

“Devil horned” *Cyphaspis* (Trilobita, Otarioninae): examples from the Middle Devonian of the Ardennes (Belgium), Eifel (Germany) and Ma’der (Morocco)

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ABSTRACT. Three new species of Middle Devonian otarionine trilobites are described: *Cyphaspis walteri* sp. nov. from the Bou Dib Formation in Morocco, *Cyphaspis rommersheimensis* sp. nov. from the Freilingen Formation in Germany, and *Cyphaspis heissae* sp. nov. from the Ahbach Formation in Germany. *Cyphaspis* cf. *heissae* sp. nov. is described from the Hanonet Formation in Belgium. All four taxa demonstrate a number of features linked to heterochronic processes, with in particular the long paired glabellar spines. Their designation to *Cyphaspis* is discussed.

KEYWORDS: Systematic paleontology, heterochrony, Devonian, Trilobita, Aulacopleuridae.

RÉSUMÉ. «Devil horned» *Cyphaspis* (Trilobita, Otarioninae): exemples du Dévonien moyen de l’Ardenne (Belgique), du Massif rhénan (Allemagne) et de Ma’der (Maroc). Trois nouvelles espèces de trilobites otarioninés du Dévonien moyen sont décrites: *Cyphaspis walteri* sp. nov. dans la Formation Bou Dib au Maroc, *Cyphaspis rommersheimensis* sp. nov. dans la Formation Freilingen en Allemagne, et *Cyphaspis heissae* sp. nov. dans la Formation Ahbach en Allemagne. *Cyphaspis* cf. *heissae* sp. nov. est décrite dans la Formation de Hanonet en Belgique. Toutes ces espèces montrent une série de caractéristiques liées à des processus hétérochroniques, en ce qui concerne en particulier les longues épines sur la glabella. Leur attribution à *Cyphaspis* est discutée.

MOTS-CLÉS : Paléontologie systématique, hétérochronies, Dévonien, Trilobita, Aulacopleuridae.

1. Introduction

Paired glabellar spines are assumed to be common traits among meraspid otarionines which disappeared before reaching adulthood in the majority of species (Adrain & Chatterton, 1994, 1996). Their presence in large holaspides has been recognised notably in *Namuropyge* Richter & Richter, 1939 from the Carboniferous (assignment to Otarioninae follows Adrain & Chatterton, 1994) and in Devonian species formerly placed in *Otarionella* Weyer, 1965. Until recently, these spines were not known from taxa that could be assigned to *Cyphaspis* Burmeister, 1843 according to recent definitions of this genus (Adrain & Chatterton, 1994, 1996; van Viersen & Prescher, 2007). Two (conspecific) otarionine specimens with paired glabellar spines were recorded from the Middle Devonian in Germany by Basse (2010) who assigned them to *Cyphaspis* in open nomenclature. We describe here supplementary material of Basse’s taxon and three additional species from Belgium, Germany and Morocco, all of which come from the Eifelian–Givetian transition and bear a prominent spine pair anteriorly on the glabella.

2. Geological context

2.1. Mrakib (MA14k), Ma’der, Morocco

Outcrop of the Bou Dib Formation at N30°45’ 48,60”; W04°40’ 42,70”. The trilobite specimen described in this paper was collected from the “2cc horizon” (see Gibb & Chatterton, 2010, p. 11, fig. 10), 14,9 m above the *Drotops megalomanicus* horizon. This is the type horizon of *Gerastos izius* Gibb & Chatterton, 2010. The age is late Eifelian to possibly earliest Givetian.

2.2. Ahütte (EF11b), Eifel, Germany

Former “Müllertchen” quarry in Üxheim-Ahütte. Trilobites come from marls at the top of the Olifant Member of the Müllert Subformation, which is part of the Ahbach Formation (lowermost Givetian). The reader is referred to Loboziak et al. (1990) and Basse (2010) for additional details about this locality. The specimens of *Gerastos* sp. shown on Fig. 2 in the present paper are the first to be published of this species.

2.3. Rommersheim (EF16d), Eifel, Germany

Slope of the former highway E42 at about 800 m south of Brunnen Brühlborn. See topographic map, sheet 5704 Prüm, r (25)32925

/h (55)63575. Trilobite specimens were collected from the upper Eifelian Eilenberg Member of the Freilingen Formation. This is the type locality and horizon of *Cornuproetus pruemensis* Basse, 2002, *Gerastos batrachus* van Viersen & Prescher, 2010 and *Gerastos rommersheimensis* van Viersen & Prescher, 2010.

2.4. Resteigne (Loc002), Ardennes, Belgium

Disused quarry near the village of Resteigne (see van Viersen & Prescher, 2010 and references cited therein for a description of this locality). A single trilobite specimen was discovered by Alfer van Rossum in an ex situ rock slab. Lithology of the matrix and additional sclerites belonging to other trilobite species (*Goldius goolaertsi* (van Viersen, 2007), *Gerastos* sp., *Nyterops* cf. *hollandi* van Viersen, 2007) are characteristic of the lower part of the Hanonet Formation there. Hence, the specimen is presumably of latest Eifelian age.

3. Systematic palaeontology

The figured specimens were whitened with magnesium chloride prior to photography and are housed at the “Institut royal des Sciences naturelles de Belgique” (abbreviated IRSNB) and the Maarmuseum in Manderscheid, Germany (abbreviated PWL). Morphologic terminology follows Whittington & Kelly (1997).

Family Aulacopleuridae Angelin, 1854

Subfamily Otarioninae Richter & Richter, 1926

Tribe Otarionini Richter & Richter, 1926

Genus *Cyphaspis* Burmeister, 1843

Type species. *Phacops ceratophthalmus* Goldfuss, 1843, from the Ahrdorf Formation (middle Eifelian) at the “Trilobitenfelder”, Gees, Eifel, by designation under the plenary power, Op. 1434 (Smith, 2001).

Diagnosis. Adopted from Adrain & Chatterton (1996), including modifications by van Viersen & Prescher (2007) and amended herein to accommodate the new species described below: Otarionini with glabella inflated, usually overhanging preglabellar field when occipital ring is held in vertical plane; preglabellar field short; G3 may be retained as spines or sack-shaped tubercles in large holaspides; interocular fixigenae narrow; L1 usually

small; librigenal field relatively broad and short (exsagittally); 11 thoracic segments, with long axial spine or occasionally a central tubercle on sixth; pygidium narrow and small even for subfamily, with transverse rows of tubercles on axial rings and posterior pleural bands; primitively three or four axial rings; pygidial doublure broad for family.

Discussion. The descriptions of the new species below are established on large holaspides that show characters reminiscent of known juvenile stages of the Otarioninae (see, e.g. Adrain & Chatterton, 1994). The question of which processes operated on these features hinges largely on the meraspid ontogenies of these taxa. To our knowledge no juvenile specimens have been recovered of our new species. However, the retention of similar (though not necessarily homologous) juvenile characters in large holaspides has been documented in various lineages of the Otarioninae and commonly attributed to pedomorphosis (e.g. Adrain & Chatterton, 1994; Lerosey-Aubril et al., 2008). With this knowledge, the juvenile appearances of our specimens could reasonably be accounted for as having been acquired through simple pedomorphosis. In describing *Cyphaspis* sp. Z (assigned to *Cyphaspis heissae* sp. nov. below) Basse (2010) pointed out a pedomorphic origin for certain features while referring to the paired glabellar spines in particular. Indeed these features are

likely homologous with spine pair G3 shown by known juvenile stages of the Otarionini (see e.g. Adrain & Chatterton, 1994), yet they are much longer, suggesting that they might also have evolved through peramorphosis. Among other characters of possibly pedomorphic origin is the median occipital spine of *C. heissae* sp. nov. and *Cyphaspis* cf. *heissae* sp. nov. This spine is displayed by early-degree meraspides of the Otarionini but it is diminished during ontogeny and usually reduced to a tubercle or absent in adults (Adrain & Chatterton, 1996). Large holaspides of *Cyphaspis munii* Adrain & Chatterton, 1996 from the Silurian in Canada also retain an occipital spine. Another striking feature is the presence of six tubercles on the anterior cranial border of (at least) *Cyphaspis walteri* sp. nov., *C. heissae* sp. nov. and *C. cf. heissae* sp. nov., which are similarly positioned to spines on meraspides of the Otarioninae (cf., e.g. Adrain & Chatterton, 1994; Lerosey-Aubril et al., 2008).

Putative heterochronies excepted, our new species are generally similar to known members of *Cyphaspis*. Basse (2010) assigned his *Cyphaspis* sp. Z to this genus because of strong resemblances to the thorax of *Cyphaspis ceratophthalmus* (the type species). We agree with this classification. The thorax and also the cephalon and pygidium of *C. walteri* sp. nov. are wider than those of the former two species but otherwise not significantly different. The comparatively large L1 of all our new species

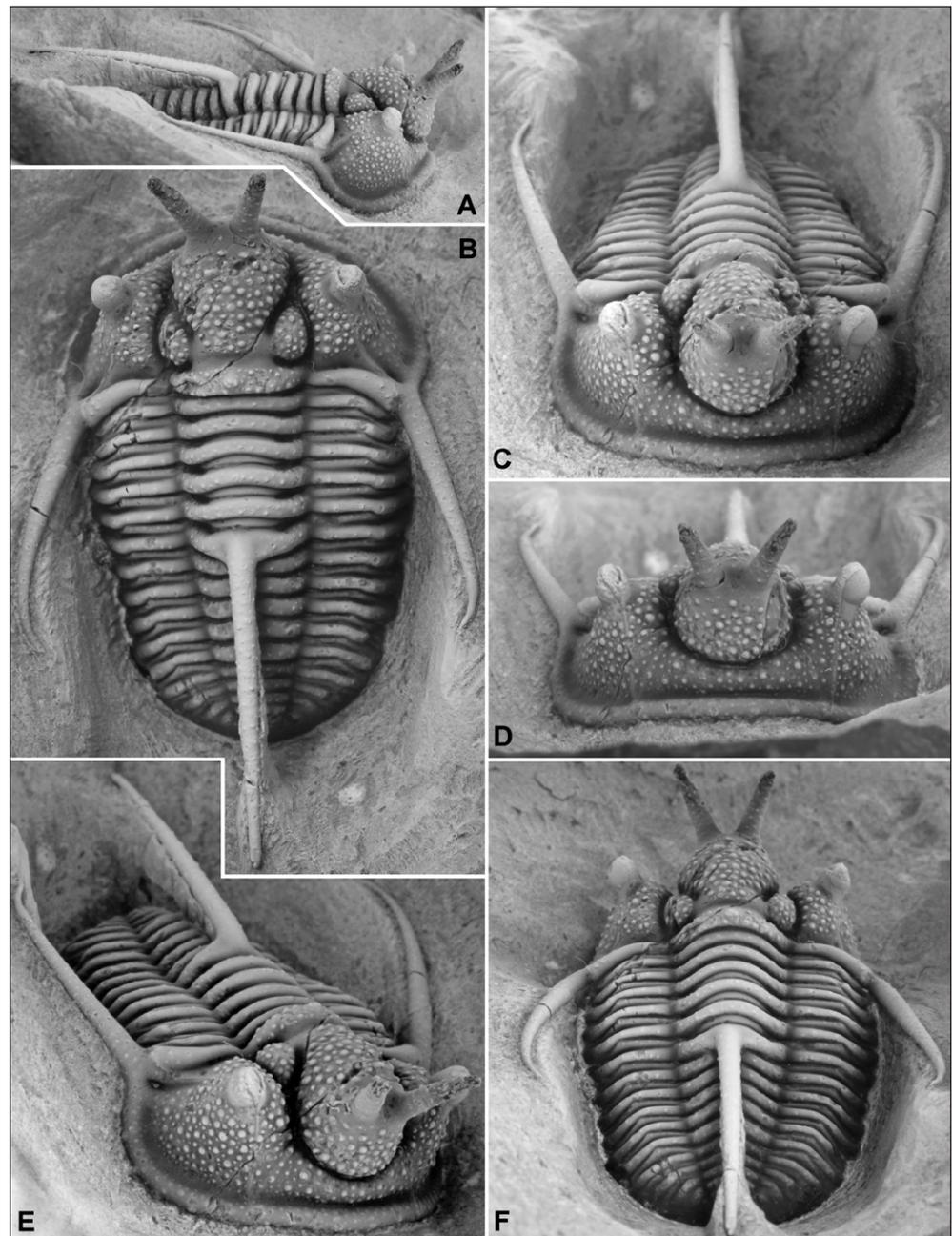


Figure 1. *Cyphaspis walteri* sp. nov. from the Bou Dib Formation in Mrakib, Morocco. Holotype complete specimen IRSNB a12875, in lateral (A), dorsal (B), anterodorsal (C), anterior (D), oblique anterior (E) and posterodorsal (F) views. Specimen is 24 mm long (sag.).

are unusual for *Cyphaspis* and remind perhaps of the otarionine *Harpidella* M'Coy, 1849 (see Adrain & Chatterton, 1995). Such resemblances are likely the result of convergent evolution. Large holaspides of *Otarionella* species (sensu Leroosey-Aubril et al., 2008), which occur in Devonian strata in Morocco and Europe, also have G3 developed as spines. However, Leroosey-Aubril et al. (2008) already provided reasons to exclude *Otarionella* from the tribe Otarionini. One of the arguments presented by those authors is the evenly spaced glabellar spine pairs of *Otarionella*, whereas in Otarionini G2 and G3 are crowded frontally on the glabella (cf., e.g., Fig. 3C). Basse (2010) restricted *Otarionella* in transferring two of its species, known from complete specimens, to his new genus *Chamaeleoaspis* (type species *Cyphaspis chamaeleo* Basse, 1997). *Chamaeleoaspis* is markedly different from *Cyphaspis* (including *C. walteri* sp. nov. and *C. heissae* sp. nov., both of which are known from complete specimens) in having only ten thoracic segments with a dorsal spine on both the fourth and sixth axial ring.

***Cyphaspis walteri* sp. nov.** (Fig. 1)

? 2009 *Cyphaspis* sp.; Bonino & Kier, pl. 164., fig. b.

Etymology. Named after Markus Walter.

Holotype. IRSNB a12875, complete specimen (Fig. 1).

Type locality and horizon. "2cc" horizon of the Bou Dib Formation, Mrakib, Morocco.

Diagnosis. Cephalon is twice as wide (tr.) as long (sag.). Preglabellar and librigenal fields bear an alternation of densely spaced granules and tubercles. G2 rudimentary or absent in large holaspides. Wide (tr.) fixigena. Adaxial two-third of thoracic pleural lobe remains subhorizontal. 5+1 pygidial axial rings.

Description. Widely rounded cephalon with marked abaxial deflection of lateral borders. Anterior glabellar lobe of ovoid to somewhat pear-shaped outline with straightened lateral, posterolateral and posterior edges, widest just in front of the eyes; weakly upward curved in lateral view between occipital ring and G3, overhanging anteriorly (>90°); dorsoventrally highest point just posterior to eyes, equating occipital ring; bearing ubiquitous, coarse, moderately small, uniformly sized tubercles except smooth, swollen area neighbouring G3; G3 developed as slightly progressively divergent but otherwise straightened, weakly tapering, robust spines, pointed anterodorsally, covered

with evenly spaced granules. L1 of elongated (exsag.) ovoid outline; covered with small tubercles; dorsoventrally highest point is halfway its length (exsag.); distinctly less inflated anteriorly. S1 deep and relatively broad opposite anterior half of L1; rudimentary opposite posterior half of L1. Axial furrows slightly overhung by glabella between S1 and G3, and concealed (dorsal view) further anteriorly from here; broadest opposite eyes from where they converge slightly toward S1, before gently curving posteriorly around L1. Preglabellar field short (sag., exsag.), overhanging anterior border as if forward deflected by anterior glabellar lobe. Anterior border furrow concave in section; moderately shallow; slightly deeper medially (tr.). Anterior border cylindrical in section (sag.); bearing moderately widely spaced granules everywhere, and six evenly spaced tubercles. Fixigena anterior to eye very steep, almost vertical; of unchanged width (tr.) and bearing moderately large tubercles sometimes alternated by granules until halfway (exsag.) between eye and anterior border furrow; quickly broadening (tr.) adaxially anterior from here and covered with small tubercles alternated by granules. Fixigena lateral and posterior to eye downward sloped adaxially; about twice as broad (tr.) posterior to eye than opposite eye; covered with small tubercles alternated by granules. Preocular sutures fairly straight; weakly convergent anteriorly. Palpebral lobe moderately small; subsemicircular to somewhat elongated (exsag.) crescent-shaped. Postocular sutures slightly divergent opposite L1; curving outward over elevated surface toward posterior border before flexing backward towards ω . Occipital ring slightly narrowing (exsag.) abaxially; covered with small tubercles alternated by granules; bearing a large median tubercle. Posterior border furrow broad (exsag.), fairly deep; distinctly groove-like near posterior border. Posterior border narrow (exsag.), transverse, smooth adaxially; broadening (exsag.) and curving posterolaterally abaxially; bearing several granules on abaxial extremity.

Librigenal field steep yet weakly vaulted (tr.); slightly lower than long (exsag.) in lateral view; very steep anteriorly and mostly concealed by eye here; slightly less sloped laterally; bearing an alternation of moderately small tubercles alternated by granules; tubercles become less common or distinctly smaller towards border furrow. Narrow (exsag.), abaxially deep, elongated (tr.) genal trunk. Eye ovoid; not particularly large; slightly abaxially and forward tilted. Lateral border furrow widely concave in section; moderately shallow; slightly broader (tr.) opposite L1; faint opposite occipital ring, adjacent to genal trunk. Border subcylindrical in section; bearing moderately widely spaced granules, and at least four, evenly spaced marginal tubercles; depicting a quarter of a circle in lateral view before curving

	<i>C. walteri</i>	<i>C. heissae</i>	<i>C. rommersheimensis</i>	<i>C. cf. heissae</i>
Cephalic width/length	≈ 2	< 1.5	≈ 1.5	?
Sculpture on glabella anterior to S0	Small, closely spaced	Moderately small, closely to somewhat more widely spaced	Alternation of closely spaced tubercles and granules	Moderately small, widely spaced
Sculpture on preglabellar and librigenal fields	Covered with an alternation of granules and tubercles	Few tubercles, concentrated around the eye	Covered with an alternation of tubercles and pits	Single row of tubercles around front of glabella (the librigena is unknown)
G2	Weak tubercles or absent	Tubercles	Tubercles	Tubercles
G3	Spines	Spines	Spines	Spines with robust bases
Shape of anterior glabellar lobe	Pear-shaped	Ovoid	Pear-shaped	Pear-shaped
Median occipital spine or tubercle	Tubercle	Spine	No spine or tubercle	Spine
Pygidial axial rings	5+1	4+1	?	?

Table 1. Comparisons of "devil horned" *Cyphaspis* species: *C. walteri* sp. nov. from Morocco, *C. heissae* sp. nov. from Germany, *C. rommersheimensis* sp. nov. from Germany and *C. cf. heissae* sp. nov. from Belgium.

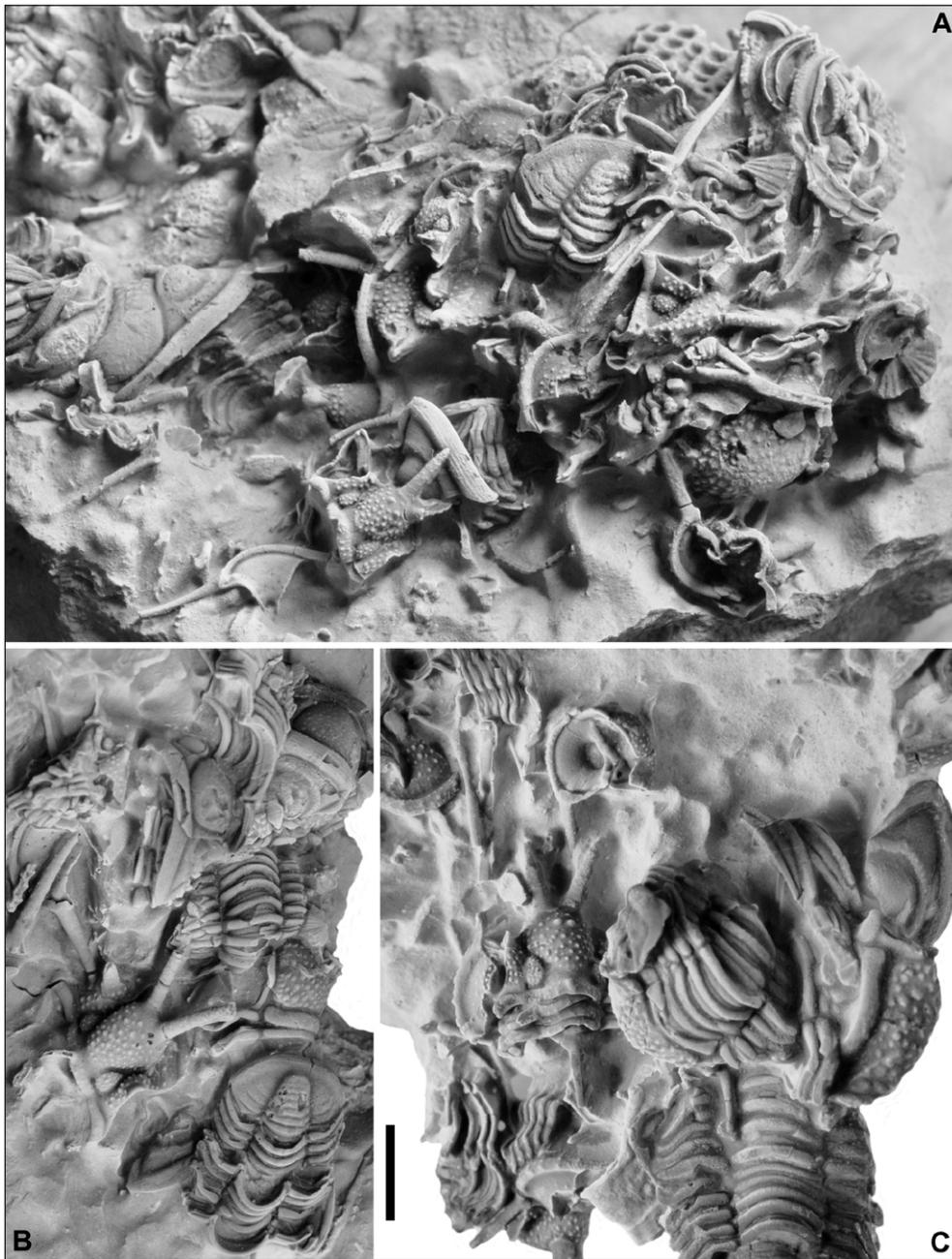


Figure 2. *Cyphaspsis heissae* sp. nov. from the Ahabach Formation in Ahütte, Germany. PWL-2014 02, rock slab containing multiple individuals along with specimens of *Gerastos* sp. (A). PWL-2014 03, rock slab with multiple specimens (B). PWL-2014 01b, complete? specimen (C). Scale bar indicates 5 mm.

backward toward genal spine. Sutural ridge moderately well developed. Genal spine moderately long; weakly posterolaterally directed; straight, weakly tapering, and bearing granules throughout most of its length; inward flexed, narrow tip without granulation.

Thorax consists of eleven segments. Wide (tr.) thoracic axial lobe (compared to *C. ceratophthalmus*); axial rings elongated (tr.) W-shaped (dorsal view); bearing fairly widely spaced, tiny tubercles that verge to forming a single row posteriorly on each segment; sixth segment is well developed centrally and bears a robust dorsal spine here. This spine tapers slightly, ascends backward slowly, curves slightly ventrally distally, and bears numerous granules. Anteriormost axial ring is broadest (tr.); subsequent four rings are of unchanged width (tr.); each subsequent ring is narrower than the previous one (tr.). Pleurae bearing few granules; with distinct pleural furrows; inner two-third weakly sloped abaxially. Anterior pleural ribs narrower (exsag.) than posterior pleural ribs and distally partially concealed by the latter.

Pygidial axial rings are about half as long (sag.) as posteriormost thoracic ring; each bearing a transverse row of small tubercles in the middle (sag., exsag.) with randomly scattered granules anterior to these on the first two or three rings. Inter-ring furrows run transversely; are deepest abaxially; anteriormost furrow is

longest (sag., exsag.), each successive one shorter. Four pleurae devoid of prosopon; posterior bands of anterior two pleurae are slightly widened (exsag.) abaxially and much more inflated than anterior bands; in the posterior two pleurae the anterior pleural band is not developed. Only anteriormost pleural furrow is long (exsag.) halfway along its length (tr.); second pleural furrow and all interpleural furrows are rudimentary. Border is broadest (sag., exsag.) medially (tr.) and bears fine granules.

Discussion. Numerous *Cyphaspsis* specimens with paired glabellar spines from the Moroccan Devonian have been offered for sale on fossil markets and the Internet where they are commonly termed “devil horned” or “devil’s horn” *Cyphaspsis*. We have seen several distinct species coming from Morocco, possibly the commonest of which is described in the present note. The glabellar, genal and thoracic spines are frequently modified or entirely fabricated during preparation. The angle of the dorsal spine on the sixth thoracic segment appears to be incorrect in most of the specimens that we have seen, by displaying a distinct curvature or dorsal direction. Normally, this spine is almost entirely straight and only slightly ascends backward, as shown in the figures of the holotype.

The rounded tubercles that are scattered all over the dorsal exoskeleton of the holotype have undergone slight abrasion.

As a preliminary note it should be mentioned that in rare, exquisitely preserved parts of the cephalon of some *C. walteri* sp. nov. specimens, many tubercles bear a single, exceedingly thin, centrally positioned spine. These structures are somewhat comparable to Størmer's (1980) spiny pit-tubercles and perhaps in a way analogous to tube-like cuticular pedestals described in the contemporary ant species *Echinopla melanarctos* (see Gnatzy & Maschwitz, 2006). In *C. walteri* sp. nov., however, the spines are placed on top of the tubercles; i.e., their bases are far thinner than the founding tubercles rather than being a smoothly tapered, spiny extension of the whole tubercle as figured by Størmer (1980, fig. 1f). The remaining thin, broken spine bases on the tubercle surface are easily abraded or overlooked so that only the underlying canal is recognised. Consequently, the cephalic prosopon of *C. walteri* sp. nov. could be misconceived as consisting of ordinary pitted tubercles (cf. Størmer, fig. 1d). We have seen similar cases in additional *Cyphaspis* species from Morocco and believe that they can also be found in congeners from other countries provided that preservation has been favourable. None of the specimens that we have examined are silicified and they cannot be prepared with conventional tools. The spines will be elaborated on further by us in a future paper.

Cyphaspis walteri sp. nov. and the other new species are contrasted in Table 1.

***Cyphaspis heissae* sp. nov.** (Figs 2, 3)

v 2010 *Cyphaspis* sp. Z; Basse, 100-103, pl. 4, figs 33, 34.

Etymology. Named after Marion Heiss, spouse of Philipp Krüger who made the type material available for study.

Holotype. PWL-2014 01a, complete specimen (Fig. 3).

Paratypes. PWL-2014 01b, complete? specimen (Fig. 2C) on other side of the rock slab that bears the holotype; PWL-2014 02, rock slab with several cranidia and other sclerites (Fig. 2A); PWL-2014 03, rock slab with a cranidium and several sclerites (Fig. 2B); PWL-2014 04, complete, tectonically distorted specimen (unfigured). All from the type locality and horizon.

The current whereabouts of specimens in the private collection of the late Robert Leunissen described and illustrated by Basse

(2010), are unknown to that author (pers. comm.) and to us. As such they are not included as paratypes.

Type locality and horizon. Olifant Member of the Müllert Subformation, Ahbach Formation, Ahütte, Germany.

Diagnosis. Anterior glabellar lobe of ovoid outline. Occipital ring longest (sag.) medially (tr.) and bearing a long median spine. Axial furrow weakly impressed opposite L1. Sutural ridge weakly inflated. Librigenal field bearing few large tubercles concentrated around the eye. Small pygidium of subtrapezoidal outline. Pygidial border upturned posteromedially. 4+1 pygidial axial rings. Posterior pleural bands of pygidium bear bladder-like swellings abaxially.

Description. See Basse (2010). Furthermore: Median glabellar lobe weakly upward curved in lateral view between S0 and G3, overhanging anteriorly ($>90^\circ$); dorsoventrally highest point lateral to eyes; bearing ubiquitous, coarse, moderately small, uniformly sized tubercles more widely spaced in some specimens than others, except smooth, swollen area neighbouring G3; G3 developed as slightly divergent, anterodorsally pointed, very weakly tapering spines. L1 covered with moderately small tubercles; dorsoventrally highest point is posteriorly. S1 deep and relatively broad opposite anterior half of L1; shallow to rudimentary opposite posterior half of L1. Axial furrows visible almost throughout in dorsal view; broadest opposite eyes from where they converge slightly toward S1, before gently curving posteriorly around L1. Preglabellar field short (sag., exsag.); bearing a few small tubercles. Anterior border furrow concave in section; moderately deep, and deepest medially (tr.). Anterior border inflated; bearing six tubercles or short thorns. Fixigena bearing moderately large tubercles throughout; comparatively weakly sloped anterior to eye (when compared to the other new species). Postocular sutures divergent toward posterior border before flexing backward towards ω . Occipital ring with small tubercles positioned somewhat abaxially and a posteriorly curved median spine. Posterior border furrow broad (exsag.). Posterior border narrow (exsag.), transverse, smooth; broadening (exsag.) and curving posterolaterally abaxially.

Librigenal field not very steep (compared to the other new species); not concealed by the eye in dorsal view. Small, pit-like

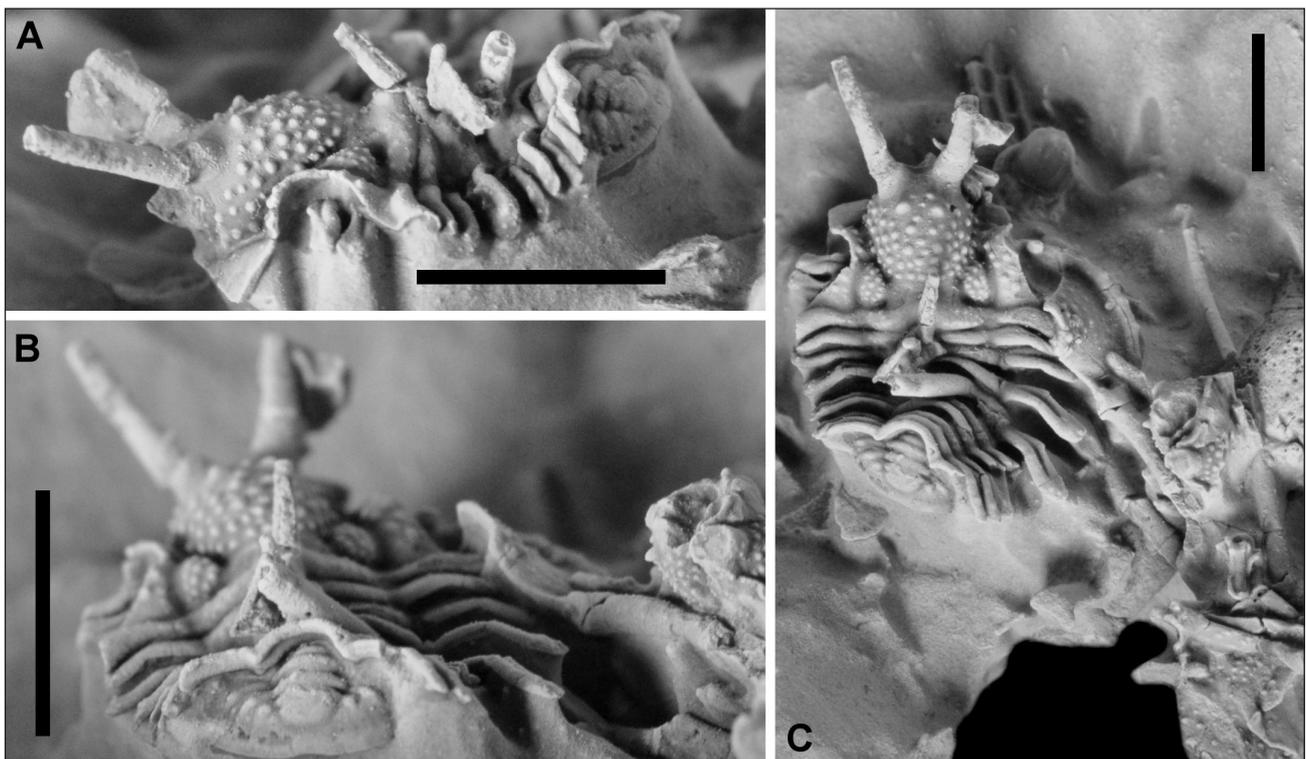
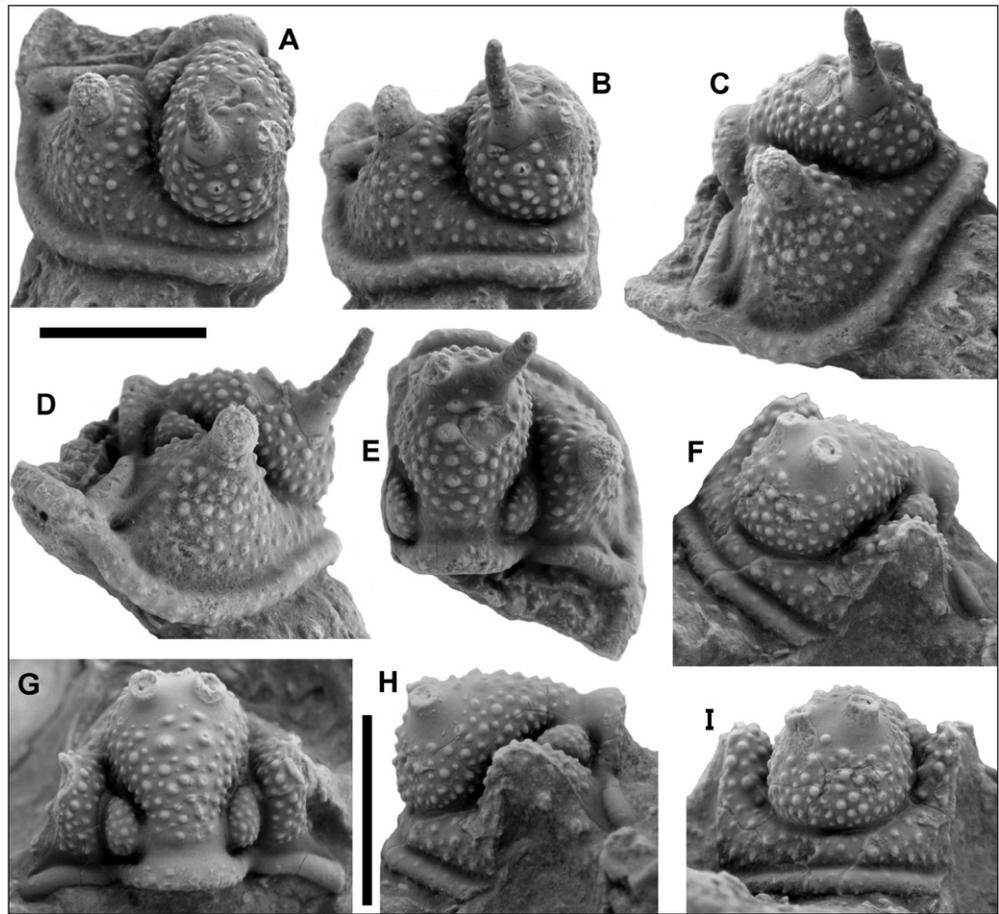


Figure 3. *Cyphaspis heissae* sp. nov. from the Ahbach Formation in Ahütte, Germany. Holotype disarticulated specimen PWL-2014 01a, in lateral (A), dorsal (B) and posterior (C) views. Scale bars indicate 5 mm.

Figure 4. *Cyphaspis rommersheimensis* sp. nov. from the Freilingen Formation in Rommersheim, Germany. Holotype, incomplete cephalon PWL-2014 05, in anterodorsal (A), anterior (B), oblique anterior (C), lateral (D) and dorsal (E) views. Paratype, cranidium PWL-2014 06, in oblique anterior (F), dorsal (G), lateral (H) and anterior (I) views. Scale bars indicate 5 mm.



genal trunk. Lateral border furrow widely concave in section; shallower than anterior border; slightly broader (tr.) opposite eyes. Border subcylindrical in section; bearing few granules, and several evenly spaced tubercles; depicting a quarter of a circle in lateral view before curving backward toward genal spine; slightly abaxially rounded in dorsal view and running adaxially towards genal corner. Genal spine moderately long; weakly posterolaterally directed; straight, weakly tapering.

Thorax consists of eleven segments. Axial rings elongated (tr.) W-shaped (dorsal view); bearing fairly widely spaced tubercles; sixth segment is well developed centrally and bears a robust dorsal spine here. Distinct pleural furrows; inner half weakly sloped abaxially.

Pygidial axial rings are about half as long (sag.) as posteriormost thoracic ring; seemingly devoid of prosopon (possibly not preserved). Inter-ring furrows run transversely; are deepest abaxially; anterior two furrows are much better developed than third one. Three pleurae devoid of prosopon; posterior band of anterior pleura is much better developed than anterior band; in the posterior two pleurae the anterior pleural band is not developed. Border is uniformly broad (sag., exsag.) throughout.

***Cyphaspis rommersheimensis* sp. nov.** (Fig. 4)

Etymology. After the type locality.

Holotype. PWL-2014 05, incomplete cephalon (Fig. 4A-E).

Paratype. PWL-2014 06, cranidium (Fig. 4F-I) from the type locality and horizon.

Type locality and horizon. Eilenberg Member of the Freilingen Formation, Rommersheim, Germany.

Diagnosis. Occipital ring narrower (tr.) than widest point of anterior glabellar lobe; without spine or distinct median tubercle. Fixigena is very strongly vaulted (tr.) lateral to eye. Librigenal field bears an alternation of moderately large tubercles and pits.

Description. Anterior glabellar lobe of pear-shaped outline, widest in front of the eyes; weakly upward curved in lateral view between S0 and G3, overhanging anteriorly; dorsoventrally highest point lateral to eyes, equating occipital ring; bearing an alternation of granules and tubercles; posterior to G3 there is usually a large tubercle pair which is presumed to represent G2; G3 developed as slightly inward curved, weakly tapering, robust spines, pointed more dorsally than anteriorly, covered with evenly spaced granules. L1 of elongated (exsag.) ovoid outline; covered with small tubercles; dorsoventrally highest point is just posterior to halfway its length (exsag.); markedly less inflated anteriorly. S1 deep and relatively broad opposite anterior half of L1; rudimentary opposite posterior half of L1. Axial furrows deep anterior to S0; broadest opposite eyes from where they converge slightly towards S1 before gently curving posteriorly around L1; slightly overhung by glabella between S1 and G2, and concealed (dorsal view) anteriorly from here. Preglabellar field short (sag., exsag.), overhanging anterior border as if forward deflected by glabella; bearing few tubercles alternated by granules. Anterior border furrow concave in section; moderately shallow. Anterior border subcylindrical; slightly dorsally flattened in section (sag.); bearing randomly scattered, large granules. Fixigena is very steep and of unchanged width (tr.) anterior to eye; bears large, widely spaced tubercles. Preocular sutures weakly convergent anteriorly throughout. Postocular sutures run exsagittally opposite L1 before flexing backward towards ω . Occipital ring slightly narrowing (exsag.) abaxially; bearing a few randomly positioned tubercles. Posterior border furrow broad (exsag.), fairly deep. Posterior border smooth; moderately narrow (exsag.), transverse; broadening slightly (exsag.) and curving posterolaterally abaxially.

Librigenal field weakly vaulted (tr.); mostly concealed in dorsal view; slightly lower than long (exsag.) in lateral view; very steep anteriorly and laterally. Narrow (exsag.), abaxially deep, elongated (tr.) genal trunk. Eye ovoid; slightly abaxially and forward tilted. Lateral border furrow widely concave in section; shallow; faint opposite occipital ring, adjacent to genal trunk. Border subcylindrical in section; bearing paired, moderately

large epiborder and marginal tubercles; depicting a quarter of a circle in lateral view before curving backward toward genal spine; hardly rounded in dorsal view and running subexsagittally towards genal corner. Sutural ridge moderately well developed. Genal spine is not known completely but initially straight and backward directed.

Cyphaspis cf. heissae sp. nov. (Fig. 5)

Material. IRSNB a12876, one cranium from the Hanonet Formation at Resteigne, Belgium.

Description. Anterior glabellar lobe of pear-shaped outline, widest anteriorly; weakly upward curved in lateral view between S0 and G3, overhanging anteriorly ($>90^\circ$); bearing small to medium sized tubercles, except in smooth, swollen area neighbouring G3; G3 developed as proximally robust (when compared to above described species) spines. L1 covered with moderately small tubercles; dorsoventrally highest point is anteriorly. Only anterior part of S1 is developed. Axial furrows visible almost throughout in dorsal view. Preglabellar field short (sag., exsag.); bearing a row of tubercles around the glabella. Anterior border furrow concave in section; moderately deep, and deepest medially (tr.). Anterior border inflated; bearing six, evenly spaced tubercles and a few randomly scattered granules. Occipital ring slightly tapers abaxially; bearing small tubercles positioned somewhat abaxially and a median spine. Posterior border slightly widened (exsag.) abaxially; without prosopon.

Discussion. According to Lerosey-Aubril et al. (2008, p. 69), among typical characters of *Otarionella* are the median occipital spine, single tubercle row surrounding the front of the glabella, and six evenly spaced cranial border spines. *Cyphaspis cf. heissae* sp. nov. shows the same features although it has border tubercles instead of spines. We nonetheless prefer to assign the Belgian taxon to *Cyphaspis* for having G2 and G3 crowded anteriorly on the glabella and for sharing with *Cyphaspis heissae*

sp. nov. the abaxially positioned tubercles and a median spine on the occipital ring as well as similar prosopon on the anterior glabellar lobe.

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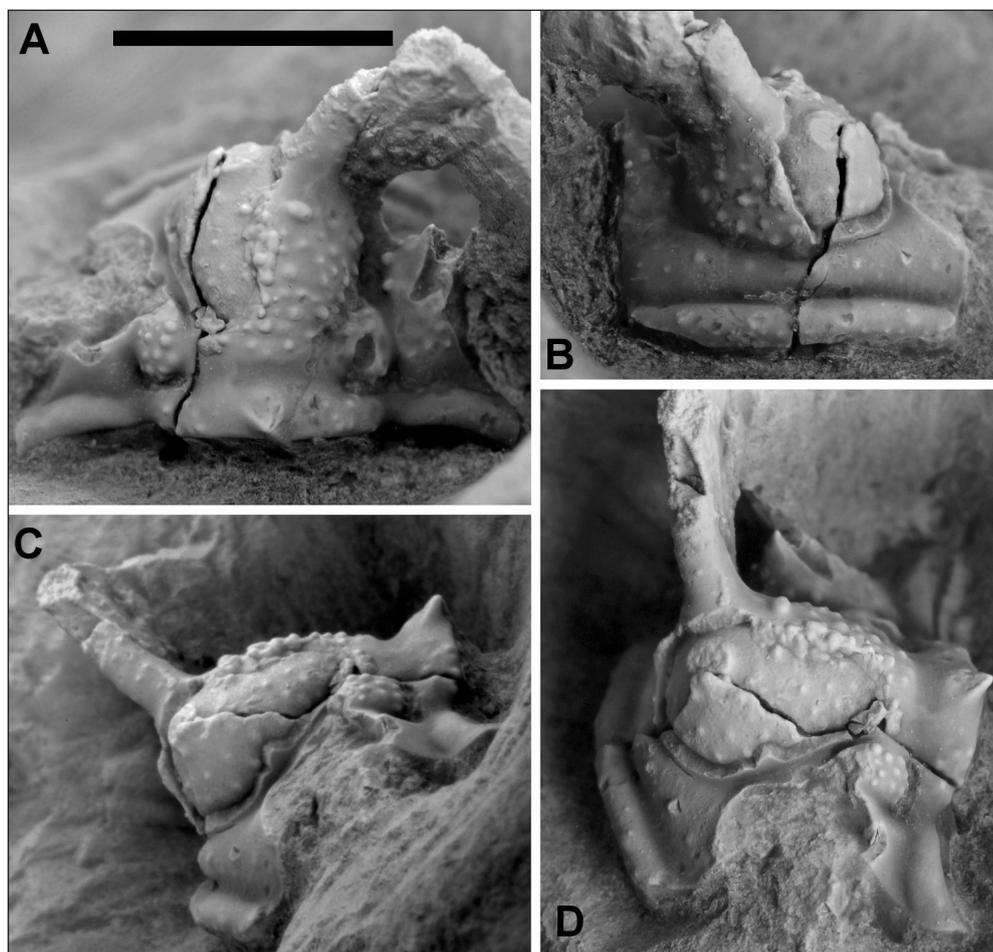


Figure 5. *Cyphaspis cf. heissae* sp. nov. from the Hanonet Formation in Resteigne, Belgium. Cranidium IRSNB a12876, in dorsal (A), anterior (B), lateral (C) and oblique lateral (D) views. Scale bar indicates 5 mm.

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