The middle Cambrian cosmopolitan key species *Lejopyge laevigata* and its biozone: new data from Sweden

NIKLAS AXHEIMER*‡, MATS E. ERIKSSON*, PER AHLBERG* & ANDERS BENGTSSON†

*Department of Geology, GeoBiosphere Science Centre, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden †Kronoborgsgatan 11, SE-252 22 Helsingborg, Sweden

(Received 1 March 2005; accepted 6 December 2005)

Abstract – The middle Cambrian *Lejopyge laevigata* Zone is poorly exposed in Scandinavia. Both this zone, however, and the succeeding *Agnostus pisiformis* Zone are well exposed at a classic locality at Gudhem, Västergötland, south-central Sweden. The sequences consist of finely laminated alum shale with scattered stinkstone (*orsten*) lenses. Three measured and sampled sections yielded a diverse fossil fauna, dominated by trilobites, in particular agnostoids, and the bradoriid *Anabarochilina primordialis*. Fossils are excellently preserved but restricted to the stinkstones. The *L. laevigata* Zone at Gudhem includes several geographically widespread key agnostoid species, notably *Tomagnostella sulcifera*, *Clavagnostus spinosus*, *Glaberagnostus altaicus*, *Lejopyge laevigata* and *L. armata*. The *L. laevigata* Zone, and its lower boundary is defined by the FAD of *L. laevigata*. Trilobite evidence shows that the upper part of the Scandinavian *L. laevigata* Zone approximately correlates with the *Proagnostus bulbus* Zone of China and elsewhere.

Keywords: Global correlation, biostratigraphy, middle Cambrian, Lejopyge laevigata Zone, Sweden.

1. Introduction

Agnostoids are by far the most important fossils for long-distance chronocorrelation in the upper half of the Cambrian, traditionally referred to as middle and upper Cambrian. Many agnostoid species and genera have distinct morphological features and a wide geographical distribution, and are hence widely used for intercontinental correlations (e.g. Daily & Jago, 1975; Robison et al. 1977; Rowell, Robison & Strickland, 1982; Robison, 1988; Peng & Robison, 2000; Ahlberg, 2003). Since Westergård's (1946) classic study of the middle Cambrian agnostoids of Sweden, the temporal and lateral distribution of agnostoid faunas have been studied at an accelerating rate, and there are now sufficient data available for a global agnostoid zonation of middle Cambrian open-marine successions (Robison, 1982, 1984; Peng & Robison, 2000). Eight more or less globally recognizable zones have been defined for that part of the Cambrian System, extending from the base of the Ptychagnostus gibbus Zone to the base of the Glyptagnostus reticulatus Zone. In ascending order these are the Ptychagnostus gibbus, P. atavus, P. punctuosus, Goniagnostus nathorsti, Lejopyge laevigata, Proagnostus bulbus, Linguagnostus reconditus and Glyptagnostus stolidotus zones (Robison, 1984; Peng & Robison, 2000). The base of each zone is defined by the lowest stratigraphical

occurrence of its eponymous species and the absence of characterizing species from the zones above (Peng & Robison, 2000).

Work currently in progress by the International Subcommission on Cambrian Stratigraphy (ISCS) is aimed at developing a scheme of globally applicable stage and series subdivisions of the Cambrian System. A Global Standard Stratotype-section and Point (GSSP) of the Furongian Series (uppermost series of the Cambrian System) and the Paibian Stage (lowermost stage of the Furongian Series) was recently defined and ratified at the first appearance datum (FAD) of the cosmopolitan agnostoid G. reticulatus (Angelin, 1851) in the Paibi section, northwestern Hunan Province, China (Peng et al. 2004a). At least ten other biohorizons seem to have potential for global correlation in the upper half of the Cambrian (Geyer & Shergold, 2000; Shergold & Geyer, 2003). These biostratigraphical key levels include the FAD of various agnostoid trilobites, such as G. stolidotus Öpik, 1961, L. reconditus Poletaeva & Romanenko, 1970, L. laevigata (Dalman, 1828), P. punctuosus (Angelin, 1851), P. atavus (Tullberg, 1880) and P. gibbus (Linnarsson, 1869); see Geyer & Shergold (2000).

Lejopyge laevigata is a globally distributed agnostoid trilobite that is used in many areas of the world as a zonal index fossil (e.g. Robison, 1984; Laurie, 1989; Peng & Robison, 2000; Geyer & Shergold, 2000). Its FAD is one of the most clearly recognizable levels in the Cambrian, and is now considered as a potential stage



http://journals.cambridge.org

[‡]Author for correspondence: Niklas.Axheimer@geol.lu.se

Series Superzones		Scandinavian zonation	Global zonation			
middle Cambrian			Glyptagnostus stolidotus			
		Agnosius pisnomnis	Linguagnostus reconditus			
		Lejopyge laevigata	Proagnostus bulbus			
	Paradoxides forchhammeri	Solenopleura? brachymetopa	Lejopyge laevigata			
	<i>ioronna</i>	Ptychagnostus lundgreni–Goniagnostus nathorsti	Goniagnostus nathorsti			
		Ptychagnostus punctuosus	Ptychagnostus punctuosus			
	Paradoxides	Hypagnostus parvifrons	Ptychagnostus atavus			
	paradoxissimus	Tomagnostus fissus-Ptychagnostus atavus				
		Ptychagnostus gibbus	Ptychagnostus gibbus			
	Acadoparadoxides	Ptychagnostus praecurrens	Ptychagnostus praecurrens			
	oelandicus	Eccaparadoxides insularis				

Figure 1. Traditional middle Cambrian biostratigraphy of Scandinavia (Westergård, 1946; Ahlberg, 1989), and the global zonation proposed by Robison (1984) and Peng & Robison (2000).

boundary level (Peng *et al.* 2004*b*). Assuming that a four-fold division of the Cambrian (e.g. Palmer, 1998; Peng, 2003) will ultimately be adopted, the FAD of *L. laevigata* is a potential candidate as a marker for the base of the upper stage of the third Cambrian series (Babcock *et al.* 2005).

The aim of this paper is to describe and discuss the faunal succession in the *L. laevigata* Zone at the classic locality of Gudhem in Västergötland, southcentral Sweden.

2. The *Lejopyge laevigata* Zone and its new Scandinavian definition

In pioneer studies during the 19th century (e.g. Linnarsson, 1869; Nathorst, 1869, 1877; Tullberg, 1882), a stratigraphical framework of trilobite zones was established for the traditional middle and upper Cambrian of Sweden. The *Lejopyge laevigata* Zone was first established by Linnarsson (1868) on the basis of the faunal succession in Västergötland, south-central Sweden. This zone has been subsequently studied by

Wallerius (1895, 1930), among others, and in Sweden it has become common practice to use it to define the succession between the top of the Solenopleura? (or Erratojincella) brachvmetopa Zone to the base of the Agnostus pisiformis Zone (Fig. 1; Westergård, 1946). Although the S.? brachymetopa Zone is of considerable importance for regional correlations, it reflects a facies change, recorded by the Andrarum Limestone and the Exporrecta Conglomerate. Westergård (1944, p. 24, 1946, p. 89; cf. Daily & Jago, 1975) noted that L. laevigata already appears near the base of the S.? brachymetopa Zone. Recently, the senior author (NA) identified the species even below this zonal base in the Andrarum-3 drill core from Scania, Sweden. As noted by Peng & Robison (2000, p. 7), the L. laevigata Zone of Sweden was seemingly based on local taxon abundance and not stratigraphical range. Therefore we suggest that the L. laevigata Zone in Scandinavia should be extended to include the traditional S.? brachymetopa Zone, and its lower boundary should be defined by the FAD of L. laevigata.

The base of the succeeding *A. pisiformis* Zone is traditionally defined by the lowest level where the index taxon occurs in abundance, or at the last appearance datum (LAD) of *L. laevigata* (Peng & Robison, 2000). We concur with the latter and place the base of the *A. pisiformis* Zone at the LAD of *L. laevigata*.

Peng & Robison (2000) defined two replacement zones for Robison's (1984) *L. laevigata* Zone, a revised and restricted *L. laevigata* Zone and a *Proagnostus bulbus* Zone above. These zones, and the North American *L. laevigata* Zone, correlate with the new *L. laevigata* Zone in Scandinavia as here defined (Fig. 2).

The *L. laevigata* Zone has been recognized throughout most of southern Scandinavia (Martinsson, 1974), but it is generally poorly exposed. In Västergötland, this zone is up to *c*. 4.3 m thick. It consists of the Exporrecta Conglomerate (a thin glauconitic and phosphoritic limestone conglomerate) and, predominantly, finely laminated black shale (alum shale) with scattered lenses

SCANDINAVIA		GF	GREAT BRITAIN		NORTH AMERICA		AUSTRALIA		SOUTH CHINA		SIBERIA		KAZAKHSTAN	
	Agnostus pisiformis		Agnostus pisiformis		С	repicephalus		Glyptagnostus stolidotus	Youshuian	Glyptagnostus stolidotus	Tuorian	Glyptagnostus stolidotus	anian	Glyptagnostus stolidotus
						Cedaria	dyallan	Acmarhachis quasivespa		Linguagnostus reconditus		Agnostus pisiformis - Homagnostus fecundus		Kormagnostus simplex
eri	Lejopyge laevigata	Paradoxides forchhammeri	eri		_ ا		Min	4	Wancunian	Proagnostus bulbus	Mayan	Proagnostus bulbus	8 K	
Paradoxides forchhamm			Lejopyge Leevigata Leovigata	Marjumar		ellopyge laevigata		Erediaspis eretes					Aryus	Lejopyge
					della		Boomerangian	Lejopyge laevigata						laeviyala
			Solenopleura?	Bolasnic	Bolaspi					Lejopyge laevigata		Lejopyge laevigata - Aldanaspis truncata		
			brachymetopa										Zhana.	Lejopyge armata

Figure 2. Correlation chart of the middle Cambrian *Lejopyge laevigata* Zone, and its new extension in Scandinavia. Compiled from numerous sources, mainly Astashkin *et al.* (1991), Pratt (1992), Peng & Robison (2000), Lazarenko & Pegel (2001), Rushton & Berg-Madsen (2002), Shergold & Geyer (2003) and Jago, Bao & Baillie (2004).



http://journals.cambridge.org



Figure 3. Map of Västergötland, Sweden, showing Cambrian outcrop areas and the location of the Gudhem quarry.

of dark-grey to black limestone (stinkstone or orsten). One important locality exposing the *L. laevigata* Zone is the old quarry at Gudhem in the Falbygden area, Västergötland.

3. Geological setting

The almost flat-lying and undisturbed Lower Palaeozoic successions of Västergötland occur as erosional outliers resting on a Precambrian crystalline basement. These outliers are grouped into four main districts: Halleberg and Hunneberg in the west, Kinnekulle in the central-north and Lugnåsberget and Billingen-Falbygden in the east (Fig. 3).

The middle and upper Cambrian succession has a total thickness of 21–22 m and predominantly consists of alum shale and beds and lenses of stinkstone, locally with interbedded conglomerates and sandstones (for general reviews, see Martinsson, 1974; Ahlberg, 1998). Most of this succession is stratigraphically condensed and there are several gaps in the sequence. The Andrarum Limestone of the lower *L. laevigata* Zone is poorly developed in Västergötland, and generally replaced by a conspicuous conglomerate, the Exporrecta Conglomerate, which locally extends down into the *G. nathorsti* and *P. punctuosus* zones (Weidner *et al.* 2004).

In most areas, the Exporrecta Conglomerate, named after the brachiopod *Oligomys exporrecta* (Linnarsson, 1869), is overlain by a succession of alum shale and scattered, diagenetically formed stinkstone lenses, comprising the remainder of the *L. laevigata* Zone and the *A. pisiformis* Zone. The thickness of the

L. laevigata Zone generally ranges from 2.5 m to *c.* 4.3 m (Wallerius, 1895; Westergård *in* Lundqvist, Högbom & Westergård, 1931; Westergård *in* Johansson, Sundius & Westergård, 1943). On Halleberg and Hunneberg, the zone is very thin or missing (Westergård, 1946, p. 16). A stinkstone bed of considerable lateral persistence (the 'Great Stinkstone Bed') occurs in the *Agnostus* (*Homagnotus*) obesus/Olenus Zone of the basal Furongian (upper Cambrian) Series, locally extending down into the *A. pisiformis* Zone and up into the *Parabolina spinulosa* Zone (Westergård, 1922).

4. The Gudhem quarry

The *L. laevigata* Zone and the lower part of the *A. pisiformis* Zone are well exposed in the old quarry situated *c.* 0.7 km W of Gudhem church and *c.* 9 km NW of the city of Falköping (Fig. 3). The succession and its faunal content were first described by Wallerius (1894, 1895, 1930). Three sections (lettered A–C) in the quarry were recently reinvestigated and sampled (Fig. 4). These sections are well exposed with three to four levels of stinkstone within a homogeneous succession of alum shale. Each stinkstone lens is between 0.20 and 2.30 m in length, and between 0.05 and 0.60 m in thickness. The Exporrecta Conglomerate was formerly exposed at the quarry floor, and the total thickness of the *L. laevigata* Zone is *c.* 4.3 m (Wallerius, 1895), that is, thickest in Västergötland.

The upper part of the *L. laevigata* Zone contains a diverse and characteristic fauna, and was formerly known as the 'Exsculptus-layer' (Wallerius, 1895, 1896), after the common occurrence of two supposed





Figure 4. Lithological succession, ranges of fossils, and biostratigraphical subdivision of sections A-C in the Gudhem quarry, Västergötland, Sweden.

varieties of 'Agnostus exsculptus', A. exsculptus forma sulcifera Wallerius, 1895 (= Tomagnostella sulcifera; Peng & Robison, 2000), and A. exsculptus forma integra Wallerius, 1895 (= Tomagnostella sulcifera; Peng & Robison, 2000).

At the northwest entrance of the quarry, along a small stream, there are exposures of the 'Hypagnostus limestone bank' (*Hypagnostus parvifrons* Zone), which is overlain by a thin, up to 15 cm thick, conglomeratic limestone with mixed faunas from the *P. punctuosus* and *G. nathorsti* zones (Weidner *et al.* 2004).

The Gudhem quarry is the type locality for several agnostoid and polymerid trilobites, notably the geographically widespread agnostoid *T. sulcifera*

(Wallerius, 1895). Moreover, Gudhem may be the type locality for *L. armata* (Linnarsson, 1869) (see Westergård, 1946, p. 89).

5. Faunal composition

In the Gudhem quarry, fossils are excellently preserved but restricted to the stinkstones. Section A, described by Wallerius (1895, 1930), is situated in the northeastern part of the quarry (Figs 4, 5). The lower part is sparsely fossiliferous. The lowermost stinkstone (-2.9 m) yielded fragments of an indeterminate agnostoid along with *Lejopyge* sp.



Figure 5. Photograph of section A in the Gudhem quarry showing the succession of Alum Shale and the continuous bed of stinkstones at c. -1.3 m, outlined by a broken white line.





Figure 6. Fossils from the *Lejopyge laevigata* Zone at Gudhem, Sweden. (a, b) *Lejopyge laevigata*. (a₁) cephalon from section B (-0.9 m), × 7, LO9600t. (a₂) pygidium from section C (-0.3 m), × 7, LO9601t. (b₁) cephalon from section B (-0.9 m), × 8, LO9602t. (b₂) pygidium from section B (-0.9 m), × 8, LO9603t. (c, d) *Lejopyge armata*. (c₁) cephalon from section C (-1.1 m), × 6, LO9604t. (c₂) pygidium from section B (-2.7 m), × 6, LO9605t. (d₁) cephalon from section B (-2.7 m), × 8, LO9606t. (d₂) pygidium from section B (-2.7 m), × 6, LO9607t. (e) *Clavagnostus spinosus*. (e₁) cephalon from section B (-0.9 m), × 11, LO9608t. (e₂) pygidium from section B (-0.9 m), × 8, LO9609t. (f) *Peronopsis insignis*. (f₁) cephalon from section C (-0.3 m), × 5, LO9610t. (f₂) pygidium from section C (-1.1 m), × 7, LO9611t. (g) *Tomagnostella sulcifera*. (g₁) cephalon from section B (-0.9 m), × 6, LO9612t. (g₂) pygidium from section C (-0.3 m), × 6, LO9613t. (h) *Proceratopyge conifrons*. (h₁) cranidium from section B (-0.9 m), × 4, LO9614t. (h₂) pygidium from section C (-0.3 m), × 7, LO9615t. (i) Indeterminate polymerid hypostome from section B (-0.9 m), × 8, LO9616t. (j) *Anabarochilina primordialis*. (j₁) left valve from section B (-0.9 m), × 7, LO9619t. (l) *Agnostus pater*, pygidium from section C (-2.1 m), × 11, LO9620t. (m) *Diplagnostus planicauda*, cephalon from section B (-0.90 m), × 12, LO9621t. (n) *Peregrinaspis*? sp., cranidium from section B (-0.9 m), × 1, LO9622t. (o) *Acrocephalites stenometopus*, cranidium from section B (-0.9 m), × 4, LO9623t.

and *L*. cf. *armata*. Approximately 1 m above this (-1.8 m), fragmentary specimens of *Lejopyge* sp. and the bradoriid *Anabarochilina primordialis* (Linnarsson, 1869) were recorded. The next fossiliferous level,

a continuous bed of stinkstones (-1.2 m), yielded a diverse fauna characteristic of the *L. laevigata* Zone. Common species include the zonal index, *A. primordialis* (Fig. 6j₁, j₂), *Diplagnostus planicauda*



(Angelin, 1851), *Peronopsis insignis* (Wallerius, 1895), *Lejopyge* sp., an indeterminate brachiopod and an indeterminate agnostoid. *Lejopyge armata*, *T. sulcifera*, *A. pisiformis* (Wahlenberg, 1818) and *Clavagnostus spinosus* (Resser, 1938) are rare. Two moderately common brachiopod species were tentatively assigned to '*Lingula agnostorum*' Wallerius, 1895 and '*Obolella parvula*' Wallerius, 1895. The upper part of section A belongs to the *A. pisiformis* Zone, which contains the eponymous zonal index in abundance.

Section B is situated in the northwestern part of the quarry and contains four levels with stinkstones (Fig. 4). The stinkstones in the basal part of the section (-2.7 m) generally are richly fossiliferous. *Lejopyge* sp., L. armata (Fig. $6c_2$, d_1 , d_2), L. cf. laevigata, 'L. agnostorum', and an indeterminate brachiopod were recorded, of which the first two taxa are the most common. In the next stinkstone level (-1.9 m)only two specimens of *Lejopyge* sp. were identified. Approximately 1 m above the latter there is a laterally continuous bed of stinkstones (-0.9 m). This level yielded a diverse fauna dominated by T. sulcifera (Fig. 6g₁), L. laevigata (Fig. 6a₁, b₁, b₂), L. armata, D. planicauda (Fig. 6m) and A. primordialis. In addition, Lejopyge sp., an indeterminate agnostoid, 'L. agnostorum' and 'O. parvula' are fairly common. Infrequent trilobites include A. pisiformis, A. neglectus Westergård, 1946, Acrocephalites stenometopus (Angelin, 1851; Fig. 60), C. spinosus (Fig. 6e₁, e₂), Toxotis pusilla Wallerius, 1895, Proceratopyge conifrons Wallerius, 1895 (Fig. 6h₁), Peregrinaspis? sp. (Fig. 6n), Glaberagnostus altaicus Romanenko, 1985 (Fig. 6k) and an indeterminate polymerid hypostome (Fig. 6i). The stinkstone in the uppermost part of the section (-0.1 m) belongs stratigraphically to the A. pisiformis Zone, yielding the zonal index only.

Section C is situated in the southwestern part of the quarry (Fig. 4). The lowermost stinkstone (-2.1 m)is dominated by Lejopyge sp. and an indeterminate agnostoid. In addition, T. sulcifera, L. armata, D. planicauda, A. primordialis, 'O. parvula', 'L. agnostorum' and an indeterminate brachiopod were recorded. Less common species include L. laevigata, A. neglectus, A. pater Westergård, 1930 in Holm & Westergård, 1930 (Fig. 61), A. stenometopus and A. pisiformis. The next stinkstone (-1.1 m) yielded generally poorly preserved fossils with a fauna dominated by Lejopyge sp. and an indeterminate agnostoid. Lejopyge laevigata, L. armata (Fig. 6c₁), T. sulcifera, D. planicauda, P. insignis (Fig. 6f₂), A. primordialis, 'L. agnostorum', 'O. parvula' and an indeterminate brachiopod are rare. The uppermost stinkstone level (-0.3 m) yielded a diverse fauna, including L. laevigata (Fig. 6a2), P. insignis (Fig. 6f1), T. sulcifera (Fig. 6g₂) and P. conifrons (Fig. 6h₂). This fauna is closely similar to that of the topmost stinkstone (-0.9 m) of the *L*. *laevigata* Zone in section B. The only taxa not recorded in the latter are A. pater, P. insignis and the indeterminate brachiopod.

6. Intercontinental correlations

The Gudhem succession includes several geographically widespread key agnostoid species, notably T. sulcifera, C. spinosus, G. altaicus, L. laevigata and L. armata. Moreover, the long-ranging D. planicauda has some biostratigraphical significance. Tomagnostella sulcifera is known from Sweden, England, Siberia, South China and possibly Kazakhstan (e.g. Westergård, 1946; Rushton, 1978; Peng & Robison, 2000). In South China it ranges from the topmost P. bulbus Zone to the basal G. stolidotus Zone (Peng & Robison, 2000). Clavagnostus spinosus has a total stratigraphical range from the P. bulbus Zone to the lower L. reconditus Zone (Peng & Robison, 2000). The effaced agnostoid G. altaicus is known from Antarctica, China, England and Russia (Peng & Robison, 2000), and has not previously been recorded with certainty from Sweden. Its total stratigraphical range seems to extend from the P. bulbus Zone to the G. reticulatus Zone (Peng & Robison, 2000). Diplagnostus planicauda is a distinctive species known from Scandinavia, Siberia, North Greenland, the western United States, Australia and Argentina (Robison, 1988; Peng & Robison, 2000). Its stratigraphical range seems to extend from near the base of the P. atavus Zone to the upper L. laevigata Zone (Robison, 1994; Peng & Robison, 2000), and it is therefore of limited correlative value.

Peng & Robison (2000) suggested that the traditional *L. laevigata* Zone in the Scandinavian biostratigraphical scheme (Fig. 1; Westergård, 1946; Martinsson, 1974) correlates with the *P. bulbus* Zone of South China and equivalent strata elsewhere. The presence of *T. sulcifera*, *C. spinosus* and *G. altaicus* in the *L. laevigata* Zone in the Gudhem quarry strongly supports the correlation of the *P. bulbus* Zone with the upper *L. laevigata* Zone as here defined (Fig. 2).

7. Selected systematic palaeontology

All figured specimens are deposited at the Department of Geology, Lund University (depository acronym LO).

All agnostoid species recovered from the Gudhem quarry are very well known and have been described in detail (e.g. Westergård, 1946; Robison, 1984, 1988; Laurie, 1989; Peng & Robison, 2000). Because the FAD of *L. laevigata* is currently under discussion as a potential stage base marker, only this species and the closely related *L. armata* are briefly commented upon below.

> Order AGNOSTIDA Salter, 1864 Family PTYCHAGNOSTIDAE Kobayashi, 1939 Genus *Lejopvge* Hawle & Corda, 1847

Type species. *Battus laevigatus* Dalman, 1828, pp. 136–7; by monotopy.

Lejopyge laevigata (Dalman, 1828) Figure 6a, b



Material. 45 cephala and 126 pygidia.

Remarks. The concept and taxonomy of *Lejopyge laevigata* have been reviewed comprehensively by Robison (1984). The differences in morphology between *L. laevigata laevigata* and *L. l. armata* (Linnarsson, 1869) were listed and discussed by Daily & Jago (1975), Robison (1984, 1994) and Laurie (1989), among others. These two subspecies or varieties are closely similar, but *L. l. laevigata* lacks prominent spines on both the cephalon and pygidium, in contrast to *L. l. armata*. However, the latter is now recognized as a separate species (e.g. Robison, 1984, 1988; Laurie, 1989; Peng & Robison, 2000), although minute marginal spines are occasionally present in *L. laevigata* (Daily & Jago, 1975; Laurie, 1989; Peng & Robison, 2000; Babcock *et al.* 2005).

Specimens from Gudhem, like elsewhere in the world, show variation in the degree of effacement of furrows on the acrolobes. These minor differences are attributed to intraspecific variability.

Occurrence. In the Gudhem quarry, L. laevigata ranges throughout the exposed part of the L. laevigata Zone, although it has not been recorded from the lower and middle part of the zone in section A (Fig. 4).

Lejopyge laevigata is cosmopolitan in open-marine lithofacies and has been recorded from all major Cambrian palaeocontinents (see, e.g. Daily & Jago, 1975; Öpik, 1979; Robison, 1984; Tortello & Bordonaro, 1997; Peng & Robison, 2000; Jago & Brown, 2001). It has a stratigraphical range extending from the base of the *L. laevigata* Zone (*sensu* Peng & Robison, 2000) to the upper *P. bulbus* Zone (Peng & Robison, 2000; Peng *et al.* 2004*a*, fig. 5).

Lejopyge armata (Linnarsson, 1869) Figure 6c–d

Material. 41 cephala and 50 pygidia, which are more or less complete.

Remarks. Lejopyge armata has been described at length by Robison (1984) and Laurie (1989). It is the only species of *Lejopyge* to possess fully developed marginal spines on both the cephalon and the pygidium. Another diagnostic feature of *L. armata* is the presence of weak indentations of the pygidial acrolobe adjacent to the bases of the spines (Robison, 1984; Laurie, 1989). Marginal spines are present also on the pygidium of *L. cos* Öpik, 1967 and, following Daily & Jago (1975), Robison (1984) regarded the latter name as a junior synonym of *L. armata*. However, the pygidial spines of *L. cos* are very small, and therefore it may prove to be a junior synonym of *L. laevigata* (Laurie, 1989; cf. Peng & Robison, 2000, p. 77).

The Gudhem material of L. armata exhibits variations in the length of the cephalic and pygidial spines, but the spines are always long and prominent and the pygidial acrolobe is indented adjacent to the spines. Westergård (1946, pl. 13, figs 30, 31) illustrated two pygidia from Gudhem with small posterolateral spines.

We agree with Laurie (1989) that these specimens represent *L. laevigata* rather than *L. armata*.

Occurrence. In the Gudhem quarry, *L. armata* ranges throughout the exposed fossiliferous part of the *L. laevigata* Zone (Fig. 4). Wallerius (1895) noted that this species does not occur in the lower part of the zone, but Westergård (1946, pl. 13, figs 32–34) illustrated specimens from the basal beds of the *L. laevigata* Zone at Gudhem.

Lejopyge armata is a widely distributed species that, outside Sweden, is known from North Greenland, Siberia, Kazakhstan, Canada, Great Basin, Himalaya, South China, Australia, Tasmania, Antarctica and South Korea (Hong, Lee & Choi, 2003). It has a stratigraphical range extending from the upper *G. nathorsti* Zone to the middle *P. bulbus* Zone (Peng & Robison, 2000; Peng *et al.* 2004*a*, fig. 5).

Acknowledgements. Financial support has been received from the Crafoord Foundation, the Swedish Natural Science Research Council (NFR) and the Swedish Research Council (VR). Euan N. K. Clarkson, David L. Bruton and Richard A. Robison critically read the manuscript and suggested valuable improvements.

References

- AHLBERG, P. 1989. Cambrian stratigraphy of the När 1 deep well, Gotland. Geologiska Föreningens i Stockholm Förhandlingar 111, 137–48.
- AHLBERG, P. (ed.) 1998. Guide to excursions in Scania and Västergötland, southern Sweden. IV Field Conference of the Cambrian Stage Subdivision Working Group. International Subcommission on Cambrian Stratigraphy. Sweden, 24–31 August 1998. Lund Publications in Geology 141, 1–47.
- AHLBERG, P. 2003. Trilobites and intercontinental tie points in the Upper Cambrian of Scandinavia. *Geologica Acta* 1, 127–34.
- ANGELIN, N. P. 1851. Palaeontologia Svecica. I: Iconographia crustaceorum formationis transitionis. Fasc. 1. Lund, 24 pp.
- ASTASHKIN, V. A., PEGEL, T. V., SHABANOV, Y. YA., SUKHOV, S. S., SUNDUKOV, V. M., REPINA, L. N., ROZANOV, A. YU. & ZHURAVLEV, A. YU. 1991. The Cambrian System on the Siberian platform. *International Union* of Geological Sciences Publication 27, 1–133.
- BABCOCK, L. E., PENG, S., GEYER, G. & SHERGOLD, J. H. 2005. Changing perspectives on Cambrian chronostratigraphy and progress toward subdivision of the Cambrian System. *Geosciences Journal* 9, 101–6.
- DAILY, B. & JAGO, J. B. 1975. The trilobite *Lejopyge* Hawle and Corda and the middle-upper Cambrian boundary. *Palaeontology* **18**, 527–50.
- DALMAN, J. W. 1828. Årsberättelse om nyare zoologiska arbeten och upptäckter, till Kongliga Vetenskaps-Academien afgifven den 31 mars 1828. Stockholm: P. A. Norstedt & Söner, 138 pp.
- GEYER, G. & SHERGOLD, J. H. 2000. The quest for internationally recognized divisions of Cambrian time. *Episodes* 23, 188–95.
- HAWLE, I. & CORDA, A. J. C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. Prague: J. G. Calve, 176 pp.



- HOLM, G. & WESTERGÅRD, A. H. 1930. A Middle Cambrian fauna from Bennett Island. *Mémoires de l'Académie des Sciences de L'URSS* **8**(21), 1–25.
- HONG, P. S., LEE, J. G. & CHOI, D. K. 2003. Trilobites from the *Lejopyge armata* Zone (upper Middle Cambrian) of the Machari Formation, Yongwol Group, Korea. *Journal* of *Paleontology* 77, 895–907.
- JAGO, J. B., BAO, J. S. & BAILLIE, P. W. 2004. Late Middle Cambrian trilobites from St Valentines Peak and Native Track Tier, northwestern Tasmania. *Alcheringa* 28, 21– 52.
- JAGO, J. B. & BROWN, A. V. 2001. Late Middle Cambrian trilobites from Trial Ridge, southwestern Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 135, 1–14.
- JOHANSSON, S., SUNDIUS, N. & WESTERGÅRD, A. H. 1943. Beskrivning till kartbladet Lidköping. Sveriges Geologiska Undersökning Aa182, 1–191.
- KOBAYASHI, T. 1939. On the agnostids (Part 1). Journal of the Faculty of Science, Imperial University of Tokyo, Section II 5(5), 69–198.
- LAURIE, J. R. 1989. Revision of species of *Goniagnostus* Howell and *Lejopyge* Corda from Australia (Agnostida, Cambrian). *Alcheringa* 13, 175–91.
- LAZARENKO, N. P. & PEGEL, T. V. 2001. Upper Cambrian levels of biostratigraphical correlation in the Khos-Nelege River reference section (northeastern flank of the Siberian platform). In *Cambrian System of South China* (eds S. Peng, L. E. Babcock and M. Zhu), pp. 276–9. Palaeoworld 13. Hefei: Press of University of Science and Technology of China.
- LINNARSSON, J. G. O. 1868. Bidrag till Westergötlands geologi. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 1868(1), 53–61.
- LINNARSSON, J. G. O. 1869. Om Vestergötlands cambriska och siluriska aflagringar. Kongliga Svenska Vetenskaps-Akademiens Handlingar 8(2), 1–89.
- LUNDQVIST, G., HÖGBOM, A. & WESTERGÅRD, A. H. 1931. Beskrivning till kartbladet Lugnås. Sveriges Geologiska Undersökning Aa172, 1–177.
- MARTINSSON, A. 1974. The Cambrian of Norden. In Lower Palaeozoic Rocks of the World. Volume 2. Cambrian of the British Isles, Norden, and Spitsbergen (ed. C. H. Holland), pp. 185–283. London: John Wiley & Sons.
- NATHORST, A. G. 1869. Om lagerföljden inom Cambriska formationen vid Andrarum i Skåne. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 1869(1), 61–5.
- NATHORST, A. G. 1877. Om de kambriska och siluriska lagren vid Kiviks Esperöd i Skåne, jemte anmärkningar om primordialfaunans lager vid Andrarum. *Geologiska Föreningens i Stockholm Förhandlingar* **3**, 263–72.
- ÖPIK, A. A. 1961. Alimentary caeca of agnostids and other trilobites. *Palaeontology* **3**, 410–38.
- ÖPIK, A. A. 1967. The Mindyallan Fauna of North-Western Queensland. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* **74**, 1–404.
- ÖPIK, A. A. 1979. Middle Cambrian agnostids: Systematics and biostratigraphy. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* **172**, 1–188.
- PALMER, A. R. 1998. A proposed nomenclature for stages and series for the Cambrian of Laurentia. *Canadian Journal* of Earth Sciences 35, 323–8.
- PENG, S. 2003. Chronostratigraphic subdivision of the Cambrian of China. *Geologica Acta* 1, 135–44.

- PENG, S., BABCOCK, L. E., ROBISON, R. A., LIN, H., REES, M. N. & SALTZMAN, M. R. 2004a. Global Standard Stratotype-section and Point (GSSP) of the Furongian Series and Paibian Stage (Cambrian). *Lethaia* 37, 365– 79.
- PENG, S. & ROBISON, R. A. 2000. Agnostoid biostratigraphy across the Middle–Upper Cambrian boundary in Hunan, China. *Paleontological Society Memoir* 53, 1–104.
- PENG, S., ZHU, X., BABCOCK, L. E. & WANG, H. 2004b. Potential global stratotype sections and points in China for defining Cambrian stages and series. *Geobios* 73, 253–8.
- POLETAEVA, O. K. & ROMANENKO, E. V. 1970. Nekotoryye trilobity Srednego i pozdnego Kembriya Altaya [Middle and Late Cambrian trilobites of the Altay]. *Paleontologicheskiy Zhurnal* 1970(2), 72–83 [in Russian].
- PRATT, B. R. 1992. Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. *Palaeontographica Canadiana* 9, 1–179.
- RESSER, C. E. 1938. Cambrian System (restricted) of the southern Appalachians. *Geological Society of America*, *Special Paper* 15, 1–140.
- ROBISON, R. A. 1982. Some Middle Cambrian agnostoid trilobites from western North America. *Journal of Paleontology* 56, 132–60.
- ROBISON, R. A. 1984. Cambrian Agnostida of North America and Greenland. Part I, Ptychagnostidae. *The University* of Kansas Paleontological Contributions 109, 1–59.
- ROBISON, R. A. 1988. Trilobites of the Holm Dal Formation (late Middle Cambrian), central North Greenland. *Meddelelser om Grønland, Geoscience* **20**, 23–103.
- ROBISON, R. A. 1994. Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bulletin Grønlands geologiske* Undersøgelse 169, 25–77.
- ROBISON, R. A., ROSOVA, A. V., ROWELL, A. J. & FLETCHER, T. P. 1977. Cambrian boundaries and divisions. *Lethaia* 10, 257–62.
- ROMANENKO, E. V. 1985. Trilobity iz pogranichnykh otlozheniy Srednego i Verkhnego Kembriya Altaya [Trilobites from the Middle-Upper Cambrian boundary beds of Altay]. *Paleontologicheskiy Zhurnal* **1985**(4), 54–63 [in Russian].
- ROWELL, A. J., ROBISON, R. A. & STRICKLAND, D. K. 1982. Aspects of Cambrian agnostoid phylogeny and chronocorrelation. *Journal of Paleontology* 56, 161– 82.
- RUSHTON, A. W. A. 1978. Fossils from the middle-upper Cambrian transition in the Nuneaton district. *Palaeontology* **21**, 245–83.
- RUSHTON, A. W. A. & BERG-MADSEN, V. 2002. The age of the Middle Cambrian 'Paradoxides forchhammeri Grit' of the Wrekin district, Shropshire, England. Transactions of the Royal Society of Edinburgh: Earth Sciences 92, 335–46.
- SALTER, J. W. 1864. A monograph of the British trilobites from the Cambrian, Silurian, and Devonian formations. Monographs of the Palaeontographical Society, 1–80.
- SHERGOLD, J. H. & GEYER, G. 2003. The Subcommission on Cambrian Stratigraphy: the status quo. *Geologica Acta* 1, 5–9.
- TORTELLO, M. F. & BORDONARO, O. L. 1997. Cambrian agnostoid trilobites from Mendoza, Argentina: A systematic revision and biostratigraphic implications. *Journal of Paleontology* 71, 74–86.

- TULLBERG, S. A. 1880. Om Agnostus-arterna i de kambriska aflagringarne vid Andrarum. Sveriges Geologiska Undersökning C42, 1–37.
- TULLBERG, S. A. 1882. Skånes graptoliter. I. Allmän öfversigt öfver de siluriska bildningarne i Skåne och jemförelse med öfriga kända samtidiga aflagringar. Sveriges Geologiska Undersökning C50, 1–44.
- WAHLENBERG, G. 1818. Petrificata telluris svecanae. Nova Acta Regiae Societatis Scientiarum Upsaliensis 8, 1– 116.
- WALLERIUS, I. D. 1894. Geologiska studier i Vestergötland. Geologiska Föreningens i Stockholm Förhandlingar 16, 298–306.
- WALLERIUS, I. D. 1895. Undersökningar öfver zonen med Agnostus laevigatus i Vestergötland, jämte en inledande öfversikt af Vestergötlands samtliga Paradoxideslager. Lund: Gleerupska Universitetsbokhandeln, 72 pp.
- WALLERIUS, I. D. 1896. Undersökningar öfver zonen med Agnostus laevigatus i Vestergötland, jämte en inledande

öfversikt af Vestergötlands samtliga Paradoxideslager. *Geologiska Föreningens i Stockholm Förhandlingar* **18**, 165–70.

- WALLERIUS, I. D. 1930. Från Västergötlands mellankambrium. Geologiska Föreningens i Stockholm Förhandlingar 52, 47–62.
- WEIDNER, T. R., AHLBERG, P., AXHEIMER, N. & CLARKSON, E. N. K. 2004. The middle Cambrian Ptychagnostus punctuosus and Goniagnostus nathorsti zones in Västergötland, Sweden. Bulletin of the Geological Society of Denmark 50, 39– 45.
- WESTERGÅRD, A. H. 1922. Sveriges Olenidskiffer. Sveriges Geologiska Undersökning Ca18, 1–205.
- WESTERGÅRD, A. H. 1944. Borrningar genom Skånes alunskiffer 1941–42. Sveriges Geologiska Undersökning C459, 1–45.
- WESTERGÅRD, A. H. 1946. Agnostidea of the Middle Cambrian of Sweden. Sveriges Geologiska Undersökning C477, 1–141.