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The latest Devonian (Famennian) phacopid trilobite *Omegops* from Belgium

CATHERINE CRÔNIER

Université de Lille, CNRS, UMR 8198 Évo-Éco-Paléo, F-59000 Lille, France; ***corresponding author:*** *catherine.cronier@univ-lille.fr.*

JULIEN DENAYER

Evolution & Diversity Dynamics Lab, Geology Department, University of Liège, allée du Six-Août, B18, 4000 Liège, Belgium; julien.denayer@uliege.be.

RAIMUND FEIST

Institut des Sciences de l'Évolution, Laboratoire de Paléontologie, Université de Montpellier II, F-34095 Montpellier cedex 05, France; raimundfeist@gmail.com.

BERNARD MOTTEQUIN

D.O. Terre et Histoire de la Vie, Institut royal des Sciences naturelles de Belgique, rue Vautier 29, B 1000 Brussels, Belgium; bmottequin@naturalsciences.be.

ABSTRACT

The Strunian regional substage corresponding to the uppermost Famennian of Belgium and northern France (Avesnois area) is marked by the occurrence of trilobites after an almost complete absence that began at the top of the Frasnian. The Strunian phacopid trilobites represented by *Omegops*, i.e., *O. accipitrinus* and *O. maretiolensis*, are recorded and illustrated from two Belgian sections (Spontin and Chansin) situated in the central part of the Dinant Synclinorium. These belong to the youngest known phacopids and they rank among the victims of the Hangenberg Crisis that took place near the Devonian–Carboniferous boundary. The phacopid fauna formed a trilobite association inhabiting a shallow shelf together with diverse brachiopod but also coral, crinoid, mollusc communities. These Belgian trilobites are compared with *Omegops bergicus* encountered in the northern France (Avesnois area).

KEYWORDS

Trilobita,
Phacopida,
Strunian,
Dinant Synclinorium

Article history

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1. Introduction

The uppermost Famennian of Belgium and northern France (Avesnois area), which corresponds to the Strunian regional substage in this area (Conil & Lys, 1980; Streel et al., 2006), is marked by the significant reappearance of trilobites. Indeed, the absence of trilobites extends from the end of the Frasnian–Famennian biotic crisis to the base of the Strunian. So far, only a single pygidium of an unidentified phacopid genus, which was collected by M. Mourlon in 1883, has been reported from the upper Famennian of southern Belgium by Van Viersen & Koppka (2021).

In northern France (Avesnois area) (Fig. 1), the latest Famennian phacopids were first reported by Hébert (1855) and Gosselet (1857, 1860, 1871, 1880) as *Phacops latifrons* (Bronn, 1825), but it was not until several decades later that they were illustrated by Dehée (1929) as *Phacops bergicus* Drevermann, 1902. From the historical viewpoint, they were first mentioned in southern Belgium, to our knowledge, as *Phacops granulosus* by Mourlon (1882, 1883a, b; in Dupont & Mourlon, 1883), who used them for characterising the *Calcaire de Comblain-au-Pont* (Comblain-au-Pont Formation; see Mottequin et al., 2024). Although Gosselet (1888) noted that *P. granulosus* may be conspecific with *P. granulatus* (Münster, 1840) (see Brauckmann et al., 1993), he kept the name previously proposed by Mourlon (1882, 1883a, b) pending a formal description of this taxon, which was never published; therefore, rightly explained by Richter & Richter (1933), *P. granulosus* Mourlon

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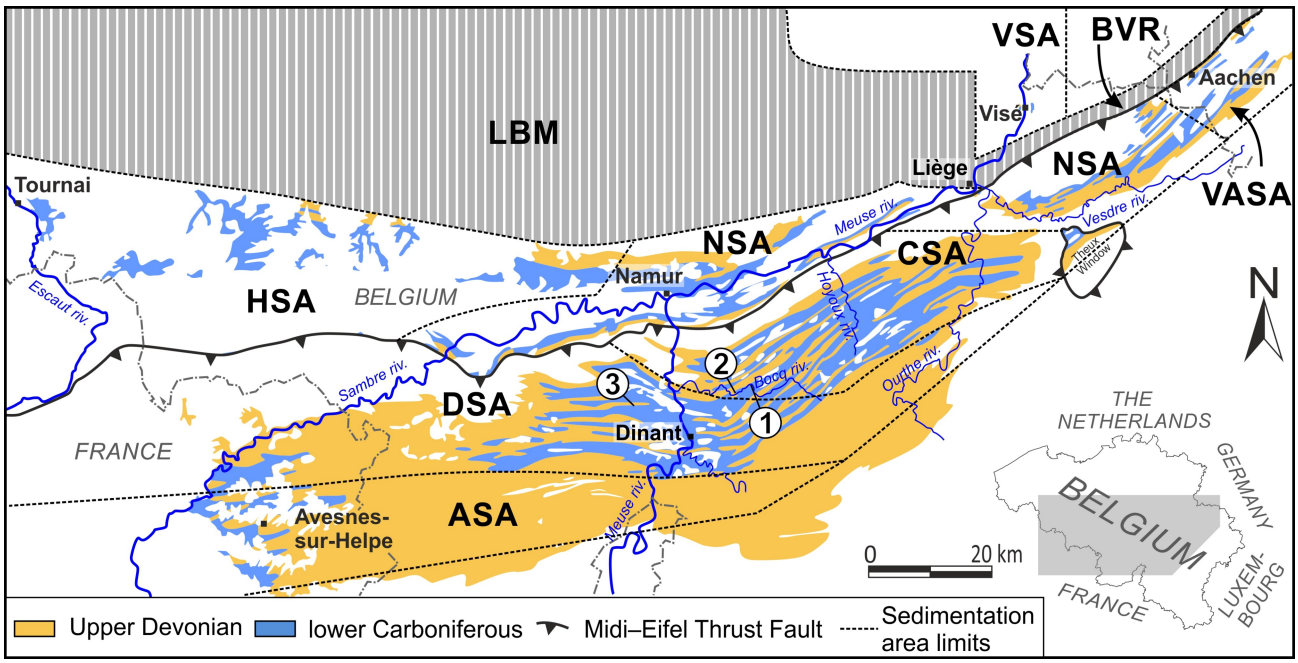


Figure 1. Sedimentation areas in the Namur–Dinant Basin (modified from Poty, 2016) and location map of the sections cited in the text (1, Spontin; 2, Chansin; 3, Maredsous). Abbreviations: ASA, South Avesnois sedimentation area; BVR, Booze–Le-Val-Dieu ridge; CSA, Condroz sedimentation area; DSA, Dinant sedimentation area; HSA, Hainaut sedimentation area; LBM, London–Brabant Massif; NSA, Namur sedimentation area; VASA, Vesdre–Aachen sedimentation area; VSA, Visé–Maastricht sedimentation area.

must be considered as a nomen nudum. Phacopid trilobites were of great importance to the pioneers of stratigraphy as they were mentioned in the four first editions of the *Légende de la Carte géologique de la Belgique* as typical macrofossil of the Famennian *assise de Comblain-au-Pont (Fa2d)*: *P. granulosus* (Conseil de Direction de la Carte, 1892) and *P. granulatus* (Conseil de Direction de la Carte, 1896, 1900, 1909). A further step was taken by Richter & Richter (1933), who provided the first description of the Strunian trilobites of Belgium and erected the new subspecies *Phacops* (*Phacops*) *accipitrinus maretiolensis* based on material from Maredsous (Fig. 1). The latter was later ascribed by Struve (1976) to his new subgenus *Phacops* (*Omegops*).

In Belgium, as the rocks yielding the phacopid trilobites were alternatively placed at the top of the Devonian or in the basal Carboniferous, their presence has frequently attracted the attention of geologists, and this interest continues to this day (e.g. Maillieux, 1933; Mortelmans & Bourguignon, 1954; Demanet, 1958; Conil et al., 1967, 1977, 1986; Austin et al., 1970; Dreesen et al., 1976; Denayer et al., 2019, 2021); indeed, these are the youngest known phacopids and they rank among the victims of the Hangenberg Crisis that took place near the Devonian–Carboniferous boundary (DCB) (e.g. Bault, 2023).

The aim of this paper is to document the last phacopid trilobites from the Upper Devonian (uppermost Famennian, Strunian) from the strata of the Belgian part of the Dinant Synclinorium equivalent of the Hangenberg Sandstone.

2. Geological setting

The Namur–Dinant Basin formed a vast, shallow-water shelf along the southern margin of the Laurussia continent during the Devonian and Carboniferous (e.g. Hance et al., 2001; Mottequin & Denayer, 2024). Nowadays, the Namur–Dinant Basin is preserved in several tectonic structures, mostly cropping out in southern Belgium, but also in the Avesnois area of northern France and Aachen area in western Germany (Fig. 1). The Upper Devonian–lower Carboniferous succession of the Namur–Dinant Basin is well exposed in the Dinant Synclinorium and Vesdre area (Fig. 1). The Famennian (Upper Devonian) is particularly well developed in the Dinant Synclinorium where it comprises a 600 m thick sequence, which is dominated by siliciclastic sediments with some carbonate levels in its middle and uppermost parts (Thorez et al., 2006; Mottequin et al., 2024). The uppermost Famennian (Strunian regional substage) is characterised by a mixed carbonate–siliciclastic sedimentation, which strongly contrasts with the rest of the Famennian succession that is strongly dominated by siliciclastic deposits (Poty, 2016). The uppermost Famennian facies indicate an inner- to median-shelf environment close to the base of the fair-weather wave zone that was influenced by detrital and marine inputs, with frequent storm deposits (Paproth et al., 1986; Thorez & Dreesen, 1986; Van Steenwinkel, 1990).

The material studied here was collected in two sections (Chansin and Spontin, see below) at the top of the Strunian succession, more precisely in the topmost part of the Comblain-au-Pont Formation and in the lowest part of the Hastière Formation. Both units were described in detail by Denayer et al. (2019, 2021). At the end of the Devonian, the two sections were situated on the southern margin of the Condroz sedimentation area (Fig. 1) sensu Hance et al. (2001) and Poty (2016). In the Dinant and Condroz sedimentation areas, the Comblain-au-Pont Formation, which consists of an alternation of bioclastic limestone and shale beds, yielded a diverse rugose coral fauna (Poty, 1999; Poty et al., 2006; Denayer et al., 2019, 2021) and numerous brachiopods (Legrand-Blain, 1995; Mottequin & Brice, 2016; Denayer et al., 2021). Tabulate corals (Tourneur et al., 1989) and bryozoans (Tolokonnikova et al., 2015) are not uncommon, but deserve to be investigated further as is the case of the molluscs and vertebrate microremains (Denayer et al., 2021). The Hastière Formation is mostly Tournaisian (Hastarian) in age, but its basal bed yields faunas (e.g. campophyllid rugose corals, phacopid trilobites) that indicate a Strunian age (Poty, 2016; Denayer et al., 2021).

3. Material and methods

Both sampled sections are situated along the touristy Bocq railway, to the east of the Meuse River valley (for more information, see Denayer et al., 2019, 2021) (Fig. 1). The specimens were collected in beds rich in macrofauna and in calcareous intraclasts.

Chansin. The material was collected within the topmost part of the Comblain-au-Pont Formation (beds 103 and 105) and in the basal part of the overlying Hastière Formation (beds 107 and 108) (Fig. 2).

Spontin. The phacopids are from the Comblain-au-Pont (beds 7, 8, and 14) and Hastière (bed 23, and 26) formations (Fig. 2).

All the specimens studied herein are deposited at the Evolution & Diversity Dynamics Lab of the Liège University (Belgium), prefixed PA.ULg.

The illustrated specimens were lightly coated with ammonium chloride before being photographed using a Nikon digital camera. The morphological terminology follows Whittington & Kelly (1997). The synonymy lists are not intended to be exhaustive and focus essentially on records with illustrations.

4. Systematic palaeontology

Order Phacopida Salter, 1864
Superfamily Phacopoidea Hawle & Corda, 1847
Family Phacopidae Hawle & Corda, 1847
Subfamily Phacopinae Hawle & Corda, 1847
Genus *Omegops* Struve, 1976

Type species. Calymene accipitrina Phillips, 1841; from the Upper Devonian Pilton Beds, England.

Species assigned. Omegops accipitrinus (Phillips, 1841), Famennian (do VI), Belgium, England, Germany, Morocco (see Richter & Richter, 1933); *O.* cf. *accipitrinus* (Phillips, 1841), Famennian, Armenia (see Crônier et al., 2021); *O. bergicus* (Drevermann, 1902), Famennian (do VI), Germany, northern France see Dehée, 1929); *O. cornelius* (Richter & Richter, 1933), Famennian (do VI), Germany, Central Iran (see Mistiaen et al., 2000); *O.* cf. *cornelius* (Richter & Richter, 1933), late Famennian, Eastern Iran (see Feist et al., 2003); *O.*? *cornelius* (Richter & Richter, 1933), late Famennian (Strunian), Afghanistan (see Ghobadi Pour et al., 2018 for discussion on the species affiliation); *O. insolatus* (Struve, 1976), Famennian (do VI), Morocco; *O. maretiolensis* (Richter & Richter, 1933), Famennian (do VI), Belgium; *O. mobilis* (Xiang, 1981), late Famennian, NW China (Xinjiang); *O. multisegmentatus* (Weber, 1937), Famennian (? do VI), Kazakhstan; *O. paiensis* Farsan, 1998, late Famennian (Strunian), Afghanistan; *O. tilabadensis* Ghobadi Pour et al., 2018, late Famennian, Northern Iran; *O.* sp. *M* (see Struve, 1976, p. 435–436 for this assignation of Moravian representatives described by Chlupáč (1966) as *O. accipitrinus*), Famennian (do VI), Moravia; *O.* sp. *T* (see Struve, 1976, p. 438–439), Famennian (do VI), Morocco; *O.* sp. (see Yuan & Xiang, 1998), Famennian (do VI), South China (Guangxi).

Remarks. The main characters of *Omegops* were presented by Struve (1976), i.e., a reduced preoccipital ring as a narrow flat band, 15–16 dorso-ventral files with a maximum of four to five lenses, a distinct postocular pad, a marginulate lateral border, and coarse tubercles on glabella. But similar genera have meanwhile been erected, and species have been added to *Omegops* and the main *Omegops* characters of Struve may now

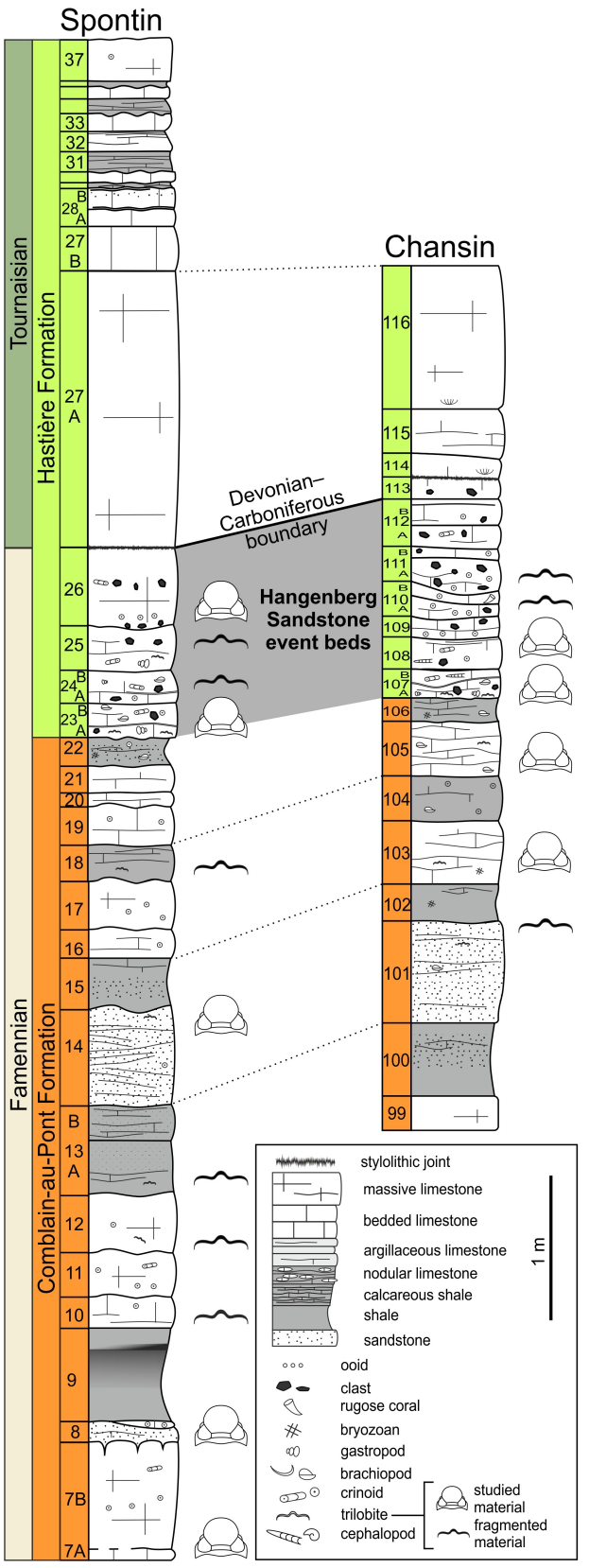


Figure 2. Lithological columns of the Spontin and Chansin sections showing the Devonian–Carboniferous transition in neritic facies (modified from Denayer et al., 2019, 2021).

refer to a range of Devonian phacopid genera. Especially the "reduced" preoccipital ring could equally be posited as to represent a broader trend among Late Devonian phacopids (i.e., the blind Famennian *Dianops* Richter & Richter, 1923). This reduced preoccipital ring is also consistent with the representatives of *Boekops* (Chlupáč, 1972) from the Lower Devonian as underlined by Chlupáč (1977, p. 76). The large-eyed mid-Frasnian *Magreanops* van Viersen & Vanherle, 2018, which has a small and flat preoccipital ring marked merely by a few crowded tubercles (van Viersen & Vanherle, 2018, fig.10N), differs in having a less significant sagittal reduction of L1 than in species of *Omegops* (Fig. 3c, g).

The assignment to *Omegops* of two newly described species from western Junggar, Xinjiang, northwest China remains questionable. *Omegops honggulelengensis* Zong, 2023a, from the middle–upper Famennian, was previously assigned to *Omegops cornelius* and *O. mobilis* from the upper Famennian; and *O. xiangi* Zong, 2023a, from the middle Famennian, was previously assigned by Crônier in Crônier & Waters (2023) to their new genus and species *Clarksonops junggariensis*. Subsequently, Zong (2023b) reclassified these two species, i.e., *Omegops honggulelengensis* and *O. xiangi* respectively to *O. mobilis* (Xiang, 1981) n. comb. and *O. junggariensis* (Crônier in Crônier & Waters, 2023) n. comb. to respect the Art. 23 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). In the diagnosis of *Omegops* (see Struve, 1976), it is clearly stated that the preoccipital ring is erased and depressed, or barely detectable in oblique light. Neither *junggariensis* nor *xiangi* meet this criterion and are therefore not *Omegops*. Furthermore, *Omegops* is until recently confined to the uppermost Famennian (Crônier & François, 2014). It therefore seems to us that the affiliation to the genus *Clarksonops* is justified for these specimens. *Omegops honggulelengensis* includes the holotype of *O. mobilis*; *honggulelengensis* should be a junior synonym of *mobilis*. Accepting the junior synonymy of the middle–upper Famennian *O. honggulelengensis* with the latest Famennian *O. mobilis*, the exclusively uppermost Famennian age for *Omegops* is questionable. Without a re-evaluation of this material to validate whether there are any notable differences between the specimens from the middle Famennian and the upper Famennian, it is best to consider all specimens as *honggulelengensis* specimens (sensu Zong, 2023a).

In Belgium, the studied material from Chansin (40 sclerites: 24 cephala and 16 pygidia) and Spontin (12 sclerites: 8 cephala and 4 pygidia) is most often incomplete, difficult to prepare and often preserved as internal moulds. Due to the smaller number of well-preserved cephala available, additional material is required, but specimens are assigned to *Omegops maretiolensis* (Richter & Richter, 1933), a common taxon in Belgium, and to *O. accipitrinus* (Phillips, 1841) on account of the cephalic shape and sculpture. *Omegops accipitrinus* and *O. maretiolensis* are present in the same levels and therefore they are considered as separate species and as not subspecies as previously stated by Richter & Richter (1933).

Omegops accipitrinus is a Late Devonian index fossil (latest Famennian, Strunian regional substage).

***Omegops accipitrinus* (Phillips, 1841)**
(Figs 3a–p, 4a)

1841 *Calymene accipitrina* Phillips, p. 128, 152, pl. 56, fig. 249 a–c.
1933 *Phacops* (*Phacops*) *accipitrinus accipitrinus* (Phillips, 1841); Richter & Richter, p. 5–12, pl. 1, figs 1–8 [cum syn.].
cf. 1937 *Phacops* (*Phacops*) cf. *accipitrinus* (Phillips, 1841); Weber, p. 114, pl. 1, figs 1–5.
1955 *Phacops* (*Phacops*) *accipitrinus accipitrinus* (Phillips, 1841); Goldring, p. 46–47.
non 1966 *Phacops* (*Phacops*) *accipitrinus* (Phillips, 1841); Chlupáč, p. 103–104, pl. 21, figs 1–5, 12, text-fig. 32.
1969 *Phacops* (*Phacops*) *accipitrinus* (Phillips, 1841); Pillet & de Lapparent, p. 329–330, pl. 39, figs 2–7, 9–18.
1972 *Phacops* (*Phacops*) *accipitrinus* (Phillips, 1841); Alberti, p. 4–21, figs 1–11.
1974 *Phacops accipitrinus* (Phillips, 1841); Levitskiy, p. 54–56, pl. 1, figs 10–22, text-fig. 3b.
1976 *Phacops* (*Omegops*) *accipitrinus accipitrinus* (Phillips, 1841); Struve, p. 439, pl. 2, fig. 8.
non 1977 *Phacops* (subg.?) *accipitrinus* (Phillips, 1841); Chlupáč, p. 76, pl. XXXII, figs 8–9.
2021 *Omegops* cf. *accipitrinus* (Phillips, 1841); Crônier in Crônier et al., p. 4, fig. 2a–d, k.

Type material. From the Upper Devonian Pilton Beds, England: original number Nr. 7055 (lectotype: cephalon), Museum of Practical Geology (i.e., The British Museum), London.

Studied material. Eight cephala and eight pygidia from the Comblain-au-Pont Formation to Hastière Formation (uppermost Famennian) of the Chansin and Spontin sections, Belgium.

Diagnosis. See Richter & Richter (1933).

Remarks. See remarks for *Omegops maretiolensis*.

***Omegops maretiolensis* (Richter & Richter, 1933)**
(Figs 3q–w, 4b)

1933 *Phacops* (*Phacops*) *accipitrinus maretiolensis* Richter & Richter, p. 12–15, pl. 2, figs 9–14 [cum syn.].
? 1936 *Phacops* (*Ph.*) *accipitrinus maretiolensis* Richter & Richter, 1933; Rome, p. 1–7, pl. 1, figs 1–6, pl. 2, figs 7–12.
1976 *Phacops* (*Omegops*) *accipitrinus maretiolensis* Richter & Richter, 1933; Struve, p. 435, figs 6–7, 16, 19, 28, pl. 1, figs 1–6.
2021 *Omegops maretiolensis* (Richter & Richter, 1933); Mottequin, p. 37, 59–61, fig. 21A–O.
2024 *Omegops maretiolensis*; Mottequin et al., p. 213, pl. 4.EE [copy of Mottequin, 2021, fig. 21A].

Type material. From the Comblain-au-Pont Formation (latest Famennian, 'Strunian') of Maredsous (Bioul 525), Belgium: RBINS a7812 (holotype: cephalon), a7813–7817 (paratypes: 3 cephala and 2 pygidia), Royal Belgian Institute of Natural Sciences, Brussels; CGF 020.11.10/12 (paratype: 1 pygidium), Centre Grégoire Fournier, Maredsous (Mottequin, 2021).

Studied material. Four cephala including two illustrated from the Comblain-au-Pont Formation to Hastière Formation (uppermost Famennian) of the Chansin section, Belgium.

Diagnosis. See Richter & Richter (1933).

Remarks. Detailed descriptions of *O. accipitrinus* and *O. maretiolensis* were presented by Richter & Richter (1933) and supplemented by Struve (1976). *Omegops accipitrinus* is characterised by a postocular area that is smooth adaxially and

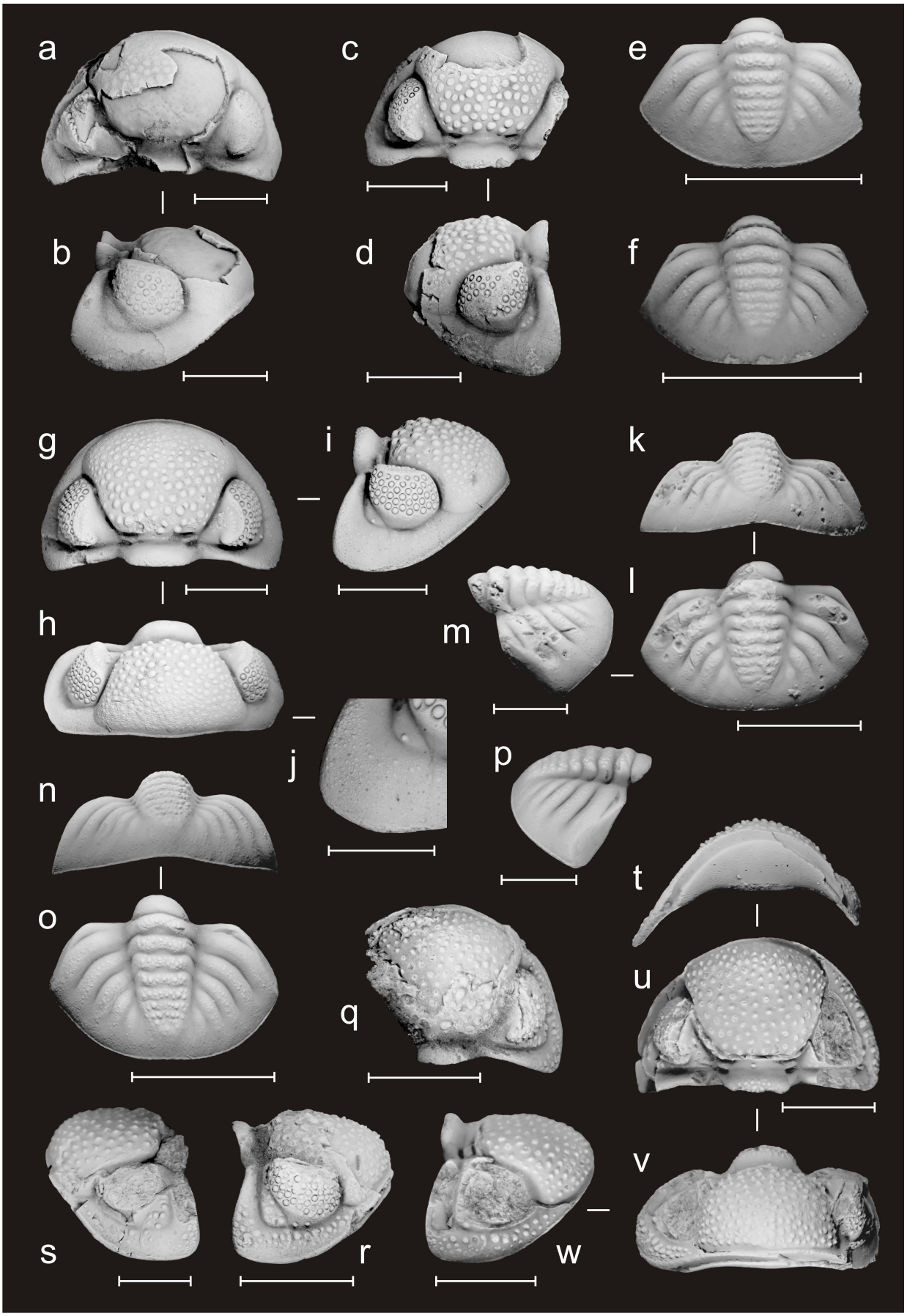


Figure 3. Phacopid trilobites from the Dinant Synclinorium (southern Belgium); all specimens are from the Chansin section (see Figs 1–2). **a–p** *Omegops accipitrinus* (Phillips, 1841). **a–b** Cephalon in dorsal and lateral views (PA.ULg.20240613-1; bed 107). **c–d** Cephalon in dorsal and lateral views (PA.ULg.20240613-2; bed 107). **e** Pygidium in dorsal view (PA.ULg.20240613-3; bed 105). **f** Pygidium in dorsal view (PA.ULg.20240613-4; bed 105). **g–j** Cephalon in dorsal, frontal and lateral views, and detail of the genal angle (PA.ULg.20240613-5; bed 107). **k–m** Pygidium in frontal, dorsal and lateral views (PA.ULg.20240613-6; bed 105). **n–p** Pygidium in frontal, dorsal and lateral views (PA.ULg.20240613-7; bed 107). **q–w** *Omegops maretiolensis* (Richter & Richter, 1933). **q–r** Cephalon in dorsal and lateral views (PA.ULg.20240613-8; bed 107). **s** Cephalon in lateral view (PA.ULg.20240613-9; bed 107). **t–w** Cephalon in ventral, dorsal, frontal and lateral views (PA.ULg.20240613-10; bed 108). Scale bars: 5 mm for all, except e, j, m and p: 3 mm.

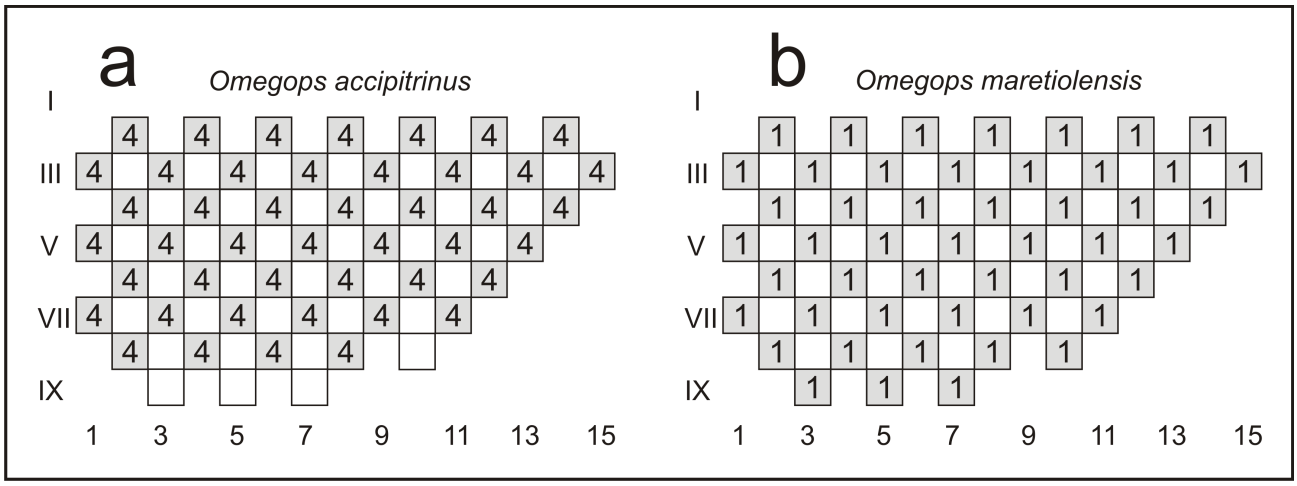


Figure 4. Schematic representation of (**a**) four visual surfaces in *Omegops accipitrinus* (Phillips, 1841) and (**b**) one visual surface in *Omegops maretiolensis* (Richter & Richter, 1933), following the method of Thomas (1998). Front of visual surface is left; numbers below drawing denominate individual dorso-ventral files, counting from the front (1–15); roman numerals denote successive horizontal rows; numbers in boxes indicate a surface having that lens present in all visual surfaces.

covered with a few tubercles abaxially, up to five lenses in a dorso-ventral file in the eye (with 56–70 lenses recorded), axial glabellar furrows diverging forwards at about 45–60°, and two small granules medially on the reduced preoccipital ring. The pygidium of *O. accipitrinus* according to available data (illustration from Salter, 1864, pl. 1, figs 10, 14 with a reassignment by Richter & Richter, 1933, description from Richter & Richter, 1933), has six pleural ribs but the last two are sometimes indistinct or only recognizable as nodes (see Richter & Richter, 1933, p. 8). Our cephala affiliated to *Omegops accipitrinus* fit rather well with this description in having 15 dorso-ventral files with a maximum of four lenses (but with only 45 lenses recorded in four visual surfaces), a postocular area that is smooth or with only few tubercles (see Fig. 3b, d). In addition, on the postero-lateral border, small granules and pits are present on the best preserved specimen (Fig. 3i–j). However, our well-preserved pygidia show rather 5 distinct pleural rib pairs and 8 axial rings plus the terminal piece. *Omegops maretiolensis* is characterised by a postocular pad covered with several tubercles, a row of coarse tubercles on the lateral border, up to five lenses in a dorso-ventral file. The pygidium of *O. maretiolensis* has seven to nine axial rings and six pleural ribs also, with a relatively long pygidial axis (Struve, 1976), and coarse tubercles (see Mottequin, 2021: fig. 21l–o). Our specimens affiliated to *Omegops maretiolensis* fit rather well with this description in having 15 dorso-ventral files with a maximum of four lenses (with 49 lenses recorded in the best preserved visual surface). Both taxa co-occur in the same samples and exhibit almost the same distributional pattern of eye-lenses, while they can be discriminated by differences in cephalic sculpture (lateral border and postocular area with numerous coarse tubercles for *Omegops maretiolensis* and with small granules for *O. accipitrinus*). While bimodal variability in eye lenses is documented for some phacopids (e.g. Campbell, 1967; Crônier et al., 2015), this pattern has not been reported for any species of *Omegops*.

Chlupáč (1966, 1977) described some Moravian specimens he assigned to *Phacops* (subg.?) *accipitrinus* encountered in the same levels and exhibiting variability in the density and spacing of tubercles. The subspecies *O. accipitrinus maretiolensis* was erected on the basis of its lateral border granulation and was not taxonomically justified according to Chlupáč (1966, 1977). However, the absence of a morphological continuum in this character between *O. accipitrinus* and *O. maretiolensis* suggests the presence of two distinct species. If additional new material may confirm whether these differences are taxonomically significant, the presence of two morphologically distinct pygidia seems to confirm the presence of two distinct species.

5. Discussion

The new illustrated specimens of *Omegops* are partially consistent in pygidial morphology with the taxa originally described from the upper Famennian of Western Europe (Richter & Richter, 1933; Struve, 1976); i.e., in having six pygidial pleural ribs. If *Omegops maretiolensis* exhibits 6 pleural rib pairs, *O. accipitrinus* from Belgium seems to show only 5 distinct pleural rib pairs. Based on small but consistent differences in the number of pleural ribs, Ghobadi Pour et al. (2018) suggested the existence of two geographically isolated *Omegops* lineages which diverged in pre-Strunian time, i.e. taxa with four to five pleural ribs from the Middle East and Northwest China (Junggar) and taxa from Western Europe and North Africa with six or more pygidial pleural ribs. The Belgian *Omegops accipitrinus* seems to contradict this trend.

Crônier & François (2014) commented on a bathymetrical gradient in the distribution of Famennian phacopid taxa with *Omegops* restricted to shallow-water deposits influenced by current activity (as previously reported by Chlupáč, 1977), along both the palaeogeographical South Laurussia and North Peri-Gondwana margins. The *Omegops* association is encountered in shallow water clastic limestones probable of lower shoreface to upper offshore origin in the upper Famennian. This pattern established by Crônier & François (2014) is consistent in the Dinant synclinorium where *O. accipitrinus* and *O. maretiolensis* are significant components of the benthic fauna with abundant brachiopods (e.g. spiriferides, rhynchonellides) that inhabited a limestone substrate rich in bioclasts within an offshore shallow shelf setting. Almost all documented *Omegops* occurrences, except those of the North African part of Gondwana, were confined to the tropics and subtropics. All phacopid genera became extinct at the end-Famennian Hangenberg Crisis. In this regard, the Famennian is notable for its taxonomic turnovers and the decline in phacopid diversity. Biostratigraphically, the Belgian levels yielding phacopids are of very late Famennian age, corresponding to the Hangenberg Sandstone event, just below the entry of the conodont *Protognathodus kockeli*.

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Author contribution

JD and BM collected the fossil material (a few specimens by CC during the IPC5 congress) whereas CC and RF described it. All authors participated to the writing of the paper.

Data availability

All studied specimens are housed in official repositories guaranteeing their long-term safekeeping and availability to other researchers for future studies.

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