



# The phacopid trilobites *Austerops* MCKELLAR & CHATTERTON, 2009, *Hottonops* gen. nov. and *Loreleiops* gen. nov. from the Devonian of the Ardenno-Rhenish Mountains

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With 6 figures

**Abstract:** Phacopids with reduced sculpture are recorded from Emsian to Givetian strata in the Ardenno-Rhenish Mountains and Brittany. *Austerops couvinensis* sp. nov. and *Austerops hottonensis* sp. nov. are described from Eifelian strata in the Ardennes and represent the first known occurrences of members of this genus outside Gondwana. *Loreleiops suffeleersi* gen. & sp. nov. and *Hottonops daumeriesi* gen. & sp. nov. are recorded from Eifelian strata in the Ardennes. *Pedinopariops simulator* BASSE, 1998 and *Pedinopariops hoelleri* VAN VIERSSEN, PRESCHER & SAVELSBERGH, 2009, from the Givetian and Eifelian (respectively) in the Rhenish Mountains, are transferred to *Loreleiops* gen. nov. *Austerops* cf. *menchikoffi* (LE MAÎTRE, 1952) is reported from the Emsian of Brittany, confirming the occurrence of this genus in peri-Gondwana.

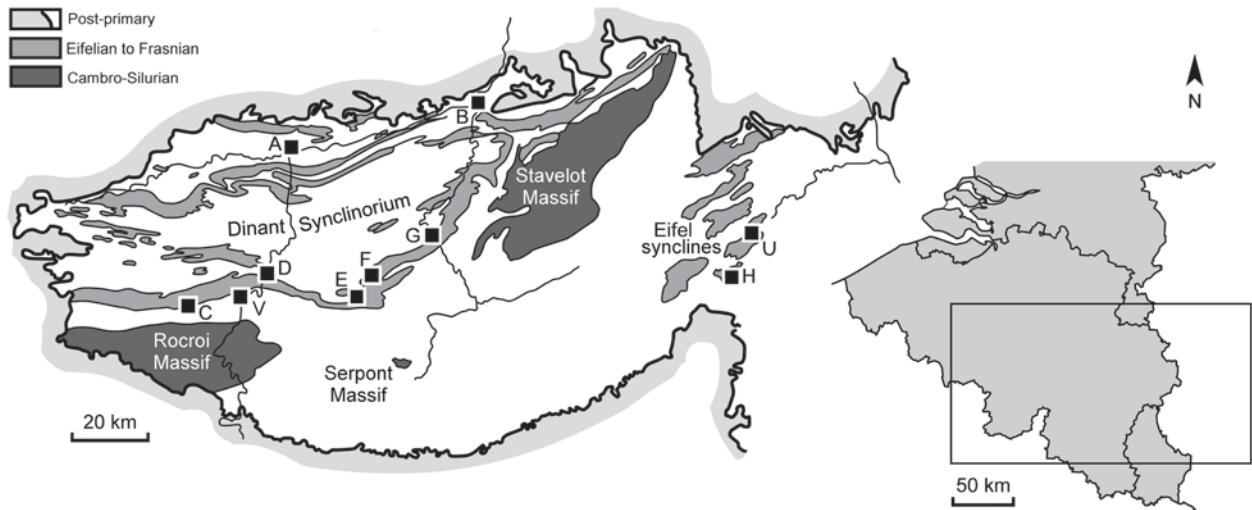
**Key words:** Trilobita, taxonomy, palaeobiogeography, Belgium, Germany, France.

## 1. Introduction

Phacopids are a major component of neritic trilobite associations from the Lower to lower Middle Devonian of Western Europe and North Africa. Most taxa bear pronounced dorsal sculpture consisting of bladder- to cone-shaped tubercles or, in rare cases, spines. Recently, MCKELLAR & CHATTERTON (2009) recognised a group of phacopids with subdued dorsal sculpture from Emsian to Eifelian strata in Morocco that they assigned to a new genus *Austerops*. Here, we record rare phacopids with reduced sculpture that mainly come from Eifelian strata in the Ardennes region (SE Belgium). These include the genera *Austerops*, *Hottonops* nov., and *Loreleiops* nov. Additionally, a cephalon of *Austerops* cf. *menchikoffi* (LE MAÎTRE, 1952) is recorded from the Emsian of Brittany, complementing material ascribed previously to *Phacops* EMMRICH, 1839 by MORZADEC (1969).

## 2. Localities

During the Eifelian the Ardennes were located on the passive southern margin of Avalonia. A mixed siliciclastic-carbonate ramp developed there that ranged from temporary deltaic swamps to open marine environments. Basin inwards the main lithostratigraphic unit is the Jemelle Formation. This unit, which crops out along the southern to southeastern borders of the Dinant Synclinorium (Fig. 1), is comprised of early Eifelian siltstones and shales to late Eifelian shales alternated by calcareous nodules. A biostrome (Couvin Formation) developed at the base of the Jemelle Formation in the Couvin area. Outside this area the biostrome is greatly reduced or replaced by the basal part of the Jemelle Formation; e.g., in Vireux-Molhain (classic “Mur des douaniers” trilobite locality) and Jemelle (stratotype) (Fig. 2).



**Fig. 1.** Generalised geological map of the Ardennes and Eifel with key places indicated (modified after VAN VIERSEN 2006: 230, fig. 1). A. Namur. B. Liège. C. Couvain. V. Vireux-Molhain. D. Givet. E. Resteigne. F. Jemelle. G. Hotton. H. Gees. U. Üxheim.

The Jemelle Formation is the main source of Devonian trilobites from Belgium. The trilobite fauna is comprised of frequent phacopids, proetids and aulacopleurids. Tropidocoryphids, scutelluids, harpetids, lichids, odontopleurids and acastids are comparatively rare (VAN VIERSEN 2015). Trilobite biodiversity has been subjected to preliminary analyses that indicated peak diversity in the (middle Eifelian) middle part of the Jemelle Formation (BIGNON et al. 2008; CRÔNIER & VAN VIERSEN 2007). All of the localities investigated by us are situated in this part of the formation; they are interpreted as open marine environments (middle ramp to outer shelf). Phacopids, the focus of this study, are represented in each of our localities by three to five species of different genera. This amount is high compared to the other trilobite families that occur there (only proetids are represented by up to three species in a single locality).

'Couvain 8011' locality of VAN VIERSEN (2015); on the western outskirts of Couvain (Fig. 1). This site is a 60 by 80 m large agricultural field that has yielded an abundance of loose calcareous nodules. It was first mentioned by MAILLIEUX (1938) and is indicated on his field maps kept by the IRSNB. According to the revised geological map (MARION & BARCHY 1999) this zone belongs to the middle part of the Chavées Member of the Jemelle Formation. This is in line with MAILLIEUX (1938) who studied the macrofauna there and considered the rocks to belong to "Co2c", an old term for the

middle and upper parts of the Jemelle Formation (BULTYNCK et al. 1991). Trilobite specimens were collected from loose calcareous nodules and thus, under limited stratigraphic control. However, steeply inclined *in situ* strata with a NW–SE orientation are located < 1 m below the surface. Samples taken from these banks indicate that they are consistent with the lithology of the nodules and the macrofauna that they enclose.

The trilobite association is richly diversified and specimens were often found as well preserved, articulated exoskeletons. These include members of Proetidae (*Cornuproetus* sp. and *Dohmiella* sp. of VAN VIERSEN 2015, *Gerastos* spp.), Tropidocoryphidae (*Phaetonellus lelubrei* VAN VIERSEN, 2015, *Tropidocoryphe* sp.), Aulacopleuridae (*Cyphaspis* spp. of the *hamidi* and *ceratophthalmus* groups of VAN VIERSEN & HOLLAND 2016), Odontopleuridae (*Kettneraspis* cf. *elliptica* of VAN VIERSEN 2015, *Koneprusia* sp.), Lichidae (*Ceratarges* sp.), Scutelluidae (*Goldius endelsi* VAN VIERSEN, 2015, *Scabriscutellum* sp.), Harpetidae (*Harpes* sp.), and Phacopidae (*Austerops couvinensis* sp. nov., *Pedinopariops* sp., *Phacops* sp.). *Gerastos* specimens are dominant whereas *Austerops* is comparatively rare.

'La Folie' locality of MAGREAN (2007) and TAGHON et al. (2012); east of Couvain. Coordinates are (Belgian Lambert system; East–North): 160.803–82.763. This outcrop in the Jemelle Formation was temporarily accessible during the constructions of buildings on both sides of the route N99. Limestones of the Chavées

	Couvin	Vireux	Jemelle	Eifel	Endorf
Givetian	HNT	HNT	HNT	Loogh	Wiedenest
				Ahbach	Meinkenbracht
Eifelian				Freilingen	Waldbach
	JEM Chavées Mbr	JEM Chavées Mbr	JEM Chavées Mbr	Junkerberg	Unnenberg
				Ahrdorf	Ohle
	CVN Abîme Mbr	CVN		Nohn	Mühlenberg
	CVN Foulerie Mbr	JEM Vieux Moulin Mbr	JEM Cimetière Mbr		Lauch
				Heisdorf	
Emsian	ENR	ENR	ENR		
	STJ	STJ	STJ		

**Fig. 2.** Formations in the Ardennes (southern border of Dinant Synclinorium, standard; BULTYNCK et al. 2000), Eifel (standard; BASSE 1996) and Endorf (Sauerland; BASSE 1996).

Member yielded a trilobite fauna inclusive of Proetidae (*Gerastos dhondtae* MAGREAN, 2007, *Cornuproetus* sp., *Dohmiella* sp.), Tropidocoryphidae (*Tropidocoryphe* sp.), Aulacopleuridae (*Cyphaspis* spp.), Lichidae (*Ohleum magreani* TAGHON, BONINO & MOTTEQUIN, 2012, *Ceratarges* sp.), Scutelluidae (*Goldius* spp., *Scabriscutellum* sp.), Harpetidae (*Harpes* sp.), and Phacopidae (*Austerops* cf. *couvinensis* sp. nov., *Phacops* sp., *Pedinopariops* sp.).

'Hampteau 086' locality; southeast of Hotton (Fig. 1) (not the same as the Hotton locality mentioned by

VAN VIERSEN et al. 2009). Coordinates are 50°15'21.6" N 5°28'01.2" W. This locality was a temporary outcrop during the foundation works of a house on the outskirts of Hampteau. Alternations of green-grey shales and nodular limestones were exposed that belong to the Chavées Member of the Jemelle Formation (DEJONGHE 2008). Trilobites were comparatively common in the shales yet poorly preserved as internal moulds. The material recorded herein stems from calcareous nodules, some of which enclosed clusters of articulated and well preserved trilobite specimens.

Disarticulated sclerites were rare in these nodules. The majority of phacopid trilobites were found in nodules, enrolled in various orientations. Of note is that most of these specimens have a pygidium that is forced into the body cavity. MCKELLAR & CHATTERTON (2009) reported similar observations on Devonian phacopids from Morocco and referred to SPEYER (1987) for forcible degassing as a likely cause.

Trilobites discovered at the Hampteau locality by two of us (BM, PT) include Proetidae (*Cornuproetus* sp., *Diademaproetus* cf. *menzeni* of VAN VIERSEN 2015, *Gerastos* sp.), Aulacopleuridae (*Cyphaspis* sp.), Phacopidae (*Austerops hottonensis* sp. nov., *Hottonops daumeriesi* gen. & sp. nov., *Geesops* sp., *Pedinopariops* sp.), and Odontopleuridae.

'Jemelle 026B' locality; east of Rochefort (Fig. 1). Coordinates are 50°15'56.4" N 5°26'05.4" W. The trilobite fauna is similar to that of the nearby 'Jemelle 004' locality from where VAN VIERSEN & PRESCHER (2008) reported at least 21 unique species. Phacopids are represented by *Geesops* sp., *Loreleiops suffeleersi* gen. & sp. nov., *Pedinopariops* sp., and *Phacops* sp.

### 3. Systematic palaeontology

The specimens were whitened with ammonium chloride prior to photography and are housed by the Natuurhistorisch Museum Maastricht (NHMM), Forschungsinstitut und Naturmuseum Senckenberg (SMF), and the Institut royal des Sciences naturelles de Belgique (IRSNB). Morphological terminology follows WHITTINGTON & KELLY (1997).

Phacopidae HAWLE & CORDA, 1847

Phacopinae HAWLE & CORDA, 1847

**Remarks:** The classification of late Early to early Middle Devonian phacopines similar to *Phacops* remains a topic of debate. For over a century the majority of species had been assigned to *Phacops* EMMRICH, 1839 until extensive splitting started in the 1970s. STRUVE (1972, 1976) erected many new subgenera; these were later promoted to generic rank by STRUVE (1982). The most extensive review of STRUVE's

concepts to date is that of BASSE (2006). MCKELLAR & CHATTERTON (2009) performed a cladistic analysis on Devonian phacopines with emphasis on Emsian and Eifelian taxa from Morocco. Several of STRUVE's genera were included in the analysis and most of these were sustained. However, little support was found for the various phacopine tribes proposed by STRUVE (see STRUVE 1995 for an overview). Hence we have refrained from their usage here.

#### Genus *Austerops* MCKELLAR & CHATTERTON, 2009

**Type species:** *Austerops kermi* MCKELLAR & CHATTERTON, 2009, from the late Emsian to Eifelian El Otfal Formation (Eifelian part) in Morocco, by original designation.

**Diagnosis:** Adopted from MCKELLAR & CHATTERTON (2009) with modification of the eye lens formula to include *Austerops hottonensis* sp. nov.: cephalic sculpture of low, sparse tubercles becoming more dense anteroventrally (coalescing into discontinuous terrace lines in some species), and fading upon lateral surfaces; doublure with prominent terrace lines continuous across most of surface. Eyes large to very large, with 16 to typically 18 vertical rows containing generalised maximum of 7-10 lenses (16-18/7-10), and thin interlensar sclera that thickens slightly dorsally; subocular and postocular pads weakly demarcated and form very narrow bands due to size of eye; lateral border furrow effaced. Glabella bulbous or gently sloping, but with minor anterior projection; divergence angle of frontal lobe usually 55-65°. Lobes and furrows effaced; S2 and S3 very faint; S1 fading medially, but deep laterally; L2 and L3 relatively flat; palpebral furrows faint or absent; ventral border non-marginulate; vincular furrow ranging from deeply incised to shallow in some species. Thorax and pygidium with subdued sculpture isolated to dorsal extremes, and with weakly defined lateral axial lobes and pleural ribs; pygidium with prominent inter-annular rings.

**Other species:** *Austerops couvinensis* sp. nov., middle Eifelian, Belgium; *Austerops hottonensis* sp. nov., middle Eifelian, Belgium; *Austerops legrandi* KHALDI, CRÔNIER, HAINAUT, ABBACHE & OUALI MEHADJI, 2016, upper Emsian, Algeria; *Austerops lemaitreae* HAINAUT, 2015, upper Emsian, Algeria; *Phacops menchikoffi* LE MAÎTRE, 1952, upper Emsian, Algeria; *Austerops punctatus* MCKELLAR & CHATTERTON, 2009, upper Emsian, Morocco; *Austerops salamander* MCKELLAR & CHATTERTON, 2009, Eifelian, Morocco; *Phacops (Phacops) speculator* ALBERTI, 1970, Eifelian?,

**Fig. 3.** *Austerops couvinensis* sp. nov. from the Jemelle Formation in Couvin 8011. **A-E, G** – Holotype, complete specimen, NHMM 2016 049, in dorsal view on cephalon (A), lateral view (B), dorsal view on thorax (C), oblique anterior view (D), anterior view (E) and dorsal view on pygidium (G). **F, H-K** – Paratype, complete specimen, NHMM 2016 050, in anterior view (H), ventral view on cephalon (I), dorsal view on pygidium (J) and dorsal view on cephalon (K). All scale bars indicate 3 mm.

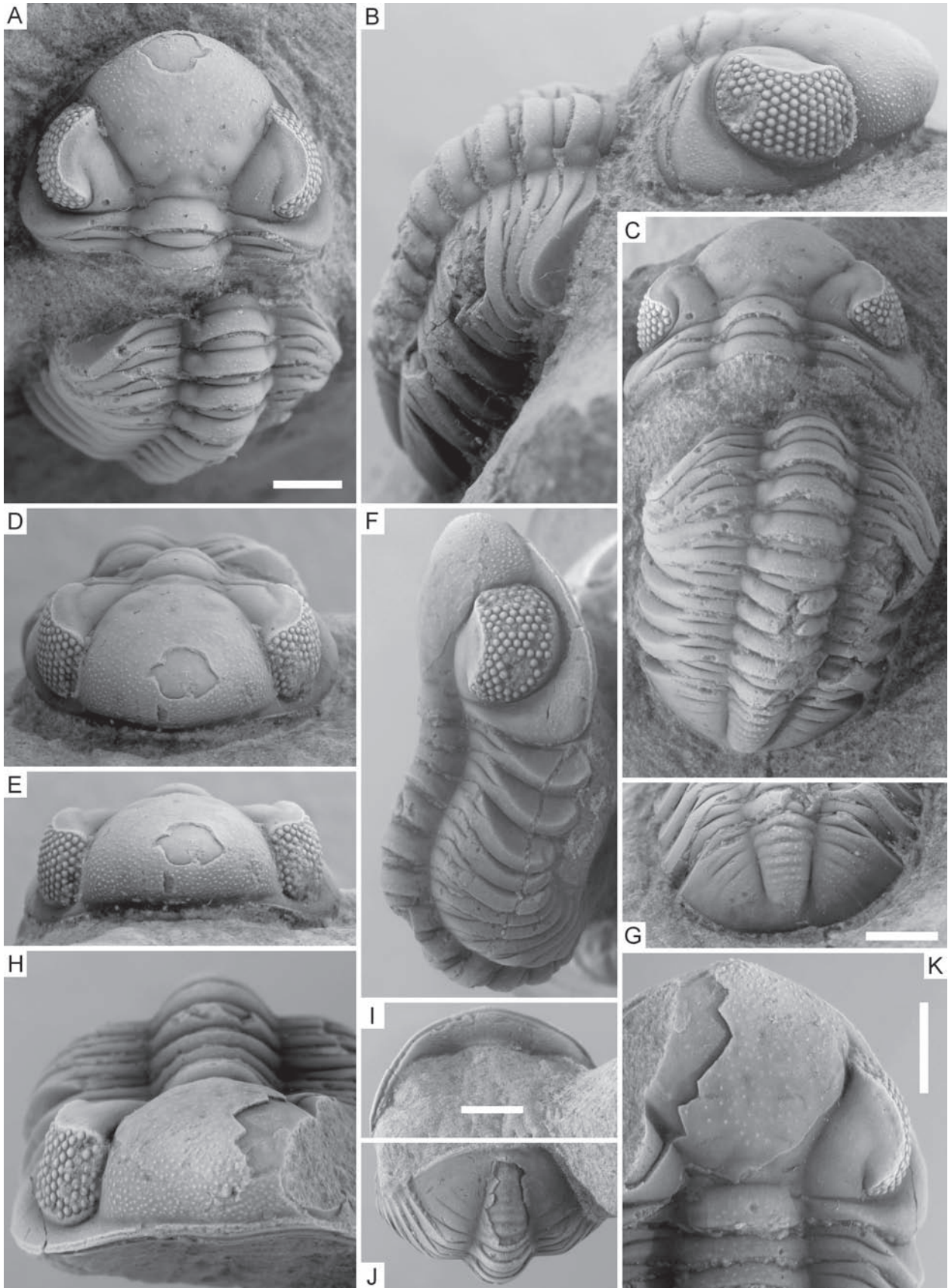


Fig. 3.

Morocco. Other taxa: *Austerops* cf. *couvinensis* sp. nov., middle Eifelian, Belgium; *Austerops* cf. *menchikoffi* (herein), upper Emsian, France; *Austerops speculator speculator* of KHALDI et al. (2016), upper Emsian, Algeria. Tentatively assigned: *Phacops* (*Chotecops*) *glabrens* CHLUPÁČ, 1977, Eifelian, Czech Republic; *Chotecops glabrens* ssp. of BASSE (1996), upper Emsian or lower Eifelian, Germany.

**Remarks:** The cladistic analysis of MCKELLAR & CHATTERTON (2009) revealed that *Austerops* species are united by sparse tubercles, an effaced lateral border furrow, a faint palpebral furrow and prominent and continuous terrace lines upon the doublure. Although its members show some of the characteristic features of other genera with reduced sculpture, MCKELLAR & CHATTERTON (2009) argued that *Austerops* is clearly distinct through the different glabellar proportions, doublure sculpture, and the size and position of the eyes upon the cephalon. These arguments are accepted herein although admittedly, *Austerops* shows a fair amount of variation in terms of eye size and position. Some of the basal members have comparatively small eyes that remain at a certain distance from the lateral cephalic border (compare, e.g., CHATTERTON et al. 2006, pl. 4, figs. 4, 8, pl. 5, fig. 10, pl. 6, fig. 12; Fig. 4A-D herein). In most stratigraphically higher species of *Austerops* the eye is of significantly increased size and located close to the lateral border (compare, e.g., MCKELLAR & CHATTERTON 2009, pl. 8, figs. 1, 2, 5, 6, 10; Fig. 3B, E, F herein). Eye size increase seems to be a general trend in *Austerops* for which there can be many reasons. With merely 16 dorsoventral files and a maximum of 7 lenses per file, the stratigraphically high *Austerops hottonensis* is clearly exceptional.

Heretofore, *Austerops* had only been recorded with certainty from Emsian to Eifelian strata in Morocco and Algeria. Its palaeogeographical distribution may be interpreted as northern Gondwanan (SCOTSE 2014). Along with the description of *Austerops* MCKELLAR & CHATTERTON (2009) pointed out that some of MORZADEC's (1969) material from Brittany could also belong to this genus. One of these taxa is assigned here to *Austerops* cf. *menchikoffi* and is believed by us to evidence the occurrence of *Austerops* in peri-Gondwana. The close similarities between *A.* cf. *menchikoffi* from France and *A. menchikoffi* from Morocco and Algeria suggests that these taxa are closely related. This observation may be of use to future interregional biostratigraphic correlations. *Austerops hottonensis* and *Austerops couvinensis* from Belgium represent the first evidence of members of

this genus in Avalonia. Still, *Austerops* appears to be restricted to the middle Eifelian of the Ardennes and could not be traced by us elsewhere north of the Rheic Ocean. This is remarkable since the exchange of trilobite associations on the southern and northern margins of the Rheic Ocean started at around the Pragian/Emsian boundary and continued far into the Devonian (e.g., BASSE & FRANKE 2006; BASSE et al. 2006; CHLUPÁČ & KOLÁŘ 2001; SCHRAUT & FEIST 2004; VAN VIERSSEN 2013, 2015; VAN VIERSSEN & PRESCHER 2009). While *Austerops* species already occurred in the upper Emsian of Gondwana and peri-Gondwana, the presently available data suggest that it took until the middle Eifelian for a member of the genus to cross the Rheic Ocean. Perhaps this relatively late timing might be explained by a strong facies preference or an above average dependency on suitable shallow-water migration routes in the closing Rheic Ocean. However, it must be recollected that Emsian strata in the Ardenno-Rhenish Mountains remain comparatively poorly prospected (VAN VIERSSEN 2015).

**Nomenclatorial notes:** HAINAUT's (2015) original spelling of *Austerops lemaitrii* is in conflict with the International Code of Zoological Nomenclature on the subject of the spelling of species-group names formed from personal names (article 31.1) and should be revised. This species was named after the French geologist and palaeontologist DOROTHÉE LE MAÎTRE (female); the name is changed here into *Austerops lemaitreae* accordingly.

*Austerops menchikoffi* is a senior subjective synonym of *Phacops smoothops* CHATTERTON, FORTEY, BRETT, GIBB & MCKELLAR, 2006, according to HAINAUT (2015) and KHALDI et al. (2016).

KHALDI et al. (2016) reported specimens from the upper Emsian of Algeria that they assigned to *Austerops speculator speculator*. However, we find that the Algerian material cannot be compared with ALBERTI's (1970) holotype from Morocco because the latter is too poorly preserved. For this same reason we consider *Austerops punctatus* – described by MCKELLAR & CHATTERTON (2009) as a subspecies of *A. speculator* – to be a distinct species, at least until more material of ALBERTI's species becomes available for comparison. MCKELLAR & CHATTERTON (2009) reported specimens of *A. punctatus* from the 'Treveropyge couche' and 'Lobopyge couche' in Morocco while referring to MORZADEC (2001) for an Eifelian age. However, MORZADEC regarded these levels basally in the El Otfal Formation as upper Emsian; we concur with the latter.

**Fig. 4. A-D** – *Austerops* cf. *menchikoffi* (LE MAÎTRE, 1952), silicone cast of external mould of cephalon, NHMM 2016 054, Kerdréolet Formation, Section K2, in dorsal (A), oblique anterolateral (B), anterior (C) and lateral (D) views. **E-G, K** – *Austerops hottonensis* sp. nov., holotype, complete specimen, NHMM 2016 053, Jemelle Formation, Hampteau 086, in dorsal view on cephalon (E), dorsal view on pygidium (F), lateral view (G) and oblique anterior view (K). **H-J** – *Austerops* cf. *couvinensis* sp. nov., complete specimen, NHMM 2016 052, Jemelle Formation, la Folie, in anterior (H), lateral (I) and dorsal (J) views. **L-N** – *Austerops couvinensis* sp. nov., paratype, juvenile complete specimen, NHMM 2016 051, Jemelle Formation, Couvin 8011, in dorsal view on pygidium (L), dorsal view on cephalon (M) and lateral view (N). All scale bars indicate 3 mm.

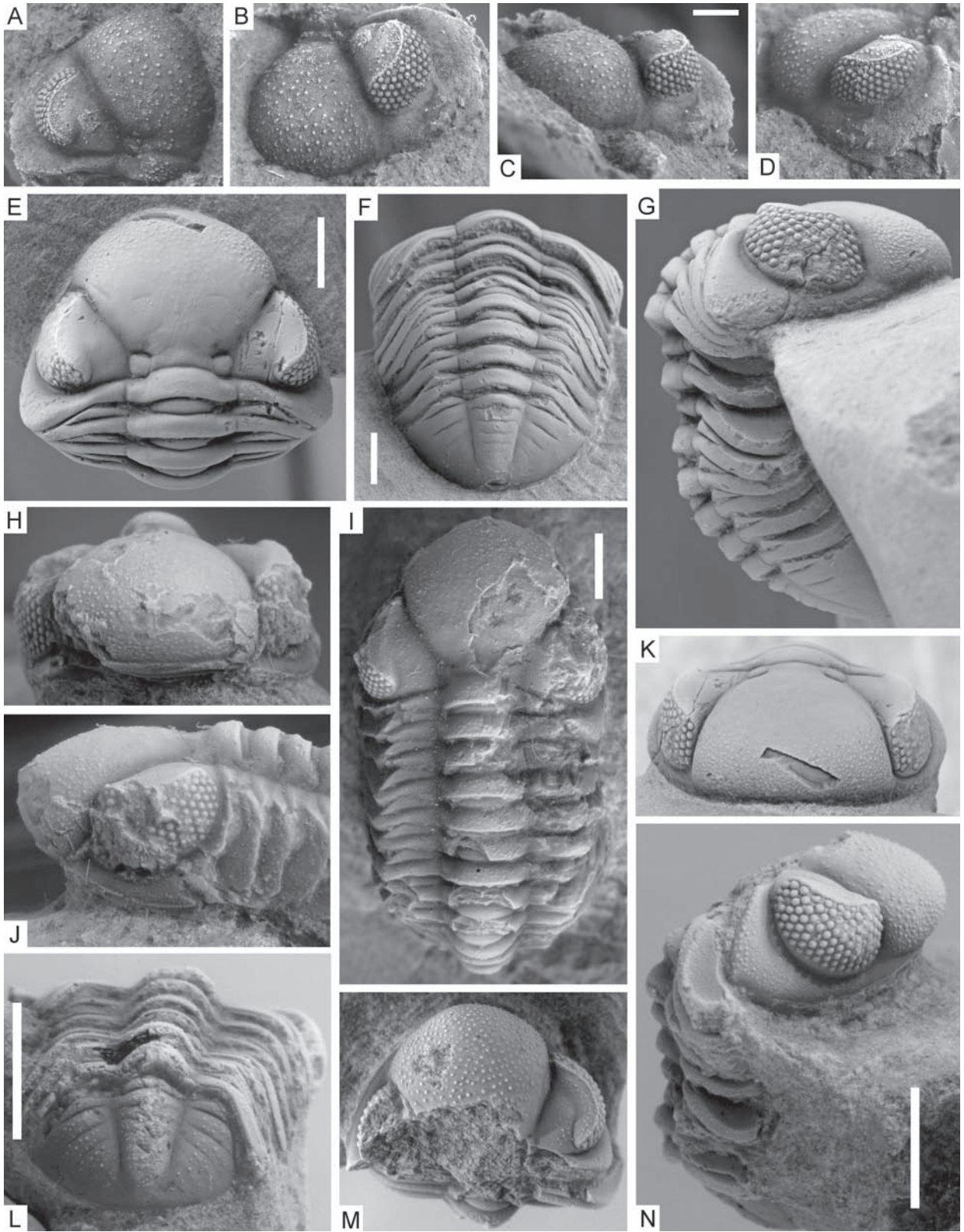


Fig. 4.

*Austerops couvinensis* sp. nov.

Figs. 3A-K, 4L-N

v 2014 *Pedinopariops* sp. – MAGREAN & TAGHON, p. 27, fig. 7.v 2015 *Austerops* – VAN VIERSSEN, p. 15.**Etymology:** After the type locality.**Holotype:** A complete specimen NHMM 2016 049 (Fig. 3 A-E, G).**Type locality:** ‘Couvin 8011’ locality in Couvin, Belgium.**Type horizon:** Chavées Member, Jemelle Formation.**Paratypes:** One complete specimen NHMM 2016 050; one juvenile complete specimen with damaged cephalon NHMM 2016 051.**Diagnosis:** Moderately widely spaced, small tubercles all over dorsal side of exoskeleton; these are scant on lateral glabellar lobes, palpebral area, thoracic anterior pleural bands and pygidial border; slightly larger tubercles on pygidial axial rings. L1 divided into two lobes separated by shallow, broad (exsag.) transverse depression. Palpebral furrow comparatively well-defined for an *Austerops* species. One or two well-defined, continuous terrace lines on the anterolateral cephalic border. Rounded-angular gena, typically bearing a small node.**Description:** Cephalon of rounded subtriangular outline. Occipital ring as high as glabella anterior to S0; bearing small tubercles centrally and posteriorly; deflated, weakly demarcated lateral lobes. Intercalating ring is separated from occipital ring by a narrow (sag., exsag.), firmly impressed furrow, laterally connected to L1, and not well demarcated anteriorly; bearing a few small tubercles. S1 short and very deep. S2 and S3 weakly impressed. Moderately large, dorsally flattened, only anteriorly and posteriorly distinctly demarcated L1 lateral lobes of angular outline. Axial furrows moderately shallow except anterior to S3 where they are deep; diverging at around 65°. Moderately weakly inflated glabella with rounded to somewhat anteriorly pointed outline and substantial anterior overhang; tubercles near anterior border transversely elongated; tubercles in front of the eyes exsagittally elongated. Moderately wide palpebral area. Crescent-shaped, palpebral lobe; centrally (exsag.) elevated and bearing a row of tubercles here; abaxially demarcated by a row of closely spaced tubercles. Visual surface consisting of 18 dorsoventral files with typically up to 8 lenses (rarely 9) per file (18/8-9). Lens formula of holotype (front to back): 6, 7, 8, 8, 8, 8, 8, 8, 7, 8, 7, 7, 6, 6, 4, 4, 2 = 120. Thin sclera horizontally between lenses in the upper part of the eyes, absent horizontally in the lower part of the eyes and vertically between lenses. Eye positioned close to lateral border. Gena bears small tubercles that are elongated (exsag.) lateral to anterior part of the eye. Glabellar cuticle moderately thin. Tubercles on glabella are barely visible on internal moulds.

Eleven thorax segments. Axial lobe as wide as pleural lobes; bearing small tubercles similar to those on occipital ring; lateral lobes smooth and only clearly defined anteriorly. Anterior pleural bands shorter than posterior pleural bands; bearing few granules (posterior thorax segments) or a row of pits along central line (tr.) (anterior thorax segments). Pleural furrow deep throughout; narrowing abaxially. Posterior pleural bands long and posteriorly curved, bearing similar ornament to anterior pleural bands.

Pygidium of broadly rounded outline. Long axis comprising 7-8 axial rings plus terminal piece. Anterior three rings W-shaped, indented posteromedially through the development of a small interannular ring. Posterior rings straight (tr.) separated by very weakly impressed interrering furrows. 3 distinct pairs of pleurae and about 2 additional weakly defined ones. First three pleural furrows much deeper than interpleural furrows which are faint everywhere. Moderately broad, smooth pygidial border; a single, continuous terrace line is developed on the posterior margin.

**Comparisons:** *Austerops couvinensis* bears many similarities to *A. kermi* and *A. salamandar* from Eifelian strata in Morocco. Those species can be discriminated from ours by their effaced palpebral furrow, the less steeply inclined visual surfaces (tr.), more numerous tubercles on glabella that form terrace lines, narrower palpebral area, and less pronounced pygidial axial sculpture. *Austerops kermi* furthermore has larger eyes (18/9-10), and shallower glabellar and axial furrows; *Austerops salamandar* has more inflated L1 and smaller eyes (18/7).**Remarks:** The genae of juveniles (small holaspides) are angular and bear a large genal node. In large holaspides the genae are rounded and bear a small node, although this last feature is not always developed (compare, e.g., Fig. 3F).*Austerops* cf. *couvinensis* sp. nov.

Fig. 4H-J

**Material:** One complete specimen (NHMM 2016 052) from the Chavées Member of the Jemelle Formation at the ‘La Folie’ locality in Couvin, Belgium.**Remark:** A single complete specimen was found. Although this is generally very similar to specimens of *Austerops couvinensis* from the same area, the poor preservation of the former precludes a detailed comparison.*Austerops hottonensis* sp. nov.

Fig. 4E-G, K

**Etymology:** After the type locality.**Holotype:** A complete specimen NHMM 2016 053 (Fig. 4E-G, K).



**Type locality:** ‘Hampteau 086’ locality near Hotton, Belgium.

**Type horizon:** Chavées Member, Jemelle Formation.

**Diagnosis:** Anteriorly arched occipital ring with inflated lateral lobes. Large eyes with comparatively few but large lenses; visual surface comprises 16 dorsoventral files with up to 7 lenses (16/7). Cephalon bears numerous small tubercles anteriorly on glabella and much weaker versions centrally between S2–S2 and S3–S3, on the posterior border, and along the outer edge of the palpebral lobe; otherwise smooth. Occipital plus thoracic and pygidial axial rings all bear small pits centrally. Posterior interranging furrows distally more firmly impressed than centrally. Broad pygidial axis.

**Description:** Widely rounded cephalon with glabella protruding anteriorly from cephalic outline. Occipital ring lower than glabella anterior to S0. Intercalating ring is very weakly inflated, separated from occipital ring by a narrow (sag., exsag.), firmly impressed furrow. S1 short and very deep. S2 and S3 moderately weakly impressed. Moderately large, inflated, isolated L1 lateral lobes of angular outline. Axial furrows deep anterior to S3; diverging at around 70°. Comparatively large, moderately inflated but distinctly demarcated L1 lateral lobes of angular outline. Moderately weakly inflated glabella with slight anterior overhang. Moderately wide palpebral area. Palpebral furrow effaced. Anteriorly slightly downwardly tilted eye; thick sclera horizontally between lenses in the upper part of the eyes, absent horizontally in the lower part of the eyes, and rudimentary vertically between lenses. Lens formula (front to back): 5, 6, 7, 7, 7, 7, 7, 6, 6, 5, 5, 4, 3, 2 = 91.

Eleven thorax segments. Axial lobe slightly wider than pleural lobes; bearing small pits centrally and posteriorly similar to those on occipital ring; lateral lobes only very weakly developed on first axial ring, otherwise not discernible. Anterior and posterior pleural bands with smooth surface dorsally.

Pygidium of broadly rounded outline. Long axis comprised of 7 rings plus terminal piece. Anterior axial rings are W-shaped but without the development of an interannular ring (not well visible between first two axial rings in the holotype which is damaged here). 4 pairs of pleurae; a 5th pair is barely developed. First two pleural furrows much deeper than interpleural furrows which are faint everywhere. Moderately broad, smooth pygidial border bearing a few pits; a single, continuous terrace line is developed on the posterior margin.

**Comparisons:** The morphologically closest species to *Austerops hottonensis* is probably *Austerops salamander* from Morocco. The new species is distinct from the latter, and from *A. kermiti* and *A. couvinensis*, in the following features: anteriorly arched occipital ring, smaller eyes, tubercles restricted to the anterior part of the glabella and posterior border, occipital plus thoracic and pygidial axial rings bearing pits instead of tubercles, and broader pygidial axis.

*Austerops* cf. *menchikoffi* (LE MAÎTRE, 1952)

Fig. 4A–D

1969 *Phacops* sp. B cf. *fecundus degener.* – MORZADEC, pp. 9, 15, 27, pl. 3, fig. 6, pl. 4, figs. 3, 4, 12.

**Material:** One external mould of a cephalon plus silicone cast (NHMM 2016 054) from the basal part (section K2 of MORZADEC 1983) of the Kerdréolet Formation (upper Emsian) at Kerdréolet en l’Hôpital-Camfrout, Brittany, France.

**Remarks:** The Kerdréolet Formation is interpreted as a distal offshore setting in the middle of a major transgressive cycle that commenced in the upper Pragian (GUILLOCHEAU 1991; LARDEUX et al. 2003). Various locations in the vicinity of the rade de Brest were sampled by two of us (BM, PT) but to date *Austerops* cf. *menchikoffi* remains the sole representative of this genus discovered there. It should be noted, however, that tectonic deformation and unfavourable taphonomic conditions often make it difficult to identify the phacopids of the rade de Brest (see, e.g., MORZADEC 1969; HOFFMAN et al. 2014).

MORZADEC’s (1969) material and our cephalon are similar to specimens of *Austerops menchikoffi* recorded from the upper Emsian in Morocco and Algeria by CHATTERTON et al. (2006) and KHALDI et al. (2016), respectively. The cephalon figured herein counts fewer lenses; from front to back: 3, 4, 5, 5, 6, 5, 5, 5, 4, 4, 4, 4, 3, 3, 2, 2, 1 = 69.

#### Genus *Hottonops* nov.

**Etymology:** Combination of ‘Hotton’ (the origin of the type species) and ‘ops’ (Greek: eye), a common suffix for phacopine genus names.

**Type species:** *Hottonops daumeriesi* gen. & sp. nov., from the early to late Eifelian Jemelle Formation (middle Eifelian part) in Belgium.

**Other species:** Only the type species. Tentatively assigned are *Geesops?* sp. E and *Geesops?* sp. nov. L of BASSE (2006), middle Eifelian, Germany.

**Diagnosis:** As for the type species.

**Comparisons:** The dorsoventrally low cephalic to pygidial axial morphology of *Hottonops daumeriesi* is unlike any known phacopine from the Ardenno-Rhenish Mountains. *Austerops* and *Loreleiops* must be compared in view of their evenly subdued sculpture. However, the cephalic proportions of these genera are principally different and the new genus can easily be discriminated by its weakly vaulted and anteriorly downward sloped glabella and palpebral lobes, smaller eyes with fewer lenses, tiny L1, pronounced postocular pads, and very weakly vaulted (tr.) thoracic and pygidial axes.

*Geesops* STRUVE, 1972 has a similarly shaped, pitted genal angle and slightly more lenses in the eye (usually 18/6 as opposed to 18/4-5) but it is otherwise distinct from *Hottonops* in having a higher cephalic outline, inflated and well-demarcated intercalating ring, strongly vaulted glabella, the absence of a postocular pad, a narrower palpebral area, numerous pronounced tubercles all over the dorsal exoskeleton and often a distinct row of tubercles on the posterior cephalic border. BASSE (2006) reported *Geesops?* sp. E and *Geesops?* sp. nov. L from the Rhenish Mountains. His specimens bear some similarities to *H. daumeriesi* such as the fully effaced S2 and S3, lens formula 18/4, and the weakly vaulted pygidial axis, but their limited preservation makes it difficult to assess their affinity with the new genus. BASSE (2006) assigned these and other potential *Geesops* species with reduced eye size to his *Geesops?* *dolosus* (STRUVE, 1970) group. At the same time he pointed out that there is significant morphologic disparity within the group and that all of its members occur in transgressive facies (event equivalent). Thus, he assumed that the generally reduced eye size may be the result of convergent evolution. Our tentative assignments of *G.?* sp. E and *G.?* sp. nov. L to *Hottonops*, as opposed to some of the other members of the *dolosus* group which have pronounced tubercles, appear to be in line with BASSE's remarks.

*Hottonops daumeriesi* gen. & sp. nov.

Fig. 5A-E, G, H

**Etymology:** Named after the late GUY DAUMERIES, in recognition of his friendship and extensive knowledge about the Devonian macrofauna of the Ardennes.

**Holotype:** A complete specimen NHMM 2016 055 (Fig. 5 A-E, G, H).

**Type locality:** 'Hampteau 086' locality near Hotton, Belgium.

**Type horizon:** Chavées Member, Jemelle Formation.

**Diagnosis:** Very weakly vaulted (tr.) phacopine with slightly dorsally arched thoracic and pygidial axes. Intercalating ring fully deflated. Cephalic border only clearly demarcated by a border furrow anterior to the glabella, and mostly

recognisable by few, continuous terrace lines. S2 and S3 completely effaced. Glabella and palpebral lobes markedly downward sloped towards the front. Central part of glabella smooth, bearing very few, randomly scattered pits; frontal part bears an alternation of large pits and terrace lines; these lines are border parallel except medially near anterior border where they are randomly oriented. Palpebral lobe is much lower than palpebral area. Eyes typically with 18 dorsoventral files and a maximum of 4 (occasionally a small fifth may be developed; compare Fig. 5 H) lenses per file (18/4-5). Thoracic axis without the development of lateral lobes. Pygidial axis hardly ascending above pleural fields.

**Description:** Cephalon of widely rounded subtrapezoidal outline. Low occipital ring, slightly wider than distance across L3-L3; lateral lobes not developed. Intercalating ring smooth; only distinctly demarcated posteriorly by occipital furrow. Axial furrows divergent at around 65°. Comparatively small, moderately inflated L1 lateral lobes of angular outline. Very weakly inflated glabella with slight anterior overhang. Wide palpebral area. Palpebral furrow completely effaced. Anteriorly downwardly tilted eye; thin sclera horizontally between lenses in the upper part of the eyes, absent horizontally in the lower part of the eyes, and rudimentary vertically between lenses. Lens formula (front to back): 2, 3, 4, 4, 4, 4, 5, 4, 5, 4, 4, 3, 4, 3, 3, 2, 2, 1 = 61. Ornament: generally smooth, except for occipital ring, posterior border, abaxial part of palpebral lobe, genal field and anterior half of glabella, which all bear pits. Pits on glabella increase in size anteriorly. Abaxial margin of palpebral lobe devoid of tubercles.

Eleven thorax segments. Axial lobe narrower than pleural lobes; bearing few pits posteriorly. Anterior pleural bands short; bearing few pits. Pleural furrows deep throughout. Posterior pleural bands long and comparatively weakly posteriorly curved; bearing numerous pits.

Weakly vaulted pygidium of widely rounded outline. Moderately long axis comprising 7 axial rings plus terminal piece. Anteriormost ring slightly indented posteromedially but an interannular ring is not developed. Remaining rings fairly straight. Posterior interring furrows very weakly impressed. 5 pairs of pleurae plus a 6th rudimentary pair. Pleural furrows are not developed. Towards posterior each consecutive interpleural furrow is more effaced. Ornament: similar as on thorax. Additionally, few tubercles are concentrated centrally on the axis; border covered with closely spaced pits.

**Fig. 5. A-E, G, H** – *Hottonops daumeriesi* gen. & sp. nov., holotype, complete specimen, NHMM 2016 055, Jemelle Formation, Hampteau 086, in lateral view (A), anterior view (B), dorsal view on cephalon (C), oblique anterolateral view on cephalon (D), dorsal view on pygidium (E), close-up of right anterior part of glabella (G), close-up of right eye (H). **F, J, K** – *Loreleiops hoelleri* (VAN VIERSEN, PRESCHER & SAVELSBERGH, 2009), holotype, complete specimen, IRSNB a12671, Ahrdorf Formation, "Trilobitenfelder" (Gees, Eifel), in dorsal view on cephalon (F), lateral view on cephalon (J) and dorsal view on pygidium (K). **I, L, M** – *Loreleiops? simulator* (BASSE, 1998), holotype, complete specimen (silicone cast of external mould), SMF 79908a+b, Meinkenbracht Formation, Endorf (Sauerland), in dorsal (I), lateral (L) and posterior (M) views. All scale bars indicate 3 mm.

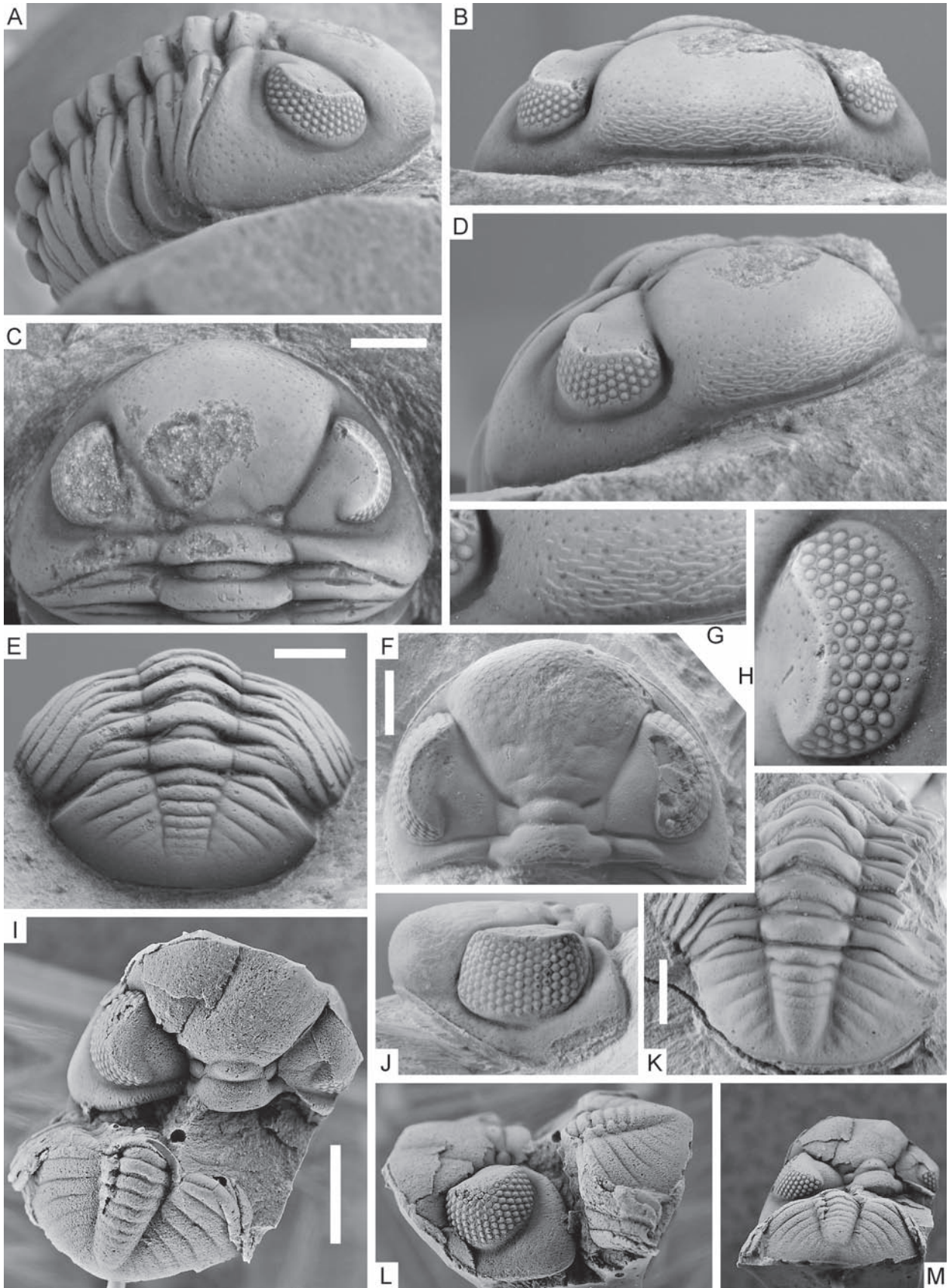
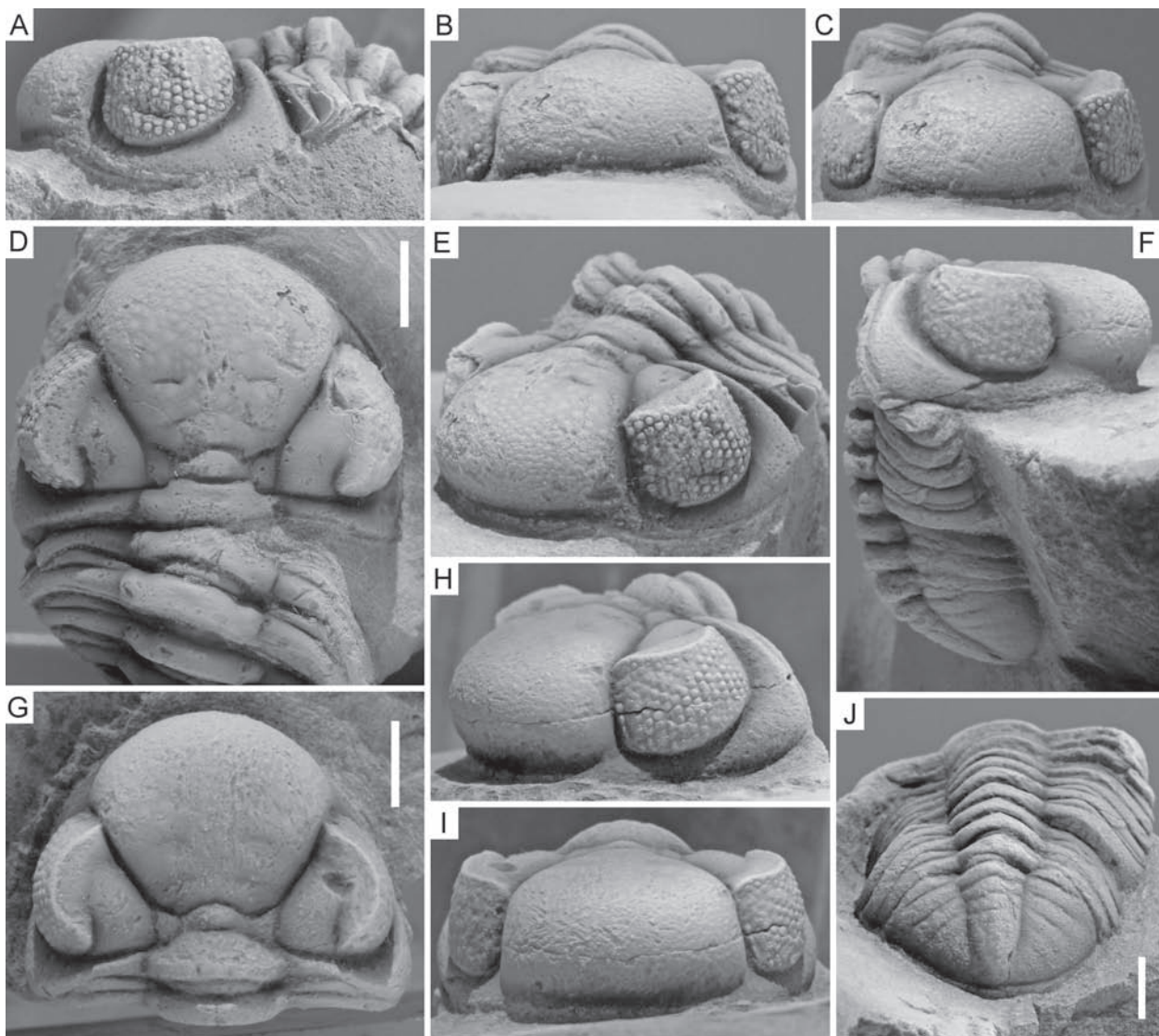


Fig. 5.



**Fig. 6.** *Loreleiops suffeleersi* gen. & sp. nov. from the Jemelle Formation in Jemelle 026B. **A-E** – Holotype, cephalon with thorax, NHMM 2016 056, in lateral (A), anterior (B), oblique anterior (C), dorsal (D) and oblique anterolateral (E) views. **F, H-K** – paratype, complete specimen, NHMM 2016 057, in lateral view (F), dorsal view on cephalon (G), oblique anterolateral view (H), oblique anterior view (I) and dorsal view on pygidium (J). All scale bars indicate 3 mm.

#### Genus *Loreleiops* nov.

**Etymology:** Combination of ‘Lorelei’, a German mythological figure from the Rhineland, and ‘ops’.

**Type species:** *Pedinopariops hoelleri* VAN VIERSEN, PRESCHER & SAVELSBERGH, 2009, from the Gees Subformation of the Ahrdorf Formation (middle Eifelian) at the classic “Trilobitenfelder” locality near Gees (see VAN VIERSEN et al. 2009) in Germany.

**Other species:** *Loreleiops suffeleersi* gen. & sp. nov., mid-

dle Eifelian, Belgium. Tentatively assigned is *Pedinopariops simulator* BASSE, 1998, basal Givetian, Germany.

**Diagnosis:** Large, dorsoventrally low occipital ring bearing pits posteromedially. Intercalating ring large, weakly vaulted, poorly demarcated laterally. L1 large, dorsally flattened, longer (exsag.) than wide (tr.). Glabella is dorsally flattened, forming a horizontal plane along with the palpebral lobes, palpebral area and occipital ring; anterior part of glabella bears a mixture of large, weakly inflated tubercles, accentuated by short terrace lines and alternated by pits. Palpebral area bears numerous pits; otherwise devoid of ornament.

Massive, smooth, uniformly vaulted palpebral area. Sclera between lenses in the dorsal half of the eye not any thicker than in ventral half. Pygidium entirely covered with densely spaced pits. Posterior thoracic and anterior pygidial axial rings bear a ridge-like bulge anteromedially, which may be accentuated by several tubercles.

**Comparisons:** *Loreleiops* encompasses species that were originally assigned to *Pedinopariops* STRUVE, 1972. As currently perceived, *Pedinopariops* includes a wide variety of taxa from the upper Emsian to Givetian of Germany, Belgium and the Czech Republic, with comparatively large eyes, thin dorsal cuticle and glabellar ornament consisting of numerous pronounced, rounded to dome-shaped tubercles. BASSE (2006) and VAN VIERSEN (2007) expressed their doubts about the monophyly of *Pedinopariops* and a critical review of this genus would be timely indeed. The cladistic analysis of MCKELLAR & CHATTERTON (2009) included the type species of *Pedinopariops*, *P. lentigifer* (STRUVE, 1970) from the middle Eifelian in the Eifel. None of the other species assigned to this genus (see BASSE 2006) were coded and so that analysis did little to resolve the ingroup structure of *Pedinopariops*. BASSE (2006, pl. 15, figs. 147-151, pl. 16, figs. 152-161) figured well-preserved specimens of *P. lentigifer*. These and other species of *Pedinopariops* are easily distinguished from *Loreleiops* in having a weakly inflated, narrow (tr.) palpebral area, small L1, dome-shaped, isolated intercalating ring, smaller visual surface with well-developed interlensar sclera, and a smoothly rounded glabella (sag.). Only specimens assigned to *Pedinopariops brongniarti* (STEININGER, 1831) by BASSE (2006) from the middle Eifelian in the Eifel have similarly large eyes. This species also has posteriormost point of ocular suture ( $\epsilon$ ) aligned (tr.) with centre of the occipital ring, but it is otherwise morphologically much closer to other members of *Pedinopariops*.

The similarities of *Loreleiops* to *Austerops* are mostly restricted to the generally reduced sculpture and the shape of L1. *Loreleiops hoelleri* (comb. nov.) and *L. suffeleersi* have large eyes that are positioned close to the lateral border. As discussed above, this is a widespread feature in Eifelian species of *Austerops* but it is also shown by all species of *Pedinopariops*. For the rest *Loreleiops* species are so distinctive that their inclusion in *Austerops* would almost certainly render the latter polyphyletic. Differences include the large but weak, bladder-like tubercles centrally on the dorsally flattened, angular (lateral view) glabella of *Loreleiops*, the massive palpebral area, firmly impressed S2 and S3 lateral glabellar furrows, rudimentary interlensar sclera, the presence of large pits (instead of small tubercles) all over the dorsal exoskeleton except centrally on the glabella and in the palpebral area, and the lack of pygidial interannular rings. Further evidence in support of the independent generic ranks of *Loreleiops* and *Austerops* comes from their unique late ontogenies. Small holaspid cephalons of *Austerops* are covered with numerous granules. This is demonstrated by juvenile specimens of *A. menchikoffi* (compare CHATTERTON et al. 2006, pl. 6, figs. 1, 2, 4) and *A. couvinensis* (compare Fig. 4M, N). Those granules are transformed into small tubercles in large holaspides (e.g., *A. menchikoffi*) or they disappear fully (e.g., *A. kermi*). A juvenile cephalon of *L. hoelleri* illustrated by VAN VIERSEN et al. (2009, pl. 1,

figs. 2, 4, 5) fully lacks such granules. Instead, its sculpture consists of large but weakly pronounced, flattened tubercles that are not different from those of large holaspides.

There are two other phacopines with subdued sculpture that should be compared to *Loreleiops*. These are *Chotecops* CHLUPÁČ, 1971 from the Eifelian of the Czech Republic, Morocco and Germany and *Arduennops* STRUVE, 1972 from the upper Emsian of Luxembourg and Germany. Members of both these genera are readily discriminated from the new genus in having much smaller eyes that are positioned farther from the lateral border, thicker interlensar sclera, and numerous small tubercles all over the cephalon. According to BASSE (2006) *Chotecops* and *Arduennops* are difficult to distinguish from one another. Future investigations may point out that those genera are synonyms.

*Loreleiops? simulator* (comb. nov.) from the Meinckenbracht Formation (Givetian part; Fig. 2) near Endorf (Sauerland) is not as well-preserved as the material of *L. hoelleri* from Gees but appears to bear most of the characteristic features of this genus. Additional photos of the holotype are illustrated here for comparison (Fig. 5I, L, M). BASSE (1998: 21) reported specimens of various stratigraphic origins in the Sauerland that he tentatively assigned to this same species. These must be examined in order to assess whether they belong to the new genus.

*Loreleiops suffeleersi* gen. & sp. nov.  
Fig. 6A-J

**Etymology:** Named after TIM SUFFELEERS, the discoverer of the holotype.

**Holotype:** A cephalon with thorax NHMM 2016 056 (Fig. 6A-E).

**Type locality:** 'Jemelle 026B' locality near Rochefort, Belgium.

**Type horizon:** Chavées Member, Jemelle Formation.

**Paratype:** One complete specimen NHMM 2016 057.

**Diagnosis:** Occipital ring posteriorly ascending. Intercalating ring well demarcated anteriorly by deep furrow. L1 well demarcated abaxially by deep furrow. Eyes overhanging lateral border (dorsal view), with visual surface typically containing 18 dorsoventral files and a maximum of 9 lenses per file (18/9). Subocular and postocular pads rudimentary. Lateral border narrow (tr.) lateral of eye. Glabella with significant anterior overhang. Broad (sag., exsag.) anterior border furrow.

**Comparison:** This species is similar to *Loreleiops hoelleri* described by VAN VIERSEN et al. (2009) from coeval strata in the Eifel. The differences are subtle but so numerous that we decided to designate a new species for the Belgian material. Among these differences are the more anteriorly overhanging glabella of *Loreleiops suffeleersi* and the more firmly incised axial and lateral glabellar furrows near the

intercalating ring and L1. Furthermore, the gena is much more angular (as against smoothly rounded) and the lateral border remains closer to the eye. Other differences include the larger eyes (>140 lenses as against ~121-127 lenses in *L. hoelleri* as according to VAN VIERSEN et al. 2009), posteriorly ascending occipital ring (this feature appears to be particularly well developed in a small holaspide of *L. hoelleri* that was illustrated by VAN VIERSEN et al. 2009, pl. 1, figs. 2, 4, 5), less pronounced subocular and postocular pads, and the fully developed anterior border furrow.

#### 4. Conclusions

Phacopids with subdued sculpture from the upper Emsian to Eifelian of the Ardenno-Rhenish Mountains have previously been referred to *Arduennops*, *Chotecops* and *Pedinopariops*. Based on our investigations, at least four genera with reduced sculpture can be identified there: *Arduennops*, which is restricted to upper Emsian strata in Luxembourg and Germany; *Loreleiops*, which is restricted to the middle Eifelian (and possibly basal Givetian) of Belgium and Germany; the monotypic *Hottonops* which is restricted to the middle Eifelian of Belgium (however, see list of tentatively assigned taxa from Germany above); and *Austerops*, species of which occur in the middle Eifelian of Belgium. Heretofore, *Austerops* had been regarded as Gondwana-exclusive. The herein recorded species represent the first evidence of this genus from the Ardenno-Rhenish Mountains, thus extending its palaeogeographic distribution to Avalonia. *Austerops* cf. *menchikoffi* is the sole confirmed member of *Austerops* from France and demonstrates the occurrence of this genus in peri-Gondwana during the upper Emsian. Both *Austerops* and *Loreleiops* have a very limited stratigraphic range in the Ardenno-Rhenish Mountains; this may indicate a strong dependency on palaeoenvironmental conditions that remain to be identified.

Despite recent advances in phacopid research a lot of work remains ahead. The cladistic analysis performed by MCKELLAR & CHATTERTON (2009) has provided a sound basis for future investigations. Future studies should include a wider range of genera and species in order to come to a more comprehensive understanding of phacopid evolution in the Rheic Ocean during the Devonian.

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