Anopolenus henrici Salter, a middle Cambrian (Drumian) centropleurid trilobite from the Alum Shale Formation of Scandinavia

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Centropleurid trilobites include five genera of which *Centropleura* Angelin, *Anopolenus* Salter, *Clarella* Howell and *Luhops* Šnajdr are known from eight species in the traditional middle Cambrian (Miaolingian Series, Drumian Stage) of Sweden and Denmark (Bornholm). *Beishanella* Xiang & Zhang has not been recorded in Scandinavia so far, and no centropleurids have been reported from Norway. Of these taxa, only *Centropleura* is common in Scandinavia. Two pygidia previously identified as *Centropleura* sp. and *Anopolenus* sp. from erratics in Germany and Bornholm, respectively, as well as a new pygidum from Scania in Sweden are here identified as *Anopolenus henrici* Salter. Elsewhere, the species is known from Wales, Avalonian Canada, Siberia, Alaska, and Sardinia, occurring in the *A. atavus* and *P. punctuosus* zones (the former in Siberia only). The presence of this species increases the known diversity of Centropleuridae in Scandinavia and is important for correlation between Baltica and Avalonia.

Keywords: Centropleurid trilobite, Miaolingian, Drumian, Alum Shale Formation, Bornholm, Scania, Scandinavia.

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New specimens of *Anopolenus henrici* Salter from Scandinavia (Fig. 1) give fresh insight into the morphology and distribution of centropleurid trilobites. The Miaolingian family Centropleuridae Angelin 1854 includes *Centropleura* Angelin 1854, *Beishanella* Xiang & Zhang 1985, *Anopolenus* Salter 1864, *Clarella* Howell 1933 and *Luhops* Šnajdr 1957 (Dean & Rushton 1997; Fortey & Rushton 2007) (Fig. 2). In Scandinavia, only *Centropleura* is common; *Anopolenus*, *Clarella* and *Luhops* are known from rare findings, while *Beishanella* has not been encountered.

Centropleura is represented in Scandinavia by three species: *C. lovéni* (Angelin 1851) (Sweden and Bornholm, Denmark) and *C. angelini* Westergård 1950 (Sweden), both from the lower part of the *Lejopyge laevigata* Zone (formerly *Solenopleura brachymetopa* Zone) and *C. angustata* Westergård 1950 (Sweden), probably originating from the *Ptychagnostus punctuosus* Zone (Westergård 1950). *Anopolenus* is known from one pygidium in the upper part of the *Acidusus atavus* Zone on Bornholm (Weidner & Nielsen 2014), where also *Clarella impar* (Hicks 1872) occurs frequently in the uppermost part of the same zone (Weidner & Nielsen 2014). Additional species of *Clarella* on Bornholm are *C. groenwalli* Howell & Poulsen 1933 (? = *Luhops expectans*, see below) known from one cranidium in the *P. punctuosus* Zone, and *C. steenstrupi* (Angelin 1878) known from the lower part of the *L. laevigata* Zone. Westergård (1950) reported a single cranidium of *Clarella* cf. *impar* from the *P. punctuosus* Zone at Andrarum, Scania, Sweden. *Luhops expectans* (Barrande 1852) is known from one fragmentary pygidium reported from the upper part of the *A. atavus* Zone on Bornholm (Weidner & Nielsen 2014), but it is noted that Rushton (2011) questionably reassigned *C. groenwalli* to *L. expectans*. Centropleurid trilobites have not been described from Norway so far, but one damaged pygidium of *Luhops* has been found in the *A. atavus* Zone of the Oslo Region in Norway (M. Høyberget, personal communication 2018). For world-wide distribution of the Centropleuridae, we refer to Dean & Rushton (1997) and Rushton (2011).

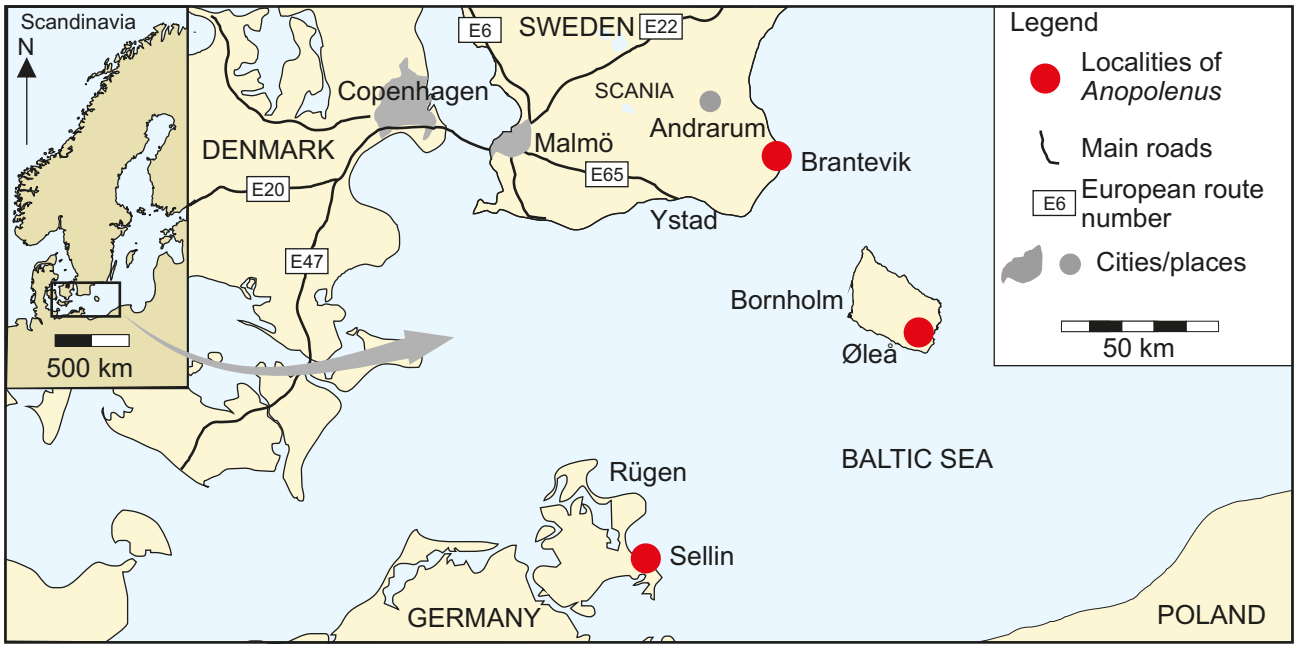

Fig. 1. Map of southern Sweden and northern Germany showing the localities mentioned for the material described herein.

Chronostratigraphy				Trilobite biostratigraphy			Ranges of Centropleuridae in Scandinavia
System	Series	Global Stage	Local Stage	Superzones	Polymerid Zonation	Agnostoid zonation	
Cambrian	Miaolingian	Guzhangian	Not defined	*Paradoxides forchhammeri*	*Simulolenus alpha*	*Agnostus pisiformis*	
					Not defined	*Lejopyge laevigata*	
					Solenopleura? brachymetopa		
		Drumian	Almbackenian	*Paradoxides paradoxissimus*	Not defined	*Goniagnostus nathorsti*	
					Paradoxides davidis	*Ptychagnostus punctuosus*	
					Bailiella ornata	*Acidusus atavus* Upper	
						Lower	
		Wuliuan			*Ctenocephalus exsulans*	*Triplagnostus gibbus*	
			Bödan	*Acadoparadoxides oelandicus*	*Acadoparadoxides pinus*	*Pentagnostus praecurrens*	
					Eccaparadoxides insularis	Not defined	

Fig. 2. Biozonation of the Miaolingian Series with ranges and occurrences of Centropleuridae in Scandinavia. Occurrences are given with S = Sweden, B = Bornholm. The ranges of the different taxa are colour coded for clarity. Revised zonation according to Weidner & Nielsen (2015); regional stages according to Nielsen & Schovsbo (2015).

Howell (1933) used the curvature of the palpebral lobes to differentiate the genera and this approach was adopted by Dean & Rushton (1997). Westergård (1950) observed the same difference between *Centropleura* and *Anopolenus* but pointed out that it was less marked in juvenile specimens. Most of the illustrations of *A. henrici* show cranidia. Complete specimens have been figured as well (Egorova *et al.* 1982; Levi-Setti 1993), while other complete specimens are displayed on private homepages, but illustrated pygidia are scarce and the photos are generally of low standard and quality.

Two pygidia previously referred to *Centropleura* sp. (Buchholz 1991; Rudolph 1994) and *Anopolenus* sp. (Weidner & Nielsen 2014) and an additional new specimen are now identified as *Anopolenus henrici* and described herein. The presence of this species

increases the known diversity of Centropleuridae in Scandinavia and is important for the correlation between Baltica and Avalonia.

Illustrated and cited material is housed in the collections at the Natural History Museum, University of Copenhagen (MGUH), the Palaeontological collections, Museum of Evolution, Uppsala University, Sweden (PMU), the collection of Buchholz, Stralsund (SB-MK), and the Sedgwick Museum of Earth Sciences, Cambridge, England (SM).

Systematic palaeontology

Family Centropleuridae Angelin 1854

Genus *Anopolenus* Salter 1864

Type species (by monotypy). *Anopolenus henrici* Salter 1864; Menevian Beds (*Hypagnostus parvifrons* and *Ptychagnostus punctuosus* agnostoid zones), St. David's, Wales.

Diagnosis. See Lake (1934) and Dean & Rushton (1997).

Anopolenus henrici Salter 1864
Figure 3A1–C4

1864 *Anopolenus henrici* n.sp. – Salter, p. 236, pl. 13, figs 4–5.
1865 *Anopolenus henrici* Salter – Salter, pp. 476–477, 480–482, figs 2–3.
1865 *Anopolenus salteri* n.sp. – Hicks, pp. 477–480, fig. 1.
1934 *Centropleura henrici* (Salter) – Lake, pp. 189–192, pl. 24, figs 1–12.
1962 *Anopolenus henrici* Salter – Hutchinson, p. 112, pl. 17, figs 12–18.
1982 *Anopolenus henrici* Salter – Egorova *et al*., p. 78, pl. 6, figs 8–9; pl. 10, figs 1–2; pl. 12, fig. 14; pl. 13, figs 1–3; pl. 14, fig. 4; pl. 15, figs 6–7; pl. 17, figs 9–11; pl. 56, fig. 9; pl. 61, fig. 8.
1991 *Centropleura* sp. – Buchholz, p. 220, pl. 2, fig. 9.
1993 *Anopolenus henrici* Salter – Levi-Setti, pl. 95.
1994 *Centropleura* sp. 1 – Rudolph, p. 176, pl. 18, fig. 14.
cf. 1995 *Anopolenus* cf. *Henrici* – Loi *et al*., pl. 4, fig. 21.
1995 *Anopolenus henrici* Salter – St. John & Babcock, fig. 7J.
1997 *Anopolenus henrici* Salter – Dean & Rushton, pp. 478–479, fig. 309:2a–c.
2014 *Anopolenus henrici* Salter – Rees *et al*., figs 1.11a, 1.12c, f.
2014 *Anopolenus* sp. – Weidner & Nielsen, p. 70, fig. 42L.
2016 *Anopolenus henrici* Salter – Bushuev & Makarova, p. 21, pl. 2, fig. 4.

Lectotype (designated by Morris 1988). Latex cast of external mould of a cephalon, SM A5367, from the *Ptychagnostus punctuosus* Zone at Porth-y-rhaw, Wales. It was originally figured by Lake (1934, pl. 24, fig. 1).

Occurrence. Anopolenus henrici is previously reported from Wales (Lake 1934; Rees *et al*. 2014), Avalonian Canada (Hutchinson 1962; Levi-Setti 1993) and Siberia (Egorova *et al*. 1982; Bushuev & Makarova 2016). It is very rare in Alaska (St. John & Babcock 1995) and on Sardinia, Italy (Loi *et al*. 1995). In Siberia, the species occurs in the lower and upper part of the *A. atavus* Zone; in the other areas in the *P. punctuosus* Zone or equivalent strata.

Material. Three pygidia are available (Fig. 3). One is from the upper part of the *Acidusus atavus* Zone at Øleå, Bornholm, Denmark (Fig. 3A_1–A_4, 0.62 cm long) (MGUH 30155, figured by Weidner & Nielsen 2014, fig. 42L as *Anopolenus* sp.). The second is from an ice-rafted limestone block found at Sellin on the island of Rügen, Germany, with provenance from the Bornholm area (figured by Buchholz 1991, pl. 2, fig. 9, SB-MK 143.53, and Rudolph 1994, pl.18, fig. 14 as *Centropleura* sp.; a cast is kept at the Museum of Evolution, PMU 31754). It derives from the *P. punctuosus* Zone (Fig. 3B_1–B_4, 0.93 cm long). The third specimen is from a boulder of the *P. punctuosus* Zone found at the shore near Brantevik, Scania, Sweden (Fig. 3C_1–C_4, 1.44 cm long) (PMU 31755). Measurements of the three specimens are listed in Table 1.

Table 1. Measurements of the available specimens of *Anopolenus henrici* Salter 1864

Specimen	Width (cm)	Length (cm)	Width axis (cm)	Length axis (cm)
Fig. 3A, MGUH 30155	1.10	0.62	0.40	0.47
Fig. 3B, SB-MK 143.53 (PMU 31754, cast)	1.43	0.93	0.46	0.64
Fig. 3C, PMU 31755	2.50	1.44	0.88	1.06

Length measurements do not include the articulating half ring.

Description. Since Lake (1934), no new descriptions of *A. henrici* have been published. Lake's meticulous description of the pygidium is repeated here with some modifications using modern terminology (Lake 1934, pp. 190–191):

- rather wide, without any definite antero-lateral angle, anterior border arching backwards at the sides and passing into the lateral border.

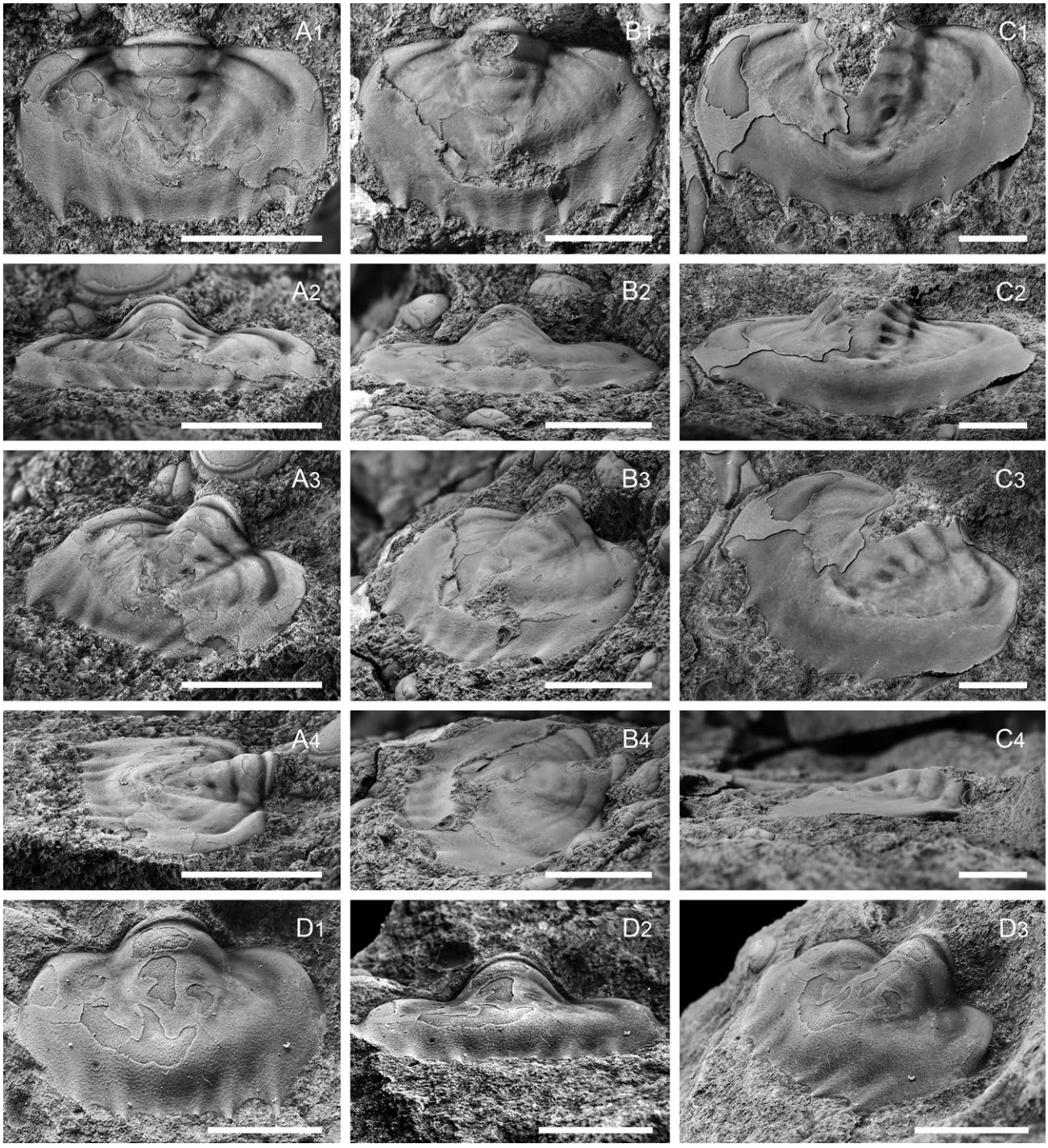

Fig. 3. $\mathbf{A_1}$–$\mathbf{C_4}$: pygidia of *Anopolenus henrici* Salter 1864 in dorsal, posterior, oblique and lateral views. $\mathbf{A_1}$–$\mathbf{A_4}$: MGUH 30155, *Acidusus atavus* Zone, Øleå, Bornholm, Denmark. This was previously figured by Weidner & Nielsen (2014). $\mathbf{B_1}$–$\mathbf{B_4}$: SB-MK 143.53, *Ptychagnostus punctuosus* Zone, Sellin, island of Rügen, Germany; cast PMU 31754 kept at the Museum of Evolution, Uppsala. This was previously figured by Buchholz (1991) and Rudolph (1994). $\mathbf{C_1}$–$\mathbf{C_4}$: PMU 31755, *P. punctuosus* Zone, Brantevik, Scania, Sweden, collected by H.-J. Schmütz. $\mathbf{D_1}$–$\mathbf{D_3}$: MGUH 30153, pygidium of *Clarella impar* (Hicks 1872) for comparison in dorsal, posterior and oblique views. *Acidusus atavus* Zone at Øleå, Bornholm, Denmark. This was figured previously by Weidner & Nielsen (2014). Scale bars represent 5 mm.

- the posterior border nearly straight, but with at least three projecting points on each side (i.e. three pairs of spines), of which the one at the postero-lateral angle is most prominent.
- there is a broad and slightly concave margin with a raised interior edge, the doublure of the margin carries terrace lines.
- axis prominent, conical, occupying about a third of the total width at the anterior margin, not quite reaching the concave margin, consisting of four rings in addition to the terminal piece.
- the lateral lobes show indications of several pleurae of which the anterior is well defined, broadens outwards and curves backwards; the next two are recognizable, the rest are obscure; all are totally effaced on the external surface of the concave margin.
- on the internal cast they are represented by ridges crossing the doublure and ending in points on the posterior border.
- on each side three of these ridges and points are usually visible and correspond with the first three pleurae, but there are several less distinct ridges interior to these (Fig. $3B_1$) which may have ended in smaller points.

The pygidia figured here agree with the description provided by Lake (1934). As indicated by him, all specimens have in addition to three distinct pairs of spines an inner pair of incipient spines. In the largest pygidium (Fig. 3C), the pleurae on the posterior border are less pronounced than in the other two specimens. Lake (1934) stated that the posterior margin is almost straight, however, in all well-preserved pygidia the margin is somewhat rounded (Lake 1934, pl. 24, fig. 10–12; Levi-Setti 1993, pl. 95; Dean & Rushton 1997, fig. 309:2c). Weidner & Nielsen (2014) discussed the three specimens we describe here and tentatively suggested that they could represent different species.

On Bornholm, *Clarella impar* (Hicks 1872) may occur associated with *Anopolenus henrici*. It differs from *A. henrici* in having a longer axis, obscured axial furrows, less pronounced segmentation of the axis and especially of the pleural fields, the lack of a border, and by having a straight posterior margin (Fig. $3D_1$–D_3; Weidner & Nielsen 2014, fig. 42E–G, I).

Only one pygidium tentatively assigned to *Centropleura lovéni* (Angelin 1851) has been illustrated (Westergård 1950). The specimen is from the Andrarum Limestone Bed of the lower part of the *L. laevigata* Zone in Scania and is distinguished from *A. henrici* by having three axial rings plus the terminal piece, two distinct pleurae that terminate in posterior border spines and one fainter pleura that ends in a small point at the posterior margin. A border is not developed.

Conclusion

Anopolenus and *Clarella* are typical members of the Avalonian faunas of England, Wales, and eastern Newfoundland (Howell 1933). *Luhops* was originally described from Bohemia, Czech Republic (Šnajdr 1957) and subsequently also reported from England (Rushton 2011). The occurrence of *Anopolenus*, *Clarella*, and *Luhops* on Bornholm confirms the close biogeographic relationship between faunas from the middle Miaolingian of Bornholm and Avalonia (Weidner & Nielsen 2014). The relationship between Bornholm and the remainder of Scandinavia is less pronounced.

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