

Middle Devonian trilobites from the Mont d’Hairs section in Givet, France, with two new species of *Dechenella*

Arnaud Bignon and Catherine Crônier

Université Lille 1, USTL Sciences de la Terre, FRE 3298 GEOSYSTEMES, 59655 Villeneuve d’Ascq Cedex, France
Email: arnaud.bignon@ed.univ-lille1.fr; catherine.cronier@univ-lille1.fr

ABSTRACT: Recent investigation of the historical Mont d’Hairs section near Givet yielded numerous trilobites from Middle Devonian carbonate deposits. The trilobite fauna described in the present paper comprises a number of taxa from the basal Givetian, including two new ones: *Dechenella givetensis* sp. n.; *Dechenella calxensis* sp. n.; *Dechenella zieglerei* Struve, 1992; *Goldius* cf. *capitellum* (Archinal, 1994); and *Nyterops* cf. *hollandi* van Viersen, 2007a. This fauna confirms the previously recognised taxonomic diversity pattern and the *Dechenella* and *Nyterops* Association from the middle Middle Devonian in the Ardenne area.

KEY WORDS: Association, diversity, French Ardenne, Hanonet Formation, Middle Devonian, Terres d’Hairs Formation, Trilobita, Trois Fontaines Formation



A stratigraphic revision (Bultynck *et al.* 1991; Bultynck & Dejonghe 2001) and a better understanding of the geodynamic contexts of the Ardenne area (Goffette 1991; Lacquement 2001) have led to revision of the geological map of Givet (Lacquement *et al.* 2003) and improved palaeoenvironmental knowledge of numerous formations, such as those outcropping in the Mont d’Hairs section in the French Ardenne (see Hubert 2008a). Such work must be based on revision of the sedimentological and faunal contents, i.e. it should include a detailed lithology of the succession, as well as stratigraphic occurrences and relative abundance of faunas, in order to interpret palaeoenvironments and their palaeogeography. Similar work has been conducted by Hubert (2008b) and Hubert & Pinte (2009) on the sedimentological and faunal contents of the Givetian section in the southern Ardenne.

Trilobites are characteristic elements of the macrofauna of the Devonian (Crônier & van Viersen 2007), and they are particularly helpful in understanding ecosystem organisation in the Ardenne Massif, as shown in some recent works (e.g., Magrean & van Viersen 2005; van Viersen 2006, 2007a; Crônier & van Viersen 2008; van Viersen & Prescher 2008; van Viersen & De Wilde 2010).

The investigations of the present study are focused on the trilobite material collected from the Mont d’Hairs fortifications, a Middle Devonian trilobite-bearing section of the Ardenne Massif. The basal part of this historical section comprises early Givetian deposits, which yielded numerous trilobites. Hubert (2008a) described the palaeoenvironments, showing evidence for quiet or agitated conditions from bed-by-bed microfacies study. Disarticulated specimens and low size sorting in a few of the beds suggest that transport cannot be rejected, but the lack of substantial wear on the samples suggests transport over short distances. These arguments suggest a parautochthonous origin of trilobites from the Mont d’Hairs section.

The aims of this paper are to (1) describe trilobite specimens from the basal part of the Givetian in Givet; (2) evaluate taxonomic diversity patterns of middle Middle Devonian age; and (3) determine the trilobite association during this period.

1. Geological setting

The Mont d’Hairs section at Givet, France (50°07′14.20″N/4°50′16.10″E; Fig. 1) are an historical Givetian section located on the eastern bank of the Meuse river (northern France) in the southwestern border of the Dinant Synclinoorium (Fig. 1). The lower Givetian is represented by the Hanonet, Trois Fontaines and Terres d’Hairs formations (Préat & Bultynck 2006; Hubert 2008a), and the basal part of the section has yielded numerous trilobites (Fig. 2).

The Hanonet Formation is a major source of late Eifelian to early Givetian trilobites (van Viersen 2007a). The facies change markedly laterally, consisting of argillaceous limestones alternated by calcareous shale beds sometimes rich in brachiopods, crinoids and trilobites in the Mont d’Hairs fortifications. The upper part is represented by a biostromal unit, with stromatoporoids and tabulate corals separated by argillaceous limestones and shales. Argillaceous crinoidal limestones constitute the first metres of the Trois Fontaines Formation. Further on, a rich stromatoporoid biostromal unit is present, followed by coquinoid beds with stringocephalids. The upper part of this formation is a micritic limestone. The Terres d’Hairs Formation is composed mainly of limestones, with crinoids, corals, brachiopods and trilobites (Bultynck & Dejonghe 2001; Préat & Bultynck 2006; Hubert 2008a).

Conodont data (*Icriodus obliquimarginatus* and *Icriodus brevis* Zones (Bultynck 1987), corresponding to the global *Polygnathus hemiansatus* and lower *Polygnathus varcus* zones) indicate an early to middle Givetian age (Weddige & Ziegler 1996).

More than 500 trilobites have been sampled from the Mont d’Hairs section, all of which are disarticulated or fragmented. *Dechenella* Kayser, 1880, which is represented here by three species, is the dominant genus of the assemblage (92%), followed by *Goldius* cf. *capitellum* (Archinal, 1994) (7%) and *Nyterops* cf. *hollandi* van Viersen, 2007a (1%). *Dechenella givetensis* sp. n. was recovered from the upper part of the Hanonet Formation and the lower part of the Trois Fontaines Formation (Fig. 2). This species is coeval with *Dechenella*

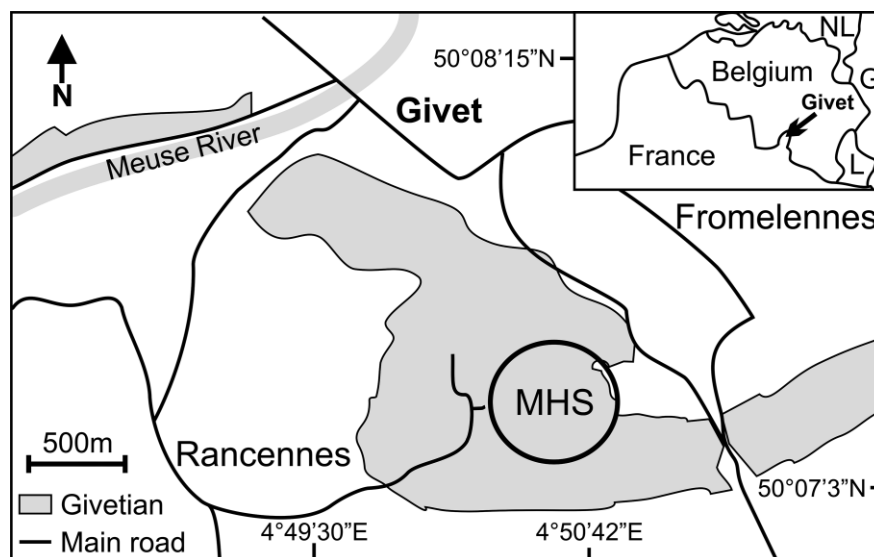


Figure 1 Location of the Mont d'Hairs section (MHS) near Givet, Ardennes, France.

calxensis sp. n. *Dechenella zieglerei* Struve, 1992, a species known from the Eifel basin, and is only found in the lower half of the Terres d'Hairs Formation (Fig. 2). *Goldius* cf. *capitulum* occurs mainly in the Hanonet Formation; only one specimen was found in the Trois Fontaines Formation (Fig. 2). *Nyterops* cf. *hollandi* is confined to Hanonet Formation (Fig. 2).

2. Systematic palaeontology

2.1. Terminology

Morphological terminology follows mainly Whittington (1997). Abbreviations: α = anteriormost point of facial suture; β = most abaxial point of anterior branch of facial suture on the anterior border; γ = intersection between anterior branch of facial suture and palpebral suture; δ = most lateral point of the palpebral suture above the eye; ϵ = intersection between posterior branch of facial suture and palpebral suture; η = intersection between facial suture and posterior border furrow; ω = point where posterior branch of facial suture reaches posterior margin; exsag. = exsagittal; sag. = sagittal; tr. = transverse.

The described and figured material is housed in the collections of the University Lille 1, France. (USTL: Université des Sciences et Technologies de Lille).

2.2. Systematics

Family Proetidae Salter, 1864
Subfamily Dechenellinae Přibyl, 1946
Genus *Dechenella* Kayser, 1880

Type species. Original designation; *Phillipsia verneuili* Barrande, 1852, Givetian, Germany.

Diagnosis. Well developed anterior border; thin preglabellar field generally present; tapering forward glabella, with a usually pronounced lateral constriction in front γ ; pronounced glabellar furrows converging anteriorly to S3; S1–S3 well defined, long and narrow, S1 in contact or not with S0; well-developed eyes; occipital ring curve anteriorly; broad pygidium with a rather thin rachis compared to pleurae; pygidial interpleural furrows very faint or absent; pygidium with 13 to 21 axial rings; pygidial border clearly define.

Remarks. *Dechenella* is one of the most diversified genera among Devonian proetids. The considerable number of species attributed to this genus makes the taxonomy clouded.

Several authors have improved the systematics, with the identification of the subgenera *D. (Basidechenella)* Richter, 1912, *D. (Monodechenella)* Stumm, 1953a and *D. (Pedinodechenella)* Ormiston, 1967. However, these subgenera were subsequently removed from *Dechenella* and given generic status by Lieberman (1994), who considered *Basidechenella* and *Pedinodechenella* to be distantly related and *Monodechenella* as not a member of the Proetinae but of the Crassiproetinae (Owen 2006). In spite of these subdivisions, the genus has kept a large number of species (Basse 1996, 1997, 2002; Basse & Müller 2004; van Viersen & Prescher 2008), augmented by recently discovered new species. Basse (2002) revised the systematics of *Dechenella* based on the recognition of five configurations of the pygidial axial rings (types A–E). Further, he identified six groups of *Dechenella* species, but not based on the five axial ring configurations. Further systematic investigations need to be performed, especially on the cephalon and pleural field organisation.

The dechenelline classification proposed by Lieberman (1994) contains a number of mistakes, as noted by Zhou *et al.* (2000). Lieberman (1994) rejects *D. (Basidechenella)* as a subgenus of *Dechenella* on the basis of several ancestral characters, including a thin and rounded pygidial posterior border; *Dechenella*'s is wide and flat. This author was probably right, but other *Dechenella* species such as *D. zieglerei* and *D. granulata* Richter, 1912 share this thin and rounded pygidial posterior border with constant width.

Yolkin (1979) described several species of *Dechenella* from the lower Devonian of Russia, *D. aspera*, *D. modica*, *D. ormistoni* and *D. prisca*, but these were already removed from the genus by Basse (1996). The present authors support Basse's judgement, mainly due to the strong bulge present on the genal field and behind the frontal lobe of these species, which is not present in *Dechenella*, and their transverse pygidium, which in *Dechenella* is mostly elongated.

According to Zhou *et al.* (2000), *Dechenella* may have originated from the species *prisca*, or from one of the four Russian species described by Yolkin (1979). These species share a large preglabellar field, a pyriform glabella, three glabellar furrows, a rather thin pygidial axis and numerous pygidial axial rings and pleurae. Nevertheless, the transverse pygidium, the faint S2 and S3 glabellar furrows, and the rather straight occipital ring suggest that the Russian species are intermediate between *Dechenella* and the proetine *Lacunoporaspis* Yolkin, 1966.

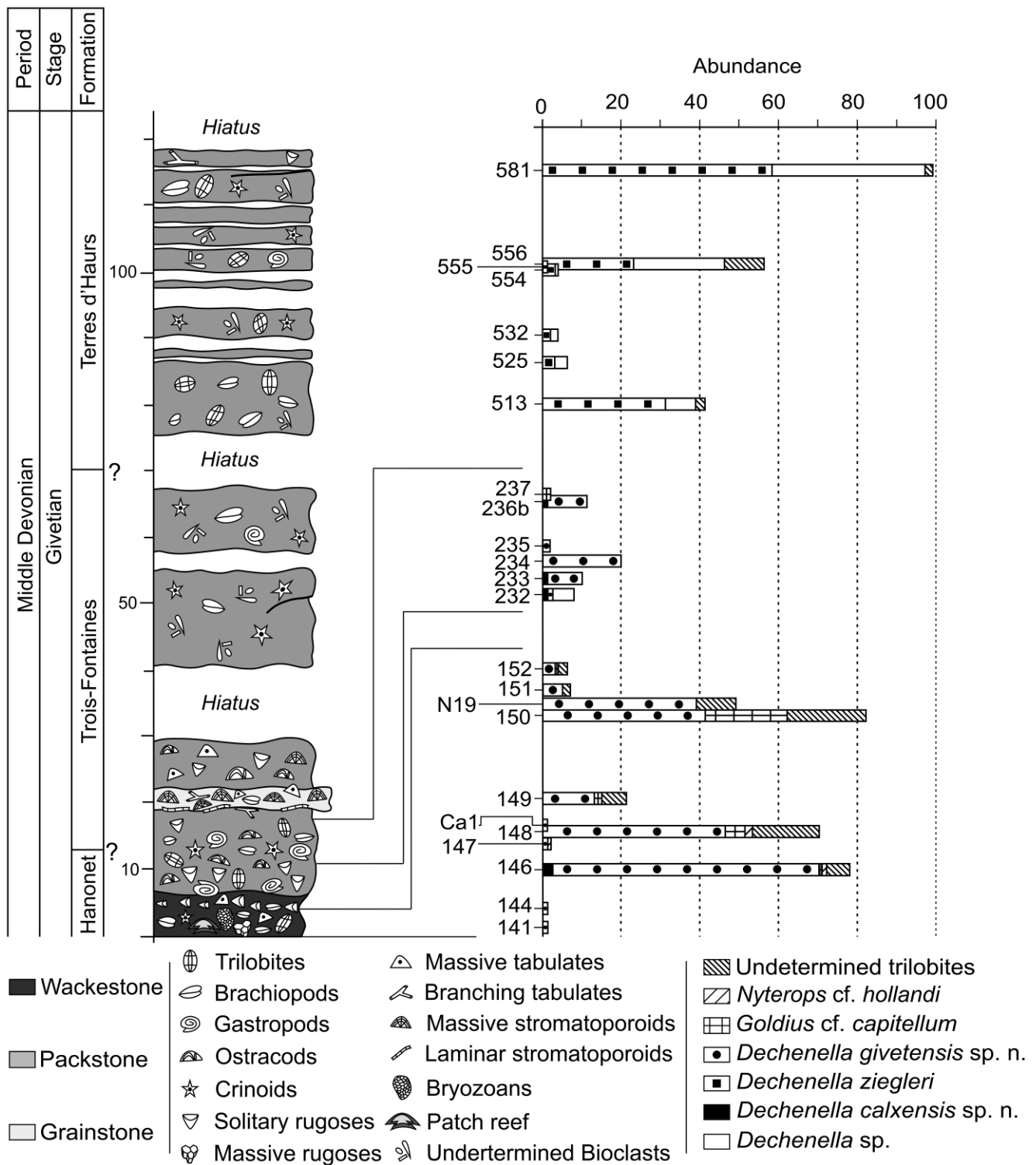


Figure 2 Lithostratigraphic succession, fossil occurrence and numerical abundance of trilobites in the Mont d'Hours section (modified from Hubert 2008a).

The first record of *Dechenella* comes from the Emsian of Canada (Ormiston 1967, 1971; Uyeno 1990) where the genus is well-represented (seven species). Its occurrence in this area is less important in the Eifelian (three species), but the genus was common in the USA and Europe in the Eifelian (11 species). The maximum diversity and distribution of this genus is found in the Givetian (30 species), mainly in Europe. *Dechenella* spread into Gondwana with two species in Morocco, while it was already declining in North America, with only two species recorded in the USA.

The Devonian proetid fauna of the Ardenne shows strong affinities with that of the Rhenish Massif. Because of a gap of

sixty years in research, the trilobites from the Ardenne Massif are not as well known as those from the Eifel. Up to now, *Dechenella* ranged to the middle of the *Polygnathus hemiansatus* Zone in the Ardenne (van Viersen & Prescher 2008), and the new material extends the range of this genus, and also Proetidae, in the Ardenne Massif to the Lower *Polygnathus varcus* Zone. Nevertheless, Basse (1996) had already referred the presence of two pieces of *Dechenella* sp. B from the Givetian limestone of Mont d'Hours. Additionally, Asselbergs (1912) mentioned a *Dechenella* species on the basis of two pygidia in the lower Frasnian of the Namur Synclinorium, and this was named *D. (D.)* ex. aff. *verneuili* sp. c by Richter (1912)

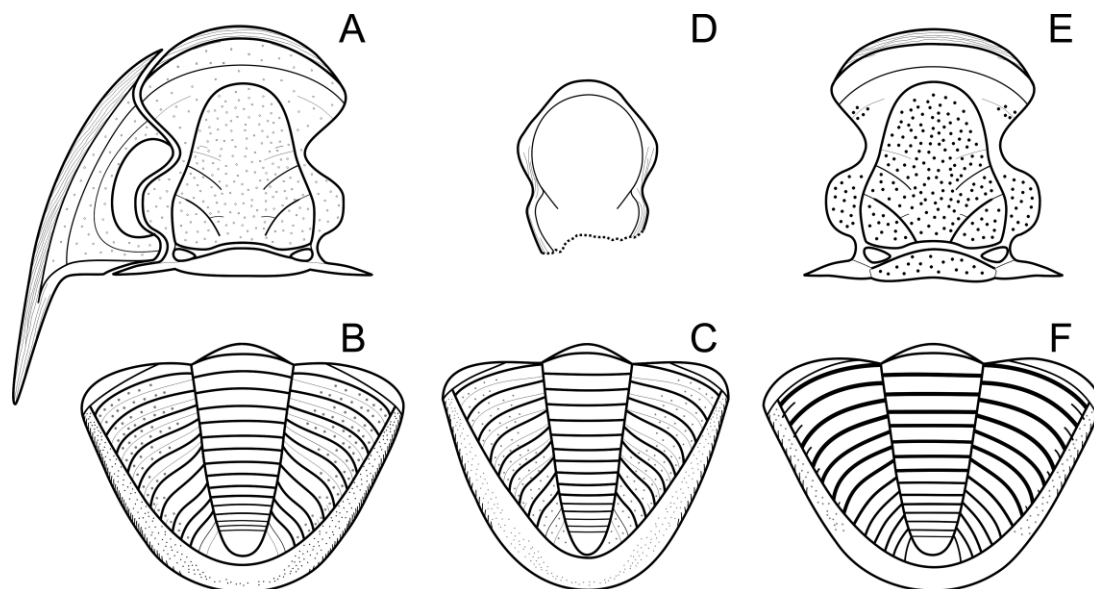


Figure 3 Reconstruction of cephalon (a) and pygidium (b) of *Dechenella givetensis* sp. n.; pygidium (c) of *D. calxensis* sp. n.; hypostome (d), cephalon (e) and pygidium (f) of *D. ziegleri* Struve, 1992.

and Richter & Richter (1926). Unfortunately, these pygidia are too small to allow a reliable determination, and the lower Frasnian age is not confirmed. The genus *Dechenella* has a typical natant hypostome (Fortey 1990), as illustrated herein with *Dechenella ziegleri* or for other *Dechenella* species (Richter 1912; Ormiston 1967). This observation, and the presence of a preglabellar field and a short glabella, are important clues for a natant hypostomal condition (Fortey & Chatterton 1988) for most of *Dechenella* species. Indeed, only a large rostral plate, unknown in this genus, could connect the hypostome to the cephalic doublure (Fortey 1990; Lerosee-Aubril & Feist 2006). A natant hypostome could imply a particle feeding habit (Fortey & Owens 1999). This assumption is supported by the high relative abundance of *Dechenella* in the Mont d'Haurs section and other Ardenne Massif assemblages (Crónier & van Viersen 2007) and by the small size of *Dechenella* in general, all suggesting a low level in the trophic chain (Fortey & Owens 1999). This observation is particularly noteworthy with the large size and the poor representation of *Goldius* cf. *capitellum* and *Nyterops* cf. *hollandi* in the assemblages. These taxa are commonly suggested as predators/scavengers (Fortey 1990; Fortey & Owens 1999), though this assumption is still not completely accepted (Bruton & Hass 1997, 2003).

Otherwise, Fortey & Owens (1999) and Lerosee-Aubril & Feist (2006) have demonstrated that tiny forks occurring at the posterior end of a natant hypostome may correspond to a predatory/scavenging feeding habit. Such forks have been illustrated for *Dechenella* (Richter 1912), but are not present in all species (Ormiston 1967). Thus, the present authors believe that most *Dechenella* were deposit feeders, but some of them, that have tiny forks, could have been opportunistic (predators)/scavengers.

Species assigned. *Dechenella algida* Ormiston, 1967: Eifelian, Canada; *D. allendorfensis* Basse, 1996: Givetian, Germany; *D. alpenensis* Stumm, 1953a: Eifelian–Givetian, Canada–USA; *D. altenae* Basse, 1996: Givetian, Germany; *D. ardennothenana* Basse, 2002: Givetian, Germany; *D. burmeisteri* Richter, 1909: Givetian, Germany; *D. carvalhoae* Lieberman, 1994: Givetian, Poland; *D. crista* Ormiston, 1967: Givetian, Canada; *D. crespuscula* Ormiston, 1967: Givetian, Canada; *D. daumeriesi* van Viersen & Prescher, 2008: Eifelian,

Belgium; *D. delsternensis* Basse, 1996: Givetian, Germany; *D. ebbighauseni* Basse in Basse & Müller, 2004: Givetian, Germany; *D. gigouti* Richter & Richter, 1950: Givetian, Morocco; *D. granulata* Richter, 1912: Givetian, Germany; *D. haldemani* (Hall, 1861): Eifelian, USA; *D. iserlohnensis* Basse, 1997: Eifelian–Givetian, Germany; *D. maclareni* Ormiston, 1967: Emsian, Canada; *D. neotesca* Ormiston, 1967: Emsian, Canada; *D. osborni* Ormiston, 1967: Emsian, Canada; *D. paramaclareni* Ormiston, 1967: Emsian, Canada; *D. perscheii* Lieberman, 1994: Eifelian, Canada; *D. praeverneuili* Struve, 1992: Eifelian, Germany; *D. pruemensis* Basse, 2002: Givetian, Germany; *D. polonica* Gürich, 1896: Givetian, France, Poland; *D. rittbergensis* Zimmermann, 1892: Eifelian–Givetian, Czech Republic, England; *D. romanovski* Tschernyschew, 1887: Middle Devonian (Eifelian and/or Givetian?), Russia; *D. rospensis* Basse, 1996: Givetian, Germany; *D. setosa* Whidborne, 1889: Eifelian–Givetian, Czech Republic, England; *D. spaekkassensis* (Tolmachoff, 1926): Eifelian, Canada; *D. soetenica* Basse, 2002: Givetian, Germany; *D. struvei* Richter & Richter, 1950: Givetian, Germany; *D. trigonalis* Basse, 2002: Givetian, Germany; *D. uexheimensis* Basse, 2002: Givetian, Germany; *D. valentini* Stumm, 1953b: Eifelian, USA; *D. vates* Basse in Basse & Müller, 2004: Givetian, Germany; *D. verneuili* (Barrande 1852): Givetian, Germany; *D. walsdorfensis* Basse, 2002: Givetian, Germany; *D. welleri* (Stauffer, 1909): Eifelian, USA; *D. werdohlsensis* Basse, 1996: Givetian, Germany; *D. wotanica* Basse, 2002: Givetian, Germany; *D. ziatensis* Feist & Orth, 2000: Givetian, Morocco; *D. ziegleri* Struve, 1992: Givetian, Germany.

Occurrence. Emsian–Givetian; Europe (Belgium, Czech Republic, England, France, Germany, Poland), North America (Canada, USA), Africa (Morocco), Russia.

Dechenella givetensis sp. n.
Figs 3a–b; 4a–z

Derivation of name. After the locality of Givet.

Holotype. Holaspid cranium, USTL 0520, from the *Polygnathus hemiansatus* Zone (lower Givetian); Givet, Ardennes, France; Fig. 4g–i.

Studied material. Thirty-seven cranidia, 22 librigenae and 75 pygidia from the Hanonet Formation to the lower part of

the Trois Fontaines Formation, lower Givetian; Mont d'Haurs fortifications, Givet, Ardennes, France.

Diagnosis. Species of *Dechenella* with the following characteristics: glabella with a stricture between S1 and S3; posterior tip of S1 is not connected to S0; facial suture at the most abaxial point on the anterior border (β) slightly more displaced distally than the most lateral point of the eye (δ); cephalon covered with small pits. Pygidium slightly compressed (tr.) posteriorly; axial anterior border shorter (tr.) than maximal pleural field; 15 (+1) smooth and slightly anteromedially flexed axial rings; 12 pleural segments with sparse granules; pygidial border broader posteromedially and bearing small granules.

Description. Glabella tapering anteriorly, moderately rounded anteromedially, strongly constricted between S1 and S3; glabellar length (sag.) is 130% ($\pm 13\%$) compared to maximum glabellar width (tr.); axial furrows deep, converging anteriorly more sharply between distal tip of S1 and S2 than between S2 and S3, slightly outwardly curved opposite distal tip of S1; S1 rather deep, divergent posteriorly at a 43° ($\pm 7^\circ$) angle; bifurcation of S1 in posterior part with a tiny, transverse, slightly curved anterior branch and a straight posterior branch which does not reach S0; L1 inflated; S2 shallower than S1, slightly straightened, and convergent posteriorly at a 54° ($\pm 9^\circ$) angle, with an exsagittal line running towards the distal tip; S3 shallow, shorter than S2, slightly curved, and convergent posteriorly at a 64° ($\pm 11.5^\circ$) angle, with an exsagittal line running towards the distal tip; S4 rarely visible, very faint, very short, straight, isolated from the axial furrows; length (exsag.) between distal tips of S1 and S2 1.6 times (± 0.2) length between distal tips of S2 and S3; S0 deep and quite large; occipital ring broad medially, narrowing abaxially, without a tubercle, with an anterior border curved anteriorly and a posterior border less curved, rather straight; lateral occipital lobes roughly triangular, mostly extended transversely; maximal length inclined at a 58.5° ($\pm 8.5^\circ$) angle, with an exsagittal line running towards the intersection between S0 and axial furrow; preglabellar field developed; very weak bulge on anterior fixigenal field on either side of frontal lobe; anterior border furrow broad and quite deep; anterior border broad bearing four to five closely spaced terrace lines (see Fig. 4m), slightly oriented ventrally backwards; α - α gently curved, close to maximal glabellar width (tr.); α - β somewhat straightened, strongly diverging backward; β - γ straight, converging backward at a 38.5° ($\pm 10^\circ$) angle, with an exsagittal line running towards γ ; long (exsag.) palpebral lobe (half of maximal glabellar length), thin (one-fifth of maximal glabellar width) located between S2 and S3 distal tips anteriorly and S0 distal tip posteriorly; γ - δ rounded, diverging backward at a 52° ($\pm 11^\circ$) angle, with an exsagittal line running towards γ ; β slightly more displaced laterally than δ ; δ - ϵ rounded, converging backward at a 35° angle, with an exsagittal line running towards ϵ ; γ and ϵ very close to axial furrow; ϵ - η slightly diverging backwards at a 15° angle, with an exsagittal line running towards η , with η located at the intersection between facial suture and posterior border furrows; η - ω diverging backward at a 100° angle, with an exsagittal line running towards η ; faint and broad furrow situated between lateral occipital lobe and η ; posterior border rather broad (exsag.), close to the half of the occipital ring width (sag.) and gently narrowing laterally. In lateral view, glabella inflated, strongly flexed anteriorly and subhorizontal posteriorly to the internal tip of S2; occipital ring horizontal, slightly inflated and beneath glabella; anterior border high, long and flat; palpebral lobe slightly bended anteriorly. In posterior view, posterior border of glabella is inflated; occipital ring is strongly inflated. Fine pits on the entire cranidium, more concentrated on glabella than on fixigenal field.

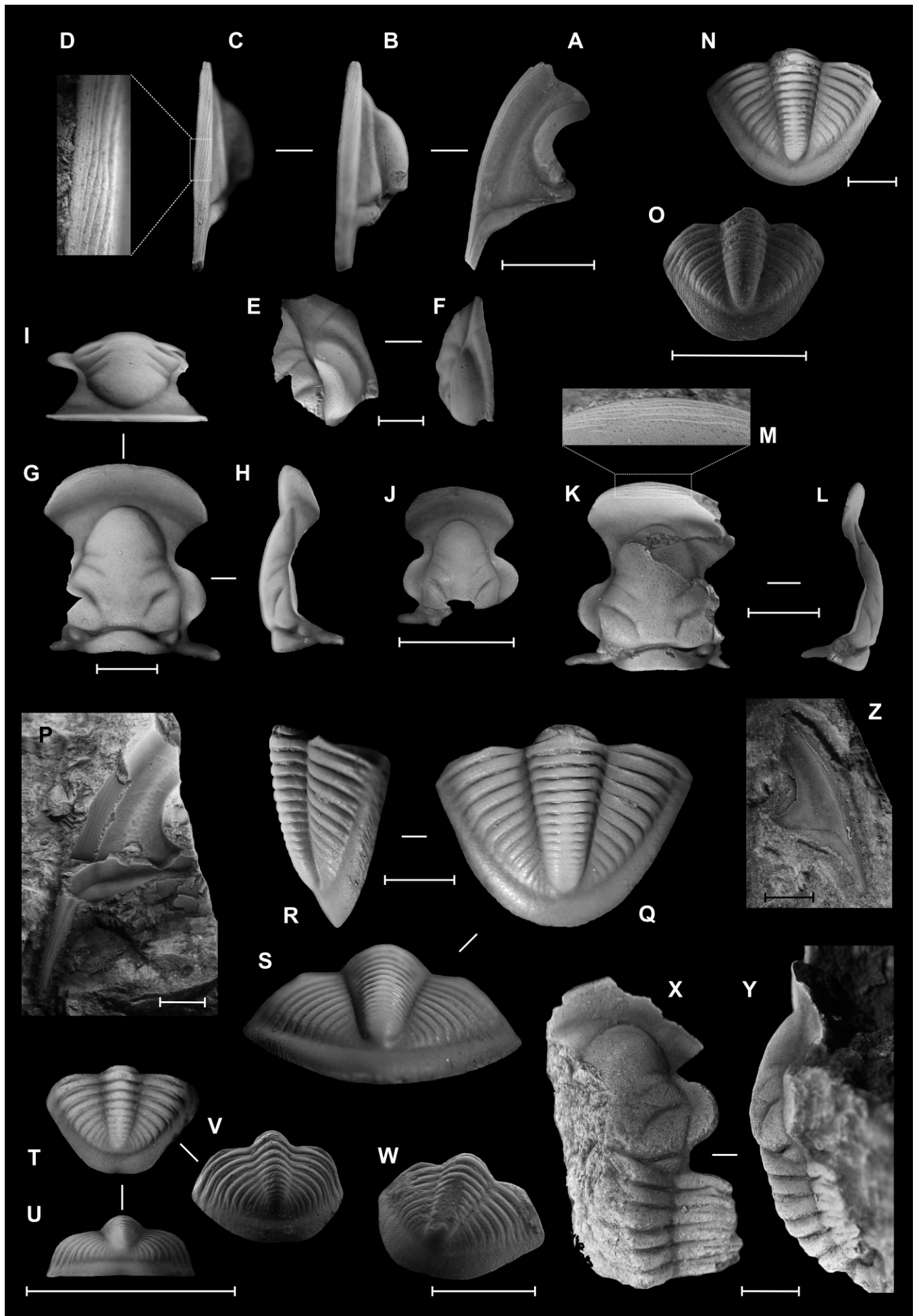
Librigena with high, kidney-shaped eye comprising a broad and almost vertical visual surface, surrounded by a prominent and large eye socle; genal field strongly sloped, narrow, widening behind the eye, separated from lateral border by a well-defined lateral furrow; lateral border bearing five dorsal terrace lines which are slightly oriented ventrally backwards (Fig. 4d); genal spine rather short, around one-third of maximum length of librigena, rather sharp, slightly inflated, base as broad as lateral border, very slightly narrowing posteriorly, forming a 110 – 115° angle (maybe up to 125°) with posterior border, bearing six terrace lines, four on outer margin, the upper line resulting of fusion of three lines of lateral border and two on inner ones; posterior border broad (exsag.) separated from genal field by a deep and straight posterior border furrow. Fine pits on the entire librigena.

Pygidium is of parabolic outline and has a slightly laterally compressed posterior margin; axis triangular, rounded and rather well-differentiated from postaxial field posteriorly, long, more than four-fifth of maximum length (sag.) of pygidium but rather narrow (anterior border corresponding to more than one-third of maximum width (tr.) of pygidium and less to three-quarter of anterior border of a pleural field); axial furrows less converging posteriorly after fifth ring; 15 interring furrows which are very slightly anteriorly curved medially, rather deep and thin, shallowing and thinning backwardly, the last four very faintly, delimiting 15 smooth axial rings and a terminal piece; a median bridge is present after the seventh ring; pleural region divided into a pleural field and a border by a deep, broad border furrow shallower at the two first pleural segments; pleural field composed of 12 segments where the two last are very faint, bearing faint small granules that become less numerous backwardly; interpleural furrows sinusoidal, shallow to inconspicuous backwardly, slightly more visible at proximal and distal tips; pleural furrows sinusoidal, deep, rather thin and gently narrowing and shallowing backwardly, the last two of which are faint; pygidial border slightly inflated, widening posteriorly until opposite the seventh segment, bearing small granules and numerous little oblique terrace lines oriented postero-ventrally on the outer-half of the entire lateral border; pygidial posterior margin without terrace lines and less numerous small granules. In lateral view, axis rather straight, with a posterior half very slightly curved, posterior tip differentiated from border; axial rings rather flat, slightly anteriorly sloped anteriorly; pleural segments rather flat, slightly incline anteriorly; posterior border flat. In posterior view, axis inflated; pleural field subhorizontal adaxially and sloping distally; border furrow well defined except for two first segments; pleural field subhorizontal adaxially and sloped distally.

Smaller cranidia, less than 3 mm long and 2.5 mm wide, differ from taller cranidia by a straighter and less defined S1, a same height between L0 and glabella with or without faint pits. Smaller pygidia, less than 2.5 mm long and 4 mm wide, have less than 15+1 axial rings, 10 pleural segments, better-defined pleural furrows, a larger posterior border and a postero-medial notch.

Comparisons. *Dechenella givetensis* sp. n. is well integrated in the 'type C' pygidial configuration that was defined by Basse (2002) based upon the anteriorly curved axial rings and a median bridge in the posterior part of the axis. This species also belongs to 'group D': "*Dechenella verneuili* and morphologically close taxa" defined by Basse (2002), with the presence of an important glabellar stricture, posterior tip of S1 is not connected to S0, faint interpleural furrows and bearing fine pits on the exoskeleton.

The new species is close to *D. verneuili* (Barrande, 1852). Nevertheless, this latter species has a glabellar length (sag.) equal to its width (tr.), only ten pleural segments, a pygidial



increasingly broad border posteriorly until the ninth pleural segment, the first axial ring width (tr.) close to anteriormost pleural segment width (tr.) and a more triangular pygidial outline.

Basse (1996) described and illustrated a cranidium and a pygidium from the Mont d'Haurs section, which he designated *Dechenella* sp. B. These pieces have been sampled in a compact dark-grey shaley limestone dated as Givetian. These specimens, in spite of their resemblance to *D. givetensis* sp. n., could be differentiated, with δ more laterally displaced than β , and a faintly pointed and thin pygidial border which does not grow after the fourth pleural segment.

D. daumeriesi van Viersen and Prescher, 2008 from the upper Eifelian in Belgium differs from *D. givetensis* sp. n. in having δ further displaced laterally than β , axial rings more flexed anteriorly and a more widely rounded posterior pygidial border.

D. givetensis presents some affinities with *D. (D.)* aff. *polonica* described by Morzadec (1988) from the Givetian of Boulonnais (northern France). Nevertheless, *D. (D.)* aff. *polonica* has 14 axial rings, nine pleural segments, and a more triangular and more inflated pygidium.

Occurrence. Lower Givetian, Hanonet Formation to the lower part of the Trois Fontaines Formation; Mont d'Haurs fortifications, Givet, Ardennes, France.

Dechenella calxensis sp. n.
Figs 3c; 5i–m

Derivation of name. After the area of Calestian (latin name: Calx).

Holotype. Holaspid pygidium, USTL 0533, from the *Polygnathus hemiansatus* Zone (lower Givetian); Givet, Ardennes, France; Fig. 5i–j.

Studied material. Five pygidia from the Hanonet Formation to the early part of the Trois Fontaines Formation, lower Givetian; Mont d'Haurs fortifications, Givet, Ardennes, France.

Diagnosis. Species of *Dechenella* with the following characteristics: pygidium strongly laterally compressed; pygidial length (sag.) close to maximal pygidial width (tr.); narrow (tr.) axial anterior border; 16 (+1) axial rings slightly posteriorly curved; axial furrows more converging posteriorly to the sixth ring; 11 pleural segments with faint large granules; shallow interpleural furrows; sigmoid pleural furrows; pygidial border broader posteromedially and flat in lateral view.

Description. Pygidium slightly parabolic in outline and strongly laterally compressed; axis roughly pointed and well-differentiated from post-axial field posteriorly, long (more than four-fifth of maximum length (sag.) of pygidium); axial fur-

rows less converging posteriorly to the sixth ring; 16 inter-ring furrows slightly posteriorly oriented medially, rather deep and thin, shallowing and thinning backwardly, the last four of which are very faint, delimiting 16 smooth axial rings and a terminal piece; a median bridge is developed from the seventh ring; pleural region divided into a pleural field and a border by a deep, broad border furrow shallower at the two first pleural segments; pleural field composed of 11 segments, the last two of which are very faint and bear large, very faint granules; interpleural furrows sinusoidal, shallow to inconspicuous backwardly, slightly more pronounced at proximal and distal tips; pleural furrows sinusoidal, slightly deep, thin and gently narrowing and shallowing backwardly, the last two of which are faint; border flat, widening posteriorly until the seventh segment, bearing very faint granules and some small oblique terrace lines oriented postero-ventrally on outer-half of anterior two-third of lateral border. In lateral view, axis rather straight with a slightly curved posterior half, a posterior end differentiated from border by a break in slope; axial rings slightly inflated, slightly sloping anteriorly; pleural segments rather flat, slightly incline anteriorly; posterior border flat. In posterior view, axis inflated; pleural field subhorizontal adaxially and sloping distally; border furrow well defined except for the two first segments; same slope between distal pleural field and pygidial border.

Comparisons. At present, *Dechenella calxensis* sp. n. is only known from pygidia.

D. calxensis sp. n. is similar in age to the German subspecies *D. soetenica* Basse, 2002, which differs from *D. calxensis* sp. n. in having more or less 14 axial rings, an axis width most of the time narrower than adjacent pleurae width, lateral furrows less converging posteriorly after the seventh ring, pleurae less compressed laterally and less inflated in posterior view.

The English and Czech species *D. setosa* Whidborne, 1889 is close to *D. calxensis* sp. n., as shown by the pygidial outline of the 'group B' described by Selwood (1965). *D. setosa* is distinct from the other species due to its 18–20 axial rings: 12 recognisable pleural segments, axial furrows straight or slightly constricted after the seventh ring, and a posterior border widening posteriorly until the ninth pleural segment.

D. calxensis sp. n. resembles *D. wotanica* Basse, 2002, but this species has 17 axial rings which are slightly more posteriorly flexed, an axial width close to the corresponding pleural width, axial posterior tips not well-distinguished from the posterior border. These German species seem to be slightly older.

D. givetensis sp. n. and *D. calxensis* sp. n. share the pleural field organisation, with faint interpleural furrows and narrow (sag.) pleural furrows and their pygidial border is broad, straight and distally inclined (Table 1). However, they can be

Figure 4 Proetidae from the Givetian of the Mont d'Haurs fortifications, French Ardenne Massif. Specimens have been whitened prior to photography, except for three views (o, v, w) based on scanning electron microscopy. Scale bars=2.5 mm. (a–d) *Dechenella givetensis* sp. n., Hanonet Formation: librigena, USTL 0544, in dorsal (a), lateral (b, c) and detail (d) views. (e–f) *Dechenella givetensis* sp. n., Hanonet Formation: fragment comprising eye, USTL 0521, in dorsal (e) and lateral (f) views. (g–i) *Dechenella givetensis* sp. n., Hanonet Formation: holotype, cranidium, USTL 0520, in dorsal (g), lateral (h) and frontal (i) views. (j) *Dechenella givetensis* sp. n., Hanonet Formation: cranidium, USTL 0541, in dorsal view. (k–m) *Dechenella givetensis* sp. n., Hanonet Formation: cranidium, USTL 0522, in dorsal (k), lateral (l) and detail (m) views. (n) *Dechenella givetensis* sp. n., Hanonet Formation: pygidium, USTL 0523, in dorsal view. (o) *Dechenella givetensis* sp. n., Hanonet Formation: pygidium, USTL 0524, in dorsal view. (p) *Dechenella givetensis* sp. n., Hanonet Formation: librigena partially exfoliated with its genal spine, USTL 0525, in dorsal view. (q–s) *Dechenella givetensis* sp. n., Hanonet Formation: pygidium, USTL 0526, in dorsal (q), lateral (r) and frontal (s) views. (t–v) *Dechenella givetensis* sp. n., Hanonet Formation: pygidium, USTL 0527, in dorsal (t), frontal (u) and postero-lateral (v) views. (w) *Dechenella givetensis* sp. n., Hanonet Formation: pygidium, USTL 0542, in postero-lateral view. (x–y) *Dechenella givetensis* sp. n., Hanonet Formation: fragmented cranidiothorax, USTL 0543, in dorsal (x) and lateral (y) views. (z) *Dechenella givetensis* sp. n., Hanonet Formation: librigena partially fragmented with its genal spine, USTL 0528, in dorsal view.

Table 1 Major features of the three *Dechenella* species from the Mont d'Haus Section, near Givet, France.

Sclerites	Features	<i>Dechenella givetensis</i> sp. n.	<i>Dechenella soetenica calxensis</i> ssp. n.	<i>Dechenella ziegléri</i>
Cranidium	S1	not contact S0 rather deep	/	contact S0 deep
	Fixigenal field	β further displaced distally than δ	/	β less displaced distally than δ
	Anterior portion of occipital ring	closed to a transverse line tangent to distal tip of S0	/	flexes anteriorly beyond anterior portion of S0
	Sculpture	small pits	/	large granules
Pygidium	Number of axial rings (+terminal piece)	15 (+1)	16 (+1)	15–16 (+1)
	Shape of axial rings	flex very slightly anteromedially	flex very slightly posteromedially	straight
	Inter-ring furrows	narrow	narrow	broad
	Axial furrows less converging posteriorly after	5th axial ring	6th axial ring	6th axial ring
	Axial and pleural width (tr.)	pleurae wider	same width	pleurae wider
	Number of pygidial pleural segments	12	11	13
	Pleural furrows	narrow	narrow	broad
	Interpleural furrows	faint	faint	absent
	Pleurae in cross section	flattened	flattened	rounded
	Posterior border	broad flattened sloped	broad flattened sloped	narrow rounded horizontal
	Shape	parabolic	laterally compressed	parabolic
	Posterior view	rounded	strongly rounded	rounded
Sculpture of pygidial pleurae	faint small granules	faint large granules	rather smooth	
Sculpture of pygidial border	small granules	very small granules	rather smooth	
Terrace lines	on outer-half of entire lateral border	on outer-half of anterior two-third of lateral border	sparse on anterior half of border	

differentiated because *D. givetensis* has axial rings oriented anteriorly, a wider (tr.) pleural field than rachis, 12 pleural segments, and the lateral border covered by terrace lines.

Occurrence. Lower Givetian, Hanonet Formation to the early part of Trois Fontaines Formation; Mont d'Haus fortifications, Givet, Ardennes, France.

Dechenella zieglerei Struve, 1992
Figs 3d–f; 5a–h, n–p

Studied material. Thirteen cranidia, one hypostome, seven librigenae and 75 pygidia from the Terres d'Haus Formation, lower Givetian; Mont d'Haus fortifications, Givet, Ardennes, France.

Diagnosis. See Struve 1992.

Description. Specimens of *Dechenella* with the following characteristics: glabella with a stricture between S1 and S3; glabellar maximum length (sag.) longer than maximum width (tr.); posterior tip of S1 contact S0; facial suture at the most abaxial point on the anterior border; (β) less displaced distally as the most lateral point of eye (δ); preglabellar field present; cephalon entirely covered with large pits. Pygidium parabolic, rather smooth; axial anterior border (tr.) shorter than maximal pleural field width (tr.), 15–16 axial rings and large inter-ring furrows; 13 pleural segments, interpleural furrows absent and large pleural furrows width (sag.); short pygidial border, rounded in lateral view. Hypostome subrectangular, with maximal width (tr.) across anterior wings; middle body strongly inflated (tr.), rather flat (sag.) and smooth, separated from posterolateral and posterior border by deep furrows with rather deep maculae; anterior border well-developed medially, ventrally curved, separated from anterior lobe by an abrupt break in slope that dies out laterally; subtriangular anterior wings projecting mainly dorsally; lateral border is of a rather constant and narrow width in dorsal view and angular in lateral view; posterior border broken; two discontinuous terrace lines run from middle of anterior wing to the broken part.

Comparisons. One of the most characteristic cranidial features of typical *D. zieglerei* is the roughly cloverleaf-shaped glabella caused by marked lateral incisions. Furthermore, the anterior portions of the fixed cheeks are elevated. In the specimens from the Mont d'Haus fortifications, the glabella is cloverleaf-shaped (Fig. 5n) but not always so well developed in some specimens. Similarly, the elevation of the fixed cheek is present, even if it is not as important as in German specimens. In the opinion of the present authors, these differences are not sufficient to elevate the French specimens to a new species or subspecies.

As suggested by Basse (2002), *Dechenella zieglerei* is an element of his 'group E': "*Dechenella granulata* and closed morphology taxa". The members of this group share the following features: heavy granules on the exoskeleton, posterior tip of S1 is in contact with S0, δ more displaced distally than β , large (sag.) pleural furrows and narrow pygidial posterior border. Following the cladistic analysis of Lieberman (1994) this group corresponds to the most derived forms of the 'Old World clade'.

Dechenella burmeisteri Richter, 1909 is probably closest to *D. zieglerei*. Their cephalae are particularly similar, but *D. burmeisteri* has pygidial axial 18–19 rings and 14–15 pleural segments, with an axial width approaching that of the adjacent pleural fields and a larger and flat posterior border.

D. zieglerei is morphologically similar to *D. ebbighauseni* Basse in Basse and Müller, 2004, but this latter differs in having deeper glabellar furrows and stronger granulation of the glabella, a rachis composed of 16–17 rings, 11–12 pleural

segments, and interpleural furrows present on anteriormost segments.

D. zieglerei is easily distinguished from *D. granulata* Richter, 1912. The latter has a glabella wider (tr.) than longer (sag.), deeper S1 and stronger granules. The pygidium has 11 pleural segments and thinner and straighter pleural and interpleural furrows.

D. zieglerei is rather dissimilar from the other two *Dechenella* species from the Mont d'Haus fortifications. *D. zieglerei* has no interpleural furrows, large pleural furrows, rounded pleural segments in cross-section and a rounded and rather narrow pygidial border (see Table 1). Its cephalon differs also from *D. givetensis* sp. n. because the posterior tip of S1 is in contact with S0, β further displaced laterally than δ , the occipital ring larger (sag.) and the exoskeleton more granulated.

Occurrence. Middle Givetian; France, Germany.

Family Scutelluidae Richter & Richter, 1955
Subfamily Scutelluinae Richter & Richter, 1955
Genus *Goldius* de Koninck, 1841

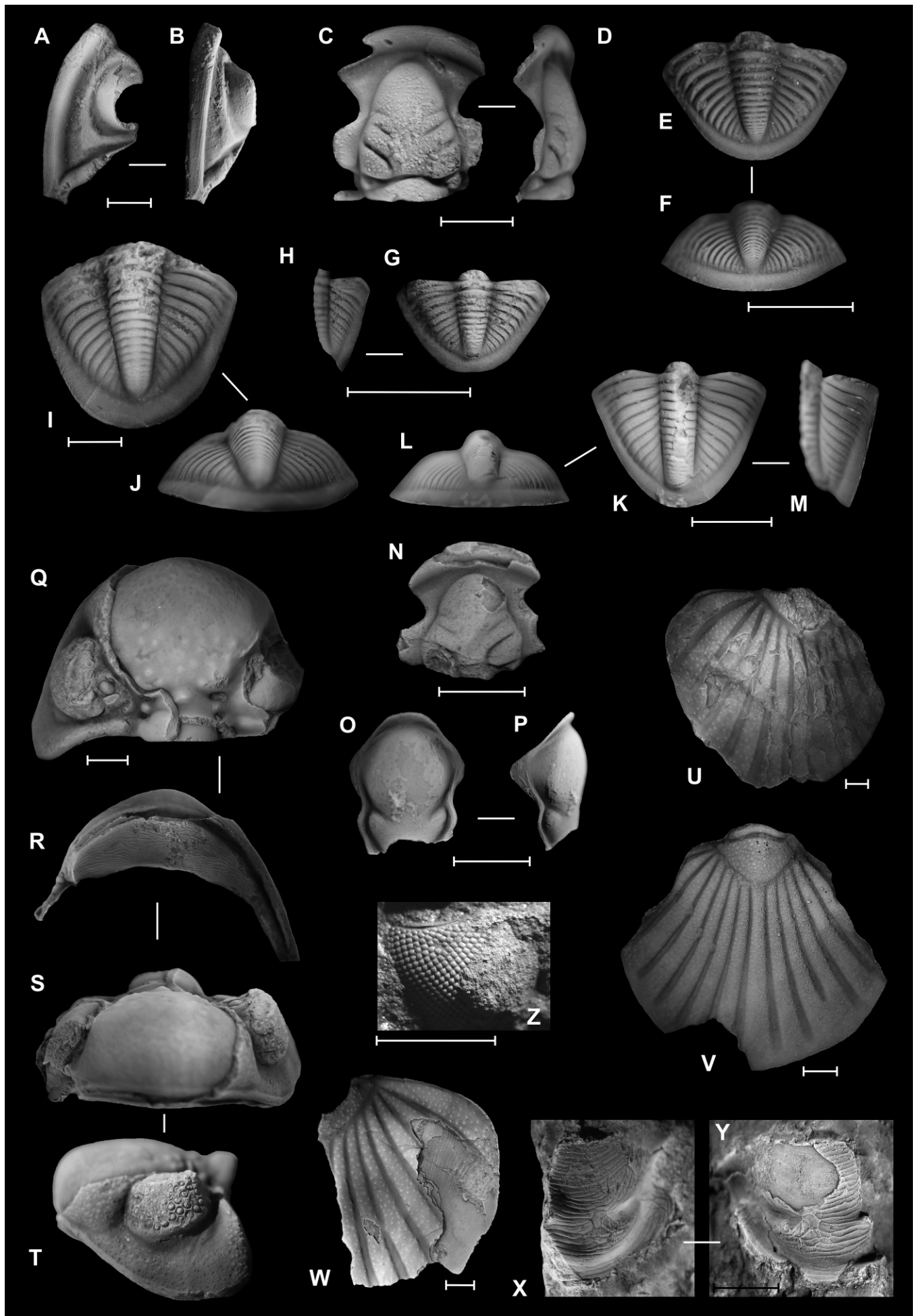
Type species. Original designation; *Brontes flabellifer* Goldfuss, 1839, Eifelian, Junkerberg Formation, Eifel, Germany.

Diagnosis. See remarks.

Remarks. The genus *Calycoscuteillum* Archinal, 1994 has been identified as a junior objective synonym, following the rediscovery of the genus *Goldius* by Basse (2007). van Viersen & De Wilde (2010) give a complete history of the name and provide justification for the restoration of the genus *Goldius*. The genus *Goldius* determined by Archinal (1994) remains a problematic concept, because several species are intermediate between *Scutellum* Pusch, 1833 and *Goldius* species, especially due to the widening of the median rib adaxially (Feist & Talent 2000; van Viersen & De Wilde 2010). Basse (1996) and Feist & Talent (2000) have rejected Archinal's concept to place it in subjective synonymy with the genus *Scutellum*. More recently, Jell & Adrain (2002) and Basse (in Basse & Müller 2004) recognised the validity of *Goldius* at generic level. Since then, this name seems to have been accepted and used in the literature (van Viersen 2007a; van Viersen & De Wilde 2010). However, without having the type material for emendation, it is better to retain Archinal's original diagnosis.

The genus *Goldius* occurs predominantly from the Eifelian to the Givetian. However, Morzadec (1988) ascribed a pygidium from the lower Frasnian in the Boulonnais to *Goldius*. Nevertheless, he did not intentionally assign his specimen to *Goldius*, since he only designated it *Scutellum* (*Scutellum*) cf. *flabelliferum*. Additionally, van Viersen & Prescher (2007) reported an occurrence in Frasnian carbonate mounds near Frasnès.

Species assigned. *G. angusticalix* van Viersen & De Wilde, 2010: Eifelian, Belgium; *G.? archinalae* Basse, 2007: Givetian, Germany; *G.? beckmanni* (Archinal, 1994): Givetian, Germany; *G.? brunopaulusi* (Archinal, 1994): Givetian, Australia, Germany; *G. capitellum* (Archinal, 1994): Givetian, Germany, France; *G. colummaris* (Archinal, 1994): Eifelian, Germany; *G.? dali* (Basse in Basse and Müller, 2004): Givetian, Germany; *G. endorfensis* (Basse, 1996): Eifelian, Germany; *G. flabellifer* (Goldfuss, 1839): Eifelian, England, France, Germany; *G.? foedus* (Maurer, 1885): Givetian, Germany; *G. goolaertsi* (van Viersen, 2007a): Eifelian, Belgium; *G. grafi* (Basse in Basse & Müller, 2004): Eifelian, Germany; *G. intermedius* (Goldfuss, 1843): Eifelian-Givetian, Germany; *G.? lovecrafti* (Basse in Basse & Müller, 2004): Givetian, Germany; *G. newberria* (Basse, 1996): Givetian, Germany; *G. sagitta* (Archinal, 1994):



Eifelian, Germany; *G. sudorus* (Holloway, 1996): Emsian, Australia; *G.? torleyi* (Archinal, 1994): Givetian, Germany; *G. uexheimensis* (Basse in Basse & Müller, 2004): Eifelian, Germany.

Occurrence. Emsian to Frasnian; Australia and Europe (Belgium, England, France, Germany).

Goldius cf. *capitellum* (Archinal, 1994)

Fig. 5u–z

Studied material. Eleven pygidia and one hypostome from the Hanonet Formation to the early part of the Trois Fontaines Formation, lower Givetian; Mont d’Hauris fortifications, Givet, Ardennes, France.

Description. Pygidium with maximal width (tr.) slightly exceeding length (sag.). Rather flat, fulcrum positioned at the anterior third of the medial rib. Axis triangular-shaped with width (tr.) longer than length (sag.), defined by rather broad axial furrows, become faint in front of median rib adjacent segments and median rib directly in contact with axis; slightly vaulted triangular in section posteriorly. Transverse and deep articulating furrow; thin articulating half-ring positioned lower than the axis in transverse section. Faint longitudinal furrows delimiting antero-lateral lobes from central lobe of the rachis. Pleural ribs are slightly convex in cross section, narrowing (tr.) progressively proximally, separated by broad and deep furrows widening posteriorly; median rib wider than other ribs, less wide anteriorly with a slight widening close to the axis and wider posteriorly about twice anterior width; lacking median furrow; first anterior rib is widest except for the median rib, with mostly a transverse orientation. Pleural ribs and furrows disappear before reaching the pygidial margin; gradual slope between gently inclined distal pleural field and flat pygidial border with no border furrow. Pygidium completely covered with fine tubercles except on the pygidial border. Dense and very short ridges are visible on the pygidial border in front of the anteriormost pleural rib.

Hypostome with a large, strongly inflated middle body, separated from posterolateral and posterior borders by deep furrows, divided into anterior and posterior lobes by a large middle furrow, smooth, straight, long and narrow maculae; middle body and posterior border entirely covered with numerous transverse terrace lines; posterior border rather thin and moderately inflated and rounded.

Comparisons. The type species *Goldius flabelliferum* (Goldfuss, 1839) from the middle Eifelian of the Eifel in Germany, shares several features with *G. cf. capitellum* such as the semicircular pygidial outline with the maximal width (tr.) slightly longer than length (sag.), the rib width (tr.) close the adjacent furrow width (tr.), the rachis organisation and fine

tubercles covering pygidium excepted the pygidial border. Nevertheless, *Goldius flabelliferum* is distinguished from *G. cf. capitellum* in having a pygidial medial rib that disappears proximally before contact with the rachis, a smaller part of the anteriormost rib with transverse orientation; i.e. a more proximal curve, wider (tr.) interpleural furrows and a narrower pygidial border.

G. goolaertsi (van Viersen, 2007a) from the uppermost Eifelian of the Ardenne Massif, differs from *G. cf. capitellum* in having a proximally thinner (tr.) median rib and generally straighter pleural ribs, but also by wider (tr.) interpleural furrows. However, the Givet population of *G. cf. capitellum* does not indicate denser tuberculation.

Occurrence. Lower Givetian; France, Germany.

Family Phacopidae Hawle & Corda, 1847

Subfamily Phacopinae Hawle & Corda, 1847

Genus *Nyterops* Struve, 1972

Type species. Original designation; *Phacops (Phacops) nyter* Struve, 1970, Givetian, Cürten Formation, Eifel, Germany.

Diagnosis (after Basse 2006). Glabella moderately strongly vaulted (tr.), bearing distinct tubercles very close to fairly spaced, always as rounded vesicular, highly convex to moderately flat. Frontal part of glabella with coarse, independent tubercles, or with transversely expanded tubercles grouped into ridge-like structures. Preoccipital lobe well-delimited medially. Visual surface with 15 dorsoventral files of lenses with maximally 4–6 lenses per file. Palpebral area of fixigena very narrow (tr.), climbing steeply to the front. Palpebral lobe quite broad. Eye socle significant to very significant. Subocular pad present. Subocular area independent, little convex, rarely granulose. Lateral border flattened or slightly convex. Vincular furrow medially continuous or shortened (sag., exsag.) and flattened. Pygidium with number of axial rings relatively low.

Remarks. In the Ardenne Massif, the phacopid fauna is dominated by *Nyterops* Struve, 1972 during the upper Eifelian and lower Givetian (Crônier & van Viersen 2007; van Viersen 2007a).

Other important phacopid taxa in the Ardenne include *Geesops* Struve, 1972 and *Pedinopariops* Struve, 1972 during the lower Eifelian and the middle Eifelian (van Viersen 2006, 2007a; Crônier & van Viersen 2008). Regarding *Phacops*, only *Phacops cf. imitator* Struve, 1970 (middle Eifelian) and *Phacops sartenaeri* Struve, 1985 (upper Eifelian) are currently known from the Ardenne with certainty (van Viersen 2007a).

Species assigned. *N. nyter* (Struve, 1970): lower Givetian, Germany; *N. yetieffiensis* Basse, 2006: upper Eifelian, Germany; *N. hollandi* van Viersen, 2007a: uppermost Eifelian, Belgium; *N. skalensis* (Kielan, 1954): Givetian, Poland.

Figure 5 Proetidae (a–p), Phacopidae (q–t) and Scutellidae (u–z) from the Givetian of the Mont d’Hauris fortifications, French Ardenne Massif. Specimens have been whitened prior to photography. Scale bars=2.5 mm. (a–b) *Dechenella ziegleri*, Struve, 1992, Terres d’Hauris Formation: librigena, USTL 0529, in dorsal (a) and lateral (b) views. (c–d) *Dechenella ziegleri* Struve, 1992, Terres d’Hauris Formation: cranidium, USTL 0530, in dorsal (c) and lateral (d) views. (e–f) *Dechenella ziegleri* Struve, 1992, Terres d’Hauris Formation: pygidium, USTL 0531, in dorsal (e) and frontal (f) views. (g–h) *Dechenella ziegleri* Struve, 1992, Terres d’Hauris Formation: pygidium, USTL 0532, in dorsal (g) and lateral (h) views. (i–j) *Dechenella calxensis* sp. n., holotype, Hanonet Formation: pygidium, USTL 0533, in dorsal (i) and frontal (j) views. (k–m) *Dechenella calxensis* sp. n., Trois Fontaines Formation: pygidium, USTL 0534, in dorsal (k), frontal (l) and lateral (m) views. (n) *Dechenella ziegleri* Struve, 1992, Terres d’Hauris Formation: partial cephalon, USTL 0545, in dorsal view. (o–p) *Dechenella ziegleri* Struve, 1992, Terres d’Hauris Formation: hypostome, USTL 0535, in dorsal (o) and lateral (p) views. (q–t) *Nyterops cf. hollandi* van Viersen, 2007a, Hanonet Formation: cephalon, USTL 0793, in dorsal (q), ventral (r), frontal (s) and lateral (t) views. (u) *Goldius* cf. *capitellum* (Archinal, 1994), Hanonet Formation: pygidium, USTL 0536, in dorsal view. (v) *Goldius* cf. *capitellum* (Archinal, 1994), Trois Fontaines Formation: pygidium, latex cast, USTL 0537, in dorsal view. (w) *Goldius* cf. *capitellum* (Archinal, 1994), Hanonet Formation: fragmented pygidium, USTL 0538, in dorsal view. (x–y) *Goldius* cf. *capitellum* (Archinal, 1994), Hanonet Formation: hypostome, USTL 0539, in counterpart (x) and dorsal (y) views; (z) *Goldius* cf. *capitellum* (Archinal, 1994), Hanonet Formation: isolated eye, latex cast, USTL 0540, in dorsal view.

Occurrence. Eifelian to Givetian; Europe (France, Belgium, Germany, Poland).

Nyterops cf. *hollandi* van Viersen, 2007a
Fig. 5q–t

Studied material. Eight cephalons from upper part of Hanonet Formation, lower Givetian; Mont d’Hairs fortifications, Givet, Ardennes, France.

Description. Cephalon wide (tr.) with weakly sloped genal fields and genal corners protruding far abaxially. Glabella anteriorly overhanging, strongly vaulted (tr.), bearing evenly spaced, coarse tubercles, with possibly expanded tubercles anterolaterally and its highest point about equal to highest point of occipital ring in lateral view. Eyes near lateral border furrows in dorsal view. Visual surface comprising fifteen dorsoventral files of lenses with maximally four lenses per file; lenses usually protruding above sclera. Reniform palpebral lobe bearing tubercles. Palpebral area inflated and bearing tubercles. Subocular area smooth and moderately wide. Anterior border furrow fine and weakly impressed anterolaterally; lateral border furrow evanescent; posterior border furrow moderately wide well-impressed until posterolateral margin; axial furrows moderately wide well-impressed posteriorly and diverging at around 60°. Lateral border with small and deep pits disappearing posteriorly and with a marginulation bearing fine terrace ridges disappearing near genal angle. Abaxial half of posterior border bearing coarse, slightly acuminate tubercles with closely spaced smaller ones in front of them. Preoccipital ring with possibly few large tubercles. Cephalic doublure bearing fine terrace ridges. Vincular furrow distally more firmly impressed than medially.

Comparisons. The specimens from the Mont d’Hairs section are similar to those from Resteigne (see van Viersen 2007a). They have a wide (tr.) cephalon with weakly sloped genal fields, a visual surface comprising fifteen dorsoventral files of lenses with maximally four lenses per file, abaxial half of posterior border bearing a row of coarse, slightly acuminate tubercles with closely spaced smaller ones in front of them, cephalic doublure bearing fine terrace ridges (Fig. 5r). Unfortunately, the partially exfoliated exoskeletons do not show the occipital ring and the sculpture of glabella that is anteriorly overhanging and strongly vaulted (tr.).

In *Nyterops hollandi* from Belgium, the glabella bears a ‘ridge complex’ of transversely expanded tubercles anteriorly. This feature also characterises *Nyterops nyter* from the lower Givetian of the Eifel. Nevertheless the maximum number of lenses per dorsoventral file varies from five to six in *Nyterops nyter*. Conversely, *Nyterops yetieffiensis* Basse, 2006 from the upper Eifelian of the Eifel bears independent tubercles on the frontal part of the glabella, and the genal fields are exceedingly rich in coarse tubercles.

Occurrence. Hanonet Formation, uppermost Eifelian to lowermost Givetian; France, Belgium.

3. Ontogeny in *Dechenella*

Various growth stages enable an assessment of the morphogenesis of the different species of *Dechenella*.

3.1. Measurements

In order to describe the growth pattern of dechenellines from the Mont d’Hairs fortifications by a numerical model, the dimensions, especially the width as a function of length of 50 cranidia and 137 pygidia in dorsal view, were obtained using an optical image analyser (tpsDig2; Rohlf 2006).

Bivariate plots of cranidia and pygidia show linear and significant, constant relative cephalic and pygidial proportions ($y=ax+b$; $p<0.001^{***}$) for each species regardless of the ontogenetic stage (Fig. 6a–b).

Additionally, in comparing two independent samples, an *F*-test provides a measure of the probability that they have the same variance or regression model (Sneath & Sokal 1973; Lomax 2007). The *F*-distribution can be found in the literature (Brandt 1983). In our samples, no significant differences between the ontogenetic trajectories of *Dechenella givetensis* sp. n. and *D. zieglerei*, respectively for cephalon and for pygidia, were detected by an *F*-test on the slopes (cranidia: $p=0.77\text{NS}$; pygidia: $p=0.84\text{NS}$). However, for pygidia, a Newman–Keuls procedure (Newman 1939; Keuls 1952) was used for testing all pairwise comparisons among size means after an *F*-test. This *post hoc* test suggests a significant difference in size means ($p<0.01^{**}$) between the two samples: *D. zieglerei* and *D. givetensis* sp. n. vs *D. calxensis* sp. n.).

3.2. Morphogenesis remarks

As in many proetids such as *Cyrtosymbole*, *Tropidocoryphe*, *Liobolina* (Feist & Lerosey-Aubril 2005) and *Drevermannia* (Lerosey-Aubril 2006) the postero-medial notch on the pygidial border of *D. givetensis* sp. n. (Fig. 4t) is gradually reduced during ontogeny until it disappears (Fig. 4q). This notch occurs in several other dechenelline species (Ormiston 1967), and is probably also present in *Dechenella zieglerei* and *D. calxensis* sp. n. This assumption would have to be verified using smaller individuals.

4. *Dechenella* and *Nyterops* association

At the Ardenne scale, a radical transgressive regime (Ziegler 1982; Bultynck *et al.* 1991) led to more diversified trilobites during the Middle Devonian. Middle Eifelian limestones yield a rich trilobite fauna, including a number of species known also from the German Eifel (Struve 1982; Basse 1996, 1997, 1998; Magrean & van Viersen 2005; van Viersen 2007b). Eifelian–Givetian transitional sequences are comparatively well-exposed in some places, especially in the Rochefort area (Crônier & van Viersen 2007) or the Givet area (this paper).

Until recently, trilobites from the Givetian were mostly poorly documented. *Goldius*, *Dechenella*, *Gerastos* (Proetidae, Proetidae) and *Nyterops* had been identified, and notably *Dechenella*, *Gerastos* and *Nyterops* in the Rochefort biota during the early Givetian (Crônier & van Viersen 2007); and now *Goldius*, *Dechenella* and *Nyterops* in the Mont d’Hairs biota during the early Givetian (this paper).

The facies development is characterised by prevailing carbonate sedimentation, including the *Dechenella/Nyterops*-dominated biota known from disarticulated and fragmented exoskeletons. The *Dechenella* and *Nyterops* Association characterises the upper Eifelian–lower Givetian in the Ardenne Massif. Dechenellinae appear to be slightly more common in the upper Eifelian in the Ardenne than in coeval strata in the adjacent German Eifel (Basse 2002). The term ‘association’ is used here for assemblages of trilobites with similar taxonomic composition (Brenchley & Harper 1998; Thomas & Lane 1999).

At a global scale, the general decline in trilobites was strongly accelerated by the late Eifelian Kacák and middle Givetian Taghanic events, and marked by stepwise diversity falls (Chlupáč 1994).

5. Acknowledgements

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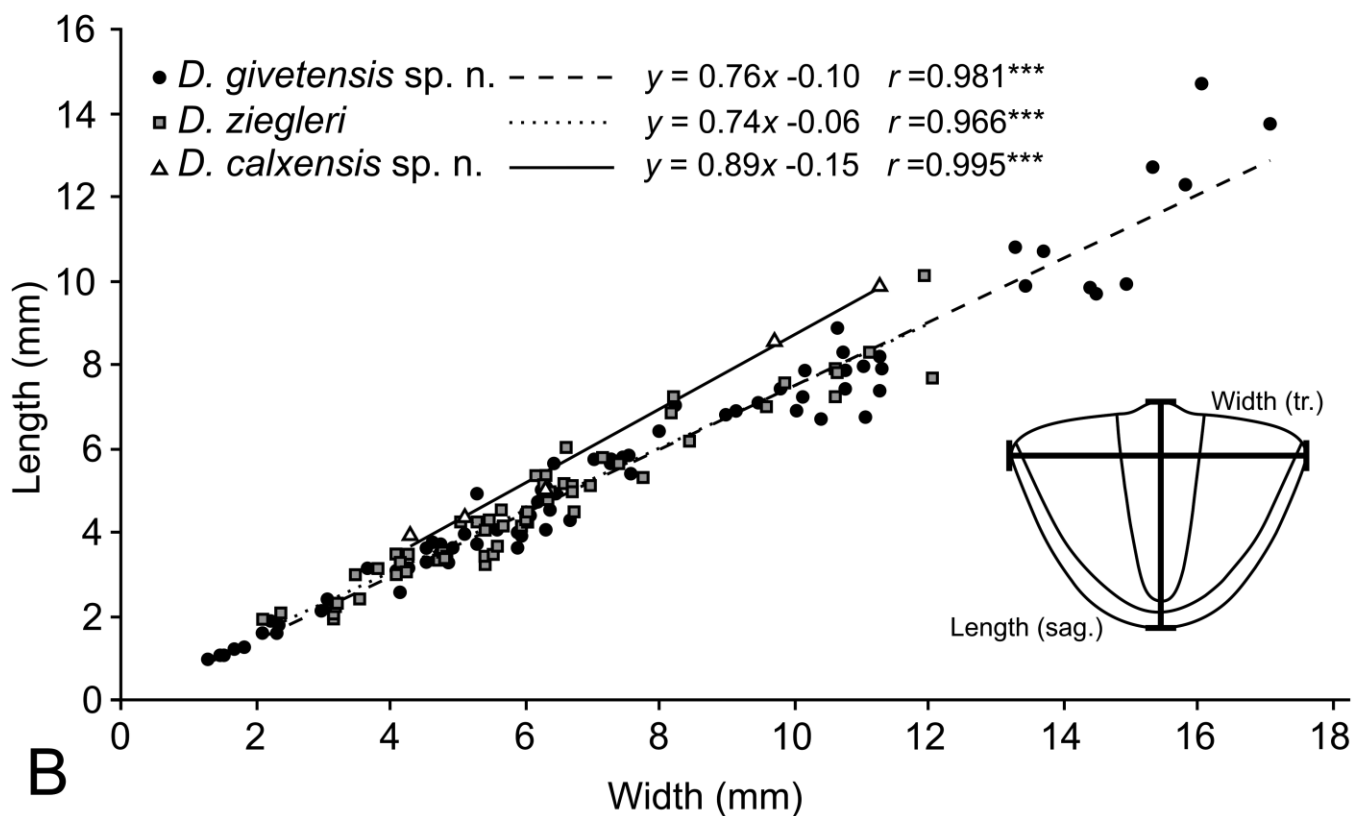
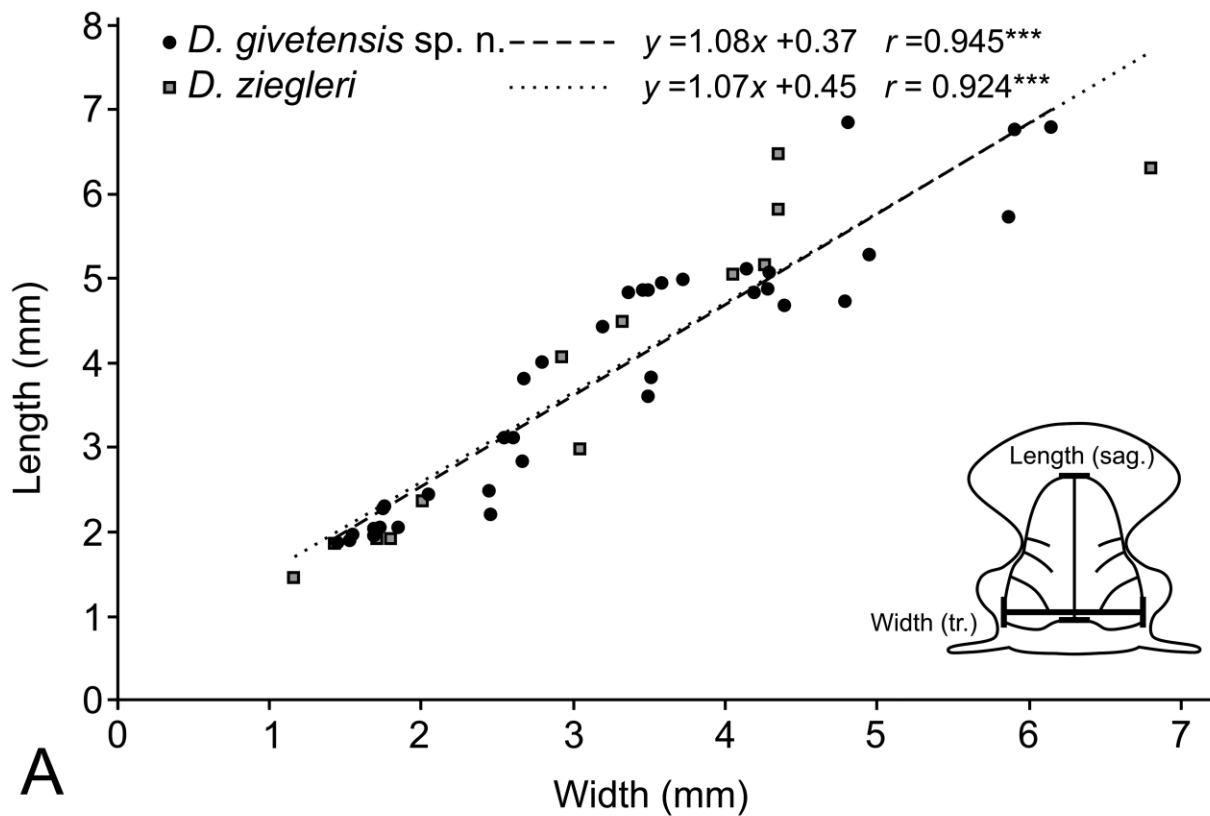


Figure 6 Scatter plot of width versus length for cranidia (a) and pygidia (b) of *Dechenella givetensis* sp. n., *D. zieglerei* Struve, 1992 and *D. calxensis* sp. n.

Technologies of Lille who facilitated access to the Mont d'Hairs fortifications. This work benefited from the helpful criticisms and constructive suggestions made by A. van Viersen (Netherlands) and M. Basse (Germany). This is a contribution of FRE 3298 Géosystèmes.

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