

Kettneraspis, *Radiaspis* and *Ceratarges* (Trilobita) from the Middle Devonian of the Rochefort area (Ardennes, Belgium)

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The Middle Eifelian trilobite fauna of the Belgian Ardennes shows close affinities with that of the German Eifel. Two trilobite taxa are recorded from Middle Eifelian strata near the town of Jemelle, on the southern border of the Dinant Synclinorium, Belgium. *Kettneraspis bayarti* sp. nov. is closely related to *Kettneraspis elliptica* (Burmeister) from the Middle Eifelian of the Rhenish Slate Mountains. *Ceratarges* cf. *armatus* (Goldfuss) is also described on the basis of a single pygidium. The odontopleurid *Charybdaspis* Basse is considered a junior subjective synonym of *Radiaspis* Richter & Richter. The lichid *Rhenarges* Basse is briefly discussed and regarded as a junior subjective synonym of *Akantharges* Phleger.

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Introduction

Middle Eifelian outcrops along the southern border of the Dinant Synclinorium are generally rich in trilobites, both individuals and species. Recent fieldwork by the author and examination of trilobites in the old Maillieux collections (Institut royal des Sciences naturelles de Belgique, Brussels) indicate close affinities between Middle Eifelian trilobite faunas of the Belgian Ardennes and those of the German Eifel. Among the genera identified in common so far are *Asteropyge*, *Astycoryphe*, *Cornuproetus*, *Cyphaspis*, *Dohmiella*, *Eifliarges*, *Geesops*, *Gerastos*, *Harpes*, *Phacops sensu stricto* and *Radiaspis*, all of which have type species that were originally described from Middle Eifelian strata in the Eifel. Many trilobite taxa from the Ardennes and Eifel are clearly related beyond a generic level and some are even considered to be conspecific (e.g., Richter & Richter, 1919, 1956; Struve, 1992, pp. 534, 535; Magrean & van Viersen, 2005). The Belgian material is commonly inadequately preserved as distorted internal moulds. Associated external moulds, if available, do not always yield many details about the original dorsal morphology of the specimens as the majority are of poor quality.

Between 2002 and 2004, the author collected trilobite material from Middle Eifelian outcrops near the town of Jemelle. Several comparatively well-preserved specimens are described and assigned here to *Kettneraspis bayarti* sp. nov. and *Ceratarges* cf. *armatus*.

The material that belongs to the new species comprises mostly internal and external moulds of disarticulated body parts, whereas the discovery of an articulated cephalothorax has permitted the unambiguous association of the loose cranidia and librigenae that were found. The cephalothorax is preserved as an internal mould in a soft, fine-grained limestone. The associated external mould shows additional details of the thorax and posterolateral parts of the cranidium although it is too fragile to prepare a silicone cast of without severely damaging it; the same applies to the external moulds of pygidia that were collected. Because the cephalic parts are obviously all conspecific, it is conservative to assume that the pygidia of *Kettneraspis* that were collected also belong to the new species, as they are all identical.

Location and stratigraphy

Embankment west of the Jemelle railway station, southern border of the Dinant Synclinorium, Belgium (see Fig. 1). At this locality, the Jemelle Formation (*Polygnathus partitus* – *Polygnathus ensensis* conodont Zone according to Bultynck *et al.*, 2000; Bultynck & Dejonghe, 2002) is comprised in ascending order the Station (40 m), Cimetière (110-115 m) and Chavées (190 m) members. The Chavées Member consists of shale beds, and argillaceous and crinoidal limestones. It yields a rich macrofauna, comprising solitary and tabulate corals, crinoid ossicles, brachiopods, bivalves and trilobites (Godefroid, 1991). This unit is comparable in age to the upper part of the Ahrdorf Formation of the German Eifel (Magrean & van Viersen, 2005, p. 88, table 1) and is the origin of the trilobite material described herein.

Systematic palaeontology

All specimens described below are housed in the Nationaal Natuurhistorisch Museum, Leiden (RGM). One further specimen is housed in the Institut royal des Sciences



Fig. 1. Embankment west of the Jemelle railway station, Belgium, indicated by a circle. Inset shows position of main map (✱) within Belgium.

naturelles de Belgique, Brussels (abbreviated IRSNB). Terminology used follows Thomas & Holloway (1988), Whittington & Kelly (1997) and Ebach & Ah Yong (2001, fig. 3). The abbreviation 'PPB' is employed to refer to the thoracic posterior pleural band. The terms 'sag.' (sagittal) and 'tr.' (transverse) are used in reference to directions along the axial line of the body and at right angle to this line, respectively. The term 'exsag.' (ex-sagittal) is used to refer to directions parallel to the axial line of the body.

Family Odontopleuridae Burmeister, 1843
Subfamily Odontopleurinae Burmeister, 1843
Genus *Kettneraspis* Prantl & Přibyl, 1949

Type species – *Acidaspis pigra* Barrande, 1872, from the Acanthopyge Limestone (Eifelian) of Koněprusy, Czech Republic, by original designation.

Remarks – Ramsköld & Chatterton (1991) revised the polyphyletic genus *Leonaspis* and assigned most of its species to *Kettneraspis*. Three groups were recognised of the latter genus. The largest of these consisted of a crown group ("*Kettneraspis* 8 spp.") and a stem group (*Kettneraspis tuberculata tuberculata* (Hall) and *Kettneraspis williamsi* type A of Campbell, 1977), and added that a number of species including *Kettneraspis elliptica* (Burmeister) and *Kettneraspis reetae* Ramsköld & Chatterton. Together, these taxa were tentatively assumed to form a monophyletic clade; character state 17:2 (two or more dorsal spines on the genal spine) was considered a possible synapomorphy. Adrain & Ramsköld (1997) reassigned five species of Ramsköld & Chatterton's 8 spp. group to their new genus *Edgecombeaspis* and discussed potential apomorphies of *Kettneraspis sensu stricto* that still require testing in broad analysis (p. 239). The remaining three species were recognised as the *Kettneraspis* cf. *williamsi* group to which *K. reetae* was added. Currently, much of the ingroup structure of *Kettneraspis* remains unclear and positioning of the stratigraphically late species *K. elliptica* and *K. bayarti* sp. nov. within the genus is difficult apart from their obvious close relationship. The position of *Kettneraspis aries* (Richter & Richter) from the Ahrdorf Formation of the Eifel is particularly ambiguous since it is only known from scanty material. Besides features common to all three species, *K. aries* shares with *K. elliptica* alone a median glabellar lobe that scarcely widens anteriorly and that bears comparatively widely distributed tubercles, and two larger tubercles on the posterolateral cranial border. However, the lack of material impedes a detailed comparison of *K. aries* with the other two at this time.

Kettneraspis was previously assumed to have become extinct at the end of the Eifelian (e.g., Ramsköld & Chatterton, 1991). Recent records by Basse (2004) from the Rhenish Slate Mountains show that it persisted until the middle part of the Givetian, although by then it had become rare. Like that of many other odontopleurids (Chlupáč, 1994), the demise of *Kettneraspis* is probably related to the mid-Givetian Taghanic event.

Previous records of *Kettneraspis* from Belgium were made by Maillieux (1919, 1933, 1938) and Asselberghs (1946), who both believed exclusively to have found the characteristically Middle Eifelian species *K. elliptica*. The material on which these records were based was actually collected from both Emsian and Eifelian strata, and thus should be reexamined. Unfortunately, the whereabouts and type numbers of the material were not specified by either one of these authors.

***Kettneraspis bayarti* sp. nov.**

Pl. 1, figs. 1-4, 6; Figs. 2, 3.

? 1919 *Acidaspis* cf. *elliptica* (Burmeister); Maillieux, p. 54.

? e.p. 1933 *Acidaspis elliptica*; Maillieux, p. 70 [*non* p. 62].

? 1938 *Acidaspis elliptica* (Burmeister); Maillieux, p. 27.

non 1946 *Acidaspis elliptica* Burmeister; Asselberghs, p. 338.

Holotype – RGM 211 460, internal mould of articulated cephalothorax with associated external mould.

Paratypes – RGM 211 461, 211 462, two internal moulds of cranidia with associated external moulds plus silicone casts; RGM 211 464, internal mould of a librigena with associated external mould plus silicone cast; RGM 211 463, internal mould of a single pygidium.

Other material – RGM 211 468, internal mould of a cranidium; RGM 211 466, internal mould of a pygidium; RGM 211 465, 211 467, external moulds of two pygidia; all from type locality and horizon.

Type locality – Embankment west of the Jemelle railway station, Belgium (see above).

Type horizon – Jemelle Formation (Chavées Member), Middle Eifelian.

Etymology – Bayart, an ancient mythical animal of the Ardennes.

Diagnosis – Anterior border furrow absent medially in front of main body of median glabellar lobe. Posterolateral cranidial border bearing three large and several randomly scattered smaller tubercles. Long median occipital spine with broad (sag. and tr.) base. Pygidium with medial border spine pair proximally wider (tr.) than third border spine pair (counting abaxially).

Description – Cephalon: Anterior margin slightly protruding medially. Anterior border bearing eleven, elongated (tr.) border tubercles. Anterior border furrow only developed as a shallow, wide (exsag.) depression in front of abaxially protruding anterolateral parts of median glabellar lobe; anteromedial margin of median glabellar lobe smoothly continuing into equally elevated anterior border and not separated from the latter by a furrow. Anterior branch of facial suture mostly exsagittal; slightly convergent anteriorly towards α . Eye ridge weakly arched abaxially; in anterior view separated from median glabellar lobe by distinct furrow; bears several tubercles, the majority on posterior half. Median glabellar lobe rectangular posteriorly, with widely rounded anterior margin; widening proportionally anteriorly, in dorsal view from about half-way (exsag.) along L2; in lateral view its outline transcribes more or less a quarter circle; surface covered with numerous, randomly scattered tubercles of varying size. L2 ovoid (exsag.), slightly more inflated than L1; tubercles more densely arranged than those on median glabellar lobe. L1 tongue-shaped, verging to subtriangular; narrowing (tr.) posteriorly; ornament mostly similar to that of L2; posteromedial margin always bearing

a single tubercle. Longitudinal furrow distinctly incising anterior widened part of median glabellar lobe; deep and pit-like at junction with S1. Axial furrow smoothly rounded in section; deepening and narrowing (tr.) only from frontal part of L2 towards anterior pit. Posterior area with dense tuberculation. Posterolateral border bearing several, randomly arranged, small tubercles and three additional, much larger, central (exsag.) tubercles: one positioned posterior (exsag.) to abaxial margin of eye, a second one on the lateral extremity near the genal spine, a third one in between. Occipital furrow shallow, but distinct anteriorly behind median glabellar lobe; posteriorly poorly demarcated, in lateral view continuing uninterruptedly into occipital ring and median spine. Occipital ring anteriorly bearing a widely rounded half circle of about seven tubercles; posterior margin bearing two tubercle pairs. Base of long occipital spine broad (sag. and tr.); occupying entire length (sag.) of occipital ring; proximally moderately dorsally oriented; distally pointed posteriorly about 20° from horizontal in lateral view and slightly decreasing in size. Hypostome covered with closely spaced, fine granules; without posterolateral spines (see Fig. 2).

Librigenal field with closely spaced tubercles high on eye-stalk, otherwise tubercles scarce. Eye higher than wide; subhemispherical. Thirteen border spines that widen distally. At least three epiborder tubercles, positioned directly above border spines 4, 6 and 9 (counting from posterior). Genal spine bearing two dorsal spines.



Fig. 2. External mould of hypostome of *Kettneraspis bayarti* sp. nov. (RGM 211 460) from the Jemelle Formation (Middle Eifelian) of Jemelle. Scale bar represents 1 mm.

Thorax: Axis cylindrically vaulted; slightly wider (tr.) than pleural region (excluding spines); posterolateral parts of axial rings showing remains of tubercles. PPB (posterior pleural band) 1 to 3 with a central (exsag.) tubercle near the fulcrum; no evidence of a tubercle near the rachis on PPB 1 and 2, probably also on PPB 3; PPB 4 to 8 bearing two central (exsag.) tubercles, one near the rachis, the other near the fulcrum. PPB 1 and 2, and especially their pleural spines, weakly developed compared to remaining PPB and spines; third PPB and spine better developed than 4 to 8. Long, posterolaterally bent pleural spines associated with PPB 3 to 8.

Pygidium: Broadly rounded; more than twice as wide (tr.) as long (sag.). Two tubercles present on anterolateral part of the pygidium (see Fig. 3). First axial ring deeply (sag.) incised posteriorly by distinct pseudo-articulating half ring. Second axial ring bearing a single tubercle pair. Postaxial field elevated medially to form a longitudinal band that bears a single tubercle pair. Pleural ridge transversally oriented proximally, then sharply flexed posteriorly; bearing a single tubercle just posterior of flexure; distally runs more or less exsagittally. Two medial spines between slightly diverging major

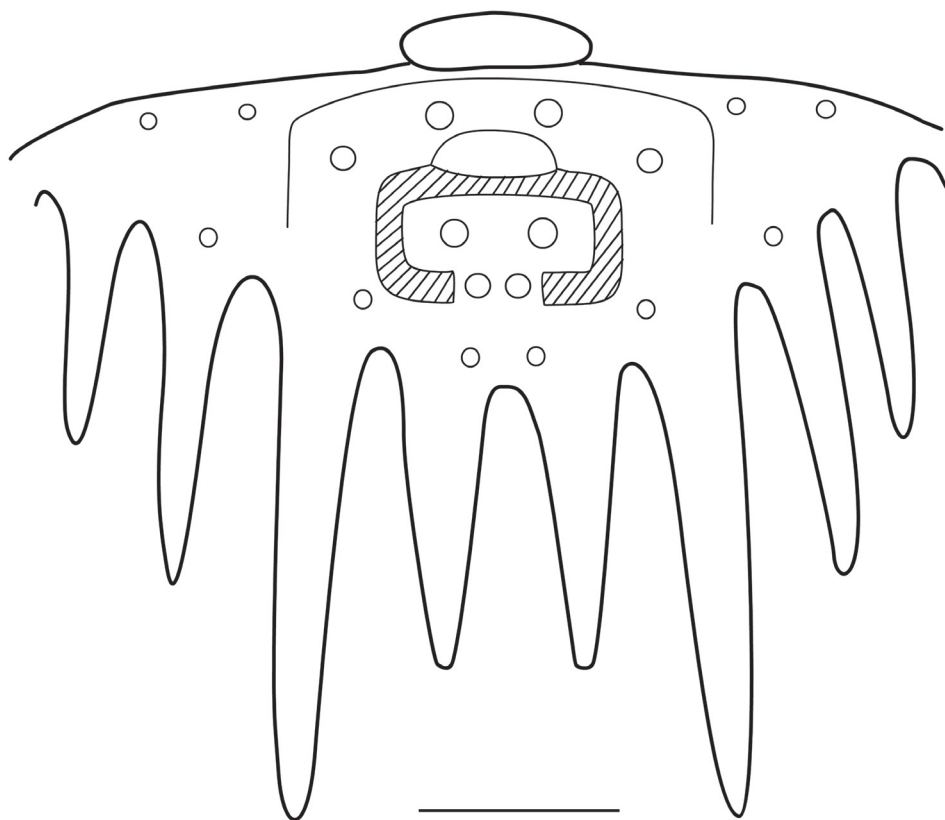


Fig. 3. Schematic drawing of the pygidium of *Kettneraspis bayarti* sp. nov. from the Jemelle Formation (Middle Eifelian) of Jemelle. Length and distal morphology of spines approximate. Scale bar represents 2 mm.

border spines. Three pairs of lateral spines. Single tubercle present centrally on base of the lateral spine abaxial to major border spine, adaxially on base of major border spine, near adaxial margin of base of medial spine.

Discussion – The right side of the eighth pleural rib pair is posteriorly enclosed by matrix which either means that a ninth pleural rib became disarticulated with the pygidium prior to final burial or that it was never there in the first place. Although *Kettneraspis sensu stricto* usually has a thorax consisting of nine segments, *K. williamsi* (Whittington) from the Haragan and Bois d'Arc formations of Oklahoma has eight segments in three out of four of its types (see, e.g., Ramsköld & Chatterton, 1991, pp. 340, 341). If the Belgian species actually has a thorax with only eight segments then this condition was developed in *Kettneraspis* at least twice and possibly independently, because of the stratigraphic separation of both species and the lack of any known morphologically intermediate form.

Occipital spines are known in *Kettneraspis* from a number of species, including *K. tuberculata tuberculata* (Hall), *K. tuberculata favonia* (Haas), *Leonaspis (Leonaspis) ruderalis* of Přibyl & Vaněk (1966) (regarded as *Kettneraspis* sp. herein), *K.? aculea* (H. Alberti) and, more rarely, *K. elliptica* (see Richter, 1909, p. 50; Ramsköld & Chatterton, 1991, p. 358), although commonly they are inadequately preserved. Only in *Edgecombeaspis* are elongate occipital spines typical of most species. In *K. bayarti* the full length of the occipital spine and the morphology of its distal part remain unknown as it is broken off in all specimens. As preserved, its length (excluding its base, measured from the posterior margin of the occipital ring) is about half that of the median glabellar lobe. It resembles the occipital spine in one of the cranidia of *Leonaspis (Kettneraspis) elliptica* of Ormiston (1967, pl. 5, fig. 7) from the Early to lower Middle Devonian (see, e.g., Rong-Yu & Jones, 2002, p. 650, fig. 2) Blue Fiord Formation of the Canadian Arctic Islands (regarded as *Kettneraspis* sp. herein). Closest to the occipital spine of the new species is that of *K. tuberculata favonia* from the Early Devonian Wenban and Rabbit Hill limestones of central Nevada. In both taxa, the occipital furrow is indistinct, the median spine is very similarly shaped and its base occupies the entire sagittal length of the occipital ring. In the subspecies of Haas (1969, p. 652, text-fig. 4) distally it does not curve towards the horizontal; rather, it retains its initial dorsal direction. Also, it is shorter than the occipital spine of the Belgian species.

Richter (1909, p. 53) reported two or three pairs of pygidial lateral border spines in topotypical specimens of *K. elliptica* and, additionally, a small fourth spine pair near the anterolateral corner in one specimen. Probably, this fourth spine pair is, in fact, part of the bifid anteriormost spine pair that was observed in the same species by Bruton (1968, p. 30). In none of the specimens of *K. bayarti* is the anteriormost spine pair completely preserved. All show a total of three pairs of lateral spines, but it is unclear whether the anteriormost pair is bifid. Three pairs of lateral spines are assumed for *K. elliptica*, following Bruton (1968) and Ramsköld & Chatterton (1991). The bifid spines are only visible if the pygidium or adjacent thoracic segment is displaced (see Bruton, 1968, p. 30) or if the pygidium is fully prepared (cf. Basse, 2004, pl. 47, fig. 598), and the lack of these conditions may have led Richter to premature conclusions.

The new species shares a number of cephalic features with *K. elliptica* which include the median glabellar lobe outlining a quarter circle in lateral view; the comparable size

and shape of the lateral glabellar lobes; the occipital ring bearing two pairs of tubercles on its posterior margin; two dorsal spines on the genal spine; and tubercles on the librigenal field concentrated below the eye. Furthermore, both species show epiborder tubercles above border spines 4, 6 and 9 (at least), which suggests close alliance. The cephalon of *K. bayarti* is readily distinguished from that of *K. elliptica* mainly by its more numerous tubercles on the median and lateral glabellar lobes, and librigenal field; the absence of a border furrow medially in front of the rectangular main body of the median glabellar lobe; the significantly wider (tr.) anterior part of the median glabellar lobe; the much better developed occipital spine, the base of which occupies most of the occipital ring and always reaches its posterior margin; and three prominent tubercles on the posterolateral cranidial border, as against two in *K. elliptica* (just adaxial of the two tubercles that are visible here in *K. elliptica* [cf., e.g., Ramsköld & Chatterton, 1991, p. 360, fig. 9; Basse, 2004, pl. 47, fig. 600] is a third one in *K. bayarti*). The neotype of *K. aries* (cf. Basse, 2004, pl. 48, fig. 607) shows a third tubercle adaxial of the other two, on its right posterolateral cranidial border. It is obviously much smaller and positioned further anteriorly, and is likely to be one of the randomly positioned smaller tubercles in this area of the cranidium.

The thorax of the Belgian species appears to be principally different from *K. elliptica* in lacking a central (exsag.) tubercle on the adaxial parts of at least the anterior two PPB. Such tubercles may be asymmetrically present in *Kettneraspis*. A well-preserved, articulated specimen of *K. tuberculata tuberculata* (Hall) illustrated by Whiteley *et al.* (2002, pl. 34) (due to a print error the captions of plates 34 and 35 were switched, according to G.J. Kloc, pers. comm., summer 2005) features tubercles positioned near the rachis on the fourth and fifth PPB exclusively on the right thoracic pleural lobe; on the left side they are absent. The dislocation of the right pleural lobe and the angle from which the photograph was taken make it somewhat difficult to observe these differences. However, G.J. Kloc (pers. comm., summer 2005) was able to corroborate that they are asymmetrically present. The holotype of *K. bayarti* lacks these two tubercles on both sides, hence their absence is assumed to be true to this species.

The pygidium of *K. bayarti* is mostly similar to that of *K. elliptica* in the arrangement of its tubercles and spines although it seems to be less variable than the German species. *Kettneraspis elliptica* has one or two tubercles on the elevated postaxial band (already observed by Richter, 1909, p. 53, in topotypical material; also compare Basse, 2004, pl. 47, fig. 597, pl. 48, fig. 601, therein on specimens from both the Eifel and Sauerland), whereas the new species appears to have two. The pygidium of *K. bayarti* is readily distinguished from that of *K. elliptica* in having a medial spine pair that is proximally wider (tr.) than the border spine pair abaxial to the major border spine pair. In the German species exactly the opposite is the case (cf. Basse, 2004, pl. 47, figs. 598-600, pl. 48, figs. 601, 605).

Distribution – Type locality and horizon only.

Genus *Radiaspis* Richter & Richter, 1917b

Type species – *Arges radiatus* Goldfuss, 1843, from the Ahrdorf Formation (Eifelian) of the Eifel, Germany, by original designation.

Synonyms – *Xanionurus* Whittington & Campbell, 1967 (according to Chatterton & Wright, 1986); *Charybdaspis* Basse, 1998 (according to Santel, 2001; also see below).

Discussion – The holotype of *Radiaspis radiata* is a pygidium with sixteen border spines. Basse (1998) pointed out that the majority of specimens from the Eifel that had previously been assigned to *R. radiata* (e.g., Richter & Richter, 1930, p. 33, fig. 2a) actually have fourteen border spines, and so he assigned these to a new genus, *Charybdaspis*. According to Santel (2001), who discussed the genera *Radiaspis* and *Xanionurus* in detail, the differences between *Charybdaspis* and *Radiaspis* that were given by Basse (1998) are insufficient for generic separation. Jell & Adrain (2003) were in agreement with Santel and considered *Charybdaspis* a junior subjective synonym of *Radiaspis*. Magrean & van Viersen (2005), who recorded several pygidia and an articulated specimen of the type species of *Charybdaspis*, *C. comes* Basse, from the Jemelle Formation of Belgium (same locality and horizon as those of *Kettneraspis bayarti* in the present paper), recognised it as a distinct species and reassigned it to *Radiaspis* following Santel and Jell & Adrain. However, Basse (2004) subsequently retained *Charybdaspis*, despite the claims of Santel (2001), and the lack of further substantial evidence to support its retention.

Basse (1998, 2004) attached great significance to thoracic morphology in distinguishing between *Radiaspis* and *Charybdaspis*. Auxiliary spines on the distal extremities of the pleurae were claimed to be fused with the pleural spines exclusively in *Charybdaspis* and, indeed, these spines are fused in *C. comes*. However, at least one undescribed species from the Moroccan Devonian clearly has fourteen pygidial border spines, but separate thoracic pleural and auxiliary spines (see Fig. 4). Thus, the latter character appears to fail as a diagnostic feature of *Charybdaspis*. The present author is aware that probably no material of the Moroccan species is currently available, apart from specimens in private collections, to provide evidence for separate thoracic pleural and auxiliary spines in at least one species that might be assigned to *Charybdaspis*. Nevertheless, because articulated carapaces of *Radiaspis* and *Charybdaspis* are known from only a few species, the use of differences in thoracic morphology to distinguish between these genera is weak and of little practical value until the thoraxes of more species become known.

The other major thoracic difference that was described by Basse (1998, 2004) is that the first seven pleural spines pairs in *R. radiata* curve strongly ventrally and usually also posteriorly, nearly exsagittally, as against smoothly and widely curved posteriorly *C. comes*. However, a reconstruction showing this feature in *R. radiata* was based on a severely distorted internal mould of a carapace (Basse, 2004, pl. 49, fig. 622). Also, only a single fragmentary thoracic segment of *R. radiata* was additionally described and illustrated. This fragment is possibly conspecific, although uncertain. The only other thoracic material of *R. radiata* that was examined was a tentatively assigned, non-figured fragment. Basse's interpretation of the thorax of *R. radiata* might be correct, but more material is needed to assess this.

The difference claimed by Basse (1998, 2004) between the pygidia of both genera is the number of border spines. Santel (2001), referring to Kříž & Pek (1974, p. 179) and to personal communication with D.L. Bruton, suggested that the taxonomic value of the number of pygidial border spines in *Radiaspis* is restricted to the species level. Furthermore, claims exist that this number is variable within some *Radiaspis* species; according to Basse (2004), both *Radiaspis formosa* Prantl & Vaněk and *Radiaspis miranda* Vaněk are known both from

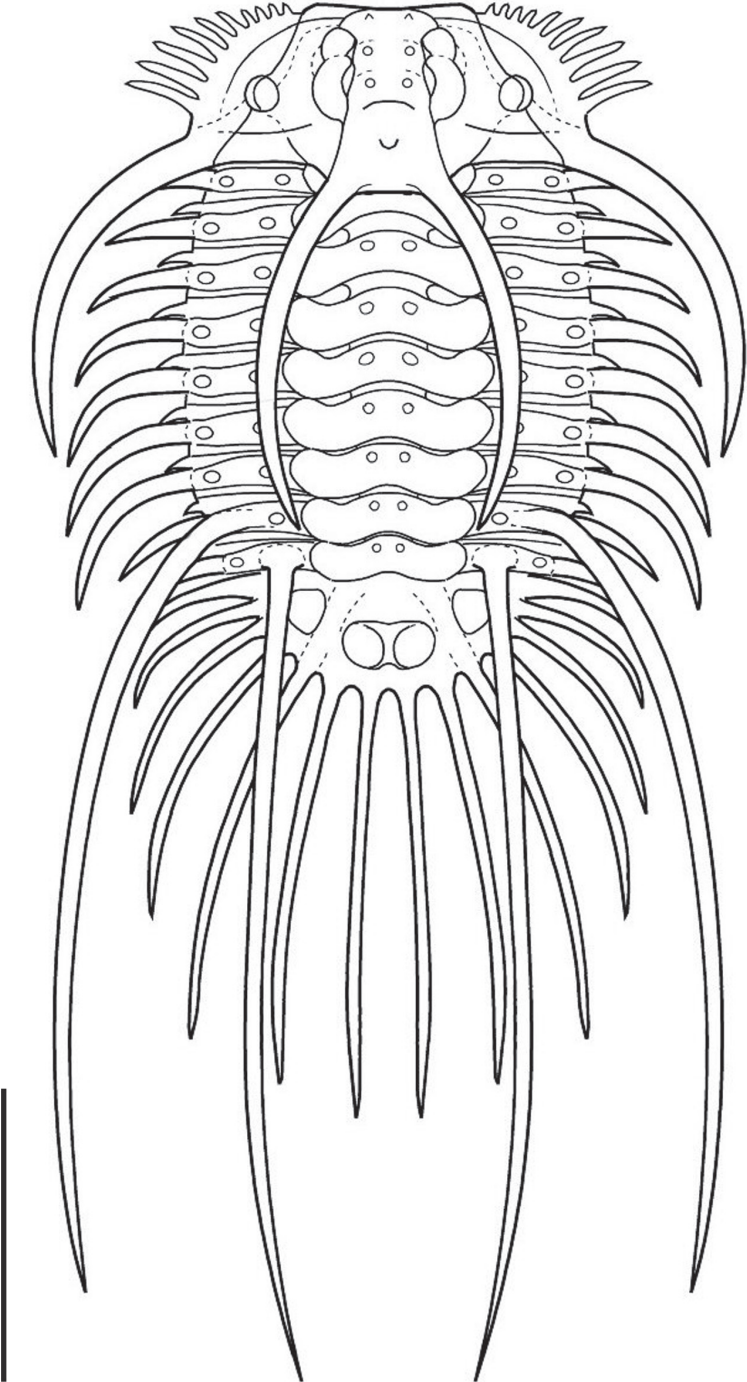


Fig. 4. Reconstruction of *Radiaspis* sp. from the Devonian of Morocco. Scale bar represents 10 mm.

specimens with twelve and fourteen pygidial border spines. If these specimens represent holaspides, then the number of pygidial border spines might best be regarded as generally having limited taxonomic value in *Radiaspis*, thus making it an unreliable character for distinguishing between *Radiaspis* and *Charybdaspis*.

It is possible that *Radiaspis sensu lato* with all of its presently included species is polyphyletic. The genus should be subjected to a large-scale phylogenetic analysis that includes Silurian and Devonian species from North Africa, western Europe and North America, probably with a species of *Diacanthaspis* as the outgroup (pers. comm. with J.M. Adrain, spring 2004; see Magrean & van Viersen, 2005). A broad analysis would also clarify the taxonomic positions of early taxa such as *Radiaspis pecten* Santel from the Silurian of the Carnic Alps, a species with twenty pygidial border spines. Until then, it remains unclear whether Basse's fourteen-spined and sixteen-spined groups are valid or whether other characters should weigh heavier in analysis. Consequently, at present there are no grounds to maintain *Charybdaspis*.

***Radiaspis comes* (Basse, 1998)**

- * 1998 *Charybdaspis comes* Basse, pp. 86, 87, pl. 13, figs. 2, 3.
2001 *R. comes* (Basse); Santel, p. 149.
- v 2004 *Charybdaspis comes* Basse; Basse, pp. 132-134, pl. 49, figs. 631-634.
- v 2005 *Radiaspis comes* (Basse); Magrean & van Viersen, pp. 89, 90, pl. 2, figs. 1-5.

Material – IRSNB a12614, internal mould of an articulated carapace, figured by Magrean & van Viersen (2005, pl. 2, figs. 1, 2); from locality VML004, Jemelle, Jemelle Formation (Middle Eifelian).

Discussion – The specimen shows the smoothly and widely posteriorly curving thoracic pleural spines very well. The reconstruction of *Radiaspis comes* by Basse (2004, p. 134, fig. 10) has the anterior pleural spine pairs curving anteriorly. In the Belgian specimen only the anteriormost pair of pleural spines is oriented slightly anteriorly, which is due to a slight dislocation of this thoracic segment. A similar situation seems to be the case in the articulated carapace from the Eifel (Basse, 2004, pl. 49, fig. 634). The more the anterior thoracic axial rings are tilted backwards, the more the associated pleural spines are oriented anteriorly.

Family Lichidae Hawle & Corda, 1847 Subfamily Trochurinae Phleger, 1936

Remark – This subfamily has been recognised as one of five main lichid clades in a recent phylogenetic analysis (Pollitt *et al.*, 2005). *Hoplolichas* and *Hoplolichoides*, both formerly assigned to the Homolichinae, were considered basal members to the Trochurinae. The diagnosis of the subfamily has been emended accordingly.

Genus *Ceratarges* Gürich, 1901

Type species – *Arges armatus* Goldfuss, 1839, from the Lauch to Ahrdorf formations (Eifelian) of the Eifel, Germany, by monotypy.

Remarks – *Ceratarges* was first discovered in Belgium by Maillieux (1904), who recorded it from Eifelian strata in the Couvin area although he erroneously identified it as *Acidaspis* cf. *vesiculosa* Beyrich. Richter & Richter (1917a, p. 54), who had examined Maillieux's original material and had topotypical specimens at hand for comparison, probably correctly designated the material as *Ceratarges armatus*. Since the concept of *Ceratarges armatus* has recently been restricted (Basse, 2004; van Viersen, 2006), Maillieux's (1904, 1907, 1912, 1919, 1933, 1938) material should be re-examined to assess if it is conspecific, the more so since it was collected from different stratigraphic units (see, e.g., Maillieux, 1938, p. 27). Maillieux (1919, 1933, 1938) later corrected his previous identifications and reported only *Ceratarges armatus* in Belgium. Consequently, *Ceratocephala vesiculosa* (Beyrich) is not assumed to also occur here.

***Ceratarges* cf. *armatus* (Goldfuss, 1839)**

Pl. 1, fig. 5; Fig. 5.

- ? 1904 *Acidaspis* cf. *vesiculosa* Beyr.; Maillieux, pp. 579, 580 [= *Ceratarges armatus* fide Richter & Richter, 1917a].
- ? 1907 *Acidaspis* cf. *vesiculosa* Beyr.; Maillieux, p. 134.
- ? 1912 *Acidaspis vesiculosa*; Maillieux, pp. 52, 53.
- ? 1919 *Ceratarges armata* (Goldfuss) [sic]; Maillieux, p. 54.
- ? 1933 *Ceratarges armata* [sic]; Maillieux, p. 70.
- ? e.p. 1938 *Ceratarges armatus* (Goldf.); Maillieux, p. 27 [non material from Co2a].

Material – RGM 211 469, internal mould of a pygidium with associated external mould plus silicone cast; from locality VML004, Jemelle, Jemelle Formation (Middle Eifelian).

Description – Pygidium convex (sag. and exsag.); wider (tr.) than long (sag.); moderately vaulted (sag. and tr.). Rachis slightly wider than pleural region (tr.); truncated posteriorly; length (sag.) about three-quarters that of pygidium; bearing one prominent ring and at least four weakly expressed additional ones (only visible in oblique lighting, both on internal mould and silicone cast); two pairs of crude granules on anterior half of rachis (see Fig. 5); base of dorsal spine on posterior half of rachis, slightly anterior to half of sagittal pygidial length. Pleural region anteriorly separated from rachis by distinct axial furrow; bearing three pleural ribs. First pleural rib only preserved on the internal mould; abaxially smoothly bending posteriorly; distally extended into a proximally somewhat ventrally oriented major border spine. Second pleural rib bearing a single, small tubercle slightly adaxial to halfway its length (tr.); proximally somewhat posterolaterally oriented, then curving transversely where it unites distally with swollen lateral border; extended into a proximally, strongly dorsally oriented major border spine. Third pleural rib running exsagittally; bearing a small tubercle at about 0.6 of sagittal pygidial length; distally merged with bifid postaxial ridge; extended into a posterolaterally, weakly dorsally oriented major border spine. Area between second and third pleural rib subtriangular; angle between second pleural rib and posterior part of swollen lateral border is about 90°. Two secondary marginal spines between second and third major border spines; two additional secondary marginal spines positioned partially below third major border spine; posteromedial margin bearing one pair of marginal border spines, with a slightly larger median spine in between.

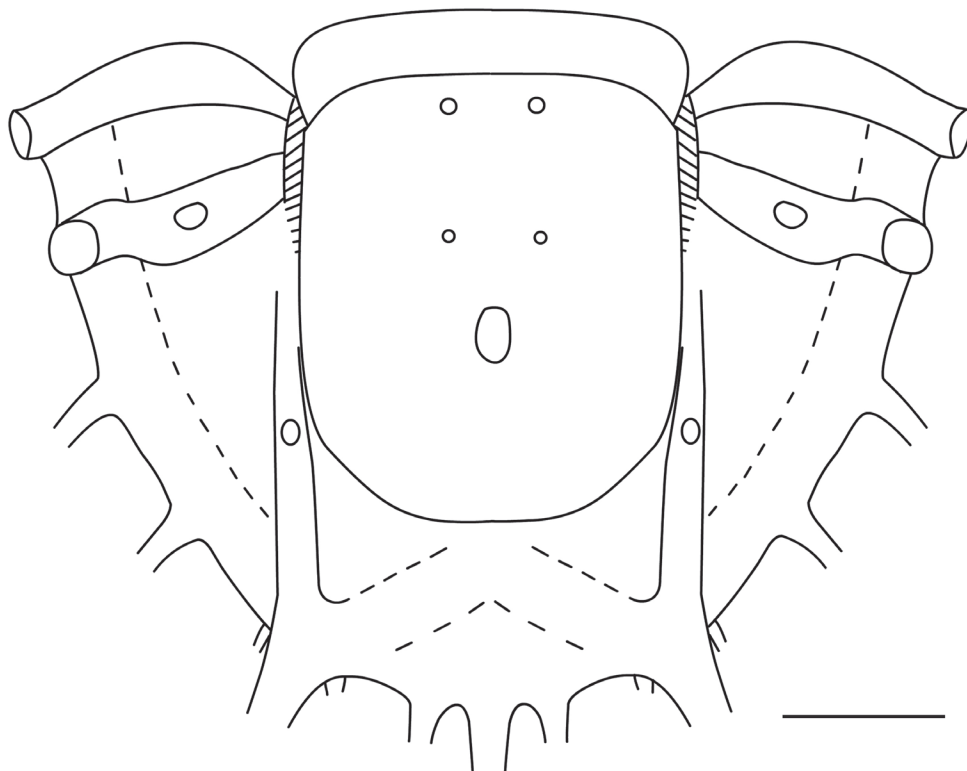


Fig. 5. Schematic drawing of the pygidium of *Ceratarges* cf. *armatus* (Goldfuss, 1839) from the Jemelle Formation (Middle Eifelian) of Jemelle, indicating the arrangement of axial symmetric tubercles. Scale bar represents 2 mm.

Remarks – Topotypical specimens of *Ceratarges armatus* (cf., e.g., Richter & Richter, 1930, pp. 36, 37, figs. 5a, b; Ormiston, 1982, pl. 1, figs. 8, 9; Thomas & Holloway, 1988, pl. 14, figs. 312-317; Basse, 2004, pl. 38, figs. 486-490, pl. 39, figs. 491-496) show many small variations, which include a changing position of the pygidial dorsal spine along the sagittal line, and variable density and arrangement of ornament on the pygidial rachis and third pleural rib. Although the pygidium from Jemelle and topotypical specimens appear to be identical, the former is nevertheless tentatively assigned to *C. armatus* until additional well-preserved material becomes available.

Note on *Rhenarges*

Basse (1998) only tentatively assigned *Acanthopyge erbeni* Meischner, 1965, to the genus *Akantharges* Phleger, 1936 (type species *Lichas gourdoni* Barrois, 1886; for generic diagnosis, see Holloway & Thomas, 2002, p. 121) because the pygidia that were known of the type species of *Akantharges*, *A. gourdoni*, were all too poorly preserved for comparison. Holloway & Thomas (2002) emphasised the assignment of *A. erbeni* to *Akantharges* because of similarities between the cranidia of this species and *A. gourdoni*,

with, in particular, the presence in both species of the curved ridge and furrow on the posterolateral cranidial lobe. Basse (2004) correctly noted the presence of this ridge and furrow in other trochurines, such as *Ceratarges* species and also *Acanthopyge* (*Lobopyge*) *niobe* Basse. However, Holloway & Thomas (2002) had already described how this ridge in *Akantharges* is unique in not bearing the eye. Basse (2004) admitted that the cranidia of *A. erbeni* and *A. gourdoni* were mostly similar, yet believed that certain differences between the pygidia of both species permitted the erection of a new genus, *Rhenarges* (type species *Acanthopyge erbeni*). These differences were not described, while for the diagnosis of *Rhenarges* reference was made to discussions on *Acanthopyge erbeni* by Meischner (1965) and Holloway & Thomas (2002). Furthermore, no reasons were given why the poorly preserved pygidia of the type species of *Akantharges* now provided sufficient insight to allow a comparison of this species with *A. erbeni*. Consequently, the present author considers *Rhenarges* to be a junior subjective synonym of *Akantharges*.

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Plate 1

Figs. 1-4, 6. *Kettneraspis bayarti* sp. nov., Middle Eifelian, Jemelle, Belgium. 

Fig. 1. RGM 211 461, paratype, silicone cast of external mould of cranidium. a, oblique view. $\times 3.3$. b, dorsal view. $\times 3.3$. c, anterior view. $\times 3.3$.

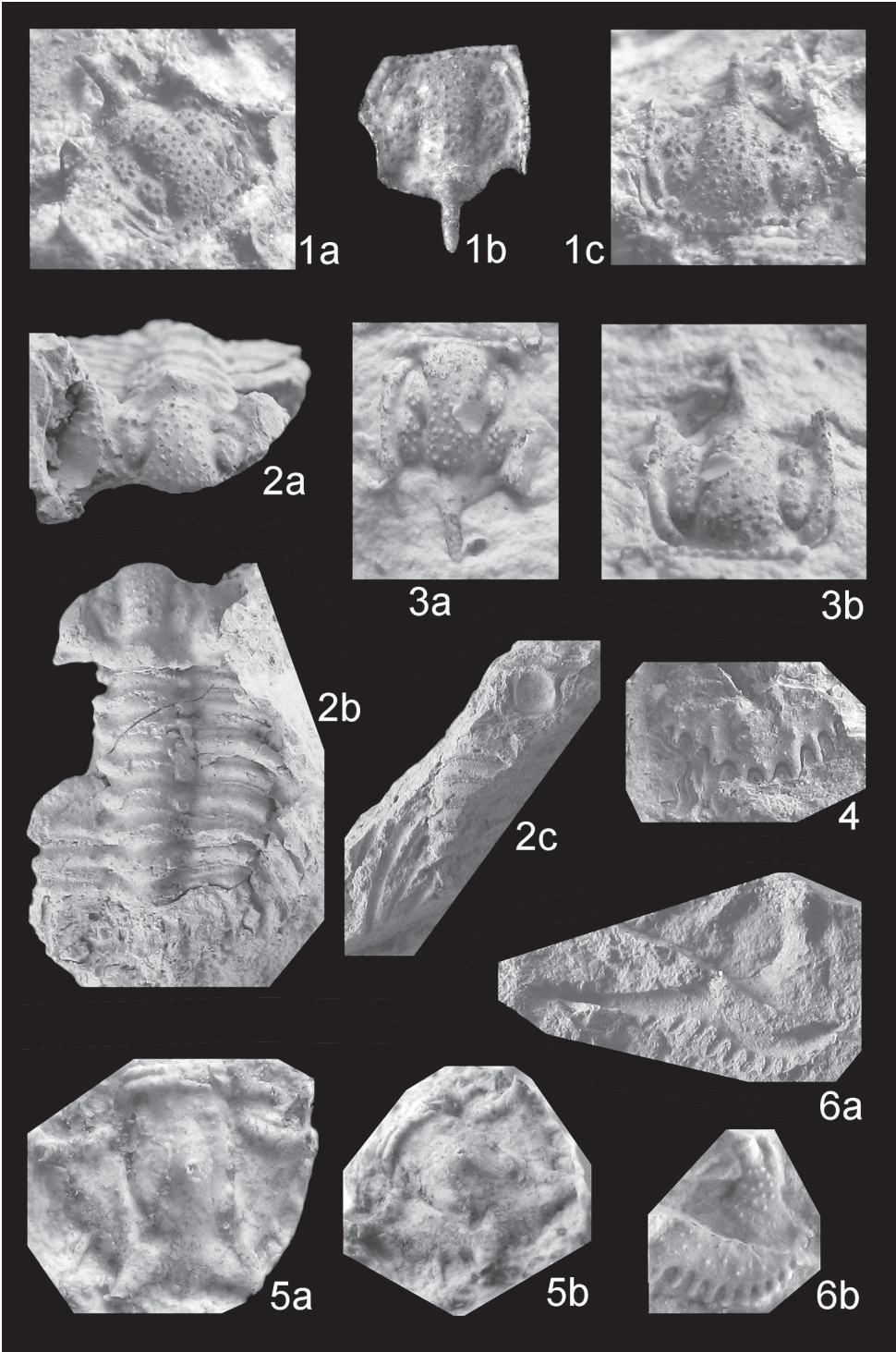
Fig. 2. RGM 211 460, holotype. a, internal mould of cephalothorax, anterior view. $\times 3.2$. b, internal mould of cephalothorax, dorsal view. $\times 2.7$. c, internal mould of anterolateral fragment of cephalothorax with external mould of hypostome in situ, dorsal view. $\times 2.0$.

Fig. 3. RGM 211 462, paratype, silicone cast of external mould of cranidium. a, dorsal view. $\times 3.2$. b, anterior view. $\times 4.0$.

Fig. 4. RGM 211 463, paratype, internal mould of pygidium. $\times 3.2$.

Fig. 6. RGM 211 464, paratype. a, internal mould of librigena, lateral view. $\times 3.4$. b, silicone cast of external mould of librigena, lateral view. $\times 3.4$.

Fig. 5. *Ceratarges* cf. *armatus* (Goldfuss, 1839), Middle Eifelian, Jemelle, Belgium. RGM 211 469, silicone cast of external mould of pygidium. a, dorsal view. $\times 3.7$. b, oblique view. $\times 3.0$.



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