

# Furongian (Cambrian) agnostoids of Scandinavia and their implications for intercontinental correlation

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**Abstract** – Out of the 14 agnostoid species/subspecies so far recorded from the Furongian of Scandinavia, seven are excellent biostratigraphical indices and important for correlation between Baltica and other palaeocontinents. *Glyptagnostus reticulatus*, *Aspidagnostus lumulosus* and *Aagnostus (Homagnostus) obesus* first appear at the base of the *G. reticulatus* Zone, allowing a precise correlation of the base of the Paibian Stage into Scandinavia. *Tomagnostella orientalis* and *Pseudagnostus cyclopyge* appear near the base of the *Parabolina brevispina* Zone, suggesting a correlation with the uppermost Paibian through the lowermost Jiangshanian stages. *Lotagnostus americanus* and *Pseudagnostus rugosus* have an intercontinental distribution and their first appearance in Scandinavia allows for a correlation with one of the most favourable levels for defining the base of Cambrian provisional Stage 10. In the Furongian of Scandinavia, agnostoids are conspicuously assembled in three different intervals: the lower *Glyptagnostus reticulatus* Zone, the lower *Pseudagnostus cyclopyge* Zone and the *Lotagnostus americanus* through lower *Trilobagnostus holmi* zones. The agnostoid-bare and largely unfossiliferous succession separating the lower and middle agnostoid-bearing intervals can be explained by means of subsequent dissolution of the calcareous fauna and/or a hostile environment. The middle agnostoid-bearing interval is succeeded by an anomalous succession dominated by the orthide brachiopod *Orusia lenticularis*, reflecting a regressive event coupled with increasing levels of oxygen at the sediment/water interface. This shallowing evidently resulted in unfavourable conditions for agnostoids.

Keywords: agnostoids, biostratigraphy, correlation, Furongian, Scandinavia.

## 1. Introduction

Agnostoids range from the traditional upper lower Cambrian (uppermost part of Cambrian provisional Series 2) through the pre-Hirnantian Ordovician and occur in a wide range of lithofacies, representing a diversity of marine environments. The agnostoids reached a maximum diversity during the latter half of the Cambrian (provisional Cambrian Epoch 3 and the early Furongian) and are most common in open-shelf lithofacies. Because of their abundance and relatively rapid evolution, agnostoids are among the most significant elements in Cambrian biostratigraphy.

Westergård (1946) monographed the agnostoids from the traditional middle Cambrian of Sweden and demonstrated their value for correlation and regional biostratigraphy. Although Westergård's biostratigraphy has been widely used as a reference standard, the zonal boundaries were not defined on the first appearance datum of eponymous species (Robison, 1976; Peng & Robison, 2000; Axheimer & Ahlberg, 2003). Since then, Cambrian agnostoids have been thoroughly studied, and it has become apparent that many genera and species have a nearly cosmopolitan distribution, hence providing the most precise tools available for intercontinental correlations in the upper half of the

Cambrian System. The subdivision of this interval (Cambrian Series 3 through the Furongian Series) into stages will accordingly be largely based on the first appearance datums (FADs) of intercontinentally distributed agnostoids (e.g. Babcock *et al.* 2005; Babcock & Peng, 2007; Peng *et al.* 2009a; Babcock, Robison & Peng, 2011).

The International Subcommittee on Cambrian Stratigraphy (ISCS) is working toward a global subdivision of the Furongian into three stages. The lowest of these, the Paibian Stage, is defined by a point in time coinciding with the FAD of *Glyptagnostus reticulatus* (Angelin, 1851) at a level 396 m above the base of the Huaqiao Formation in the Paibi section, northwestern Hunan Province, China (Peng *et al.* 2004). A proposal (Peng *et al.* 2009a) to define the base of the middle stage (Jiangshanian) on a point in time coinciding with the FAD of *Agnostotes orientalis* (Kobayashi, 1935) at 108.12 m above the base of the Huayansi Formation in the Duibian B section at Duibian village, western Zhejiang, China, was recently ratified by the International Union of Geological Sciences (IUGS). The base of the upper stage of the Furongian is expected to be drawn at the FAD of *Lotagnostus americanus* (Billings, 1860) or at a closely comparable level.

Fourteen agnostoid species/subspecies assigned to eight genera have been described from the Furongian of Scandinavia (Terfelt & Ahlberg, 2010; Terfelt, Ahlberg & Eriksson, 2011). The majority of these have been

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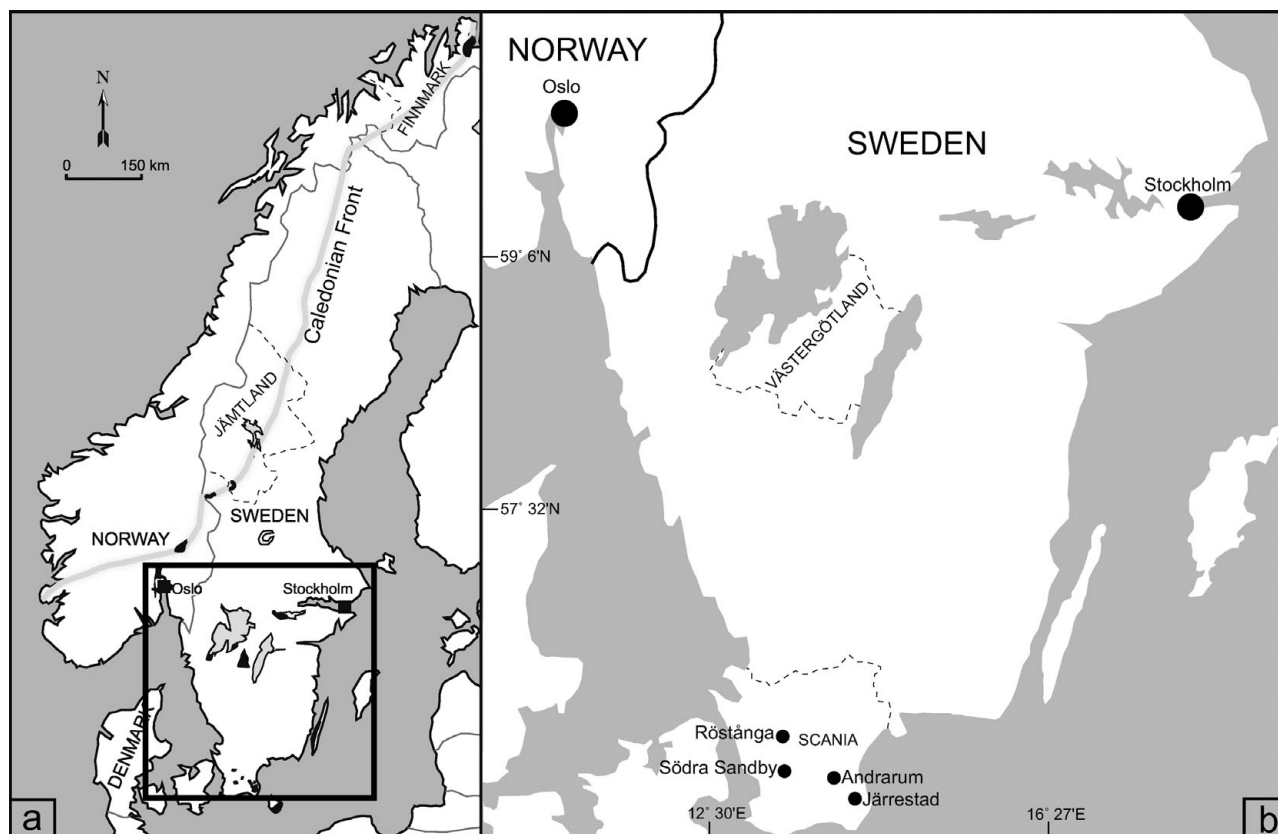


Figure 1. (a) Map of Scandinavia showing Cambrian outcrop areas (in black), the extent of the Caledonian Front, and the location of Jämtland, central Sweden, and Finnmark, northern Norway. (b) Map of southern Sweden showing provinces and localities referred to in the text.

recovered from Scania (Skåne) and Västergötland, Sweden (Fig. 1). The aim of this paper is to review their temporal and spatial distribution, and their potential for intercontinental correlation.

All illustrated specimens are housed at the Department of Geology, Lund University, Sweden (prefixed LO), and the Geological Survey of Sweden, Uppsala (SGU).

## 2. Geological setting and biostratigraphy

In Furonian times, Baltica was geographically inverted and situated at temperate to subtropical palaeolatitudes between 30 and 60° S (Torsvik & Rehnström, 2001; Cocks & Torsvik, 2002, 2005). Scandinavia formed the northeastern part of Baltica and was to a large extent covered by an oxygen-depleted and sediment-starved epicontinental sea. The Scandinavian successions are dominated by dark grey to black mudstones and shales of the condensed Alum Shale Formation (Gee, 1972; Buchardt, Nielsen & Schovsbo, 1997; Nielsen & Schovsbo, 2007), except in Finnmark, northern Norway, where the Furonian predominantly consists of thick arenaceous deposits (Reading, 1965; Nikolaisen & Henningsmoen, 1985).

The thickest and most complete Furonian successions are found in Scania, southernmost Sweden (Westergård, 1922, 1944; Buchardt, Nielsen &

Schovsbo, 1997; Ahlberg *et al.* 2009). In other parts of Scandinavia the Furonian alum shales are either tectonized (along the Caledonian Front, for instance in southern Norway) and/or interrupted by unconformities of various magnitudes. In Scania, Furonian deposits crop out in a number of areas scattered along the Colonius Shale Trough (Norling & Bergström, 1987; Erlström *et al.* 1997), notably at Andrarum, Järrestad, Södra Sandby and Röstånga.

The Furonian faunas of Scandinavia are generally dominated by low-diversity olenid trilobite assemblages (Westergård, 1922; Henningsmoen, 1957; Terfelt, Ahlberg & Eriksson, 2011). In addition, agnostoids, brachiopods, conodonts *sensu lato*, phosphatocopines and tiny crustaceans may be common in certain stratigraphical levels, notably in interbedded limestone beds and early diagenetic carbonate lenses (anthraconite or *orsten*) (e.g. Westergård, 1922; Müller & Walossek, 1985; Müller & Hintz, 1991; Ahlberg & Ahlgren, 1996; Szaniawski & Bengtson, 1998; Maas, Waloszek & Müller, 2003; Terfelt & Ahlgren, 2007; Eriksson & Terfelt, 2007).

The Furonian biostratigraphy of Scandinavia is largely based on the succession of endemic olenid trilobites. Species turnover rate was high, which enabled Westergård (1947) and Henningsmoen (1957) to establish a high-resolution biostratigraphy that has been applied also in Poland, England, Wales and East Maritime Canada. Terfelt *et al.* (2008) recently

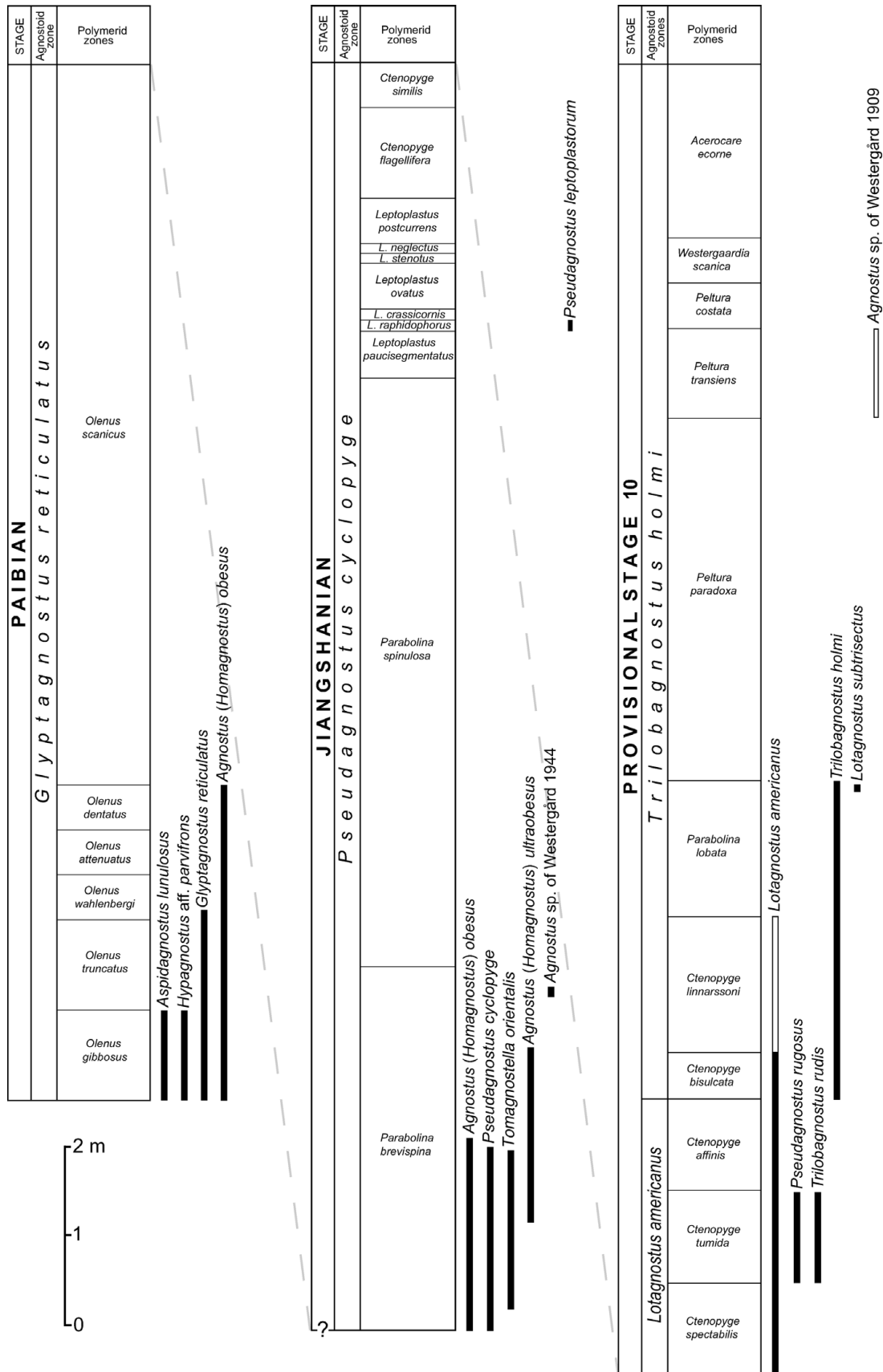


Figure 2. Biostratigraphical subdivision, relative thicknesses of the zones (as recorded in Scania) and ranges of agnostoids in the Furongian Series of Scandinavia. An open bar indicates presence in the zone, not the temporal distribution within the zone.

revised the biostratigraphy and established a two-fold interval zonation based on agnostoids and polymerids, respectively (Fig. 2). The zonation proposed was

based on the succession in Scania (except for the *Peltura costata* Zone). Four agnostoid interval zones were distinguished: the *Glyptagnostus reticulatus*,

*Pseudagnostus cyclopyge*, *Lotagnostus americanus* and *Trilobagnostus holmi* zones.

### 3. Paibian Stage

In Scandinavia, the base of the *Glyptagnostus reticulatus* Zone coincides with the base of the Paibian and the top of the zone corresponds to the top of the stage. In Scania, the stage has a thickness of approximately 11.5 m. The zonal index occurs in low to moderate numbers in the lower one-fifth of the zone, corresponding to the *Olenus gibbosus* through the lowermost *O. wahlenbergi* zones (Westergård, 1922; Clarkson, Ahlberg & Taylor, 1998; Lauridsen & Nielsen, 2005; Eriksson & Terfelt, 2007; Fig. 2). The FAD of the cosmopolitan species *Glyptagnostus reticulatus* (Fig. 3a, b) provides a globally recognized and correlatable horizon (e.g. Palmer, 1962; Rushton, 1983; Peng & Robison, 2000; Geyer & Shergold, 2000; Peng *et al.* 2004). Two other geographically widespread agnostoids are known from the lower Paibian of Baltica: *Aspidagnostus lunulosus* (Kryskov in Borovikov & Kryskov, 1963) and *Agnostus (Homagnostus) obesus* (Belt, 1867). *Aspidagnostus lunulosus* (Fig. 3f, g) is a distinctive species known from the *Glyptagnostus stolidotus* and/or *G. reticulatus* zones of southern Kazakhstan, northwestern Queensland, Australia, South Korea, Siberia and China (e.g. western Xinjiang, western Zhijiang and western Hunan; Peng & Robison, 2000; Ergaliev & Ergaliev, 2008; Lazarenko *et al.* 2008). In Sweden, this species has been described from the *Olenus gibbosus* Zone of Västergötland (Ahlberg & Ahlgren, 1996; described as *A. cf. stictus* Öpik, 1967; Fig. 2). A single specimen has been recorded from an erratic limestone boulder at Wismar in northern Germany (Weidner, 1997). The stratigraphical position is not known owing to the lack of an associated fauna.

A cephalon assigned to *Hypagnostus aff. parvifrons* (Linnarsson, 1869) (= *H. aff. correctus* Öpik, 1967 of Ahlberg & Ahlgren, 1996) is known from the *Olenus gibbosus* Zone of Västergötland, Sweden. The overall morphology of the cephalon suggests that it represents a species of *Hypagnostus*. It compares most closely with cephalons of the type species, *H. parvifrons*, a cosmopolitan and long-ranging species that is known from the Drumian and the Guzhangian stages. *Hypagnostus parvifrons* is a variable species, and, following Peng & Robison (2000) and Peng *et al.* (2009b), we consider *H. correctus* to be a junior synonym of *H. parvifrons*.

*Agnostus (Homagnostus) obesus* (Fig. 3c–e) is a common species in the interval ranging from the base of the *Olenus gibbosus* Zone through the *O. dentatus* Zone (*sensu* Terfelt *et al.* 2008) in Scandinavia (e.g. Westergård, 1944, 1947; Terfelt *et al.* 2008). It has also been recorded from the lower half of the *Parabolina brevispina* Zone (Fig. 2). The concept and intraspecific variability of *A. (H.) obesus* were discussed by Pratt (1992), who showed that a number of species, including *Homagnostus tumidosus* (Hall &

Whitfield, 1877), can be synonymized with *A. (H.) obesus*. Outside Scandinavia, *A. (H.) obesus (sensu* Pratt, 1992) has been recorded from England (Rushton, 1983), Newfoundland (Martin & Dean, 1988), Siberia (e.g. Lazarenko *et al.* 2008), Kazakhstan (Ergaliev & Ergaliev, 2008), Korea (Choi, Lee & Sheen, 2004) and North America (Pratt, 1992; Stitt & Perfetta, 2000). It ranges from the base of the Paibian into the Jiangshanian and is valuable for broad correlations in the Paibian Stage.

### 4. Jiangshanian Stage

*Pseudagnostus cyclopyge* (Tullberg, 1880) is fairly common in the lower half of the *Parabolina brevispina* Zone of Scania, southern Sweden (Figs 2, 3h, i). It has also been described from southern Mackenzie Mountains, Northwest Territories, Canada (Pratt, 1992) and Malyi Karatau, southern Kazakhstan (Ergaliev & Ergaliev, 2008), facilitating a broad correlation between these areas.

A single pygidium of *Tomagnostella orientalis* (Lazarenko, 1966) (= *Peratagnostus falanensis* Westergård, 1947 of Ahlberg & Ahlgren, 1996) is known from the lower *P. brevispina* Zone (Fig. 2) in Västergötland, south-central Sweden, where it is associated with *A. (H.) obesus* and *Protopeltura aciculata*. Two additional pygidia have recently been recovered from contemporaneous strata at Andrarum, Scania, southern Sweden. The Scanian specimens are associated with *P. brevispina* and *P. aciculata*. The pygidial axis is faintly outlined and has a clearly visible axial node, and the border is wide (Fig. 3j, k). The Swedish material agrees in all essential respects with that of *T. orientalis*, a geographically widespread species that has been described from the upper Paibian and the lower Jiangshanian in Siberia, China, Korea, Alaska and Australia (see Choi, Lee & Sheen, 2004 and references therein; Lazarenko *et al.* 2008; Peng *et al.* 2009a).

Specimens tentatively assigned to *Agnostus (Homagnostus) ultraobesus* Lermontova, 1940 are known from the middle *P. brevispina* Zone (Fig. 2) at Andrarum, southern Sweden (cf. Shergold & Webers, 1992; Ahlberg & Ahlgren, 1996). Pratt (1992) considered this species name to be a junior synonym of *A. (H.) obesus*. The former differs, however, from the latter in completely lacking a median preglabellar furrow and in having less constricted acrolobes and wider cephalic and pygidial borders. *A. (H.) ultraobesus* and *A. (H.) obesus* are herein treated as two separate species.

A single indeterminate pygidium with a fairly short and distinctly tapered axis was recorded by Westergård (1944) from the uppermost *P. brevispina* Zone (Fig. 2) at Andrarum, southern Sweden. It is herein referred to as *Agnostus* sp. of Westergård (1944).

*Pseudagnostus leptoplastorum* Westergård, 1944, is based on a flattened pygidium from the *Leptoplastus raphidophorus* Zone (Fig. 2) at Andrarum, southern Sweden. It has subsequently been recorded from roughly contemporaneous strata in central and



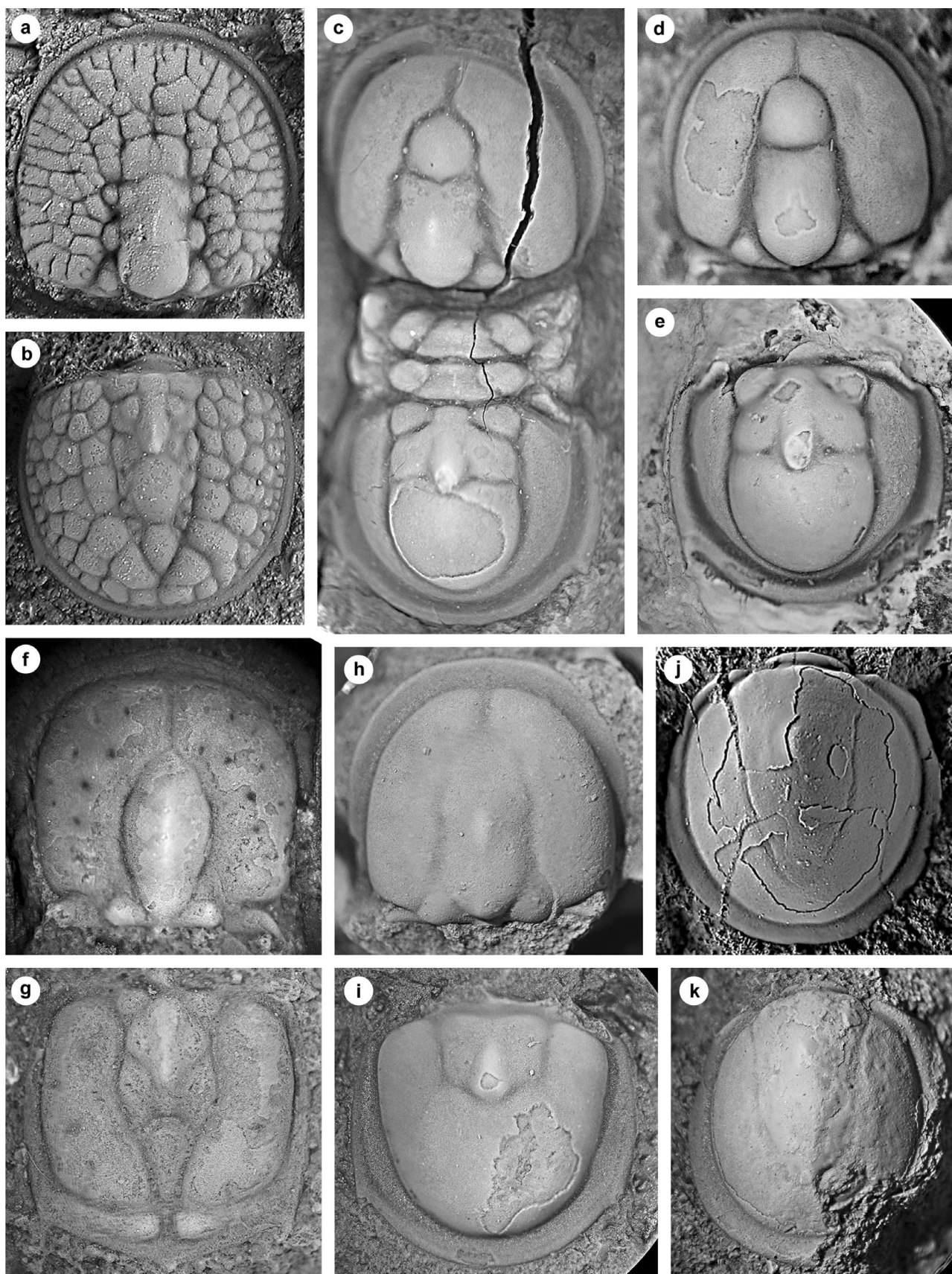


Figure 3. (a, b) *Glyptagnostus reticulatus* from the *Olenus gibbosus* Zone at Krokagården, eastern Kinnekulle, Västergötland, south-central Sweden. (a) Cephalon, original of Ahlberg & Ahlgren (1996, fig. 4I), LO 7333t,  $\times 11$ . (b) Pygidium, original of Ahlberg & Ahlgren (1996, fig. 4M), LO 7337t,  $\times 13$ . (c–e) *Aagnostus (Homagnostus) obesus* from the *Olenus wahlenbergi* Zone at Andrarum, southern Sweden. (c) Complete specimen, original of Westergård (1922, pl. 1, fig. 4a, b) and Ahlberg & Ahlgren (1996, fig. 3G), SGU 122a,  $\times 16$ . (d) Cephalon, original of Westergård (1947, pl. 1, fig. 10a, b) and Ahlberg & Ahlgren (1996, fig. 3E), SGU 6433,



southern Kazakhstan (Ivshin, 1962; Ergaliev & Ergaliev, 2008), allowing a broad correlation between lower *Leptoplastus*-bearing strata and the *Acutatagnostus acutatus*–*Erixanium* Zone in southern Kazakhstan.

### 5. Provisional Stage 10

*Lotagnostus americanus* (Billings, 1860) is a globally dispersed and easily recognizable species (Fig. 4a–f) that can be used for intercontinental correlations of upper Furongian strata (Peng & Babcock, 2005). Moreover, it is used as a zonal index in many areas, including Scandinavia (Terfelt *et al.* 2008). The ISCS has recently proposed the FAD of *L. americanus* as the primary marker horizon for correlation of the base of Stage 10 (e.g. Babcock & Peng, 2007). In Sweden, *L. americanus* (= *L. trisectus* of Westergård, 1922, 1944, 1947; Ahlberg & Ahlgren, 1996) ranges from the *Ctenopyge spectabilis* through the *C. bisulcata* zones, and possibly through the *C. linnarssoni* Zone (Westergård, 1947; Fig. 2).

*Pseudagnostus rugosus* Ergaliev, 1980 is known from the *Ctenopyge tumida* Zone of Scania and Västergötland, Sweden (Figs 2, 4g, h). The species was recently discussed comprehensively by Terfelt & Ahlberg (2010). This distinctive agnostoid has a narrow stratigraphical range and provides a precise correlation between the *C. tumida* Zone of Baltica, the lower *Eolotagnostus scrobicularis*–*Jegorovaia* Zone of Kazakhstan and the lower *Lotagnostus americanus* Zone of South China.

*Trilobagnostus rudis* (Salter, 1864) is based on material from the Dolgellau Formation at Gwynedd, North Wales (Morris, 1988; Rushton, 2009). In Sweden, it has been recorded from the *Ctenopyge tumida* Zone of Scania and Västergötland (Westergård, 1947; Ahlberg & Ahlgren, 1996; Figs 2, 4i, j). The species has subsequently been reported from the *C. tumida* Zone in the Holy Cross Mountains, Poland, and the middle *Lotagnostus americanus* Zone at the Khos-Nelege River, western Yakutia, Siberia (Żylińska, 2001; Lazarenko *et al.* 2008). Ergaliev & Ergaliev (2008) reported *T. rudis* from considerably older strata in the lower part of the *Pseudagnostus vastulus*–*Irvingella tropica* Zone in Malyi Karatau, southern Kazakhstan. This is an anomalous occurrence and the species identification needs to be confirmed.

*Trilobagnostus holmi* (Westergård, 1922) is a distinctive species and zonal index in the agnostoid zonation of Scandinavia (Terfelt *et al.* 2008; Figs 2, 4k,

l). It ranges from the *Ctenopyge bisulcata* (Westergård, 1922, p. 69) through the *Parabolina lobata* zones and is most common in the lower *P. lobata* Zone (Henningsmoen, 1958; Terfelt *et al.* 2005). The species has also been recorded from North Wales, where it is associated with *L. americanus* (Rushton, 1982, text-fig. 2).

*Lotagnostus subtrisectus* Westergård, 1944 is a poorly known species based on a single flattened pygidium from the uppermost *P. lobata* Zone (Fig. 2) at Andrarum, southern Sweden.

The last occurring agnostoid hitherto recorded from the Furongian of Scandinavia is represented by an incomplete, flattened and poorly preserved pygidium from the *Peltura transiens* Zone (Fig. 2) at Järrestad, Scania, southern Sweden. It was briefly described by Westergård (1909) and is herein referred to as *Aagnostus* sp. of Westergård (1909).

### 6. Discussion

Out of the 14 agnostoid species/subspecies so far known from Scandinavia, seven are geographically widespread and important for intercontinental correlations. *Glyptagnostus reticulatus*, *Aspidagnostus lunulosus* and *Aagnostus* (*Homagnostus*) *obesus* first appear at the base of the *G. reticulatus* Zone, allowing a precise correlation of the base of the Paibian Stage into Scandinavia (Fig. 5). The primary marker for the base of the Jiangshanian Stage, *Aagnostotes orientalis*, has hitherto not been recorded in Scandinavia. *Pseudagnostus cyclopyge* and *Tomagnostella orientalis* are, however, valuable auxiliary markers for the Paibian–Jiangshanian transitional interval (Fig. 5). In South China, the FAD of *T. orientalis* defines the base of the zone below the *A. orientalis* Zone (Peng *et al.* 2009a). *Tomagnostella orientalis* is, however, a rather long-ranging species that has been recorded from the *A. orientalis* through the *Eolotagnostus* zones (Peng *et al.* 2009a). The pygidium from the *Eugonocare borealis* Zone in the Khos-Nelege River section, Siberia (Lazarenko *et al.* 2008, pl. 16, fig. 13), is misidentified and should be transferred to another taxon. In Scandinavia, the first occurrence of *T. orientalis* and *P. cyclopyge* is in the lowermost *Parabolina brevispina* Zone, suggesting a correlation with the uppermost Paibian through the lowermost Jiangshanian stages. The record of the intercontinentally distributed polymerid *Irvingella major* in the *P. brevispina* Zone of Jämtland, central Sweden (Rushton & Weidner, 2010),

× 20. (e) Pygidium, original of Westergård (1947, pl. 1, fig. 11a, b) and Ahlberg & Ahlgren (1996, fig 3F), SGU 6434, × 18. (f, g) *Aspidagnostus lunulosus* from the *Olenus gibbosus* Zone at Hällekis, Kinnekulle, Västergötland, south-central Sweden. (f) Cephalon, original of Ahlberg & Ahlgren (1996, fig. 5K), LO 7350t, × 17. (g) Pygidium, original of Ahlberg & Ahlgren (1996, fig. 5L), LO 7351t, × 18. (h, i) *Pseudagnostus cyclopyge* from the lower *Parabolina brevispina* Zone at Andrarum, Scania, southern Sweden. (h) Cephalon; original of Ahlberg (2003, fig. 4C), LO 8308t, × 17. (i) Pygidium, original of Ahlberg (2003, fig. 4D), LO 8309t, × 15. (j, k) *Tomagnostella orientalis* from the lower *Parabolina brevispina* Zone. (j) Pygidium from Andrarum (locality 5 of Westergård, 1922, fig. 3), Scania, southern Sweden, coll. F. Terfelt, LO 11305t, × 12. (k) Pygidium from Gum, Kinnekulle, Västergötland, south-central Sweden, original of Ahlberg & Ahlgren (1996, fig. 5F), LO 7345t, × 13.



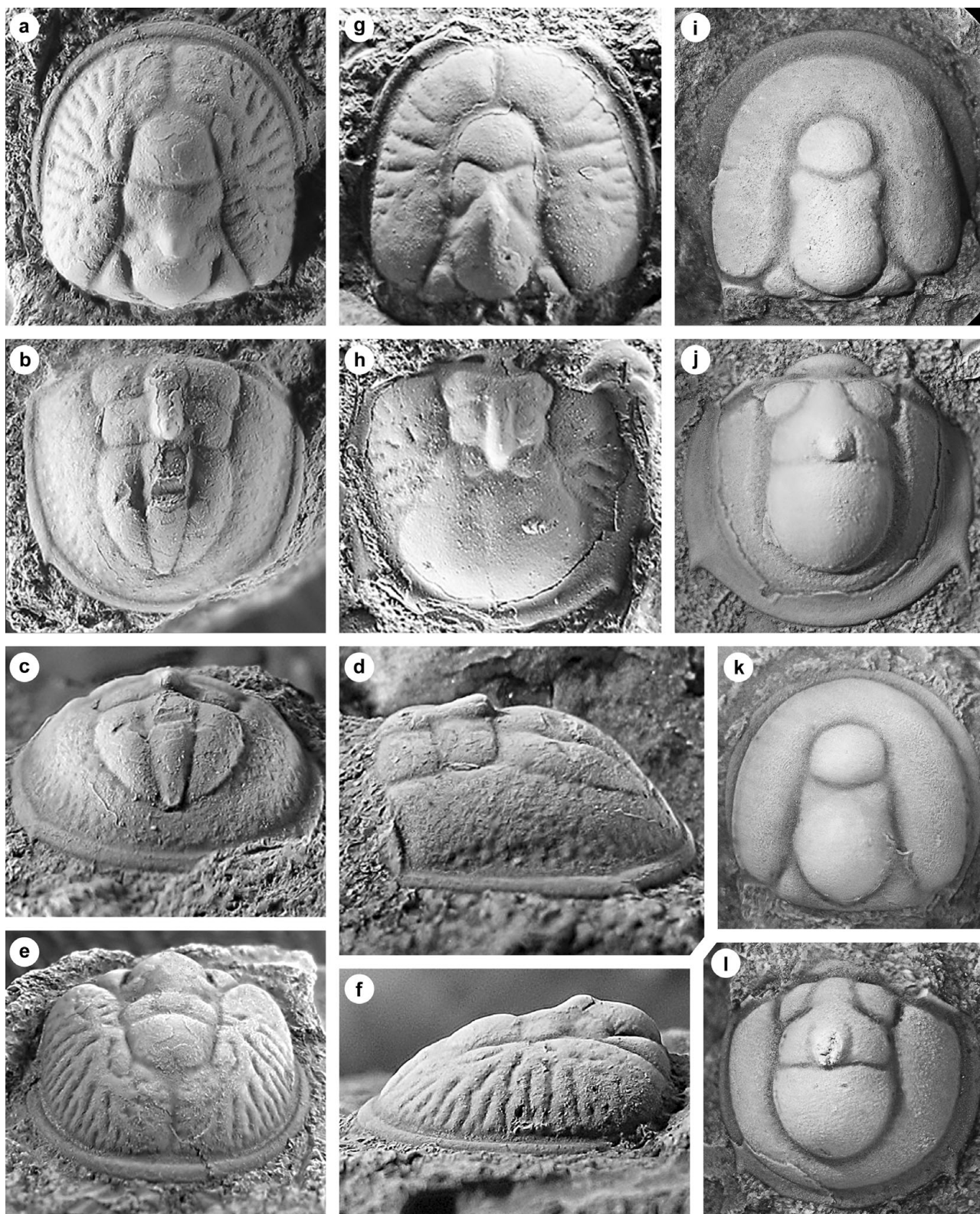


Figure 4. (a–f) *Lotagnostus americanus* from locally derived boulders of the *Ctenopyge bisulcata* Zone along the shore at Gislövshammar, Scania, southern Sweden. Coll. P. Cederström. (a, e, f) Cephalon in dorsal (a), anterodorsal (e) and left lateral (f) views, LO 11306t,  $\times 10$ . (b–d) Pygidium in dorsal (b), posterior (c) and left lateral (d) views, LO 11307t. (b)  $\times 11$ . (c)  $\times 12$ . (d)  $\times 14$ . (g, h) *Pseudagnostus rugosus* from locally derived boulders of the *Ctenopyge tumida* Zone along the shore NNE of the hamlet of Gislövshammar, Scania, southern Sweden. Coll. P. Cederström. (g) Cephalon, LO 11308t,  $\times 12$ . (h) Pygidium, LO 11309t,  $\times 11$ . (i, j) *Trilobagnostus rudis* from the *Ctenopyge tumida* Zone at Hönsäter, Kinnekulle, Västergötland, south-central Sweden. (i) Cephalon, original of Ahlberg & Ahlgren (1996, fig. 3I), LO 7321t,  $\times 15$ . (j) Pygidium, original of Ahlberg & Ahlgren (1996, fig. 3H), LO 7320t,  $\times 15$ . (k, l) *Trilobagnostus holmi* from the *Parabolina lobata* Zone. (k) Cephalon from Blomberg, Kinnekulle, Västergötland, south-central Sweden, original of Westergård (1922, pl. 1, fig. 13) and Ahlberg & Ahlgren (1996, fig. 3K), SGU 129,  $\times 21$ . (l) Lectotype, pygidium from Råbäck, Kinnekulle, Västergötland, south-central Sweden, original of Westergård (1922, pl. 1, fig. 15a–b) and Ahlberg & Ahlgren (1996, fig. 3O), SGU 131,  $\times 20$ .

GLOBAL		SOUTH CHINA		LAURENTIA		KAZAKHSTAN		SIBERIA		BALTICA		Scandinavian agnostoid zones	
FURONGIAN SERIES	STAGE 10	SERIES	NIUCHEHEAN	IBEXIAN SERIES	SKULLROCKIAN	SERIES	BATYRBAIAN	SERIES	NELEGERIAN	SERIES	STAGE 10	<i>Trilobagnostus holmi</i>	FAD of <i>Pseudagnostus americanus</i> <i>Pseudagnostus rugosus</i>
	JIANGSHANIAN		JIANGSHANIAN		SUNWAPTAN		AKSAYAN		CHEKUROVIAN		JIANGSHANIAN	<i>Lotagnostus americanus</i>	FAD of <i>Pseudagnostus cyclopyge</i> <i>Peratagnostus orientalis</i>
	PAIBIAN		PAIBIAN		STEPTOEAN		SAKIAN		PAIBIAN		PAIBIAN	??-??-??-??-??	<i>Glyptagnostus reticulatus</i>

Figure 5. Correlation chart of the Furongian Series showing the FADs of important agnostoid species and the agnostoid zonation of Baltica as compared to global stages as well as regional stages in major areas of the world.



provides evidence for a broad correlation between the *P. brevispina* Zone and the *Irvingella major* Zone of the lower Jiangshanian. *Lotagnostus americanus* and *Pseudagnostus rugosus* have an intercontinental distribution and their first appearance in Scandinavia allows for a correlation with one of the most favourable levels for defining the base of provisional Stage 10 (Figs 2, 5).

The depositional environment of the Alum Shale Formation has been debated during the past two decades, but all evidence indicates poorly oxygenated conditions at the sediment/water interface and that deposition generally took place below storm wave base. The Furongian part of the formation is seemingly fairly homogeneous; however, recent studies have shown that it is a variable unit both in terms of lithology and fossil fauna (e.g. Clarkson, Ahlberg & Taylor, 1998; Ahlberg *et al.* 2006; Eriksson & Terfelt, 2007), reflecting environmental changes. The life style of agnostoids has been extensively discussed and different life strategies have been proposed, including, for instance, a pelagic (e.g. Öpik, 1961, 1979; Robison, 1972; Jago, 1973), benthic (Jaekel, 1909), epifaunal (Pek, 1977; Havlíček, Vaněk & Fatka, 1993) and a nektobenthic (Müller & Wallosek, 1987) life. There is, however, growing evidence for a benthic mode of life in adult agnostoids (e.g. Chatterton, Collins & Ludvigsen, 2003; Fatka *et al.* 2009; Fatka & Szabad, 2011).

In the Furongian of Scandinavia, agnostoids are conspicuously assembled in three different intervals: the lower *Glyptagnostus reticulatus* Zone, the lower *Pseudagnostus cyclopyge* Zone and the *Lotagnostus americanus* through lower *Trilobagnostus holmi* zones (Fig. 2). If the assumption that the agnostoids had a benthic mode of life is correct, their distribution was strongly influenced by changes in sea-floor conditions, such as variations in temperature, oxygen levels, acidity/alkalinity, substrate composition/consistency, etc. The agnostoid-barren strata may represent time intervals during which the environment was inimical to agnostoids. A different interpretation is that the absence of agnostoids, or fossils altogether, is a result of taphonomy, notably subsequent dissolution of the calcareous fauna (Eriksson & Terfelt, 2007).

The unfossiliferous succession separating the lower and middle agnostoid-bearing intervals can be explained by means of dissolution and/or a hostile environment. The base of the lower interval coincides with the onset of the Steptoean Positive Carbon Isotope Excursion (SPICE; Ahlberg *et al.* 2009), which has recently been interpreted as reflecting transient increases in the burial of organic carbon and pyrite sulphur in sediments (Gill *et al.* 2011). According to Saltzman *et al.* (2011), massive amounts of oxygen were released as a side product of chemical reactions in the buried material. Following Schovsbo (2001), the highly elevated oxygen levels in the sulphur-rich sediments produced corrosive pore waters during the reoxidation of sulphide compounds, resulting in an adverse, acidic environment effectively prohibiting

fossilization. This model can be applied also to the unfossiliferous interval in the middle *Trilobagnostus holmi* Zone following the upper agnostoid-bearing interval. The middle agnostoid-bearing interval is succeeded by an anomalous succession dominated by the articulate brachiopod *Orusia lenticularis*, reflecting a regressive event coupled with increasing levels of oxygen at the sediment/water interface (Dworatzek, 1987). This shallowing obviously resulted in unfavourable conditions for agnostoids.

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