelf, suffered consecutive blows from the worldwide “drowning” of reef ecosystems and a decline of the shallow water environments to which they were confined (Feist, 1991, 1995). The latest Frasnian Kellwasser Event, though not by itself responsible for the demise of Frasnian trilobites, was the “coup de grâce” for many families. This event and its effects on trilobites have been the focus of investigations at various sections located in Germany, France, Morocco and NW Australia, among other countries (e.g. Becker et al., 1989; Feist & Schindler, 1994; Feist, 2002; McNamara & Feist, 2016).

Frasnian trilobites from Belgium were described mainly in the monograph on Late Devonian trilobites of Richter & Richter (1926) and in van Viersen & Bignon (2011) and van Viersen & Prescher (2011). Bignon & Crônier (2015) analysed faunal dynamics of Devonian trilobites from Belgium and northern France and recognised two poorly diversified associations in the Frasnian: the Scutellum–Goldiuss association which they considered to be restricted to reef environments, and the Bradocryphaeus association (Bradocryphaeus, Oarion, Helioyyge) of Crônier & van Viersen (2007) which occurs in lateral shales and limestones below fair-weather wave base.

The authors of the present note have made numerous excursions to Frasnian trilobite-bearing strata in Belgium over the past years. Additionally, one of us (AV) has examined the old Mâlilleux collections (see, e.g. Richter & Richter, 1926; Mâlilleux, 1927, 1940) kept by the Institut royal des Sciences naturelles de Belgique (IRSNB). Here we report newly discovered Frasnian trilobites from Belgium including palaeogeographically significant taxa that were not previously known to occur here. The selected specimens from museum and recent field collections enable a first attempt at assessing the rise and fall of the Frasnian trilobite fauna concomitant with the rapidly changing palaeoenvironment.

https://doi.org/10.20341/gb.2018.005
reef growth was able to keep up with sea-level rise. Eventually reef growth lost this contest as the mounds were ‘drowned’ and buried through clay deposition (shaly Ermitage and Boussu-en-Fagne members) (= events 3 and 7 of Da Silva et al., 2010). However, Mottequin & Poty (2015) argued that the shallow-water limestones and erosion–transgressive surface at the top of the Lion mound, disconformably overlain by the argillaceous Boussu-en-Fagne Member in Frasnes, suggest a major sea-level drop instead. They regarded this regression as being responsible for the termination of the Lion mounds and a major disruption of Frasnian carbonate production. The late Frasnian Petit-Mont mounds of the Champ Broquet Formation are principally different from their middle Frasnian predecessors in having a limited lateral extension that was caused by the more drastically changing sea and oxygen levels leading to the relative instability of the carbonate factory (Boulvain, 2007). The demise of this last mound level was caused by another sea-level drop (Mottequin & Poty, 2015).

2.2. Contemporary localities

Extensive quarry works, natural outcrops and road or railway sections in Belgian Frasnian strata have been known for many decades, providing excellent opportunities for scientific studies. Some of these places continue to serve as suitable outcrops for fossil collecting at present. They are frequented by collectors for their brachiopods, crinoids, goniatites, corals and trilobites, which is exposed there is highly fossiliferous, both in numbers and diversity (Vanherle, 2012, 2013). Two trilobite species, Cyphaspis komeiheronensis sp. nov. and Torleyiscutellum protrusifrons (van Viersen & Prescher, 2011) (= type locality and horizon), co-occur here with the brachiopods “Hypothyridina” gr. cuboides (Sowerby, 1840), Parallelepipedorhynchus trapezoides Sartenaer, 2006 and Flabellulirostrum sp. (determinations by WV). The association of these brachiopods is characteristic of coeval sections along the southern border of the Dinant Synclinorium and in the Philippeville Anticlinorium.

Loc037, Boussu-en-Fagne, “ancienne carrière du Cimetière”. This abandoned quarry was described by Coen-Aubert (1992). The top of the Lion Member of the Grands Breux Formation which is exposed there is highly fossiliferous, both in numbers and diversity (Vanherle, 2012, 2013). Two trilobite species, Cyphaspis komeiheronensis sp. nov. and Torleyiscutellum protrusifrons (van Viersen & Prescher, 2011) (= type locality and horizon), co-occur here with the brachiopods “Hypothyridina” gr. cuboides (Sowerby, 1840), Parallelepipedorhynchus trapezoides Sartenaer, 2006 and Flabellulirostrum sp. (determinations by WV). The association of these brachiopods is characteristic of coeval sections along the southern border of the Dinant Synclinorium and in the Philippeville Anticlinorium.

Loc043, Frasnes, “ancienne carrière du Lion”. Disused quarry in which the shales and limestones of the Grand Breux Formation as well as a Lion type mound are exposed. Trilobites include Bradocryphaeus neptuni neptuni (Bieumont Member = type locality and horizon), Torleyiscutellum sp. X (Lion Member), and Bradocryphaeus cf. laomedeia sp. nov. (Boussu-en-Fagne Member).

Loc051, Frasnes, “carrière de l’Arche”. Old quarry known for its Arche bioherm in the Moulin Liénaux Formation.
Torleyiscutellum decipulum (van Viersen & Prescher, 2011) (= type locality and horizon) is the only trilobite known to occur here.

Loc087, Hotton, outcrop of the Bieumont Member of the Grandes Breux Formation on the southern outskirts of town. This site was temporarily available during the construction of a house. Two trilobite species were found by P. Taghon and donated for study; these are assigned here to Bradocryphaeus neptuni howsonensis sp. nov. and Bradocryphaeus laomedeia sp. nov.

Loc088, Marloie, outcrop in the Ermitage Member of the Moulin Liénaux Formation just north of town. This site was temporarily available during the construction of a building. Trilobites were collected by P. Taghon and assigned herein to Bradocryphaeus mosanus (Richter & Richter, 1926).

Loc089, Neuville, “anciennce carrière de Beauchâteau”. This is an abandoned quarry which is well known for its “marbre rouge” mined from the Petit-Mont Member of the Champ Broquet Formation (Boulvain & Coen-Aubert, 1992). Trilobites (mostly Maillieux collection but including a specimen collected ex situ by S. Goolnaerts): Torleyiscutellum sp. A.

Loc090, Ny, former railway Melleux–Manhay. Described by Asselberghs (1914) and revisited by Coen & Coen-Aubert (1971). The site is a small outcrop just south of Ny (“section 5” of Asselberghs, 1914). A single Torleyiscutellum sp. H pygidium was recovered by WV from an ex situ, light grey limestone block along with atrypid and gypidulid brachiopods. The origin of the trilobite specimen is either the Fromelennes Formation (uppermost Givetian) or the basal part of the Nismes Formation (lowermost Frasnian).

Loc120, Hotton, outcrop in the Ermitage Member of the Moulin Liénaux Formation on the southwestern outskirts of town. This site was temporarily available during the construction of a building. Trilobite specimens belonging to two species were collected by B. Magrean and donated for study; these are assigned here to Bradocryphaeus echinatus sp. nov. and Magrenanos renatae gen. & sp. nov.

2.3. Old localities

Specimens in the old Maillieux collections housed by the IRSNB were examined in addition to the newly collected material. Names and one to four-digit numbers correspond to places indicated on Maillieux’s field maps which are kept by the IRSNB.

Loc092. “Surice 7301” locality, just north of Surice. Lion Member of the Grands Breux Formation. Trilobites: Torleyiscutellum sp. E.

Loc093. “Han-sur-Lesse 6220” locality, just ENE of Eprave. Lion Member of the Grands Breux Formation. Trilobites: Torleyiscutellum sp. I.


Loc095. “Olloy 8715” locality, “3ième terniat” (see Maillieux, 1913), southeast of Mariembourg. Petit-Mont Member of the Champ Broquet Formation. Trilobites: Pterocoryphe platyMarginata sp. nov.


Loc121. “Senzelles 7119” locality, just north of Samart. Lower (biostromal) part of the Philippineville Formation. Trilobites: Torleyiscutellum sp. C.

Loc122. Vodécée, “Carrière des Croisettes”, abandoned quarry at 1100 m southwest of Vodécée. Petit-Mont Member of the Champ Broquet Formation. Trilobites: Torleyiscutellum sp. D.

Loc123. Emines, disused quarry just northwest of Emines. Bovesse Formation. Asselberghs (1912) described the macrofauna of the Emines locality based on material in the “le major Henne collection” which, according to him, is housed by the Katholieke Universiteit Leuven. Asselberghs illustrated trilobite specimens that he assigned to Bronteus flabellifer (= Torleyiscutellum sp. F), Cryphaeus punctatus (in all probability, conspecific with Quadratispina excelsa sp. nov.) and Dechenella verticalis (pygidia of what appears to be a dechenelline indeed; referred to herein as “Dechenella verticalis”, pending revision, because that species is from the Middle Devonian of Germany and a very problematic concept as according to Richter, 1912). Unfortunately, the Henne collection could not be traced in the university at the time of this study (R. Speijer, pers. comm., April 2017). Numerous cephalas and pygidia of Quadratispina excelsa sp. nov. that come from this same locality were discovered in the Maillieux collections at the IRSNB.


Loc126. “Sautour 6147” locality, “le Rondtienne”, near Sautour. Petit-Mont Member of the Champ Broquet Formation (see, e.g. Mottequin, 2005). Trilobites: Cyphaspis sp. F.

3. Development of the Eifelian to Frasnian trilobite fauna of Belgium

3.1. Middle Devonian

During the Devonian Belgium was located on the passive southern margin of Laurussia. Lower Devonian sequences are characterised here by transgressive siliciclastic sediments, the deposition of which was controlled by substantial detritic influx from the northern lying Brabant Massif. A mixed siliciclastic-carbonate ramp settled at around the Lower–Middle Devonian transition and lasted almost throughout the Eifelian. The Jemelle Formation is the main lithostratigraphic unit on the southern to
The diachronous Hanonet Formation (uppermost Eifelian to basal Givetian) which directly overlies the Jemelle Formation where the Lomme Formation is not developed, witnessed the transformation of the Eifelian ramp into an extensive reef complex that would subsequently dominate the Givetian. Dechenella and Nyterops appear just above the base of the Hanonet Formation between Couvin and Olloy; their association with Gerastos, Goldius, Dohmiella, Cornuproetus, Astycoryphe, Radiaspis and Cyphaspis, is characteristic of the basal part of this unit. Bignon & Crônier (2015) interpreted this latest Eifelian biota as a progressive substitution of fauna during the Kačák interval, with their late Eifelian to Givetian Dechenella association replacing the mixed association. However, as explained above and shown in the graphic chart of van Viersen (2015, p. 9, fig. 6; herein repeated as Fig. 3 and updated), the decline of the Eifelian mixed association had already started in the middle Eifelian and the most significant overhaul seems to have taken place at around the transition between the *australis* and *kockelianus* Conodont zones. These changes predate the putative positioning of the Lower Kačák Event. In fact, no evidence of this event has been found in the Ardennes (Bultynck & Hollevoet, 1999; Gouwy & Bultynck, 2003). Instead, a shallowing episode was recorded here at this time (e.g. the Lomme Formation) which is likely related to Struve’s “Great Gap”, described as a series of sedimentary gaps from Middle Devonian neritic shelf environments (Struve, 1982; Walliser et al., 1995). Except for Nyterops which is the only innovation, all trilobite genera from the basal Hanonet Formation including Dechenella (van Viersen, 2007) are components of…

![Figure 3. Stratigraphic ranges of trilobite genera in the Devonian of the Ardennes; figure adopted from van Viersen (2015, fig. 6), and updated with the weakly sculptured phacopines *Austerops*, *Hottonops* and *Loreleiosops* recognised by van Viersen et al. (2017) and Frasnian taxa reported herein. Formations named are standard lithostratigraphic units on the southern border of the Dinant Synclinorium; their thickness and age may vary laterally and chronostratigraphic boundaries are approximate.](image-url)
the middle Eifelian associations of the Jemelle Formation (van Viersen, 2015). Thus, the basal part of the Hanonet Formation records a marked recovery (reinstallation) of the mixed association rather than a gradual transition to the Dechenella association.

The latest Eifelian upsurge of the mixed association would be short-lasting, however. By the earliest Givetian, the richly diversified trilobite faunas of the Eifelian mixed ramp environments in Belgium were decayed, the prooids, had lost most of its diversity (van Viersen & Prescher, 2010); odontopleurids and aulacopleurids are not known from above the Givetian boundary (van Viersen, 2015). The last occurrences of Cornuproetus, Dothiella, Astorycorphus, Cyphaspis and Radiaspis can be observed close to the Eifelian–Givetian boundary in the abandoned Resteigne quarry. Except for Cyphaspis and Radiaspis which continued elsewhere, these genera went globally extinct at around this time or shortly after. Trilobite diversity drops are witnessed in latest Eifelian to early Givetian sections worldwide and have been attributed to the Lower Kačák Event (Chlupáč, 1994) although at times perhaps somewhat arbitrarily. Further investigations will be required in order to come to a better understanding of trilobites in relation to the changing palaeoenvironment during the Eifelian-Givetian transition in Belgium.

The “main” Givetian macrofauna of Belgium was chiefly composed of stromatoporoids and brachiopods. Trilobites were poorly diversified, encompassing prooids, scutelluids and phacopids. These were mostly restricted to back-reef environments (Bignon & Crönier, 2015).

3.2 Frasnian

Gouwy & Bullynck (2000) recognised four T-R cycles in the Belgian Frasnian (Fig. 4) as opposed to three in the global T-R chart of Johnson et al. (1985). The first cycle corresponds to a general increase in faunal diversification at the end of the Givetian and the opening of the Givetian carbonate platform which was subsequently “drowned” in the basal Frasnian (Nismes Formation). No trilobite occurrence in the Nismes Formation could be corroborated during our study. However, the transgressive character of this unit and its shaly facies similar to the trilobite-bearing middle Frasnian strata of Belgium, were particularly suitable for acastids that radiated palaeogeographically during this interval. Maillieux (1940) provided lists of macrofaunal elements from units “F2a, zone à Spirifer orbелиanceus” and “F2b, zone à Spirifer binus” which correspond to the Nismes Formation (Fig. 4). He only reported trilobites in “F2b” which he identified as Asteropyge (Asteropyge supradovenica (the type species of Bradocryphaeus) and Otarion cf. ibergia (in all probability congeneric with species assigned to Cyphaspis below). We were unable to trace this material. However, in view of the circumstantial evidence it is conservative to assume the presence of Bradocryphaeus and Cyphaspis, or morphologically similar genera, in the Nismes Formation.

Second T-R cycle: Starting with the development of the Arche mounds in the Moulin Liénaux Formation near the base of the punctata Conodont Zone. Trilobites are found associated with both the mounds and lateral facies although diversity is much higher in the latter. In the northern belt a more or less coeval, fairly diverse trilobite association including prooids (Dechenellinae) and acastids (Quadrataspina) has been found. The acastids (Bradocryphaeus, Heliopyge, Quadrataspina) are the dominant trilobites in the shales and limestones of the southern and northern belts (heretofore undiscovered in the intermediate belt) although it must be emphasised that their diversity is almost entirely covered by Bradocryphaeus. Heliopyge has long been known from the southern border of the former Synclinorium (Nismes); a second occurrence in the Namur Basin (Ligny) can now be added. Scutelluids (Torelyiscutellum) are the only trilobites found associated with the reef environments but they might not be confined to these: an undescribed species occurs in the proximal facies of the Bovesse Formation (Asselberghs, 1912, p. 38, pl. 6, fig. 12a, b). However, because the original material was unavailable its sedimentology could not be assessed. In this context it is noteworthy that Dormal (1888) reported what he interpreted as small mounds, enclosed within the shales of the Bovesse Formation. Thus, the occurrence of Torelyiscutellum in the Bovesse Formation must be validated. There are also exceptional cases of scutelluids from lateral facies on the southern border of the Dinant Synclinorium but those specimens are very fragmentary and have only been found in the vicinity of the mounds. Such occurrences likely represent mechanically reworked sclerites originating from the nearby reefs (van Viersen, 2015). Phacopids (Magreanops) are rare and only known from the lateral facies in the northern and southern belts. Aulacopleurids (Cyphaspis) are restricted to the upper part of the Ermitage Member of the Moulin Liénaux Formation (southern belt).

Third T-R cycle: Starting just above the base of the hassi Conodont Zone with the diachronous Bieumont Member and the development of the Lion mounds in the Dinant Synclinorium. Trilobite faunas in the Grands Breux Formation is different from the underlying Moulin Liénaux Formation in that an increase at the genus level is observed in the reefal environments but at the cost of the lateral facies. Limestones and shales have chiefly yielded acastids although the diversity of the family is clearly reduced with Bradocryphaeus as the sole genus. Bradocryphaeus neptuni is widespread, occurring in the Bieumont Member and lower half of the Boussu-en-Fagne Member at the Lompret, Frasnes and Hotton sections, while demonstrating a marked preference for limestones. Bradocryphaeus laomediae, however, while co-occurring with B. neptuni in the basal limestones of the Bieumont Member at the Hotton section, is known in the Boussu-en-Fagne Member exclusively from shales. Dormal (1888) listed “Cryphaeus arachnoideus” (sic) and Phacops sp. for the Rhines Formation: the former is an acastid, presumably belonging to Bradocryphaeus or Quadrataspina; the latter might be a phacopid (Dormal’s original material could not be traced and he did not provide illustrations). Aulacopleurids (Cyphaspis) remain poorly diversified although by now they have invaded reef environments in the southern belt. Fairly numerous specimens of Cyphaspis koimetereoniensis have been recovered from the upper part of the Lion mound exposed at the Boussu-en-Fagne section. Scutelluids (Torelyiscutellum), while still showing no major innovations, are more diversified with several (at least two) species identified in Lion type mounds. Torelyiscutellum furthermore occurs in the biostromal lower part of the Philippeville Formation in the Philippeville Anticlinorium. Harpetids (see van Viersen & Bignon, 2011) are only known from shales near Frasnes.

Fourth T-R cycle: The semichatoae transgression represents a brief global eustatic deepening in the upper Frasnian named after the index fossil Palmatolepis semichatoae (Sandberg et al., 2002). This event was identified by Gouwy & Bullynck (2000) in the lower part of the Champ Broquet Formation. The latter unit was defined by Coen Aubert (2015) to encompass the former Neuville Formation and Petit-Mont type mounds on the southern border of the Dinant Synclinorium and is furthermore inclusive of the Les Valisettes Member in the Philippeville Anticlinorium (Fig. 4). The Petit-Mont mounds are traditionally known for their hemiactinian limestones (informally called “marbes rouges”) such as those exposed in the disused Beauchâte quarry. The origin of the red pigmentation has long remained a matter of debate but recent studies point to iron bacteria as being a likely source (Boulvain et al., 2001). The trilobites of the Champ Broquet Formation are historically associated with these mound levels. Scutelluids (Torelyiscutellum) are dominant and specimens can be fairly common locally whereas Cyphaspis is very rare. The unique discovery of a pygidium of the pteropariine Pterocoryphe is of great palaeobiogeographic importance (see 5.4.). The last facies of the Champ Broquet Formation have yielded the last confirmed Bradocryphaeus neptuni occurrences which occur high in the Neuvile Member at the Lompret section (designated Bradocryphaeus sp. N in Fig. 4); these will be described elsewhere (S. Goolaeats & AV, work in progress).

3.3 Frasnian extinction patterns

The Frasnian–Famennian extinction was named the “Kellwasser Event” by Hauge (1985) in reference to the widely distributed, blackish Lower and Upper Kellwasser Limestones. More recently, the notion was developed that rather than mass depletion as the
product of periodic elevated extinction, the Kellwasser Event reflects increased attrition rates linked to reduced origination (Bambach et al., 2004). Notwithstanding the unquestionably widespread ecosystem perturbations caused by the Kellwasser Event, its effects remain inadequately positioned in a broader, Late Devonian context (Racki, 2005).

Feist & Schindler (1994) noticed that by late Frasnian times, trilobite associations encompassed only obligate bottom-level inhabitants adapted to low-light conditions. They postulated that most trilobites from the \textit{linguiformis} Conodont Zone were blind, probably endobenthic forms, unable to cope with the sudden and widespread dysoxia of the Upper Kellwasser level. Indeed, drastic diversity drops at sections in Europe and North Africa occurred at the Upper Kellwasser level. The situation is somewhat different in the Canning Basin (NW Australia) where one of the best preserved Devonian reef complexes in the world is exposed. McNamara & Feist (2016) described how trilobite diversity was exceptionally high prior to the Lower Kellwasser level with representatives of Harpetidae, Scutelluidae, Odontopleuridae, Phacopidae, Aulacopleuridae and Proetidae (including Tropidocoryphidae). In the two regional conodont zones preceding the Lower Kellwasser level origination rates were equal to extinction rates but none of the 23 species in both zones survived the Lower Kellwasser level. The same applies to the interval between the two Kellwasser levels, until all 40 species described from the Frasnian in the Canning Basin went extinct at the Upper Kellwasser level. Here there is no evidence of dysoxia; instead, both levels are correlated with the onsets of major regressions. Such examples demonstrate the destructive effects of the Kellwasser Event on trilobite associations which is, with right, considered an extinction.

In Belgium the intensity of the Kellwasser Event and its effects on benthic biotas depended on their position along the ramp (Mottequin, 2008a). The Lower Kellwasser level is marked by the deposition of dark shales (Matagne Formation) on the southern border of the Dinant Synclinorium (Gouwy & Bultynck, 2000). The sudden but diachronous, widespread darkening of the sediments is considered to evidence the onset of hypoxic or anoxic conditions. In the Philippville Anticlinorium, the base of the Matagne Formation corresponds to the Upper Kellwasser level whereas the Lower Kellwasser level is positioned in the Les Valisettes Member of the underlying Champ Broquet Formation (Bultynck et al., 1998; Gouwy & Bultynck, 2000). The late Frasnian decline of brachiopods in shelf environments occurred in a step-wise fashion until a major crisis was recorded just below the Upper Kellwasser level (Mottequin, 2008a, b; Mottequin & Poty, 2015). Major turnovers in the ostracod fauna close to the Kellwasser Event have been interpreted as episodic hypoxia followed by a major regression close to the Frasnian–Famennian boundary (Casier, 2017). The Lower Kellwasser level had no noticeable effect on corals as it trailed the first coral extinction which corresponds to a shift in the depositional pattern at around the middle–upper Frasnian boundary (Poty & Chevalier, 2007).

The presently available data reveal that Frasnian trilobite diversity in Belgium was highest within the \textit{punctata} Conodont Zone with 14 species (including taxa in open nomenclature) in 7 genera (Fig. 4). The shales with few limestone intercalations of the Ermitage Member were particularly suitable for members of \textit{Bradocryphaeus} which are locally truly abundant. The first significant diversity cut happened in conjunction with the termination of the Arche mounds. For \textit{Torleyiscutellum} this is particularly obvious because its occurrence was restricted to reefal environments. Only \textit{Bradocryphaeus} lineages continued without noticeable interruption into the \textit{hassi} Conodont Zone as members of the genus quickly established widespread foothold in the mud- and limestones of the Bieumont Member. Trilobites
from the *hassi* and *jamiaeae* Conodont zones include a larger amount of taxa in open nomenclature: up to 13 distinct species in 4 genera potentially occur here (*Parapetacidae* included: *Acasitidae* and *Phacopidae* from the Namur Basin excluded) although the number of 6 *Torrleyiscutellum* species described in open nomenclature is likely to be much reduced as better preserved material becomes available (see below). None of these species made it until the Lower *rhenana* Conodont Zone except for *B. neuntani*. Instead, brief diversity upsurges occurs in this last zone with at least 5 species in 4 genera, none of which persisted into the Upper *rhenana* Conodont Zone.

Based on these figures a general reduction of trilobite diversity during the middle to late Frasnian in Belgium might be advocated. This is certainly true for the associations of the lateral facies which lost most of their diversity after the collapse of the Arche mound and remained at a decline. The associations of the reefal environments on the other hand, although fully recovered along with the termination of each mound level, repeatedly convalesced rather well subsequent to the reinstatements of their habitats. In fact, a modest diversity increase is observed in the mound levels throughout the Frasnian. It is striking that except for members of the highly successful and stratigraphically long-ranging *Cyphaspis* (see below), no trilobite appears to have been able to switch between the reefal and lateral environments. Thus, a distinction must be made between trilobite extinction patterns in the reefal and lateral facies of the Belgian Frasnian for they are principally different.

The role of the Kellwasser Event in the demise of the trilobite fauna remains inconclusive. No stratigraphically controlled data from around the Kellwasser levels were available during our study. Consequently, we can only possibly speculate on their impact by assessing the quality of the habitats of the trilobites. The termination of the last (Petit-Mont) mound level happened prior to the Lower Kellwasser level in the southern Dinant Synclinorium and in between both Kellwasser levels in the Philippeville Anticlinorium. Thus, if the reefal trilobite associations did in fact cease to exist with the final removal of their habitats then they could well have been present above the Lower Kellwasser level in the latter depositional area. The trilobites of the lateral facies appear to exhibit a more step-wise decline. It stands, however, that not a single trilobite is known with certainty from levels above the first darkening of the sediments. Mailleux (1936) mentioned the occurrence of *Bradorycyphaeus supraventionic* basally in the Matagne Formation but we have not been able to trace this material. Notwithstanding the devastating potential of the Kellwasser levels on trilobites as showcased in other countries, the currently available data suggest that the Belgian Frasnian trilobite fauna was already at a decline prior to this event, as a consequence of the deteriorations or losses of shallow-water habitats attested to by some other fossil groups.

4. Systematic palaeontology

All the figured specimens were whitened with ammonium chloride prior to photography. The type material is housed by the Institut royal des Sciences naturelles de Belgique (IRSNB). Occurrences provided for each of the genera below encompass exclusively records from Belgium.

Our study was based both on our contemporary fieldwork in cooperation with private collectors and examinations of old museum collections. Although research has been exhaustive it must be considered that 1) the number of latest Frasnian outcrops that are open and suitable to collectors is limited; 2) it can be assumed, a priori, that there is a sampling bias towards sections that yield a richer macrofossil; 3) trilobites were often collected under limited stratigraphic control (this is particularly the case for old museum collections which make up a major part of the data).

Family Aulacopleuridae Angelin, 1854
Subfamily Otarioninae Richter & Richter, 1926
Tribe Otarionini Richter & Richter, 1926

**Genus Cyphaspis** Burmeister, 1843

*Type species.* *Phacops ceratophthalmus* Goldfuss, 1843.

**Species assigned.** This genus is in need of revision. Van Viersen & Holland (2016) have outlined the basic problems and grouped species based on major morphological trends. However, they emphasised that none of their groups are demonstrably monophyletic, nor does their collection account for the total generic diversity.

**Discussion.** According to its present definition *Cyphaspis* ranges from the Silurian to Late Devonian. Most stratigraphically older species exhibit a strongly vaulted glabella with distinct anterior overhang. This has been considered an important distinguishing feature from its sister taxon, *Otarion* Zenker, 1833 (Adrian & Chatterson, 1994). The Emsian to Frasnian, however, gave rise to many convergences, i.e., putative *Cyphaspis* species with a weakly inflated, *Otarion*-like glabella (compare, e.g. the *hamidi* group of van Viersen & Holland, 2016). Most of the Frasnian forms (e.g. Richter & Richter, 1926; McNamara & Feist, 2016) have been assigned to *Otarion* based on their weakly vaulted median glabellar lobe. The importance of the glabellar morphology to the generic assignments of derived species is open to debate (e.g. Basse, 2002; van Viersen & Prescher, 2007). We attribute the Frasnian *otarionoides* described in this study to *Cyphaspis* based on the presence of inflated genital trunks. According to Adrian & Chatterson (1994) this feature is developed in *Cyphaspis* and several other genera but never in *Otarion*.

**Occurrence.** Members of *Cyphaspis* are widespread in Eifelian strata, occurring in the Jemelle, Couvin and Hanonet formations. They are not known from the Givetian strata where they are rare and mostly restricted to Lion type mounds. Few specimens are known from lateral shales: substantiated records come from the Ermitage (*Cyphaspis* sp. D of van Viersen & Prescher, 2007, pl. 2, fig. 8) and Boussu-en-Fagne members of the Moulin Liénaux and Grands Breux formations, respectively. Additionally, a single specimen is recorded from a Petit-Mont type mound.

**Cyphaspis koineterionensis** sp. nov. (Figs 5A-D, F-H)

v 1926 *Cyphaspis iber gia* Richter & Richter, pl. 7, fig. 10. e.p. 1927 *Otarion iber gia* R. et E. Richter, 1926; Mailleux, p. 78 [only material from “carrière du Cimetière”].

**Etymology.** Derived from κοινητερία (Greek; cemetery), in reference to the type locality “carrière du Cimetière”.

**Holotype.** IRSNB a13165, cephalon (Figs 5F-H).

**Paratypes.** IRSNB a7781, a13183 (Figs 5A-D), a13218, three cephalon, from type locality and horizon.

**Type locality and horizon.** Loc037, Boussu-en-Fagne; Lion Member of the Grands Breux Formation.

**Diagnosis.** Widely rounded cephalon with anteriorly slightly anteriorly protruding outline. Preocular suture running straight in anterior view; in dorsal view γ and β are on the same exsagittal line, with α located just adaxial to this line. Length of L1 (exsag.) relative to length of glabella anterior to 0.5 = 0.45.

**Description.** Occipital ring as high as central part of median glabellar lobe; slightly shorter (exsag.) abaxially than centrally. Teardrop-shaped L1 reaching anteriorly at least until lateral to facial suture point ε; well demarcated by deep furrows. Median glabellar lobe elongated bulb-shaped with straightened (exsag.) flanks; slightly longer than high and with minor anterior overhang. Preglabellar field short (sag., exsag.); slightly anteriorly dorsally protruding medially, where a large depression is developed in the adjacent part of the preglabellar furrow (see below). Fixigena lateral to eye as wide as L1 (tr.); highest point is much lower than occipital ring. Postocular suture running straight proximally, making a gentle curve anteriorly towards ε. Eyes not preserved; their bases are ellipsoidal (exsag.). Lateral field longer (exsag.) than wide (tr.) in lateral view; steep (tr.) with
Figure 5. A-D, F-H. *Cyphaspis kometerionensis* sp. nov. from the Lion Member of the Grands Breux Formation at Loc037, Boussu-en-Fagne. Paratype cephalon with exfoliated anterior border, IRSNB a13183, in dorsal (A), anterior (B), lateral (C) and oblique anterior (D) views. Holotype cephalon, IRSNB a13165, in lateral (F), anterior (G) and dorsal (H) views.

E, J, K, N, Q. *Bradocryphaeus neptuni* ssp. A from the Neuville Member of the Champ Broquet Formation at Loc124, Mariembourg. Complete specimen, IRSNB a13187, in dorsal (E) and oblique lateral (K) views. Pygidium, IRSNB a13185, in dorsal view (J). Pygidium, IRSNB a13186, in dorsal (N) and posterior (Q) views.

L, M, O, R, S. *Bradocryphaeus neptuni hottonensis* ssp. nov. from the Bieumont Member of the Grands Breux Formation at Loc087, Hotton. Paratype cephalon, IRSNB a13205, in dorsal (L) and lateral (M) views. Holotype pygidium, IRSNB a13206, in close-up of right anterior three pleurae (O), dorsal (R) and oblique posterior (S) views.

P. *Bradocryphaeus laomedea* sp. nov. from the Bieumont Member of the Grands Breux Formation at Loc087, Hotton. Holotype pygidium, IRSNB a13207, in dorsal view.

All scale bars represent 2 mm.
fairly well-developed genal trunk. Genal spines are short (if not broken off); their oblique bases are directed more posteriorly than laterally. Shallow, broad cephalic border furrow. Weakly inflated anterior to lateral cephalic borders; slightly flattened lateral of the eye. Entire cephalon covered with moderately closely spaced tubercles. Preglabellar field bears three pairs of slightly enlarged tubercles.

Discussion. The new species is similar to *Cyphaspis ibergia* from the Iberger Kalk (Franzian) of Germany. The latter is discriminated by its narrower (tr.) cephalic outline, narrower glabella, smaller L1, eyes positioned far posteriorly relative to glabella, and long genal spines. While describing *C. ibergia* Richter & Richter (1926, pl. 7, fig. 10) included an incompletely prepared cephalon from Boussu-en-Fagne in their type series (IRSNB a7781, examined by us and selected herein as paratype of *C. koimeterionensis* sp. nov.) and provided a drawing. This drawing, however, is misleading in that it depicts a seemingly complete cephalon in lateral view with only an exfoliated cephalic border. Possibly, this drawing was enhanced using some of the numerous other cephalas that are kept in the Maillieux collection.

Trenkner (1867) described *Cyphaspis ellipsococephalus* (sic) on the basis of a single glabella from “the Iberger Kalk of Winterberg”, Germany. Richter & Richter (1926) complemented the description of this species using specimens from various places, none of which is the type locality. We consider a single glabella to come short to warrant the description of a new species. The holotype cannot be adequately compared with the supplementary material of Richter & Richter (1926) and so their putatively conspecific relationship cannot be corroborated. Since the type locality is not known exactly and no other toptype specimens have been identified we regard *C. ellipsococephalus* as a nomen dubium.

*Cyphaspis stigmatophthalmus* (Richter, 1914) from the upper Frasnian in Germany (Richter & Richter, 1926, pl. 7, figs 11-16; Feist, 1995, p. 229, fig. 11.2; Feist & Schindler, 1994, pl. 4, figs 9, 10, 15), Montagne Noire (Feist & Schindler, 1994, pl. 4, figs 11-14) and Morocco (Feist, 2002, fig. 3J, K) has a long (sag.) upper Frasnian in Germany (Richter & Richter, 1926, pl. 7, figs 10) included an incompletely prepared cephalon from Boussu-en-Fagne in their type series (IRSNB a7781, examined by us and selected herein as paratype of *C. koimeterionensis* sp. nov.) and provided a drawing. This drawing, however, is misleading in that it depicts a seemingly complete cephalon in lateral view with only an exfoliated cephalic border. Possibly, this drawing was enhanced using some of the numerous other cephalas that are kept in the Maillieux collection.

Maillieux (1927, p. 78) reported *Otarion ibergia* in “F2j, petit récif rouge” in the Cimetière Quarry. This refers to the Petit-Mont Member. All of the specimens in the IRSNB are from a grey limestone. These are identical to our material from the top of the Lion Member. A Petit-Mont type mound is shown on the revised geological map in the northern part of the quarry but is no longer accessible at present.

*Cyphaspis* sp. E

(Fig. 6R)

**Material.** IRSNB a13171, incomplete cranidium on a single rock slab together with *Bradocoryphaeus* cf. *laomedea* sp. nov. from Loc011, Lompret; Boussu-en-Fagne Member of the Grands Breux Formation.

**Discussion.** The single cranidium is indeterminable. Of note are the long (sag., exsag.) occipital ring with densely spaced pustules and what appears to be the base of a median tubercle or thorn posteriorly, the large L1, and the smooth, wide (tr.) fixigena with large base of an eye lobe and steeply inclined front.

*Cyphaspis* sp. F

(Fig. 5I)

**Material.** IRSNB a13184, external mould of a cephalon from Loc126, Sautour; Petit-Mont Member of the Champ Broquet Formation.

**Discussion.** This is the sole confirmed *Cyphaspis* specimen from a Petit-Mont mound. The specimen is not very well preserved but easily distinguished from *Cyphaspis koimeterionensis* by the longer (sag., exsag.) occipital ring, shallow S0, shorter L1, and longer preglabellar field. These features and the stratigraphically high occurrence of *C. sp. F* suggest a closer relationship to *Cyphaspis stigmatophthalmus* instead.

Family Proetiidae Saltier, 1864

Subfamily Proetopinae Hupé, 1953

**Genus Pterocoryphe** Feist, 1976

**Type species.** *Pterocoryphe languedociana* Feist, 1976 from the Frasnian of the Montagne Noire.

**Species assigned.** *Pterocoryphe larouquettensis* Feist, 1976; *Pterocoryphe progrediens* Feist & Clarkson, 1989; *Pterocoryphe platymarginata* sp. nov.

**Occurrence.** *Pterocoryphe* is restricted to a single species from grey limestones of the Petit-Mont Member in the vicinity of Mariembourg.

*Pterocoryphe platymarginata* sp. nov.

(Fig. 10C)

v 1940 Drevermannia palpebralis R. E. Richter; Maillieux, p. 32 [material from “Olloy 8715”].

v 2015 Drevermannia; van Viersen, pp. 9, 17.

**Etymology.** Combination of παλατός (Greek; flat, broad) and marginatus (Latin; bordered).

**Holotype.** IRSNB a13194, external mould of a pygidium (Fig. 10C).

**Type locality and horizon.** Loc095, Mariembourg; Petit-Mont Member of the Champ Broquet Formation.

**Diagnosis.** Pygidium with seven or eight weakly vaulted (tr.) axial rings only the anterior four of which are separated by distinct inter-ring furrows, the remaining axial rings being recognisable through the presence of median tubercles. Long, narrow pygidial axis; fourth axial ring distinctly more tapered than third. Pygidial border of equal width throughout.

**Discussion.** Van Viersen (2015) listed “Drevermannia” in the Frasnian of Belgium, referring to the earlier identifications of *Drevermannia palpebralis* by Maillieux (1940). Having examined the original material, a pygidium in the collections of the IRSNB, it has become clear that this taxon should be assigned to *Pterocoryphe* instead.

*Pterocoryphe platymarginata* is similar to *Pterocoryphe larouquettensis* from the middle Frasnian (middle part of *hassi* Conodont Zone) in the Montagne Noire. The French species is different in having a more uniformly tapering pygidial axis with deeper inter-ring furrows and larger median tubercles; the pygidial border is broadest (sag.) postero-medially and tapers anteriorly (this is nowhere the case in the Belgian species which has much narrower pleural fields as a result). Although the discovery of a cephalon of *P. platymarginata* would be timely, the described differences are sufficient for its recognition as a distinct species.

Family Acasitidae Delo, 1935

Subfamily Asteropyginidae Delo, 1935

**Genus Bradocoryphaeus** Haas & Mensink, 1970

**Type species.** *Cyphaspis supradevonicus* Frech, 1888.

**Species assigned.** In performing a cladistic analysis on Asteropyginidae Bignon & Crônier (2014) emended the diagnosis of *Bradocoryphaeus* and revised the list of species assigned. Some of these species are referred herein to *Quadratispina* Gandl, 1972 (see below).

**Discussion.** There appear to be two morphological groups within *Bradocoryphaeus* during the middle Frasnian in Belgium.
Figure 6. A-K. Quadratispina excelsa sp. nov. from the Bovesse Formation at Loc123, Emines. Holotype pygidium, IRSNB a13195, in dorsal (A), oblique lateral (C), close-up of left pleural field (D) and oblique posterior (I) views. Paratype cephalon, IRSNB a13196, in dorsal view (B). Paratype cephalon, IRSNB a13197, in anterior (E) and dorsal (F) views. Paratype pygidium, IRSNB a13200, in dorsal view (G). Fragmentary cephalon, IRSNB a13201, close-up of left part of glabella (H). Paratype incomplete cephalon, IRSNB a13198, in dorsal view (J). Paratype incomplete cephalon, IRSNB a13199, in dorsal view with inset showing left eye in lateral view (K).

L-Q, S, T. Bradocryphaeus neptuni neptuni van Viersen & Bignon, 2011 from the Boussu-en-Fagne Member of the Grands Breux Formation at Loc011, Lompret. Cephalon, IRSNB a13169, in anterior (L), dorsal (M), oblique anterolateral (N) and lateral (Q) views. Pygidium, IRSNB a13170, in dorsal close-up of right pleural field and axis (O), lateral (P), posterior (S) and dorsal (T) views.

R. Pygidium of Bradocryphaeus cf. laomedeia sp. nov. and cranium of Cyphaspis sp. E (arrow), IRSNB a13171, from the Boussu-en-Fagne Member of the Grands Breux Formation at Loc011, Lompret.

All scale bars represent 2 mm.
(Fig. 7): one is inclusive of forms with short pygidial pleural spines (fourth pair of pleural spines ≤ length of associated pleurae), often of rounded triangular section (tr.); the other group encompasses species with long pygidial spines (fourth pair of pleural spines is at least 1.5 times length of associated pleurae) of broadly rounded section. Members of neither group are confined to certain facies. The phylogenetic importance of both groups must be assessed in a broader investigation that is to include species from other countries. This is beyond the scope of the present paper.

**Occurrence.** Bradocryphaeus occurs both in the shales and limestones of the Nismes (?), Moulin Liénaux, Grands Breux and Champ Broquet formations; it has never been found associated with any of the bioherms.

**Bradocryphaeus mosanus (Richter & Richter, 1926)**

(Fig. 7; Figs 8D-J, L)

v e.p. * 1926 Asteropyge (*Asteropyge*) mosana Richter & Richter, pp. 218, 219, pl. 12, fig. 32 [non pl. 12, fig. 33 = *B. cf. mosanus*].

e.p. 1927 *Asteropyge* (*Asteropyge*) mosana; Maillieux, pp. 82, 83 [only Givet].


**Material.** IRSNB a7789, holotype partially exfoliated pygidium, the associated negative imprint of which is refuged (digitally inverted) in Fig. 7 as “*B. mosanus*, Givet”.

Additionally: IRSNB a13208 (Figs 8D, E, G), a13209 (Figs 8F, H), two cephalas and IRSNB a13210 (Figs 8I, L), a13211 (Fig. 8J), two pygidia, from Loc088, Marloie; Ermitage Member of the Moulin Liénaux Formation.

**Discussion.** This species was described by Richter & Richter (1926) on the basis of two pygidia in the collections of the IRSNB that come from middle Frasnian strata in Givet and Boussu-en-Fagne. Van Viersen & Bignon (2011) examined cephalas in the collections of the IRSNB which, according to their labels, had been identified as *B. mosanus* by the Richters but these were all poorly preserved. As far as they could be compared by us, the cephal and especially the pygidia from Marloie are indistinguishable from the types from Givet.

The material kept by the Université de Liège from the Frasnian in the Hotton area and labelled “Cryphaeus valleeanus Dewalque” (*a nomen nudum*, as according to Asselberghs, 1912) was examined by AV and is possibly conspecific.

**Bradocryphaeus neptuni** van Viersen & Bignon, 2011

Subspecies assigned. *Bradocryphaeus neptuni neptuni*; *Bradocryphaeus neptuni hottonensis* ssp. nov.; *Bradocryphaeus neptuni* ssp. A.

**Bradocryphaeus neptuni neptuni** van Viersen & Bignon, 2011

(Figs 6L-Q, S, T; Fig. 7)

e.p. * 2011 Bradocryphaeus neptuni van Viersen & Bignon, pp. 115, 116, pl. 3, fig. G, pl. 4, figs C-J [non pl. 3, fig. H = *B. cf. laomedeia* sp. nov.].


**New material.** IRSNB a13169, cephalon (Figs 6L-N, Q; Fig. 7) and IRSNB a13170 (Figs 6O, P, S, T; Fig. 7), pygidium, from Loc011, Lompret; Boussu-en-Fagne Member of the Grands Breux Formation.

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Figure 7. Morphological groups of *Bradocryphaeus* and their dominant facies occurrences in Belgium during the middle Frasnian. For a description of *B. sp. 20* reference is made to van Viersen & Bignon (2011).
A. *Heliopyge helios* (Richter & Richter, 1926) from the Ermitage Member of the Moulin Liénaux Formation at Loc018, Nismes. Incomplete pygidium, IRSNB a13166, in dorsal view (A). Fragment of left side of a pygidium, IRSNB a13167, in dorsal view (B).


D-J, L. *Bradocryphaeus mosanus* (Richter & Richter, 1926) from the Ermitage Member of the Moulin Liénaux Formation at Loc088, Marloie. Cephalon, IRSNB a13208, in dorsal (D), oblique lateral (E) and anterior (G) views. Cephalon, IRSNB a13209, in dorsal (F) and anterior (H) views. Pygidium, IRSNB a13210, in dorsal (I) and posterior (L) views. Pygidium, IRSNB a13211, in dorsal view (J).

K, M-Q. *Bradocryphaeus echinatus* sp. nov. from the Ermitage Member of the Moulin Liénaux Formation at Loc120, Hotton. Holotype pygidium, IRSNB a13215, in dorsal (N), lateral (O) and close-up of right pleural field (Q) views. Paratype cephalon, IRSNB a13214, in anterior (K), dorsal (M) and lateral (P).

All scale bars represent 2 mm.
Discussion. This subspecies was described by van Viersen & Bignon (2011) for members of *Bradocryphaeus* from the limestones of the Grands Breux Formation in the vicinity of the Lion bioherm (Lion quarry near Frasnes). The new material from Lompret is indistinguishable except for the slightly less divergent axial furrows near L1 to anterior glabellar lobe and the maximum number of lenses per dorsoventral file in the visual surface (five, instead of seven in the holotype from Frasnes).

**Bradocryphaeus neptuni hottonensis** ssp. nov.  
(Figs 5L, M, O, R, S; Fig. 7)

**Etymology.** After the type locality.

**Holotype.** IRSNB a13206, pygidium (Figs 5O, R, S; Fig. 7).

**Paratype.** IRSNB a13205, cephalon (Figs 5L, M; Fig. 7), from type locality and horizon.

**Type locality and horizon.** Loc87, Hotton; Beumont Member of the Grands Breux Formation.

**Differential diagnosis.** Posterior border furrow abaxial to eye is transverse. Narrow (tr.) glabella. Pygidium devoid of prosopon. Pygidal axial inter-ring furrows all (except for first) rudimentary medially so that an “axial median bridge” is developed. Pygidal pleural spines of broadly rounded section.

**Discussion.** Topotype material of the nominate subspecies from Frasnes is easily distinguished from the new subspecies through its wider (tr.) glabella, the posterior curvature of the posterior border furrow of cephalon as it runs abaxially towards the genal spine, the presence of granules on the pygidal axis and pleural spines, the well-developed pygidal inter-ring furrows, and the dorsally more angular section (tr.) of the pygidal pleural spines.

**Bradocryphaeus neptuni** ssp. A  
(Figs 5E, J, K, N, Q)

**Material.** IRSNB a13187, nearly complete specimen (Figs 5E, K) and IRSNB a13185 (Fig. 5J), a13186, two pygidia (Figs 5N, Q), from Loc124, Mariembourg; Neuville Member of the Champ Broquet Formation.

**Discussion.** This is one of the stratigraphically highest members of *Bradocryphaeus* from Belgium. Despite a significant stratigraphic difference the pygidia are similar to topotype material of the nominate subspecies except, notably, for the more elevated pygidal pleural bands. The cephalon of our complete specimen is crushed and cannot be compared in detail.

**Bradocryphaeus laomedea** sp. nov.  
(Fig. 5P; Fig. 7)

**Etymology.** Λαομήδεια (Greek; Laomedea), a satellite of Neptune, referring to the occurrence of this species close to *B. neptuni* in certain localities.

**Holotype.** IRSNB a13207, pygidium.

**Type locality and horizon.** Loc87, Hotton; Beumont Member of the Grands Breux Formation.

**Diagnosis.** Anterior two pygidal inter-ring furrows deepest, especially exagittal; from there each consecutive furrow is shallower; sixth and following inter-ring furrows very narrow (exsag.). Six pairs of weakly curved pleurae which are devoid of sculpture. Anterior four pleural spine pairs are straight with slightly backward curved tips; rounded to somewhat keel-shaped in cross-section; each spine longer than the previous.

**Description.** Pygidium is smoothly rounded subtriangular; just over 1.5 times wider (tr.) than long (sag.). Axis comprised of 12 (+ terminal piece) axial rings, the first two of which are slightly anteriorly curved; the remaining rings are straightened (tr.). Axial furrows slightly more convergent posteriorly near anterior five rings than near remaining rings. First pleura is about 1.6 times longer than fifth. Proximal tip of fifth posterior pleural band reaches fifth axial ring. Posterior pleural bands are three times larger (exsag.) than anterior bands, extended onto pygidal border and extended into long, sword-shaped pleural spines. Fifth pleural spine pair is short, straight, convergent, and about as long as first spine pair. Terminal lappet rudimentary. Borders and spines are covered with densely-spaced, fine granules.

**Discussion.** The pygidia of *B. neptuni* and *B. laomedea* from Hotton are similar at first sight except for the spine lengths. We might have been inclined to make a case for sexual dimorphism. Apart from practical issues to provide evidence for such a claim, the short-spined pygidium and the cephalon from Hotton are in turn similar to *B. neptuni* specimens from Frasnes and Lompret and assigned to a new subspecies, *B. neptuni hottonensis*. The long-spined pygidium from Hotton lacks distinctive features of this species, such as the broad (tr.), subtriangular pygidal outline and the proximal fenestrae. Consequently, we assign it to a new species, *B. laomedea*. Long-spined pygidia similar to the one from Hotton have been recovered from the Boussu-en-Fagne Member of the Grands Breux Formation in Lompret and Frasnes. These are tentatively assigned to this same new species (see below).

**Bradocryphaeus vanherlei** van Viersen & Bignon, 2011 from Nismes is easily distinguished through the shallower pygidal pleural and interpleural furrows, merely 10 pygidal axial rings, and the long fifth pygidal pleural spine pair (twice as long as associated pleurae). Specimens of *B. vanherlei* are usually also smaller. *Bradocryphaeus laomedea* may well represent a broader group of comparatively large-sized species (compare, e.g. *B. cf. laomedea*).

The type species, *B. supradevonicus*, comes from the Oos Formation (*punctata* to Upper *rhenana* Conodont zones) in Büdesheim-Oos in the Eifel. Topotype specimens were figured by Kowalski (1990, p. 50, fig. 42) and Basse (2003, pl. 27, figs 444-455). Königshof et al. (2016, p. 40, fig. 6) recorded a cephalon and a pygidium from the Oos Formation in the Eifel (not the type locality) which they identified as *B. supradevonicus*. The cephalon has few, comparatively small tubercles, and the pygidal pleural pattern and spines are similar to those of *Bradocryphaeus laomedea* sp. nov. We do not regard these specimens as belonging to *B. supradevonicus* but rather believe that they represent a new species.

**Bradocryphaeus cf. laomedea** sp. nov.  
(Fig. 6R, Fig. 7)

v e.p. 2011 Bradocryphaeus neptuni van Viersen & Bignon, pp. 115, 116, pl. 3, fig. H.

**New material.** IRSNB a13171, pygidium, from Loc011, Lompret; Boussu-en-Fagne Member of the Grands Breux Formation.

**Discussion.** Along with the description of *Bradocryphaeus neptuni* van Viersen & Bignon (2011) included a poorly preserved pygidium from the shales of the Boussu-en-Fagne Member at the type locality near Frasnes in their type series. The similarities of this pygidium to *B. laomedea* suggest that it is closely related to that species instead. New collections from the Lompret quarry have yielded another similar pygidium from the Boussu-en-Fagne shales.

**Bradocryphaeus echinatus** sp. nov.  
(Fig. 7; Figs 8K, M-Q)

**Etymology.** Echinatus (Latin; spiny), an understatement, in reference to the rather long pygidal spines.

**Holotype.** IRSNB a13215, pygidium (Fig. 7; Figs 8N, O, Q).

**Paratype.** IRSNB a13214, cephalon (Fig. 7; Figs 8K, M, P), from type locality and horizon.
Type locality and horizon. Loc120, Hotten; Ermitage Member of the Moulin Liénaux Formation.

Discussion. Comparatively strongly vaulted (tr.) cephalon. Glabellar sculpture consisting of small tubercles restricted to central part. First pygidial pleural spine pair is twice as long as associated pleurae. Broad (exsag.) and deep pygidial pleural and interpleural furrows; without fenestrae.

This species shares with stratigraphically slightly younger Bradocryphaeus vanherlei from Nismes, the weakly developed subocular ridge, comparatively fine sculpture on the glabella, dorsally low pygidial posterior pleural bands, and long fifth pygidial pleural spine pair. Bradocryphaeus vanherlei is discriminated by its shallower palpebral furrows, broader cephalic outline, rudimentary pleural and interpleural furrows, short first pygidial pleural spine pair and terminal spine.

Bradocryphaeus echninus might be taken for a Helioype. However, this last genus is distinguished by its thinner, hardly tapered, longer pygidial pleural spines (especially third and fourth pair). Furthermore, the pygidium of Helioype is triangular in outline (with sharp angles), the axis hardly tapers posteriorly, exceedingly large fenestrae are developed, and the pleural spines are more outward instead of backward projected.

Genus Quadratispina Gandl, 1972

Type species. Neocalmonia (Quadratispina) quadratispinosa Gandl, 1972.

Diagnosis (translated from Gandl, 1972, with emendations). Occipital ring bearing a median tubercle. Pygidial axis comprising 10-13 (+1) narrow (sag.), sharply demarcated rings most of which bearing a median tubercle (weak or absent in posterior rings). 5-6 pairs of pleurae with a strongly modified supradevonicus pattern: these consist of steeply inclined posterior bands and moderately narrow (exsag.) yet sharply demarcated and individually vaulted anterior bands. The abaxial half of the posterior pleural band is often widened; in those cases it overhangs the anterior band of the posteriorly lying pleura; further abaxially the posterior pleural bands are extended as roof-shaped swellings on the pygidial border and into pleural lappets; border furrows at these transitional points nonetheless visible (indented). Interpleural furrows narrow and sharp. Large fenestrae may be developed. Pleural furrows equivalent to average width (exsag.) of a posterior pleural band; considerably deepened. Pleural lappets shorter than first pleural pair, lumpish, sharply keeled, and as a result subquadratical in section, always posteriorly directed, and at least the fifth pair convergent. Terminal lappet about as long as fifth pleural lappet; triangular.


Discussion. Haas & Mensink (1970) distinguished three subgenera of Neocalmonia Pillet, 1969 based on the number of pygidial pleural spines and the presence or absence of pygidial fenestrae. These are N. (Neocalmonia) (four spines; without fenestrae), N. (Helioype) (five spines; with fenestrae), and N. (Bradocryphaeus) (five spines; without fenestrae). Gandl (1972) added a fourth, N. (Quadratispina) (five spines; sometimes with fenestrae). According to Arbizu (1977), Quadratispina had been erected based on the keel-like morphology of the pygidial pleural spines. Like Haas & Mensink (1970), Arbizu (1977) attributed major significance to the presence or absence of pygidial fenestrae. He noticed that Quadratispina included species with and without pygidial fenestrae and so he reasoned that these must belong to different subgenera of Neocalmonia. This led Arbizu (1977) to reject Quadratispina. Recently, however, van Viersen & Bignon (2011) demonstrated the presence of small pygidial fenestrae in some members of Bradocryphaeus (compare, e.g. Fig. 60). Thus, this feature can no longer be used to typify Helioype.

Gandl (1972) underlined the importance of the shape of the pygidial pleural bands of Quadratispina. He pointed out similarities to Bradocryphaeus but claimed that even transitional species could be assigned to either taxon based on the strongly modified supradevonicus pygidial pleural pattern of the former. The phylogenetic analyses of Lieberman & Kloc (1997) and Bignon & Crônier (2014) did not support the usage of such patterns. Indeed, with the exception of the supradevonicus pattern the resulting groupings have been shown to be artificial. The conception that some occurrences of pygidial pleural patterns are the result of convergent evolution, however, does not disqualify them as phylogenetically informative characters. That is, we argue that the patterns may still be used to support lower taxonomic ranks, provided that they are homologous within that context.

Bignon & Crônier (2014) noticed that all former Quadratispina species share median tubercles on the pygidial axial rings. These workers considered this feature to bear significance only at the species level and referred to their phylogenetic analysis to support their suggestion. However, only one former Quadratispina species, Asteropyge hispanica Richter & Richter, 1926, was coded and this is not the type species. Consequently, the analysis of Bignon & Crônier (2014) cannot be used to validate the synonymy of Quadratispina with Bradocryphaeus. Similarly to the case of pygidial fenestrae, we believe that median tubercles on the pygidial axial rings developed independently in several lineages of the Asteropyginae. In this respect it is important to note that none of the other Bradocryphaeus species assigned to that genus by Bignon & Crônier (2014) show this feature.

We conclude that the combination of characters in Gandl’s (1972) diagnosis is adequate to discriminate Quadratispina from similar genera. We emend the diagnosis by adding the putatively synapomorphic pygidial axial tubercles and large fenestrae in some species, and furthermore by the presence of a median occipital tubercle and a maximum of 13 (as against 12 reported by Gandl) pygidial axial rings. Lastly, we promote Quadratispina to generic rank which is in line with the general trend of treating asteropygines, including former subgenera of Neocalmonia, as distinct genera – at least until a closer affinity is corroborated.

Occurrence. Quadratispina is restricted to the limestones of the Bovesse Formation on the northern border of the Namur Basin. Basse (2003, pl. 27, figs. 459, 460) illustrated pygidia from the “Givetian or Frasnian near Nismes” in the collections of the Senckenberg Museum, that he assigned to Bradocryphaeus cf. hispanica (transferred herein to Quadratispina). We agree with this identification. Unfortunately, the geographic and stratigraphic origins of the Senckenberg specimens remain unknown.

Quadratispina excelsa sp. nov.

(Figs 6A-K)

1879 Cryphaeus arachnoideus, Goldf. sp.; Malaise, p. 34.
1888 Cryphaeus arachnoideus (sic); Dormal, p. 103.
1912 Cryphaeus punctatus; Asselberghs, pp. 38-40, pl. 6, figs 13-17.
  e.p. 1926 Asteropyge (Asteropyge) hispanica Richter & Richter, pp. 211-213 [only Émines (sic)].
  e.p. 1927 Asteropyge (Asteropyge) hispanica R. et E. Richter,
    Maillieux, pp. 80, 83, pl. 4, fig. 7 [only Émine (sic)].
  e.p. 1927 Asteropyge (Asteropyge) mosana R. et E. Richter,
    Maillieux, pp. 82, 83 [only Émine (sic)].

Etymology. Derived from excelsa (Latin: exalted).

Holotype. IRSNB a13195, pygidium (Figs 6A, C, D, I).

Paratypes. IRSNB a13196-a13199 (Figs 6B, E, F, J, K), a13201 (Fig. 6H), five cephalia and IRSNB a13200 (Fig. 6G), pygidium, all from type locality and horizon.

Type locality and horizon. Loc123, Émines; Bovesse Formation.
**Material.** IRSNB a13188, pygidium, from Loc096, Ligny; Bovesse Formation.

**Discussion.** This pygidium is not well preserved but shows important similarities to *Helioptyge helios* from Nismes such as the triangular pygidial outline and the long, hardly tapered pleural spines of rounded section, the first pair of which is very thin. The axis seems to be broader (tr.) than that of *H. helios* and the terminal lappet is acuminate but spineless. Therefore, the specimen is provisionally designated *H. cf. helios*.

Family Scutellulidae Richter & Richter, 1955
Subfamily Scutellulinae Richter & Richter, 1955

**Genus Torleyiscutellum** Basse, Koch & Lemke, 2016

*Type species.* Scutellum (Scutellum) torleyi Archinal, 1994, from the Givetian of the Rhenish Mountains.

*Species assigned.* See Basse et al. (2016).

**Discussion.** *Torleyiscutellum* encompasses taxa formerly included in *Scutellum* Pusch, 1833. Basse et al. (2016) restricted *Scutellum* to its type species, *S. costatum* Pusch, 1833, because the latter is ambiguous and, in all probability, cannot be salvaged. A similar, less ideal solution was given by van Viersen (2015) who proposed a transfer of former *Scutellum* species to *Goldius* De Koninck, 1841. Differences between *Goldius* and *Torleyiscutellum* were described by Basse et al. (2016).

**Occurrence.** Members of *Torleyiscutellum* occur associated with mounds in the Moulin Liénaux, Grands Breux and Champ Broquet formations. Further specimens come from the biostromal limestones in the lower part of the Philippeville Formation.

**Torleyiscutellum spp.** (Figs 9A-Y, 10A, B)

*Material.** Dimant Syncriniorium: IRSNB a13212a+a-b (= Torleyiscutellum sp. g; Figs 9E-O), from Loc011, Lompret, Grands Breux Formation, Lion Member; IRSNB a13193 (= Torleyiscutellum sp. h; Figs 9P), from Loc090, Ny, Fromelennes or Nismes formations; IRSNB a13182 (= Torleyiscutellum sp. e; Figs 9V, W), from Loc92, Surice, Grands Breux Formation, Lion bioherm; IRSNB a13179, a13180, a13191 (= Torleyiscutellum sp. i; Figs 9U, X, Y), from Loc093, Han-sur-Lesse, Grands Breux Formation, Lion Member. IRSNB a13202-a13204, a13176-a13178 (= Torleyiscutellum sp. x; Figs 9D, E, G-K), from 043, Frasnnes, Grands Breux Formation, Lion Member. Philippeville Antichlorium: IRSNB a13168, a13174, a13175 (= Torleyiscutellum sp. a; Figs 9A, C, F), from Loc89, Neuville, Champ Broquet Formation, Petit-Mont Member; IRSNB a13172, a13173 (= Torleyiscutellum sp. b; Figs 10A, B), from Loc125, Solre St. Géry, lower part of Philippeville Formation; IRSNB a13189, a13189, a13190 (= Torleyiscutellum sp. c; Figs 9O-T), from Loc121, Senzeilles, lower part of Philippeville Formation; IRSNB a13192 (= Torleyiscutellum sp. d; Fig. 9B), from Loc122, Vodéece, Champ Broquet Formation, Petit-Mont Member.

Namur Basin: specimens figured by Asselberghs (1912, p. 38, pl. 5, fig. 12a, b), not examined (= Torleyiscutellum sp. f), from Loc123, Emites, Bovesse Formation.

**Discussion.** Van Viersen & Prescher (2011) described two new species, *Torleyiscutellum decipulum* (Arche Member, Loc051, Frasnes) and *Torleyiscutellum protrusifrons* (Lion Member, Loc037, Bousu-en-Fagne), which had been identified previously as *Scutellum costatum* by Richter & Richter (1926). No new material of either species was discovered in the meantime. The identifications of *Torleyiscutellum* specimens from other localities in Belgium have proved rather difficult and the current provisional assignments to this genus were based on similarities to the two earlier described species. Most of our material comes from Lion or Petit-Mont type mounds but exact origins within the mounds are not known. The specimens are often also incomplete, making it difficult to compare them.
Figure 9. A, C, F. *Torleyiscutellum* sp. A from the Petit-Mont Member of the Champ Broquet Formation at Loc89, Neuville. Incomplete pygidium, IRSNB a13168, in dorsal view (A). Fragmentary cranidium and pygidium, IRSNB a13174, in dorsal view (C). Fragmentary pygidium, IRSNB a13175, in dorsal view (F).

B. *Torleyiscutellum* sp. D from the Petit-Mont Member of the Champ Broquet Formation at Loc122, Vedée. Fragmentary pygidium in dorsal view.

D, E, G-K. *Torleyiscutellum* sp. X from the Lion Member of the Grands Breux Formation at Loc943, Frasnes. Holaspid cranidium, IRSNB a13202, in dorsal (D) and anterior (J) views. Librigera, IRSNB a13203, in dorsal view (E). Fragmentary pygidium, IRSNB a13178, in dorsal view (G). Pygidium, IRSNB a13176, in dorsal view (H). Pygidium, IRSNB a13177, in dorsal view (I). Fragmentary pygidium, IRSNB a13204, in dorsal view (K).

L-O. *Torleyiscutellum* sp. G from the Lion Member of the Grands Breux Formation at Loc011, Lompret. Incomplete external mould of a cranidium, IRSNB a13212b, in dorsal view (L). Incomplete pygidium, IRSNB a13213, in dorsal view (M) and close-up of axis (N). Pygidium with anomalous (short) median rib ceasing well before reaching axis, IRSNB a13212a, in dorsal view (O).

P. *Torleyiscutellum* sp. H from the Fromelennes or Nismes formations at Loc090, Ny. Incomplete pygidium, IRSNB a13193, in dorsal view.

Q-T. *Torleyiscutellum* sp. C from the lower part of the Philippeville Formation at Loc121, Senzeilles. Fragmentary cranidium, IRSNB a13181, in dorsal (Q) and anterior (R) views. Incomplete pygidium, IRSNB a13189, in dorsal view (S). Incomplete pygidium, IRSNB a13190, in dorsal view (T).

U, X, Y. *Torleyiscutellum* sp. I from the Lion Member of the Grands Breux Formation at Loc093, Han-sur-Lesse. Pygidium, IRSNB a13191, in dorsal view (U). Incomplete cranidium, IRSNB a13179, in dorsal view (X). Fragmentary pygidium, IRSNB a13180, in dorsal view (Y).

V, W. *Torleyiscutellum* sp. E from the Lion Member of the Grands Breux Formation at Loc092, Suris. Fragmentary cephalon, IRSNB a13182, in dorsal (V) and anterior (W) views.

All scale bars represent 3 mm.
Figure 10. A, B. *Torleyiscutellum* sp. B from the lower part of the Philippeville Formation at Loc125, Solre St. Géry. Partial thoracopygidium, IRSNB a13172, in dorsal view (A). Articulated specimen with fragmentary cephalon and pygidium, IRSNB a13172, in dorsal view (B).

C. *Pterocoryphe platymarginata* sp. nov. from the Petit-Mont Member of the Champ Broquet Formation at Loc095, Mariembourg. Holotype external mould of a pygidium, IRSNB a13194, in dorsal view (digitally inverted image).

D-I. *Magreanops renateae* sp. nov. from the Ermitage Member of the Moulin Liénaux Formation at Loc120, Hotton. Holotype enrolled specimen, IRSNB a13216, in dorsal view of pygidium (D), dorsal view of cephalon (E), lateral (F), anterior (G), oblique anterolateral (H) and close-up of eye (I) views.

J-N. *Magreanops monachus* sp. nov. from the Bovesse Formation at Loc094, Golzinne. Holotype cephalon, IRSNB a13217, in dorsolateral (J), lateral (K), anterior (L), close-up of right eye (M) and dorsal (N) views.

All scale bars represent 2 mm.
Further complicating are moderate morphological variations and fairly common pathologies. These often affect the pygidial median rib (see, e.g. Fig. 9O), an important marker used in the discrimination between species. All these factors hinder the definitions of species boundaries. It is conceivable that different types of mounds and even various mound growth stages can be associated with different species. Consequently, we have decided to treat the specimens from each of our localities as individual species, in open nomenclature, until more material and accurate data on stratigraphy and palaeoecology become available. Stratigraphic ranges are extended for each species in Figure 4 as assumed to occur in the entire mound, at least until known to be otherwise (e.g. T. protrusifrons).

Of note are the small eyes of Torleyiscutellatum spp. and Torleyiscutellatum protrusifrons from the Lion mounds in comparison to Torleyiscutellatum decipulum from the stratigraphically older Arche mounds. Eye size reduction has been recognised in various phylectic lineages of Late Devonian trilobites worldwide, including scutelluids (Feist, 1995; McNamara & Feist, 2016).

Family Phacopidae Hawle & Corda, 1847
Subfamily Phacopinae Hawle & Corda, 1847

Genus Magreanops nov.

Etymology. Named after Benedict Magrean who found the holotype of the type species and donated it for study. Gender masculinum.

Type species. Magreanops renateae gen. & sp. nov.

Diagnosis. Moderately small phacopid. Cephalon parabolic in outline, bearing widely spaced, cone-like pustules on glabella. Dorsoventrally low occipital ring. L1 small, flat, sunken deep below adjacent parts of the cephalon. Moderately broad palpebral area, highest point slightly ascending above palpebral lobe. Anterior half of glabella more inflated than posterior half. Lateral glabellar furrows S2 and S3 and post- and subocular pads absent. Axial furrow rudimentary anterior to eyes. Narrow glabella, with axial furrows more divergent between S1 and point opposite δ than anterior to this last point. Large visual surface (max. 18/8-9 lenses); sclera not developed horizontally between lenses and distinctly protruding from visual surface. Short (sag., exsag.) thoracic axial rings, bearing close-set tubercles anteriorly and few tubercles posteriorly; weakly defined lateral lobes. Pygidial axial rings bearing closely spaced tubercles; first three inter-ring furrows are particularly well developed. Pygidial pleurae bearing few small tubercles; pleural furrows broad (exsag.) and deep.

Species assigned. Magreanops monachus gen. & sp. nov.

Discussion. As stated below (see 5.3.), Magreanops is unique in that it is the first large-eyed phacopid to be recorded from Frasnian strata worldwide. It bears similarities to species from the Ardenno-Rhenish Mountains currently included in the problematic Pedinopariops Struve, 1972 (see Basse, 2006). The stratigraphically youngest of these species stem from the earliest Givetian. Setting aside the huge stratigraphic gap between members of both genera, the similarities are probably superficial and mostly related to the large eyes, a trait shared by a number of other phacopid genera (see van Viersen et al., 2017). The type species of Pedinopariops, P. lentigiger (Struve, 1970) from the Eifelian in the Eifel, differs in important aspects such as the inflated and intercalating ring, firmly impressed lateral glabellar furrows, gradually anteriorly descending glabella (sagittal section) with more densely spaced and larger tubercles, axial furrows that are divergent anterior to S2, well-developed posterior pads, broad and deep lateral border furrow, dense sculpture consisting of tubercles and pits on the lateral and posterior borders, less tightly packed lenses in the visual surface as a result of thicker sclera.

Furthermore reminiscent of Magreanops is Eldredgeops Struve, 1990 from the Givetian in the USA (putative Frasnian occurrences have been reported but these were never described). The contents of Eldredgeops is subject to revision. Commonly included taxa are E. milleri (Stewart, 1927) (the type species), E. rana (Green, 1832) and E. crusisituberula (Stumm, 1953). Yet even if Eldredgeops was to be restricted to these species the morphologic disparity would still be vast and the genus clearly be polyphyletic. McKellar & Chatterton (2009) performed a broad cladistic analysis on Devonian phacopids that cast doubt upon the independent generic rank of Eldredgeops. However, their conclusion cannot be sustained since they inadvertently took E. rana for the type species and coded that for analysis instead of E. milleri. These two species are rather dissimilar and likely belong to different genera. Babcock (1992) noticed that the type series of E. milleri consists of multiple species and selected a complete, partially enrolled specimen as the lectotype. This specimen is principally different from our Magreanops material in having a widely rounded cephalon, isolated L1, firmly impressed lateral glabellar furrows, gradually anteriorly descending glabella bearing large, closely spaced, flattened tubercles and without anterior overhang, presence of posterior pads, wide, weakly vaulted (tr.) thoracic and pygidial axes with long (sag., exsag.) robust rings, pygidium lacking pronounced tubercles, and narrow pygidial inter-ring and pleural furrows.

Magreanops renateae gen. & sp. nov. (Figs 10D-I)

v 2014 Phacopinae gen. et sp. indet.; Magrean & Taghon, p. 26, fig. 5.

e.p. 2015 Phacopinae indet.; van Viersen, p. 9 [Frasnian].

Etymology. Named after Renate Magrean.

Holotype. IRSNB a13216, partially exfoliated complete specimen (Figs 10D-I).

Type locality and horizon. Loc120, Hotton; Ermitage Member of the Moulin Liénaux Formation.


Magreanops monachus gen. & sp. nov. (Figs 103-N)

e.p. 2015 Phacopinae indet.; van Viersen, p. 9 [Frasnian].

Etymology. Derived from “a monk’s work” (monachus, Lat.; monk), a common regional expression, in reference to the surprisingly challenging preparation performed by F. Lerouge.

Holotype. IRSNB a13217, cephalon (Figs 10J-N).

Type locality and horizon. Loc094, Golzinne; Bovesse Formation.

Diagnosis. Genal tip reaching backward until lateral of occipital ring. Shallow posterior border furrow. Glabella with slight anterior overhang; bearing widely spaced cone-shaped tubercles. Visual surface comprising 18 dorsoventral files with maximally 8-9 lenses per file. Intercalating ring only accentuated by the presence of several densely spaced pustules.

Discussion. The cephalon of M. monachus from Golzinne and the enrolled specimen of M. renateae from Hotton are both well preserved (not tectonically deformed) in spite of having abraded or exfoliated patches. They are similar as far as they can be compared yet clearly differ in several important aspects: M. monachus has a less posteriorly projected genal angle, a shallower posterior border furrow, larger, less downward-tilted eyes but with slightly fewer lenses, elongated glabella projecting
further anteriorly beyond the eyes and with less anterior overhang (compare Fig. 10F to Fig. 10K). These differences warrant the descriptions of both species awaiting the discovery of additional material.

5. Origin and palaeogeographic relationships of the Belgian Frasnian trilobite fauna

Van Viersen (2015) recognised three intervals of increased trilobite “immigrations” in Belgium during the Devonian (Fig. 3), referring to the influx of “Hercynian” elements known to occur in older strata elsewhere in the world. The first wave commenced in the late half Pragian and is characterised by the onset of such “Hercynian” trilobites in the offshore facies of the Villé Formation (Neufchâteau Syncline). A second, very uncertain wave started in the upper Emsian: it corresponds to the putative acme of the Daleje Event (Hierges Formation), adding “Hercynian” elements to trilobite associations on the southern border of the Dinant Synclinorium and followed by other “Hercynian” taxa along with extensive carbonate production (St. Joseph–Eau Noire complex). The final wave started in the basal Frasnian and is characterised by the widespread deposition of shales and the appearance of Bradycyphaeus.

As shown above, the Frasnian trilobite fauna of Belgium is best characterised as generally coherent, with scutelluids dominating the reefal environments and acastids in the lateral facies. With each major T-R cycle an alternative of this “base” trilobite fauna was installed. Taxa accentuating these alternatives are probably primarily allochthonous elements. Trilobite genera shared between Belgium, other parts of southern Laurussia and (peri-)Gondwanan terranes during the Frasnian are shown in Figure 11.

5.1. Acastidae

Bradycyphaeus is palaeogeographically widely distributed owing much of its radiation to eustatic sea level rises that commenced in the Givetian (Morzadec, 1992). According to the revised definition of Bignon & Crônier (2014) (but see remarks in taxonomic section herein) Bradycyphaeus species occur in the Givetian of Brittany, the Cantabrian Mountains, eastern Iran, western Afghanistan and in the Frasnian of Brittany, the Boullonnais, Ardennes, Eifel, Cantabrian Mountains and eastern Iran. We add to that the occurrence of Bradycyphaeus in the Givetian of the Right Rhenish Mountains (Basse, 2003). Members of this genus are specialists of shaly sediments. They are chief components of the Frasnian “base” trilobite fauna of Belgium and in all probability settled here during regional Frasnian T-R cycle 1, for they are not known from the Givetian carbonate platform nor would there have been many suitable habitats. Phylogenetic affinities between Bradycyphaeus species worldwide remain unclear and even within Belgium the diversity is significant. The demise of the Asteropyginae including Bradycyphaeus was studied by Morzadec (1992) who suggested that the terrigenic detritic deposits triggered by tectonic uplift in Belgium were unfavourable for its members. This is not confirmed by our data which suggest that various lineages continued, with relative success, until levels just below the first darkening of the sediments in the Dinant Synclinorium (i.e. close to the Lower Kellwasser level).

Heliopyge is known outside Belgium only in Brittany where Morzadec (1983) recorded Heliopyge aff. helios from the upper Frasnian Rostivieck Formation. Bignon & Crônier (2014) pointed out that the pleural fields of the French material are not well preserved, impeding the recognition of the pleural pattern and consequently, assignment to a genus. However, the combination of a triangular pygidial outline, narrow pygidial axis, and long, hardly tapered pygidial pleural spines strongly suggests that it is a Heliopyge. Quadratispina is known outside Belgium only from the Frasnian in Spain but those occurrences are not very precisely dated.

The distribution of these acastids in southern Laurussia and peri-Gondwanan terranes points to open, shallow-water migration routes between these continents during the Frasnian.

5.2. Scutellidae

Scutelluid morphological disparity in the Belgian Frasnian is rather limited. Only the conservative Torleyiscutellum occurs here which evolved, with few changes, from a Givetian rootstock. Palaeogeographically this genus was confined to the southern margins of Laurussia. Feist (1974) recorded Scutellum gallicum from the Frasnian of the Montagne Noire but according to Basse et al. (2016) the generic affinity of that species remains uncertain.

5.3. Phacopidae

Phacopids (e.g. Cryphops, Acuticyphops, Nephrops) have been recorded from Frasnian sections in Germany, France, Morocco and NW Australia but all of these are atheloptic. In fact, we could not find any substantiated published record of a big-eyed phacopid from post-Givetian strata, except for the latest Famennian Otoecops Struve, 1976. Chlupáč (1993) recorded a large-eyed phacopid from the Givetian-Frasnian transitional (lower Szydłówek) beds in the Holy Cross Mountains that he described as Chotecops zofiae. Although the age of the Szydłówek Beds is not well defined, conodont data from the lower part suggest a latest Givetian age (Racki & Bultynck, 1993). Smeenk (1983) illustrated large-eyed phacopids from the post-Givetian Portilla Formation and basal part of the overlying Nocezo Formation in Spain, which he assigned to various species of Phacops Emmrich, 1839. Van Loevezijn (1988) added that Smeenk’s Phacops rana aff. rana in particular, is a common species in the transitional beds between these formations. According to the more recent chronostatigraphy of Fernández et al. (1997), however, these strata are all of Givetian age. Thus it appears that the middle Frasnian Magreanops is a world novelty.

According to Feist (1995) phacopid eye reduction is a universal and unidirectional trend that occurred in several lineages throughout the Givetian to Famennian. The appearance of members of Magreanops in the middle Frasnian of Belgium suggests that evolution of big-eyed phacopids took place in settings not exposed at present. The distribution of shallow-water environments to which Devonian trilobites were confined was

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**Figure 11.** Palaeogeographic map of western Europe and northwest Africa during the Frasnian. Adopted from Doupieralska et al. (2016, fig. 1) with modifications. The Ardennes, including western part of the Eifel, is indicated by a black rectangle.
limited during the Late Devonian and so could their preservational potential in the geological record be expected to be reduced (Owens, 1994). Open migration routes between Armorica, the Celtiberian–Cantabrian domain and southern Laurussia as demonstrated by other trilobite groups along with Late Devonian records of big-eyed phacopids, suggest that early Frasnian strata to potentially bear ancestors of *Magreanops* might be sought in western Europe.

5.4. *Proetidae*

Members of the *Dechenellinae* are known from strata up to Middle Givetian age in Belgium (Bignon & Crönier, 2015), the Rhenish Mountains (Struve, 1992; Basse, 2002) and Poland (Chłupáč, 1993). *Dechenella* was furthermore reported by Lombard (1952) from the middle Alvaux Member of the Bois de Bordeaux Formation (Givetian) which underlies the Bovesse Formation in the same area that the pygidia illustrated by Asselberghs (1912, pl. 6, figs 18, 19) came from. It seems possible that *Dechenellinae* persisted in Belgium from the Eifelian, throughout the Givetian, into the Frasnian.

According to Feist (2003) *tropidocoryphid* (included in *proetids herein*) were exclusive to the Montagne Noire during the Late Givetian to middle Frasnian; they were terminated at the Upper Kellwasser level. *Pterocoryphe* is a Lazarus taxon. It was perceived to range from the *falsiovalis* to *hassi* Conodont zones. Thus, it ended in the middle Frasnian, well before reaching the upper Frasnian. The discovery of a pygidium in the Lower *rhenana* Conodont Zone in Belgium is remarkable in several ways. Not only does the genus reappear after a substantial gap in the fossil record but also a member managed to find safe passage from peri-Gondwana to the outer margin of Laurussia and invade a new habitat without showing major morphological (at least pygidial) changes.

5.5. *Harpetidae*

A fragmentary harpetid cephalon was identified in the lateral facies of the Grands Breux Formation (Couvain area) but remains in a private collection (see van Viersen & Bignon, 2011). The genus could not be resolved and so a comparison to harpetids from other regions cannot be made. This occurrence was therefore omitted from the palaeogeographic map. Harpetids are characteristic components of Frasnian sections worldwide.

5.6. *Aulacopleuridae*

*Cyphaspis* is a geographically and stratigraphically widely distributed genus. It has been recorded from the *Uper rhenana* to *linguiformis* Conodont zones in Germany, France, Morocco and NW Australia. Other putatively Late Devonian records come from the USA, China and the Urals. Most of our specimens come from middle Frasnian strata; they predate the widely distributed *C. stigmatophthalmus* of late Frasnian age. Instead, the Belgian specimens are more similar to *Cyphaspis iberia* from Germany. A single cephalon of *Cyphaspis* sp. F from the upper Frasnian is perhaps closely related to *C. stigmatophthalmus*.

6. Acknowledgements

A. Folie and A. Dréze facilitated the study of trilobites in the old collections of the IRSNB with unfailing endurance. S. Goollaerts, M. Coen-Aubert and M. De Ceukelaere helped to trace information about several old localities. R. Speijer shared information on the collections of the Katholieke Universiteit Leuven. R. Endels, S. Goollaerts, I. Kesselaar, D. Leluibre, F. Lerouje, B. Magrean, P. Taghon and R. Walter donated trilobite specimens for study and/or communicated important field observations. R.T. Becker provided valuable suggestions on Devonian palaeogeography. The manuscript benefited from the review comments provided by M. Basse and A. Bignon.

7. References


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A.P. van Viersen & W. Vanherle


Manuscript received 28.10.2017, accepted in revised form 02.03.2018, available on line 31.05.2018.