



Lotagnostus? mystacinus, a rare agnostid from the Upper Cambrian of Sweden

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Agnostids afford the best means of correlating Cambrian strata, and they are widely used for intercontinental correlations. They are most common in open-marine deposits and reached a maximum diversity during the Middle and early Late Cambrian. About twenty species of agnostids are known from the Upper Cambrian of Scandinavia. *Lotagnostus? mystacinus* Tjernvik, 1953 is a rare agnostid from the Upper Cambrian Agnostus pisijormis Zone of south-central Sweden. It is redescribed following examination of the holotype and an additional pygidium. The outline and morphology of especially the **pygidial** posteroaxis, which is distinctly trilobate by a pair of deep notular furrows, suggest that the species is best classified as a species of *Lotagnostus*. If correctly assigned to *Lotagnostus*, it would be the oldest known species of that genus.

The Middle and Upper Cambrian of Scandinavia are largely represented by dark, kerogen-rich mudstones and shales with lenses or beds of dark limestone (anthraconite or stinkstone). The mudstones and shales are generally finely laminated and referred to as alum shales. The sequences are condensed and accumulated over long periods of time under dominantly anoxic or dysoxic conditions. The lithological homogeneity and the large areal extent of the alum shale facies point to a fairly uniform depositional environment in a broad epicontinental sea, prone to stagnation (e.g., Thickpenney 1987).

The alum shale sequences are generally richly fossiliferous and they have a long history of palaeontological research, extending well back into the eighteenth century. The Upper Cambrian faunas are generally dominated by olenid trilobites, except in the lowermost part of the sequence where agnostids frequently occur in abundance. The olenids have been widely used for intraregional correlations and they provide a firm basis for the biostratigraphic classification of the Upper Cambrian of Scandinavia (e.g., Westergird 1922, 1947; Henningsmoen 1957). They tend, however, to be provincial and strongly facies controlled, and hence of limited value for long-distance correlations. Agnostids are among the best indices for regional and global correlation of Cambrian strata. Some twenty species of agnostids are known from the Upper Cambrian of Scandinavia. Most of these are in the lower part of the Upper Cambrian. Higher in the sequence agnostids become very rare, and only five species seem to be present in the upper part (Westergård 1947; Ahlberg & Ahlgren 1996). The lowest zone of the Upper Cambrian, the *Agnostus pisiformis* Zone, is dominated almost entirely by the eponymous species. Other agnostids are here very rare, but include specimens of *Cristagnostus papilio* Rushton, 1978 (= *Linguagnostus recondi-*

tus Poletaeva & Romanenko, 1970), *Peratagnostus falanensis* (Westergård, 1947), *Hypagnostus* sp., and *Komzagnostus?* sp. (Ahlberg & Ahlgren 1996). In addition, Tjernvik (1953) described '*Lotagnostus(?) mystacinus* sp. n.' on the basis of a single pygidium from the *Aagnostus pisiformis* Zone in Närke, south-central Sweden. Recently, the junior author (J.A.) collected an additional pygidium of this diagnostic species from the *Aagnostus pisiformis* Zone at Honsäter on Mount Kinnekulle, Västergötland, south-central Sweden. It is clear that *L.?* *mystacinus* is in need of modern description and illustration, and it is redescribed herein.

Systematic palaeontology

The morphological terms used herein are those advocated by Robison (1982: pp. 134–135, text-fig. 2) and Shergold et al. (1990: pp. 8–16, figs 1–6). Figured and cited specimens are housed in the Palaeontological Museum, University of Uppsala (PMU), and the Department of Geology, University of Lund (LO).

Order Agnostida Salter, 1864

Family Agnostidae M'Coy, 1849

Genus *Lotagnostus* Whitehouse, 1936

Type species: *Aagnostus trisectus* Salter, 1864 (p. 10, pl. 1: 11) from the White-Leaved-Oak-Shales (*Peltura scarabaeoides* Zone) in the Malvern area, England; by original designation.

Remarks. — *Lotagnostus* was established by Whitehouse (1936: p. 101) for scrobiculate agnostids with a distinct transglabellar furrow (F3), large basal lobes, a longitudinal trisection of the pygidial axis, and a pair of posterolateral spines in the pygidium. The concept of the genus has subsequently been discussed by, e.g., Palmer (1955: p. 91), Shergold (1975: p. 49), Ludvigsen et al. (1989: pp. 11–12), and Peng (1992: p. 15). The most comprehensive discussion is by Öpik (1963: pp. 53–54), who gave a list of important characters and noted that the generic concept can be expanded to include species with partial effacement of the furrows and lobes. These largely effaced species are generally grouped in the subgenus *Lotagnostus* (*Distagnostus*) Shergold, 1972 (see Ludvigsen et al. 1989: p. 12).

The type species and other closely related species of *Lotagnostus* have a morphologically distinctive pygidium with a long and clearly defined axis, which is weakly constricted across M2. The posterior part of the axial lobe (posteroaxis) is elongate, lanceolate or semioval to ogival with a well developed terminal node (Shergold et al. 1990: p. 34). It is usually tripartite, i.e., divided into three longitudinal parts by the notular furrows. The articulating device is of the basic type (Öpik 1963: p. 54).

The genus is widely distributed and has been recorded from the middle and upper Upper Cambrian of Europe, North America, Argentina, Kazakhstan, China, and Australia (e.g., Rasetti 1945; Palmer 1955; Ergaliev 1980, 1983; Allen et al. 1981; Peng 1992; Shergold et al. 1995; Westrop 1995; Ahlberg & Ahlgren 1996; Tortello & Bordonaro 1997; Shergold & Laurie in Kaesler 1997).

Lotagnostus? *mystacinus* Tjernvik, 1953

Fig. 1A–D.

Lotagnostus(?) mystacinus sp. n.; Tjernvik, 1953: pp. 73–74, fig. 1.

Holotype by monotypy: A nearly complete pygidium (PMU ar. 4192/N 1; Fig. 1A, B) from the *Aagnostus pisiformis* Zone in an abandoned quarry at Gymninge in Närke, south-central Sweden (see Westergård 1922: p. 81 for a description of the locality). It was collected by T.E. Tjernvik in 1946.

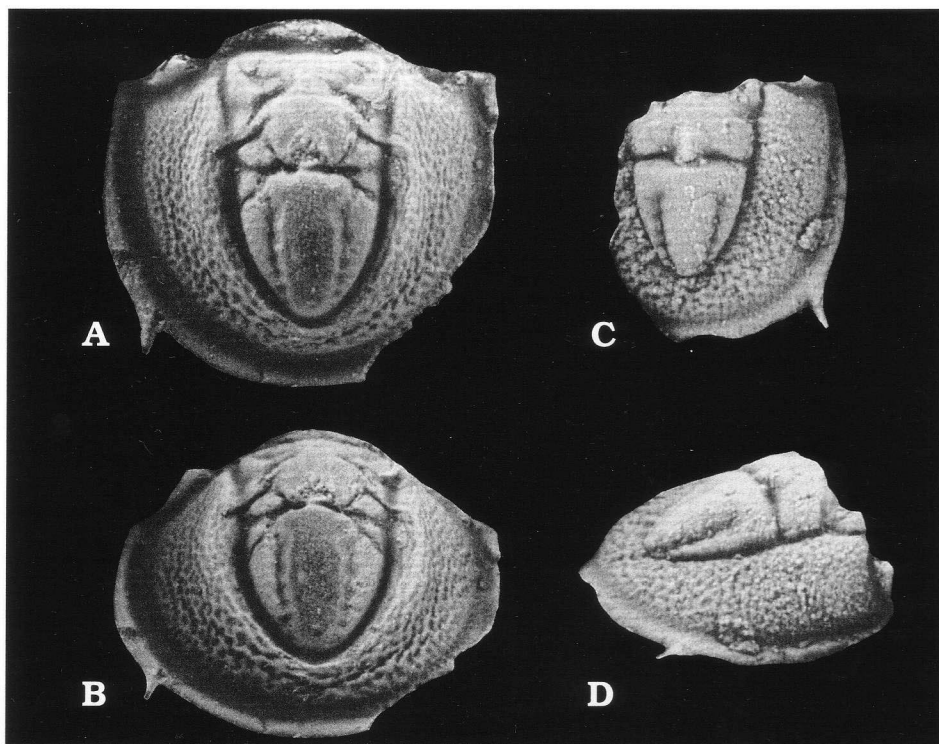


Fig. 1. A–D. *Lotagnostus? mystacinus* Tjernvik, 1953. *Agnostus pisiformis* Zone. A, B. Dorsal and posterodorsal views of pygidium, holotype, PMU ar. 4192/N 1; Gymninge, Närke, south-central Sweden; $\times 15$. C, D. Dorsal and posterolateral views of incomplete pygidium, LO 8095t; Honsater, Västergötland, south-central Sweden; $\times 16$.

Other material: An incomplete pygidium (LO 8095t; Fig. 1C, D) from the *Agnostus pisiformis* Zone at Honsater in Västergötland, south-central Sweden (locality 2 of Ahlberg & Ahlgren 1996: fig. 1). It was collected by J. Ahlgren in 1995.

Emended diagnosis.—Pleural fields non-scribulate and with distinct reticulate pattern of raised lines. Posteroaxis long, acutely rounded posteriorly, and divided into three longitudinal parts by fairly deep notular furrows. Each notular furrow with five pits. Intranotular axis wide. Prominent posterolateral spines at level of rear of axis. Differs from the type and other species of *Lotagnostus* in having a wider intranotular axis and in having a distinct reticulate pattern of raised lines on the external exoskeletal surface of the pleural fields.

Description.—The pygidium is *en grande tenue*, highly convex, subcircular in outline, and subequal in length and maximum width. The acrolobe is non-scribulate, unconstricted, and lacks a median postaxial furrow. The axis (excluding the articulating half-ring), occupying 67 to 71% of the total pygidial length, is highly convex, tapered backwards, and delimited laterally by prominent axial furrows. It is gently constricted at the posterior ring furrow (F2), acutely rounded posteriorly, and about 1.6 times as long (excluding the articulating half-ring) as its maximum width. The anterior axial segment (M1) is slightly wider (tr.) than M2. The anterior axial furrow (F1) is medially discontinuous, and directed inward and slightly for-

ward from the axial furrow, then curved strongly forward adaxially. F2 is deep and nearly straight. A pair of slightly curved ridges, and behind these a pair of furrows, are present on the anterolateral parts of the **middle** axial lobe (M2) in the holotype. The axial tubercle is poorly preserved, at least in the holotype, but it appears to have been prominent and extends backwards above F2. The posteroaxis is nearly lanceolate and 1.4 to 1.5 times longer (sag.) than the anteroaxis (M1+M2). It is distinctly tripartite and has a pair of deep notular furrows. Each notular furrow is provided with five small pits. The posteroaxis is strongly down-sloping laterally and posteriorly, and bears a faint terminal node slightly anterior to its posterior end. The articulating furrow is wide and deep, deepest laterally.

The pleural fields are strongly down-sloping and narrowest behind the axis. They bear a distinct reticulate pattern of raised lines. The border furrow is deliquiate. The border is widest posterolaterally. Sagittally, the border and border furrow combined occupy 8–9% of the total pygidial length. The posterolateral spines are prominent and commence on a transverse line passing the posterior end of the axis. The anterior border furrow is deeply incised.

Remarks. — The ridge and furrow along the anterolateral margin of M2 in the holotype are not present in the pygidium from Västergötland. These peculiar structures may be of taphonomic origin, perhaps due to compression or crushing of the anteroaxis. It is also worth noting that the acrolobe is slightly constricted in the Västergötland specimen, whereas it is unconstricted in the holotype. In most other respects, the specimens are closely similar, and there is no reason to doubt that they are conspecific.

Lotagnostus? mystacinus most closely resembles *L. punctatus* Lu in Wang, 1964 from the Upper Cambrian of South China, but the latter species differs in having a more prominent median tubercle, wider posteroaxis, and a considerably narrower intranotular axis. In addition, *L. punctatus* seems to lack a reticulate pattern of raised lines on the pleural fields (see Peng 1992: fig. 6A–G, L).

The outline and morphology of the posteroaxis, which is distinctly tripartite, suggest that *L.? mystacinus* is best classified as a species of *Lotagnostus*. But as no cephalae have been found, the generic assignment remains uncertain. The earliest known species of *Lotagnostus* previously recorded are from middle Upper Cambrian strata. If *L.? mystacinus* is correctly assigned to *Lotagnostus*, it would be the oldest known species of this genus.

In the proportions and outline of the individual parts of the pygidium, *L.? mystacinus* is similar to *Agnostus pisiformis*, but the latter species generally has a distinctly constricted axis, whereas the axial furrows are straighter in *L.? mystacinus*. Notular furrows and a distinct reticulate meshwork of raised lines are not present on the external exoskeletal surface of the adult *A. pisiformis*. It is worth noting, however, that juvenile pygidia of *A. pisiformis* can sometimes be reticulated or pitted (see Henningsmoen 1958: p. 181, pl. 5: 7–8). Notular furrows on the posteroaxis have been illustrated on rare, small holaspides of *Pseudagnostus* (Palmer 1955: pl. 20: 5, 8) and *Komagnostus* (Pratt 1992: pl. 3: 17, text-fig. 27A), but such furrows disappeared during later ontogeny. Possibly *L.? mystacinus* represents an extreme variant of *A. pisiformis*. We have, however, examined thousands of specimens of *A. pisiformis* in all stages of growth, and it is obvious that *L.? mystacinus* falls outside the variation seen in *A. pisiformis*. Consideration of the possible suppression of *Lotagnostus* as a junior synonym of *Agnostus* requires evaluation of many species, and is not attempted here.

Occurrence. — *Agnostus pisiformis* Zone at Gymninge in Närke and at Hönsäter on northern Kinnekulle, Västergötland. The species is associated with *A. pisiformis* in abundance.

Table 1. Dimensions (in mm) of *Lotagnostus? mystacinus*. Estimated values and transverse measurements achieved by doubling the width from the sagittal line are indicated with a question mark.

	PMU ar. 4192/N 1	LO 8095t
Length of pygidium (incl. articulating half-ring)	3.45	—
Length of pygidium (excl. articulating half-ring)	3.15	2.20?
Length of pygidial axis (excl. articulating half-ring)	2.45	1.65?
Length of posteroaxis	1.45	1.00
Length of posterior pygidial border (incl. border furrow)	0.30	0.20
Maximum width of pygidium	3.50	2.50?
Maximum width of pygidial axis	1.50	1.05

Acknowledgements

Financial support has been received from the Swedish Natural Science Research Council (NFR). Dr John H. Shergold, Masseret, France, provided valuable information. Professor Richard A. Robison, Lawrence, Kansas, and Mr Mats Eriksson, Lund, read the manuscript and offered helpful criticism.

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