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Some lower Middle Ordovician species of *Asaphus* (Trilobita) from SwedenMARTIN STEIN¹ and JAN BERGSTRÖM²

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Abstract: Several *Asaphus* (*Asaphus*) species concepts are in a state of flux. Here we elucidate the morphological differences and stratigraphical occurrences of *Asaphus raniceps* and *A. lamanskii*. It is shown that *Asaphus raniceps* and *A. 'raniceps'* of several authors include specimens of *A. raniceps*, *A. lamanskii*, *A. striatus*, *A. vicarius* and *A. fallax*. Specimens of the latter have commonly been labelled *A. expansus*. Angelin's '*A. acuminatus*' is interpreted as a species distinct from Boeck's *A. acuminatus*. The dorsal pattern of terrace lines is described and used in species discrimination. The number of axial rings in the anterior half of the pygidium is a second new character useful in characterising and identifying *Asaphus* species. Diagnoses and descriptions are provided for *A. raniceps*, *A. lamanskii*, *A. vicarius* and *A. angelini* n. sp. It is shown that both *A. raniceps* and *A. vicarius* occur in the *Asaphus 'raniceps'* Zone, and it is proposed to rename that zone to the *Asaphus raniceps* and *Asaphus vicarius* Zone.

Keywords: Middle Ordovician, Kunda Stage, biostratigraphy, trilobite biozones, *Asaphus*, *raniceps*, *lamanskii*, *vicarius*, *angelini* n.sp.

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Introduction

Recent studies of Middle Ordovician asaphids from Östergötland (Bergström et al. 2003) have revealed great flaws in previous understandings of Kundan (lower Darriwilian) species of *Asaphus*. This even affects common species that were regarded as well known, such as the type species *A. expansus* (Wahlenberg, 1821; see Bergström 2007).

The original basis for this report is a study of the sedimentary sequence and trilobite zonation in a quarry at Gillberga, Öland (Fig. 1; Stein, unpublished diploma thesis). The results make it necessary to continue the revision of early *Asaphus* species.

In Gillberga, the top eight meters of accessible strata in the section comprise the *Asaphus 'raniceps'* Zone, but *Asaphus raniceps* Dalman, 1827 occurs only in a narrow interval of about one meter at the base of the zone (Fig. 2). In the remaining seven meters *Asaphus vicarius* (Törnquist, 1884) occurs in abundance. Both *A. raniceps* and *A. vicarius* were previously referred to as *Asaphus 'raniceps'*. We here propose to rename the zone from the *Asaphus 'raniceps'* Zone (e.g., Jaanusson 1953, p. 406; Nielsen 1995, p. 30) to the *Asaphus raniceps* and *Asaphus vicarius* Zone. The lower boundary is defined as the first appearance of *Asaphus raniceps*. The lower boundary of the overlying *Megistaspis obtusicauda* Zone (Bohlin 1949, 1955) should be defined by the first appearance of the index species, but was not identified in the sequence at Gillberga where it should be close to the top. With this refined zonation, we remove an obstacle in the attempts to make a correct regional biostratigraphy.

Material and methods

Material is derived mostly from the Gillberga section, although material from other localities across Sweden (Fig. 1) has also been studied in different collections. Of particular interest were the collections of Dr. Harry Mutvei from sections at Hälludden and Hagudden, Öland, Sweden as well as type specimens. Relevant collections and localities are given in the descriptions of the individual species. Abbreviations for repositories are listed below. The preservation is typical for the limestone sequence in general, with the calcareous exoskeleton well preserved if not flaked off and moderately deformed by compression.

Measurements. – Measurements were taken with callipers, following the definitions of Shaw (1957) and Temple (1975). Pygidial length measures exclude the articulating half-ring.

Repositories. – Abbreviations are given as follows:

- NRM – Swedish Museum of Natural History, Stockholm
- PMO – Palaeontological Museum, University of Oslo
- MGUH – Geological Museum, University of Copenhagen
- LO – Department of Geology, Lund University.

Systematic section

Asaphus (*Asaphus*) Brongniart, 1822

Type species. – *Entomostracites expansus* Wahlenberg, 1818 (by subsequent designation: Jaanusson 1956).

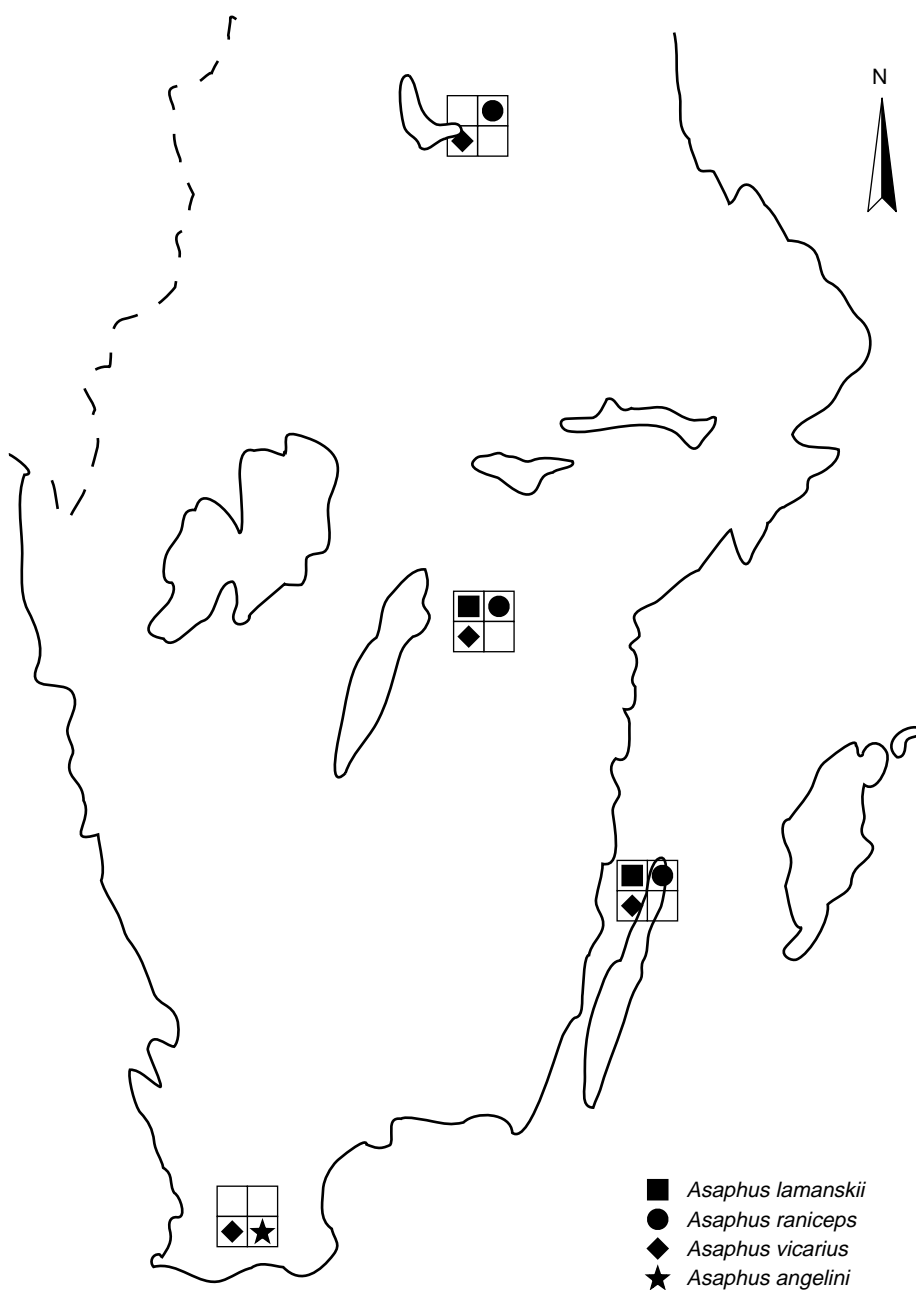


Fig. 1. Geographic distribution of the four species commonly called *Asaphus raniceps* in Sweden. The northernmost occurrence is the Siljan district, the southernmost southern Scania. The two occurrences in the centre are Östergötland to the west and northern Öland to the east.

Diagnoses of genus and subgenus. – See Jaanusson 1953, pp. 391 and 396 respectively.

Remarks. – Previous taxonomic studies of *Asaphus* (*Asaphus*) focused on cephalic features including the hypostome, and on the doublure of thorax and pygidium with particular reference to the pandertian notch. In the present contribution, additional dorsal characters, in particular the terrace line pattern on the pygidium, are applied. The absence of a true preglabellar field can be added as a diagnostic character of the cephalon.

The pattern of terrace lines on the thoracic axis (Fig. 3A) is uniform in *Asaphus* (*Asaphus*), but the distinctness varies between species. The facet carries distinct terrace lines arranged in a fan (Fig. 3B). The same pattern is seen in the pygidial facet.

In the pygidium, the fulcrum is developed only at the anterior margin, where it is seen at the inner end of the facet. Only

A. acuminatus (Boeck, 1838) as conceived by Angelin (1854) forms an exception in having a fulcrum developed throughout most of the pygidium. This taxon also has a true preglabellar field and is here provisionally excluded from *Asaphus* (*Asaphus*). In the remaining species, a division of the pleural region of the pygidium into inner and outer portions is indicated by the distribution of terrace lines. The boundary corresponds roughly to the inner margin of the pygidial doublure. The latter carries usually less than 20 (but up to 24 in *Asaphus striatus* (Boeck, 1838), see Wandås 1984, p. 218, Nielsen 1995, p. 93, and Hansen 2009, p. 79) fairly coarse terrace lines in the majority of the species.

A count of the total number of axial rings in the pygidium is impractical, because the rings tend to be effaced in the posterior part of the axis. A more feasible approximation is the number

of axial rings along the anterior half of the pygidial mid-line, excluding the articulating half-ring. Since this number is counted along a straight line it can be counted also in tectonically deformed specimens. Boeck's material of *A. acuminatus* is deformed, but appears to have about 5 rings in this position. *A. fallax* Angelin, 1854 and *A. expansus* (Wahlenberg, 1818) have 5, *A. raniceps*, *A. lamanskii* (Schmidt, 1901) and *A. lepidurus* Nieszkowski, 1859 5.5, *A. incertus* Brögger, 1882 5.5–6, *A. vicarius* Törnquist, 1884 5, *A. striatus* 6–6.5, *A. 'maximus'* Brögger, 1886 and *A. angelini* n. sp. 7.

Schmidt (1901, p. 14) noted that the pygidial segmentation is rarely visible in the pleural field of *Asaphus*. Furrows are indistinct, though inconspicuous impressions can be seen in oblique light (Fig. 4). The segmentation is best revealed by the regularity in the terrace line pattern found in *Asaphus* (*Asaphus*) except for *A. broeggeri* Schmidt, 1901. The pattern includes one more or less continuous segmental line corresponding to each pleural segment with a fan-like branching close to the margin (Fig. 4B). Close to the axis, the line gives way for an array of short, sinuous anterolaterally directed terrace lines (Fig. 3C, 4B). A similar pattern in the thorax is found in *A. vicarius* (Fig. 3A) and the Ptychopyginae. Two or three short terrace lines extend from the pleural field over the axial furrow onto the axial ring (Fig. 4B). These short lines seem to be confined to the anterior band of the pleura. About halfway to the pygidial margin the long terrace line branches into a fan-like structure. This ramification may be a serial similarity to the ramification on the pygidial facet and the pleural facet of the thorax. It is not present in all species (cf. Fig. 3C). Instead, there may be scattered lines in-between the long lines reaching the margin as e.g. in *A. expansus*. Exfoliated specimens of *A. expansus* allow the study of the distribution of terrace lines in relation to the segmentation (Fig. 4A). Both pleural and interpleural furrows are weakly impressed on the sediment filling the space between dorsal test and doublure. Imprints of terrace lines are found on the anterior band of the pleura. In *A. expansus* the short sinuous terrace lines are restricted to the anterior band whereas in others, for instance in *A. lepidurus*, they extend over the entire surface of the pleurae and connect to the line or array of the next posterior segment (Fig. 4B). In that case, they are usually interrupted or dislocated at the pleural furrows, which is in accord with Miller's (1975, p. 164) 'rules' (his quotation marks), the second of which is that terrace lines 'do not continue across or into deep furrows'. Support can be found even for his third 'rule' saying that the lines 'tend to swing so as to run tangentially to deep hollows or furrows' (therefore the sinuosity of the anterolaterally directed lines).

On the axial ring, a whole set of terrace lines typically extends forwards from the posterolateral corner via the posterior portion of the lateral swellings of the axial rings, and inwards over the midline (Figs. 3C, 4B). In addition, there is commonly a set of short transverse arches in or directly anterior to the inter-ring furrow, corresponding to lines found on the articulating half-rings of the thoracic axis (Fig. 3A). The pattern tends to be less well developed towards the posterior, particularly in the inter-ring furrow.

It appears that Schmidt (1901, p. 15) already recognised the presence of this basic pattern, though he described it only in brief and did not stress its general validity for the genus, which can be confirmed at least for *Asaphus* (*Asaphus*) with *A. broeggeri* excluded. According to his description (Schmidt

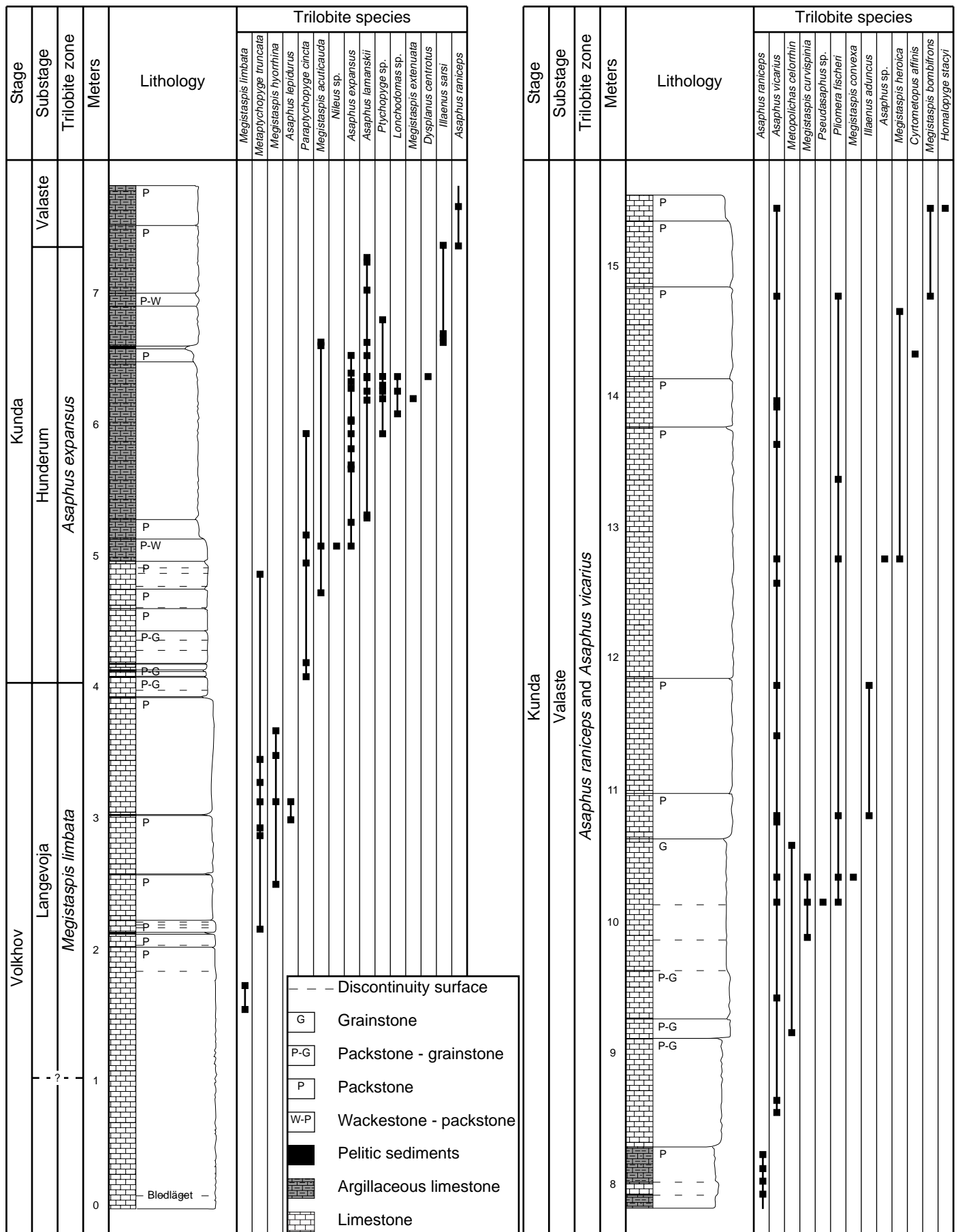
1901, p. 23), terrace lines are absent on the pleural field in the latter species, except for fine short lines in the axial furrow. Schmidt (1901, p. 23) considered *A. broeggeri* to be an odd species without close affinities to any other known species of the genus. This view was supported by the presence of an ill-defined pygidial border developed medially on the posterior margin as well as a hypostome morphology deviating from that of other *Asaphus* species. Despite these peculiarities, Balashova (1953, p. 388) placed *A. broeggeri* in her *A. (Schizophorus)*, which is a synonym of *A. (Asaphus)*.

Nielsen (1995, pp. 74–76) presented the most recent review of *Asaphus* (*Asaphus*). The investigation presented herein suggests a somewhat narrower scope of the subgenus. Thus *Asaphus broeggeri* should be excluded. Although it agrees with *Asaphus* (*Asaphus*) in features of the thoracic doublure, it differs considerably in other respects. In addition to those differences mentioned above the cephalon has a preglabellar field, the pygidial axis has 12 axial rings (5 in the anterior half) and the doublure carries more than 25 fine terrace lines.

In our view, the following taxa can be included in *Asaphus* (*Asaphus*): *A. expansus* (Wahlenberg, 1821), *A. raniceps* Dalman, 1827, *A. striatus* (Boeck, 1838), *A. fallax* Angelin, 1854, *A. lepidurus* Nieszkowski, 1859, *A. lamanskii* Schmidt, 1901, and *A. vicarius* Törnquist, 1884. *Asaphus incertus* Brögger, 1882 is considered a *nomen dubium* (Nielsen 1995, p. 75). Species which may not belong here include *A. acuminatus* (Boeck, 1838), *A. angelini* n.sp., and *Asaphus maximus* Brögger, 1886 (see Nielsen 1995, p. 75). Of these, we consider *A. acuminatus* and *A. maximus* as possible *nomina dubia*.

Asaphus (*Asaphus*) *raniceps* Dalman, 1827
Fig. 5

- Asaphus expansus* var. β *raniceps* – Dalman 1827, p. 108, pl. 3:4 (diagnosis, illustration).
? *Trilobites raniceps* – Boeck 1838, p. 36 (brief comparison with *A. expansus* and *A. acuminatus*).
Asaphus raniceps Dalm – Angelin 1854, p. 53; pl. 28:2a–c; non pl. 28:2 (diagnosis, occurrence, illustrations).
Asaphus raniceps Dalm. Burm – Nieszkowski 1857, pp. 550–551 (diagnosis, description).
Asaphus raniceps Dalm – Schmidt 1901, pp. 32–36, text figure 20; pl. 1:8, 9, 11; non pl. 2:3 (description, occurrence, photographs).
Asaphus raniceps – Lamansky 1905, pp. 58, 62–63, 168, 169 (occurrence).
Asaphus (*Schizophorus*) *raniceps* Dalman – Balashova 1953, pp. 394–395; pl. 1:5, 23, pl. 2:4 (remarks and comparison, occurrence, illustrations).
Asaphus (*Asaphus*) '*raniceps*' – Jaanusson 1953, pp. 394, 396–397 (discussion).
Asaphus (*Asaphus*) *raniceps* Dalman, 1827 – Balashova 1976, p. 9 (discussion).
non *Asaphus* "*raniceps*" – Tjernvik & Johansson 1980, pp. 190, 194, figs 1, 2, ?10B (occurrence, illustration).
non *Asaphus raniceps* – Tjernvik & Johansson 1980, fig. 10A (illustration).
non *Asaphus* (*Asaphus*) *raniceps* (Dalman, 1827) – Nielsen 1995, p. 97 fig. 75 A–D (occurrence, remarks, photographs).
non *Asaphus* (*Asaphus*) '*raniceps*' sensu Angelin – Nielsen 1995, pp. 96–98, figs. 75 E, F, 76 A–C (occurrence, remarks, photographs).



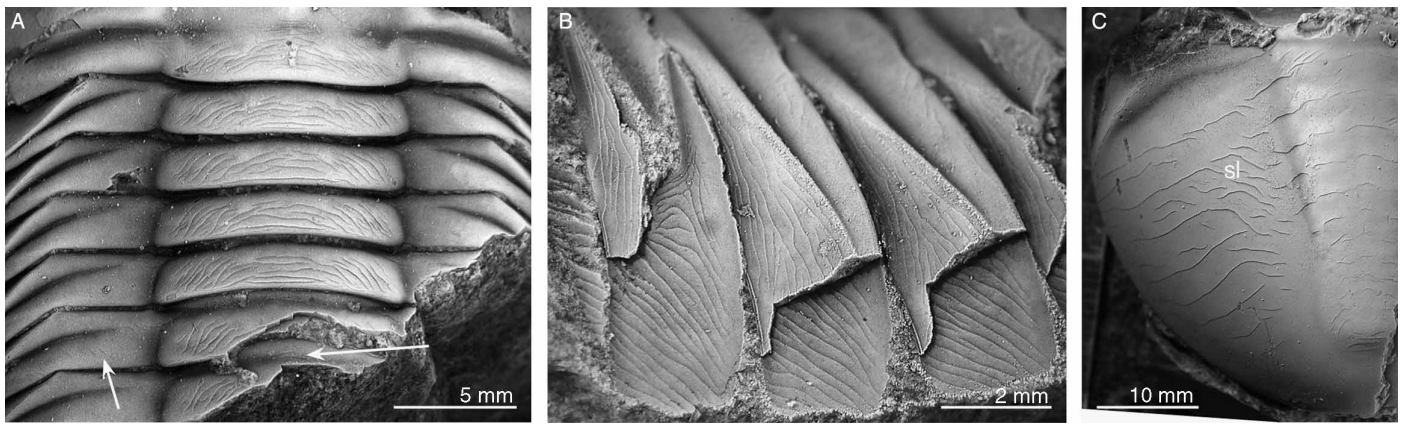


Fig. 3. Terrace line patterns in thorax and pygidium in *Asaphus vicarius* Törnquist, 1884. **A.** Thoracic axis showing distinct terrace lines in characteristic pattern found in all *Asaphus* species, note also the lines on the posterior band of the pleural field (left arrow) and the transverse terrace lines on the articulating half ring (right arrow), NRM Ar 59864. **B.** Thoracic facet, NRM Ar 59863. **C.** Pygidium, NRM Ar 59492. Abbreviations: *sl*, short sinuous terrace lines.

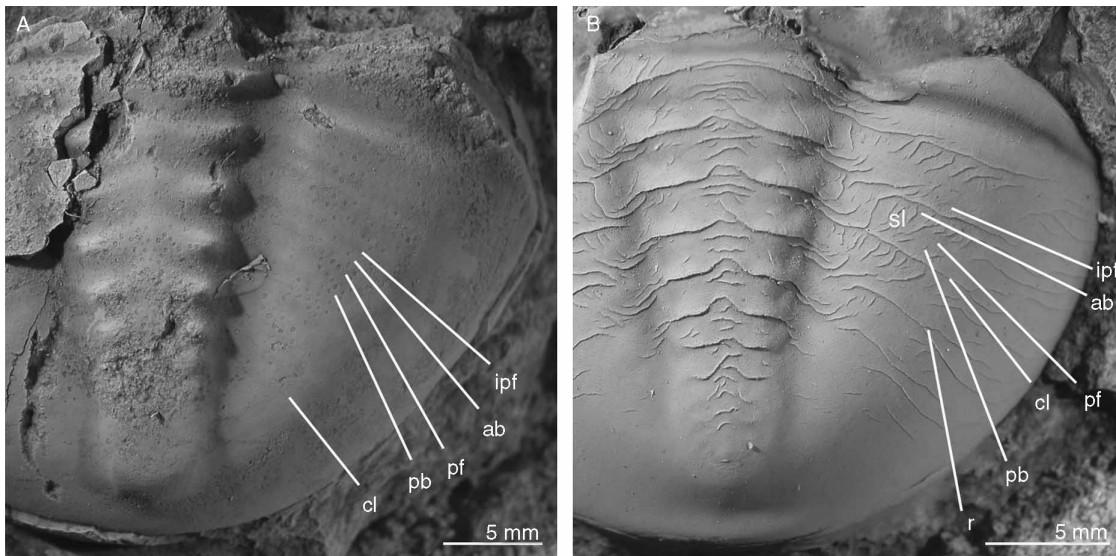


Fig. 4. Pygidial terrace line patterns and segmentation. **A.** Exfoliated pygidium of *Asaphus expansus* (Wahlenberg, 1818), NRM Ar 59459, showing pleural and interpleural furrows. **B.** Pygidium of *Asaphus lepidurus* Nieszkowski, 1859, NRM Ar 2163, showing distribution terrace lines. Abbreviations: *ab*, anterior band; *cl*, continuous segmental terrace line; *ipf*, interpleural furrow; *pb*, posterior band; *pf*, pleural furrow; *r*, ramification.

non *Asaphus* (*Asaphus*) '*maximus*' (Brögger, 1886) – Nielsen 1995, pp. 98–102 (cf. his comment p. 101).

Asaphus (*Asaphus*) *raniceps* Dalman, 1827 – Bergström et al. 2003, pp. 101–103, figs. 2C, E, 3C, 4F, G; non fig. 4D.

non *Asaphus raniceps* Dalman, 1827 – Bergström 2007, fig. 5C; the catalogue number and locality given for the specimen are incorrect, it is NRM Ar 16681 (figured here in Fig. 6A).

Lectotype. – Balashova's (1953, p. 394) designation of a lectotype is invalid according to the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 2000, article 74.1), since the specimen was not selected from Dalman's syntypes (and could therefore

only be a potential neotype). The valid lectotype (from Dalman's type series) is thus the specimen RM Ar 16531, as designated subsequently by Bergström et al. (2003, fig. 4F). The type material was collected in Västana, Östergötland, Sweden.

Syntypes. – RM Ar 16363, 16379, 16414, 16626, 16627, 16664, 51808, 51820, 52066.

Other material. – RM Ar 59467–59474 (1 complete specimen, 1 incomplete specimen, 6 pygidia) from Gillberga, Öland.

Occurrence. – The species is known from Västana and Ljungsbro in Östergötland, the type material being collected

Fig. 2. Stratigraphic distribution of trilobite species in the section at Gillberga, Öland, Sweden. The base of the Valaste substage coincides with the base of the *Asaphus raniceps* and *Asaphus vicarius* Zone, which replaces the old *Asaphus 'raniceps'* Zone.

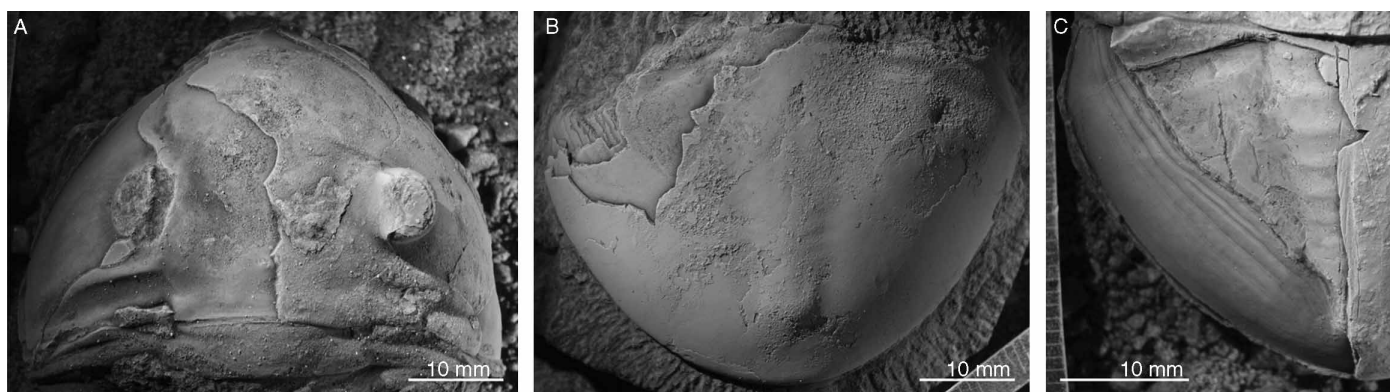


Fig. 5. *Asaphus raniceps* Dalman, 1827. **A.** Partially exfoliated cephalon, NRM Ar 52050. **B.** Pygidium with cuticle largely intact, showing effaced axis, NRM Ar 59467. **C.** Partially exfoliated pygidium with the doublure exposed to show the terrace lines, NRM Ar 58388.

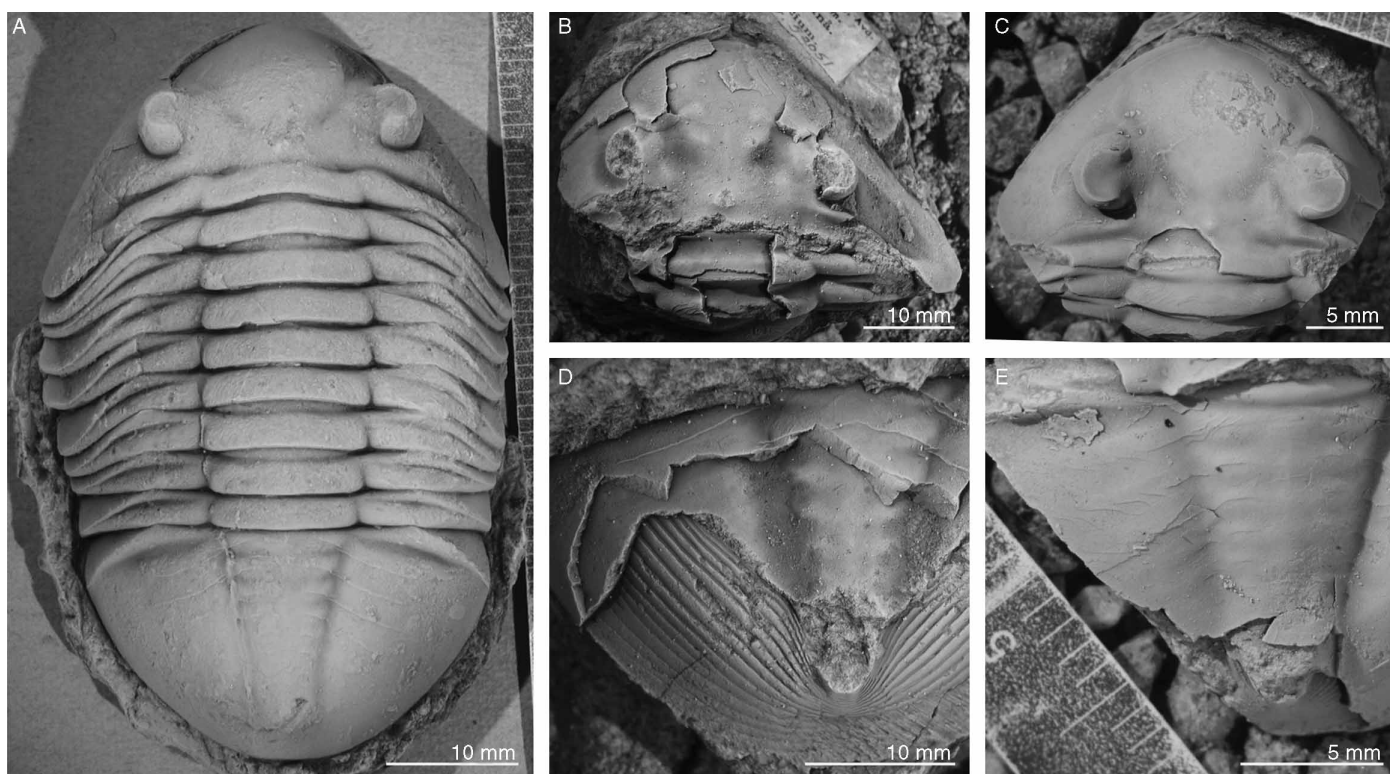


Fig. 6. *Asaphus lamanskii* Schmidt, 1901. **A.** Complete specimen, NRM Ar 16681. **B, D.** Complete, enrolled specimen NRM Ar 52051; **B.** Largely exfoliated cephalon, NRM Ar 52051, **D.** Largely exfoliated pygidium showing doublure, NRM Ar 52051. **C, E.** *Asaphus lamanskii* cf. *acuminatus*, complete, enrolled specimen NRM Ar 55574; **C.** small cephalon, **E.** pygidium showing deviating terrace line pattern.

in the former locality. It furthermore occurs on northern Öland and in Estonia. Nielsen (1995) reported it from southern Scandinavia and the Oslo region, but his determinations are incorrect (see below). *A. raniceps* occurs in the Gillberga section in a narrow interval of less than one meter above the strata with *A. expansus* and *A. lamanskii*. It could also be identified in the collections from Dalarna stored in the Swedish Museum of Natural History (RM Ar 45168 from Silvberg).

New diagnosis. – Species of *Asaphus* (*Asaphus*) with subtriangular outline of cephalon and pygidium. High degree

of effacement; cephalic furrows and bacculae indistinct. Occipital furrow largely effaced. Anterior lobe with weak nodes over two pairs of muscle scars and an indistinct median keel. Pygidium with terminal piece notably elevated. Pygidial axis with 10 axial rings, axial segmentation completely effaced in testaceous specimens. Of the axial rings, 4–5 are situated in the anterior half of the pygidium.

Description. – Descriptions are given by Schmidt (1901) and Balashova (1953). In pygidia with a well-preserved cuticle, oblique terrace lines can be observed in the axial furrow, usually one lateral to each axial ring. Terrace lines on the pleural field

are poorly defined. Those on the inner pleural field are confined to the anterior band. The lines on the outer pleural field do not fully reach the pygidial margin. The branching is not distinctly seen. Instead shorter lines are sparsely intercalated between the long lines extending across the outer field. Only the anteriormost pleural furrow is distinct, the posterior ones are very indistinct impressions in the pleural field close to the axial furrow. Poorly defined traces of interpleural furrows can be seen only in the anteriormost portion. The pygidial doublure is wide and shows about 10 to 12 coarse terrace lines (Fig. 5C).

Remarks. – This species reaches a length of about 11 cm. The pygidium figured by Schmidt (1901, pl. 2:3) carries about 17 fine terrace lines on the doublure, which is not in accord with the material investigated herein, including Dalman's material. Neither does the outline resemble that of *A. raniceps*. In the cranium figured by Tjernvik and Johansson (1980, fig. 10B), the palpebral lobes are small and separated by a comparatively wide glabella. The occipital ring is wide and the distance between the axial furrows where it reaches the posterior cephalic border and the intersection of the facial suture with the border appears to be rather small. All this resembles *A. striatus* rather than *A. raniceps*.

Discussion. – The species has been subject to discussion for half a century. Bergström et al. (2003) gave a historical review and showed that Angelin's specimens include Dalman's specimens and belong to Dalman's species. While helping to resolve the identity of *A. raniceps* with regards to other species described from Sweden, the authors did not discuss the morphologically similar but stratigraphically older *A. lamanskii* Schmidt, 1901. The latter was known from the Zone of *A. expansus* in the Baltic countries (Schmidt 1901, Balashova 1953, Ivantsov 2001), but also occurs in the same zone in Sweden (Stein 2003). See also the remarks under *A. lamanskii*.

Asaphus (Asaphus) lamanskii Schmidt, 1901
Fig. 6A, B, D; ?C, E

Asaphus raniceps Dalm. – Angelin 1854 pars, pl. 28:2; non pl. 28:2a–c.

Asaphus raniceps Dalman var. *lamanskii* – Schmidt 1901 pp. 32–36, textfigure 21; pl. 12:8–10 (comparison, occurrence, photographs).

Asaphus lamanskii – Lamansky 1905 p. 63 (brief discussion).

Asaphus (Schizophorus) lamanskii Schmidt – Balashova 1953 pp. 391–393; pl. 1:33, pl. 2:7 (description comparison, occurrence, photographs).

Asaphus (Asaphus) lamanskii Schmidt, 1901 – Balashova 1976 p. 9 (discussion).

Asaphus n. sp. – Tjernvik & Johansson 1980 p. 194, fig. 9J (occurrence, brief comparison with *A. expansus* and *A. lepidurus*, photograph).

Asaphus (Asaphus) raniceps Dalman, 1827 – Bergström et al. 2003, fig. 4D.

Asaphus (*A.*) '*raniceps*' sensu Angelin 1854 – Krueger 2003, pp. 61–62, pl. 2:1–2.

Asaphus raniceps Dalman, 1827 – Bergström 2007, fig. 5C.

Type material. – Balashova (1953) selected one specimen figured by Schmidt (1901, pl. 12:8) as the lectotype. Unfortunately, this specimen is lost (Bruton et al. 1997). Two specimens figured by Schmidt are deposited in the Central Scientific Research Geological Exploration Museum,

St. Petersburg (CNI), namely the specimens figured on plate 12:10 (CNI 13/11152, from the Langevojan-Hunderumian at Isvos – i.e. Izvos – near the river Wolchow) and in textfigure 21 (CNI 17/11152 from the Langevojan–Valasteian at Obuchowo – i.e. Obuchovo) (Bruton et al. 1997). The availability of these specimens renders Balashova's neotype (1953, p. 391) invalid. A new lectotype has to be selected from this material.

Other material. – RM Ar 59443–59451, 59457, 59466 (2 incomplete specimens, 1 incomplete cephalon, 1 cranium, 7 pygidia, all from Gillberga.)

Occurrence. – The species was first described by Schmidt from the eastern Baltic BIII α (Schmidt 1901, p. 36). We here report it from Sweden for the first time. It is present on Öland at Gillberga but also in collections from Östergötland. In fact, even some of Dalman's syntypes of *A. raniceps* can be shown to represent *A. lamanskii* (the specimens RM Ar 16410, 16681 [Fig. 6A], 16632, 51818, 52085, and 53573), as well as specimen no. RM Ar 16630, figured by Angelin (1854, pl. 28:2).

New diagnosis. – *Asaphus* species with subtriangular outline of cephalon and pygidium. Baculae fairly distinct. Occipital furrow faint. Anterior lobe with weak nodes over two pairs of muscle scars and fairly distinct median keel. Librigenae with slight depression around the eye socle. Pygidium with 9 axial rings, 4–5 of which are in the anterior half of the pygidium, terminal piece notably elevated. Axial segmentation indistinct in testaceous specimens; continuous across axis only in anteriormost two segments. More posterior inter-ring furrows incised laterally only.

Description. – The description is complementary to that of Balashova (1953, p. 392–393). Because of the strong resemblance to *A. raniceps* described above, only characters deviating from that species are described herein. The most specific characteristics are a comparatively low degree of effacement, rendering the dorsal furrows, baculae (cf. Lee & Choi 1999), and glabellar features such as muscle scars and median keel fairly distinct (Fig. 6A, B; versus the condition in *A. raniceps*, where these structures are indistinct or invisible, Fig. 5A). It generally measures only 60–90 mm (*A. raniceps*: typically 80–110 mm). The longest cephalon encountered from Gillberga measures 19.3 mm, the longest pygidium 22.6 mm, corresponding to a calculated body length of about 75 mm.

The eye varies in size. The eye-socle is about one fourth to one third as long as the cephalon. The librigena is depressed along the eye socle. This depression becomes more distinct with body size (*A. raniceps*: librigena not depressed).

The pygidial axis has 9 rings of which 5.5 are situated in the anterior half (*A. raniceps*: 10 rings). The inter-ring furrows are shallow and only the first and second ones traverse the axis in testaceous specimens (Fig. 6A, D; *A. raniceps*: inter-ring furrows only visible in exfoliated specimens, Fig. 5B; C). Posterior to that, axial segmentation is seen only abaxially, whereas the sagittal line of the axis remains uninterrupted (*A. raniceps*: axial segmentation is completely effaced). The axial furrows are fairly distinct anteriorly, but become almost effaced towards the posterior, where the axis is elevated above the pleural fields (Fig. 6A, D; *A. raniceps*: axial furrows almost effaced anteriorly, Fig. 5B). In specimens with well preserved test, oblique terrace lines can be observed in the axial furrow, usually two to three lateral to each axial ring (*A. raniceps*: only one). One of them extends onto the axial ring, but vanishes

adaxially where the axial ring becomes less distinct (Fig. 6A; *A. raniceps*: none on rings, Fig. 5B). This is even the case in the two most anterior axial rings, which are continuous across the sagittal line. Terrace lines on the pleural field are fairly distinct (*A. raniceps*: poorly defined). The pygidial doublure carries 12 to 15 fairly coarse terrace lines (Fig. 6D; *A. raniceps*: 10–12, Fig. 5C).

Discussion. – Schmidt (1901, p. 33) originally named this form *Asaphus raniceps lamanskii*, but Lamansky (1905) gave it the status of a distinct species. It is very similar to *A. raniceps*. Therefore it is hardly remarkable that Dalman (1827) and Angelin (1854) failed to recognise the difference between the two species, even though both are well represented in the collections that were available to them. About half of the collection studied by Dalman consists of Schmidt's species (for instance the specimens RM Ar 16410, 16681, 16632, 16648, 16649, 51809, 51810, 51811, 51818, 52085, 52087, 53573, 16648, 16649). Also one of the two specimens figured by Angelin (1854, plate 28, fig. 2, specimen RM Ar 16630) represents *A. lamanskii*.

Schmidt (1901, p. 34) suggested that *A. lamanskii* can be distinguished from *A. raniceps* on the presence of segmentation in the pygidial axis in testaceous specimens. Nielsen (1995, p. 89) rejected the validity of this observation, noting that Schmidt's *A. lamanskii* is generally smaller than the *A. raniceps*, and stating that the furrows generally became less distinct with individual growth. However, a large collection (RM) of material of both species from Östergötland contains large specimens of *A. lamanskii* showing axial segmentation, whereas there are specimens of *A. raniceps* of similar or even smaller size devoid of visible segmentation. Among Dalman's syntypes of *A. raniceps*, only one tiny testaceous specimen (RM Ar 16627, 13.4 mm long) shows segmentation of the pygidial axis.

In the Gillberga section, *A. lamanskii* occurs in the Zone of *Asaphus expansus*, *A. raniceps* above this zone, and there appears to be no overlap (Fig. 2). Schmidt likewise regarded his *Asaphus raniceps* var. *lamanskii* as the oldest variety of *A. raniceps* and reported it from the beds with *A. expansus*.

According to Schmidt (1901, p. 34), the eyes are generally smaller in *A. lamanskii* and situated at a greater distance from the posterior cephalic margin. This character, however, could not be affirmed in the material from Östergötland and Öland. At least in *A. lamanskii*, the size of the eye and the distance between the eye and the posterior cephalic margin appear to vary, and there is no statistical difference between the species in this respect (Stein 2003). Balashova (1953, p. 393) added further characters to define *A. lamanskii*, namely (1) the expression of the S1 glabellar furrow, (2) a narrower (sag.) and more deeply incised posterior cephalic border furrow, (3) a broader glabella, and (4) greater separation between the anterior branches of the facial sutures and the anterior cephalic margin. The two former characters are in accordance with the material from Öland and Östergötland, though the sagittal width and depth of incision of the posterior cephalic border furrows seem to be somewhat subjective. The two latter characters could not be affirmed, since plotting the maximum preoccipital glabellar width against the maximum cephalic width shows no apparent trends (Stein 2003, fig. 11B), and the distance from the anterior branch to the anterior cephalic margin is variable to some extent in both species. A further character added herein is the number of terrace lines on the pygidial doublure.

Also *Asaphus acuminatus* (Boeck, 1838) shows similarities to *A. raniceps*, and Schmidt (1901, p. 33) regarded it as a further

subspecies of the latter, which was accepted by Størmer (1941, p. 141). Ivantsov (2001, 2003) proposed the inclusion of *A. lamanskii* as a subspecies of *A. acuminatus*. Others (e.g. Balashova 1953, p. 394, Nielsen 1995, p. 84) treated *A. acuminatus* again as a distinct species. There are problems with the concept of this species, however.

Brögger's material, apparently consisting of Boeck's type series (Nielsen 1995, p. 84), includes two specimens. Størmer (1941, p. 141) selected specimen PMO 56254 (Størmer 1941, fig. 12) as the lectotype. Nielsen (1995, p. 84), being unaware of that, subsequently selected specimen PMO 20214 for lectotype. Brögger's material (1882, p. 93; pl. 8:5a, b) was refigured by Nielsen (1995 figs. 66J, 68). Jaanusson (1953, p. 394) doubted that any of the two specimens is determinable and considered *Asaphus (Asaphus) acuminatus* (Boeck, 1838) a *nomen dubium*.

It should be noticed that, outside the type area, at least two different species have been labelled *Asaphus acuminatus*. One is a species discussed and figured by Schmidt (1901, pp. 32–36; pl. 1:10, pl. 2:2; not pl. 2:1), Balashova (1953, p. 394, pl. 1:4, pl. 5:3), and Nielsen (1995, fig. 66 A–G, I). It does in fact strongly resemble *A. raniceps*. The other species, known only from Scania, is based on Angelin's (1854, pl. 29 figs. 2, 2a; RM Ar 24157–8) concept of Boeck's species; it is thus *A. acuminatus* sensu Angelin. It is herein described as a distinct species, *A. angelini* n. sp.

Boeck considered his species to be larger than *A. raniceps*, but our material shows that this is not the case. The pygidial characters displayed by the Norwegian type material make a close affinity to *A. raniceps* likely, as argued by Schmidt (1901) and Størmer (1941). One similarity is the rather ill-defined axial segmentation even in exfoliated specimens. We can also confirm that Boeck's and Brögger's specimens are similar to *A. raniceps* in the number and appearance of the terrace lines of the doublure. This makes it appear even possible that the material represents *A. raniceps*. However, there still appears to be a difference in the shape of a denser dorsal terrace line pattern in Boeck's material. Ivantsov (2004) presented drawings of *A. acuminatus* and *A. lamanskii* showing a slightly longer cephalon and more strongly defined bacculae in *A. acuminatus* as well as a more regular pattern of terrace lines with short sinuous lines in each segment of the inner pleural field of the pygidium versus one continuous line in each segment in *A. lamanskii*. While both types of pattern do occur in the material from Sweden (Fig. 6C, E), too little material is available to judge whether this is due to individual variation or if it is a character of the species. If the latter could be confirmed, establishment of a new species should be considered, given the problematic status of the type material of *A. acuminatus*. For this, a re-investigation of the type material of *A. lamanskii* is also required.

Asaphus (Asaphus) vicarius Törnquist, 1884
Figs. 3, 7

? *Asaphus rimulosus* n. sp. – Angelin 1854, p. 52, pl. 27:7 (type material RM Ar 16669).

Asaphus vicarius – Törnquist 1884, pp. 64–65; pl. 2:18–20 (diagnosis, description, occurrence, illustration of one cranidium and two pygidia).

Asaphus vicarius – Brögger 1886, p. 30.

Asaphus vicarius Törnq. – Jaanusson & Mutvei 1951, pp. 633–634 (occurrence).

Asaphus vicarius Törnq. – Jaanusson 1953, pp. 394, 397 (taxonomic notes, listed).

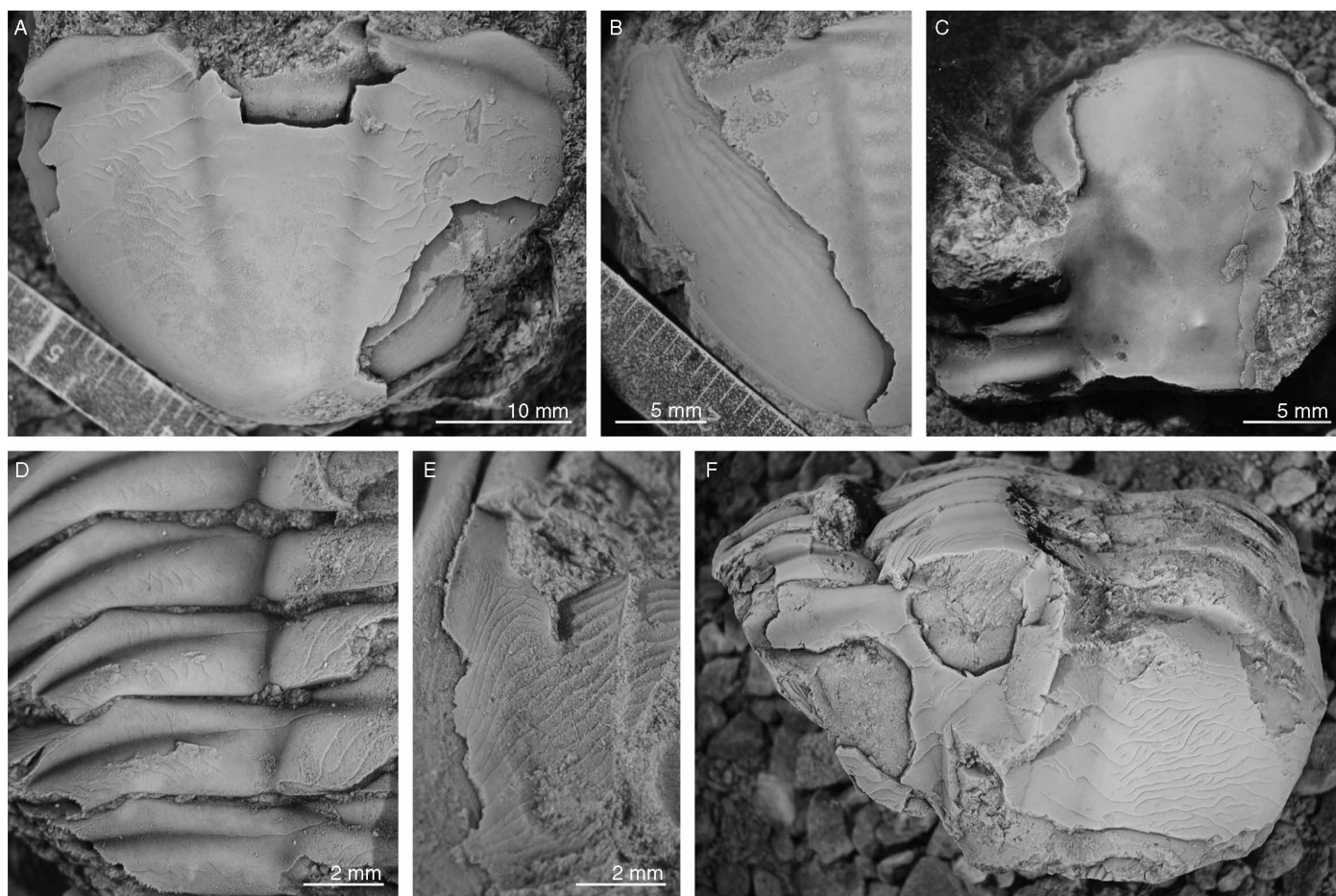


Fig. 7. *Asaphus vicarius* Törnquist, 1884. A. Pygidium, lectotype LO612T. B. Exfoliated pygidium, paratype LO613t. C. Exfoliated cranidium, NRM Ar 59489. D. Detail of thorax showing terrace lines pattern on the pleurae, NRM Ar 59863. E. Detail of thoracic doublure, showing slit-like panderian opening, NRM Ar 52087. F. *Asaphus rimulosus* Angelin, 1854, type, NRM Ar 16669.

Asaphus vicarius – Nielsen 1995, p. 76 (brief discussion).

A. 'raniceps' sensu Angelin 1854 – Nielsen 1995, pp. 96–98;

Fig. 76 A–C, possibly also Fig. 75E–F (comparison, photographs).

Type material. – Lectotype LO 612T. Paratype LO 613t. Törnquist's material was collected in Utby and at Sjurberg, Dalarna, Sweden.

Material. – Törnquist's material comprises disarticulated pygidia and cranidia. Fairly many pygidia and a few poorly preserved cranidia and free cheeks were retrieved from the Gillberga section. Two fairly complete specimens from Hagudden, Öland and one from Västanå, Östergötland are available. Angelin's specimen has 7 thoracic segments preserved.

Other material. – NRM Ar 52087 from Västanå, NRM Ar 59863 and 59864 from Hagudden, and NRM Ar 59489–59493 and 59496–59501 from Gillberga.

Occurrence. – This species has been known previously only from the Siljan district in Dalarna, central Sweden. We here report it for the first time from northern Öland and Östergötland. As in Dalarna (Törnquist 1884), it seems to be a common faunal element on northern Öland, where it appears directly above the narrow zone of *A. raniceps*. It occurs also in Scania, where it was determined as *A. raniceps* (Nielsen 1995, pp. 96–98) (see discussion).

Diagnosis. – A species of *Asaphus* with subtriangular cephalon; cranidium pointed with distinct median keel. Occipital furrow indistinct. Eyes large. Thoracic pleurae with terrace lines on posterior band. Panderian openings slit-like. Pygidium parabolic in outline, with break of slope behind axis. Axis with about 12 rings, 5 of which are in the anterior half of the pygidium. Median axial depression posterior to the second axial ring, bordered by lateral bumps with smooth posterior slope. Rich pattern of terrace lines on the inner portion of the pleural field. Pygidial doublure wide, carrying fairly fine, densely spaced terrace lines.

Description. – The cephalon is subtriangular in outline. The cranidium is pointed. The glabella carries two pairs of muscle scars level with the palpebral lobe and a distinct median keel (Fig. 7C). The eyes are large with a high socle, almost two thirds of the height of the visual surface.

The panderian openings are slit-like (Fig. 7E). The thoracic pleurae carry terrace lines on the posterior band (Fig. 7D).

The largest pygidium in the Törnquist collection is 2.9 cm long, indicating a body length of about 10 cm. The outline of the pygidium is parabolic, with a considerable variation in length/width ratio (0.60 to 0.68). It is fairly convex transversally. The sagittal profile is almost straight until the end of the axis, behind which it slopes downward.

The axis is fairly wide in front, with the transverse separation of the axial furrows being roughly one third of the maximum

pygidial width (Fig. 7A). It tapers distinctly to the seventh axial ring, behind which it is of more or less even width. Throughout its length, it is slightly elevated above the pleural fields. It slopes down gently along the three anteriormost axial rings. Posterior to that, the downward curvature decreases in distinctness towards the terminal axial piece.

The axis has about 12 axial rings, six of which are in the anterior half. The first two are expressed as complete rings, the others as smooth paired bumps, which leave a smooth median furrow along most of the axis. In exfoliated specimens also the third ring is complete. On the whole, the morphology is smooth, and the last three rings are best seen in exfoliated specimens, although weakly expressed even in them.

The axial furrows are very shallow. As Törnquist (1884, p. 65) described, they are marked rather by the elevation of the axis than by actual incision.

Exfoliated specimens often show weak impressions of pleural and interpleural furrows. Sometimes, these can be seen in oblique light even in testaceous specimens. The terrace line pattern is characteristic in showing the short sinuous lines on the inner portion of the pleural field distinctly (Figs. 3C, 7A). In the more anterior segments, they do not traverse the pleural furrows. To the posterior, they not only traverse the pleural furrows, but connect to those lines of adjacent segments. The ramification beyond the fulcral line is rather weakly expressed. The terrace lines on the pleural field are connected with the axial rings by single continuous lines (Figs. 3C, 7A), rather than an array of short lines traversing the axial furrow. The terrace line ramifies on the posterolateral corner of the axial rings. The most posterior of the branches extend almost perpendicular to the sagittal line towards the depression in the middle, and often connect across the sagittal line as an arch open to the posterior (cf. *A. lepidurus*, *A. expansus*). Behind the arch there is a set of short transversal lines (Fig. 3C).

The pygidial doublure is of moderate width, somewhat narrower than in *Asaphus (Asaphus)* and carries numerous fairly fine and rather densely spaced terrace lines (Fig. 7B). Up to twenty may occur. They frequently become less distinct towards the pygidial margin (i.e. the outer margin of the doublure). It should be noted, that material from Dalarna appears to be more variable in the development of terrace lines of the doublure. Some specimens (e.g. RM Ar 49025) have only about 13 coarser terrace lines. The test of the pygidium is densely punctate. Coarse pits are distributed more widely between the punctae.

Discussion. – Törnquist (1884) based this species on material from the Siljan district in Dalarna, central Sweden. Jaanusson (1953, p. 394), later followed by Nielsen (1995, p. 76), suggested a possible synonymy with their *A. 'raniceps'* sensu Angelin, which they considered a *nomen dubium*.

In the Gillberga section, *A. raniceps* is restricted to an interval of one meter just above the *A. expansus* Zone. Above that interval, pygidia of *Asaphus vicarius* appear in abundance over a long interval, reaching to the top of the section. They differ from pygidia of *A. raniceps* in the more parabolic outline, more elevated axis with more distinct segmentation, and the pattern and richness of the terrace line sculpture. Furthermore the doublure bears finer, more densely spaced terrace lines than in *A. raniceps*.

Angelin (1854, p. 53) reported *A. raniceps* from Östergötland and Dalarna. The material from Östergötland, still present, consists of *A. raniceps* and *A. lamanskii*. No material from his

Dalarna collections is preserved. The most common species in corresponding strata is *A. vicarius*, but there are also *A. raniceps* and perhaps *A. striatus*. What is clear, however, is that his illustrations show *A. raniceps*, not *A. vicarius* (see Bergström et al. 2003).

Collections in the University of Lund (with Törnquist's collection), the Swedish Museum of Natural History, and the Geological Survey of Sweden include a large number of pygidia and some cranidia from Törnquist's localities in Dalarna. The pygidia are indistinguishable from the Gillberga specimens, except that the terrace lines on the pleural field tend to have a slightly denser spacing. The general pattern is the same, however. The cranium has an anterior pair of muscle scars, not reported by Törnquist but seen in some specimens from Dalarna.

Three specimens figured by Nielsen (1995, fig 76 A–C) as '*Asaphus raniceps*' sensu Angelin appear to represent *A. vicarius*, as can be judged from the outline of the pygidia and the terrace line spacing on the pygidial doublure (see above in the discussion on *A. raniceps*). *Asaphus vicarius* therefore is not restricted to the Siljan region, but also occurs in southern Scania, whereas *A. raniceps* may have a narrower distribution than previously assumed. Törnquist considered *A. vicarius* to be the most common trilobite in the '*raniceps*' beds of the Siljan region, and that appears to be true for Northern Öland as well, since it is a very frequent element in collections from Northern Öland.

Affinities. – Jaanusson (1953, pp. 388, 397) assigned *A. vicarius* to *Asaphus (Asaphus)*, which can be confirmed now that the pandering opening is known.

Asaphus (Asaphus?) angelini n. sp.

Fig. 8

Asaphus acuminatus Boeck – Angelin 1854, pp. 53–54 (non 'Norvegica'), pl. 29, fig. 2, 2a (description, distribution, drawing).

Asaphus (Asaphus) acuminatus (Boeck, 1838) – Nielsen 1995, pp. 84–91, figs 66H, 67C–I, ?67A–B (non 66A–G, I, J, 68). ? *Asaphus (Asaphus)* sp. A – Nielsen 1995, p. 102, fig. 79.

Type material. – Holotype: RM Ar 24157 (Fig. 8A); syntype RM Ar 24158 (Fig. 8B).

Material. – The material includes Angelin's figured specimens (RM Ar 24157, a cranium, and Ar 24158, a pygidium), further 6 fragmentary cranidia and 2 pygidia at RM, and specimens collected and in part figured by Nielsen (1995, pp. 84–91, fig. 67 C–I).

Occurrence. – The species is known from Scania.

Diagnosis. – Cranium with wide flat shelf surrounding anterior glabellar lobe, forming preglabellar field terminating in a stout ogival projection. No constriction at anterior muscle scar. Pygidium subtriangular, smooth, axial segmentation barely visible, inner cast with 11–12 axial rings, anterior half of pygidium with 7 rings, demarcation line separating inner and outer pleural fields, the former with shallow pleural and interpleural furrows.

Description. – The cranium has an exceptionally wide, flat border around the anterior part of the glabella, and a stout pointed anterior projection. Two pairs of muscle scars are obvious in the internal mould of the glabella (Fig. 8A). There is a low median ridge in the holotype which is less distinct in other

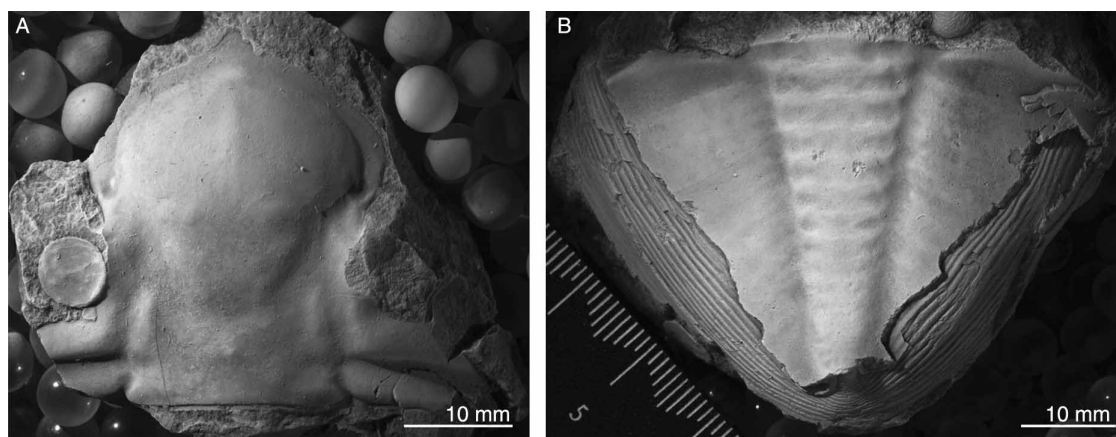


Fig. 8. *Asaphus angelini* n. sp. A. Exfoliated cranidium, NRM Ar 24157. B. Exfoliated pygidium, NRM Ar 24158.

specimens. The baccula (cf. Lee & Choi 1999) is a well-defined narrow ridge on the inner mould, a smoother elevation on the exterior. The occipital furrow is effaced (Fig. 8A). See Nielsen (1995, p. 87, Pl. 67A–B) for a description of the hypostome. The thorax is unknown.

Nielsen (1995, p. 87–89) described the pygidium. Here follow only complementary notes. It is large, up to 56 mm in length (Nielsen 1995, fig. 67H) indicating a total length of 14–15 cm for a complete exoskeleton. A fairly well defined ‘fulcral line’ divides the pleural field into inner and outer parts. The inner part is wide and flat and carries both pleural and interpleural shallow furrows that extend uniformly over the entire surface. They are terminated abruptly at the ‘fulcral line’, which probably corresponds to the position of the inner doublural margin. 12 axial rings are visible in Angelin’s type (RM Ar 24158, Fig. 8B). The spacing is tight: 7 of them are in the anterior half of the pygidium.

Discussion. – The spacing of the axial rings in the pygidium demonstrates discreteness of this species. *A. angelini* is similar only to *A. ‘maximus’* sensu Nielsen in having 7 rings in the anterior half of the pygidium. Of other species that have been compared with *A. angelini*, *A. raniceps* has about 5.5 segments. Also, the shelf extending around the anterior part of the glabella is a feature not met with in typical species of *Asaphus* (*Asaphus*). Cranidia of *A. raniceps* typically lack a preglabellar field.

The pygidia described and figured by Nielsen (1995, pp. 84–91, fig. 67 C–I) are indistinguishable from Angelin’s specimens in the general shape, in the number and spacing of rings in the axis and terrace lines on the doublure. It is clear that all these specimens are conspecific.

It is also clear that *A. angelini* is distinct from Boeck’s *A. acuminatus*. Thus, *A. angelini* has 11 to 12 axial rings (the higher number possibly correlated with slightly greater length of the pygidium), whereas in Boeck’s *A. acuminatus* no rings can be recognised beyond the eighth (cf. Brögger 1882, plate 8:5b). Furthermore, Boeck’s species has 10 (Brögger 1882, p. 93) or 11 (lectotype, PMO 56254) terrace lines, whereas Nielsen (1995, p. 89) reported 11 to 16 in *A. acuminatus*.

The sharp demarcation of inner and outer pleural field in the pygidium is alien to *A. raniceps* and other *Asaphus* (*Asaphus*) species. Such a fulcrum was reported from *A. acuminatus* by Brögger (1882, p. 93, pl. 8:5b) but it is questionable if it is truly present, since the material is poorly preserved. Brögger’s

material (Nielsen 1995, fig. 68) shows imprints of rather densely spaced terrace lines in the pattern typical for *Asaphus* (*Asaphus*), although this obviously escaped Brögger’s (1882, p. 93) notice. This pattern was described and illustrated as belonging to *A. acuminatus* by Schmidt (1901, pl. 1:10) and Balashova (1953, p. 394, pl. 5:3). Nielsen, on the other hand, described the dorsal test of the pygidium of *A. angelini* as “largely without terrace lines” except for a few transverse lines present anterolaterally (Nielsen 1995, fig. 67C, description p. 89), which is in accordance with Angelin’s type specimens.

Boeck’s species appears to be the size of *A. raniceps*. This is a difference against *A. angelini* that is much larger: its length can be calculated to 14–15 cm as compared with 11 cm for *A. raniceps*.

The new species is most similar to *A. ‘maximus’* Brögger in the sense of Nielsen (1995, pp. 96–102, figs. 77–79). The latter differs in being even larger (calculated length up to around 20 cm) and in having a wider pygidial doublure with more numerous (16–20) terrace lines. The species may be closely related phylogenetically; *A. angelini* is found in the *A. expansus* Zone, *A. ‘maximus’* in the *A. ‘raniceps’* beds. *A. angelini* and *A. ‘maximus’* are sufficiently different from *A. raniceps* and *A. lamanskii* and from typical members *Asaphus* (*Asaphus*) that the subgeneric position is in question.

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