

The *Asaphus raniceps* problem in the Ordovician of Sweden

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It has been repeatedly stated that the lower Llanvirn *Asaphus raniceps* described by Dalman in 1827 and by Angelin in 1854 may represent two different species. This has forced us to live with the concepts of both *A. raniceps* Dalman and *A. 'raniceps' sensu Angelin*, and with a zone of *A. 'raniceps'* where *A. raniceps* is supposedly not present. However, new considerations based on large old and new collections have led to the firm conclusion that Angelin was correct in his identification of Dalman's species. What has been regarded recently as the true *Asaphus raniceps*, at least by Tjernvik & Johansson in 1980 and by Nielsen in 1995, is instead identical with another generally misidentified species, *Asaphus fallax* Angelin 1854.

Key words: Ordovician, Baltoscandia, trilobites, *Asaphus*, Dalman, Angelin.

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The story began in 1826, when Jöns Jacob Berzelius, the famous chemist and secretary general of the Royal Swedish Academy of Sciences, and Johan Wilhelm Dalman, professor of zoology at the same academy, collected Ordovician fossils at Husbyfjöl while a Mr. Olivecrona did the same at Skarpåsen, in the province of Östergötland (Fig. 1). Dalman (1827) subsequently described *Asaphus raniceps* (as *Asaphus expansus* var. β *raniceps*) from the material collected. In addition to *A. expansus* (Wahlenberg, 1818), there were at that time two Östergötland species described of the currently recognised subgenus *Asaphus* (*Asaphus*) Brongniart, 1822 (not Jaanusson 1953, as cited by Nielsen 1995).

In his comprehensive treatise on the trilobites of Sweden, Nils Petter Angelin (1854, p. 53, pl. 28, figs 1e and 3–3c) added *Asaphus fallax* to the list, noting that all three species occur at the locality of Husbyfjöl. This name has such an unfortunate connotation (– it means 'the king's estate toilet' –) that it has subsequently been changed to Västana (pronounced roughly 've'stana'w'). Later, in 1905 Lamansky in-

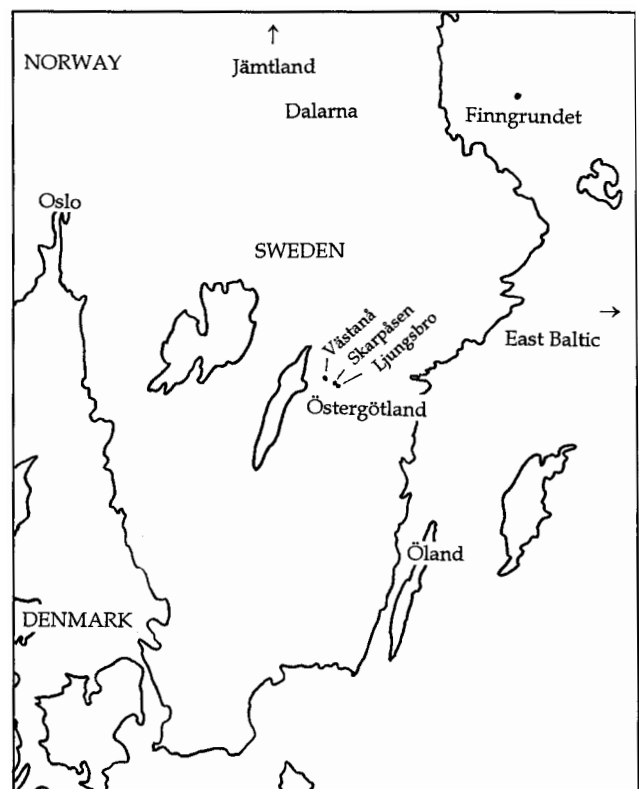


Fig. 1. Localities and areas mentioned in the text.

troduced the Zone of *Asaphus raniceps* overlying the Zone of *Asaphus expansus*.

Jaanusson (1953, p. 394), following Törnquist (1884, p. 63), compared Angelin's (1854, pl. 28, figs 2, 2a–c) concept of *Asaphus raniceps* with that of Dalman (1827). He concluded that a specimen associated with one of Angelin's drawings could not have been the type selected by Dalman, and that the latter must belong to a different species. He did not, however, supply any illustration to demonstrate his concept of this species.

Jaanusson (*in* Jaanusson & Mutvei 1953, p. 30) introduced the terms *Asaphus "raniceps"* and "*Raniceps*"-Kalkstein ("*Raniceps*" limestone), with quotation marks. In a short note the reason was given as follows, translated into English: "Following the lead of Angelin (1854), the zonal fossil of this unit is determined as *Asaphus raniceps* Dalm., although it is not identical with *Asaphus expansus* var. β *raniceps* Dalman, 1827 (see Jaanusson 1953, p. 394). As long as no correct name is established for this species, the authors will characterise it as the "*Raniceps*" limestone (after *Asaphus raniceps sensu* Angelin, 1854)."

In the offshore Finngrundet drillcore, Tjernvik & Johansson (1980, pp. 190, 194, and fig. 10A) recorded what they regarded as the true *A. raniceps* Dalman. The same specimen was again illustrated by Nielsen (1995, fig. 75A–D). Bruton *et al.* (1997, p. 108), following Nielsen (1995, p. 96), stated that Schmidt (1901, fig. 20) illustrated *Asaphus 'raniceps'* in the sense of Angelin under the name *Asaphus raniceps* Dalman. Schmidt's illustration, however, does not show the same species illustrated by Nielsen.

In summary, Jaanusson, Tjernvik & Johansson, Nielsen and Bruton *et al.* all accepted the idea that Angelin had misunderstood Dalman's species *Asaphus raniceps*. It may also be added that Brögger (1886) made a valuable contribution to the knowledge of the doublure together with the hypostome of this taxon. The species are so similar, however, and we know very few specimens from the ventral side, that this information has been of little help in this study.

The *Asaphus* species in the Östergötland *expansus-raniceps* beds

The Swedish Museum of Natural History has a fairly large collection of trilobites from the *expansus-raniceps* beds (corresponding to the upper Arenig – lower Llanvirn) in Östergötland. This collection includes specimens from Husbyfjöl/Västanå and nearby localities, brought together during almost 200 years of collecting. A special collection from Ljungsbro not far

from Husbyfjöl, assembled by the late collector Henry Pihl in the 1980s and 1990s, is of higher quality with large numbers of prepared complete specimens and is best suited to illustrate the composition of the trilobite fauna. Apart from all the other trilobites, there are three common species of *Asaphus*, all belonging to the nominal subgenus. Of these, 269 specimens belong to *Asaphus expansus*, 83 to *Asaphus raniceps* as understood by Tjernvik & Johansson (1980), and 52 to *Asaphus raniceps* as understood by Angelin (1854). In addition, there is a single specimen, which is similar to and perhaps identical with the older-established *Asaphus lepidurus* Nieszkowski, 1859; it is not known for certain if it was collected from the same beds. These four species make up 12.5% of the trilobite species in the fauna, but 51% of the specimens.

A great majority of the specimens are more or less complete skeletons, all of which have the free cheeks preserved. Five specimens are just complete cephalae, and two are cranidia representing moults. It is thus clear that, with few exceptions, the trilobites were killed by sedimentation events, which left some of them strongly inclined to the bedding in the obrution deposits.

No additional *Asaphus* species has been found at this level at any other locality in Östergötland. Jaanusson did not in any publication illustrate any specimen that he meant should correspond to Dalman's (1827) concept of *Asaphus raniceps*. Judging from the composition of the fauna, he could only have meant the species subsequently illustrated by Tjernvik & Johansson (1980, fig. 10A) and Nielsen (1995, fig. 75A–D). There is no other alternative (– the possible *Asaphus lepidurus* specimen was not present in the collections at the time –), and Tjernvik & Johansson certainly were aware of that specimen.

However, a study of Jaanusson's labels in the collections of the Swedish Museum of Natural History does not substantiate this picture. Six specimens are labelled by him "*Asaphus raniceps sensu* Angelin". Of these, five (Ar. 52066, 52073, 52087, 55569, and 55578) are typical representatives of *Asaphus raniceps* as understood by Angelin (1854), whereas one (Ar. 55570) is an *Asaphus fallax*. Four others are labelled "*Asaphus raniceps* Dalman". Three of these (Ar. 52047, 52056, 52067) belong to *Asaphus raniceps* as understood by Angelin, the fourth (Ar. 52048) to *Asaphus fallax*. One specimen of *A. raniceps* in the sense of Angelin is labelled *Asaphus expansus* (Ar. 51808), and six (Ar. 16648, 51849, 52034, 55573, 55574, 55575) are not determined to species. It appears that Jaanusson's idea about Dalman's and Angelin's supposedly different species concepts was not well founded. Although an expert on the genus *Asaphus*, he had not studied these oldest-established species closely and was apparently

deceived by the varying preservational states of the specimens.

Asaphus (Asaphus) fallax Angelin, 1854, is an additional *Asaphus (Asaphus)* species mentioned from Östergötland. This species is considered to be extremely rare and to occur only at Husbyfjöl (see Nielsen 1995, p. 80). As will be seen below, *A. fallax* is identical to *Asaphus raniceps* in the sense of Tjernvik & Johansson (1980). This means that we can be confident that the three species presented in Angelin's (1854) volume indeed represent the three that are common in the collection. It is easy to identify Angelin's three species one by one. The problem concerns Dalman's concept of *Asaphus raniceps*. No type specimen has been selected, but there are a number of extant specimens collected in 1826 by Dalman, Berzelius and Olivecrona.

Asaphus raniceps in the sense of Tjernvik & Johansson 1980

The affinities of *Asaphus fallax* are briefly discussed by Nielsen (1995, pp. 80–81). He compared it only with the similar *A. expansus*. Of the two, *A. fallax* has a lower cephalic relief, and the facial sutures are separated from the cephalic margin until they meet and form a small triangular tip at the anterior end of the cranium. The eyes tend to be slightly lower, and the posterior border furrow is narrower, rather more V-shaped in cross section than the U-shaped furrow of *A. expansus*. The hypostome and pygidium of the two species appear to be inseparable. It can be added that the axial ring of the thorax is less vaulted in longitudinal section in *A. fallax*, and not contracted in the midline as it is in many specimens of *A. expansus*.

Like *A. expansus* and *A. fallax*, *A. raniceps* in the sense of Tjernvik & Johansson (1980) is considered to be a member of the *A. expansus* group within the nominate subgenus (Nielsen 1995, p. 75). Nielsen (1995, p. 80) compared it with *A. expansus*, but not with *A. fallax*. The comparison is too vague to be instructive, and it is confusing that he stated that there are only two asaphid species in the Dalman collection, rather than three.

Anyway, the large Holger Pihl collection shows that there is no distinction between *Asaphus fallax* and *A. raniceps* in the sense of Tjernvik & Johansson (1980) and Nielsen (1995). The deeply impressed glabellar muscle scars, thought by Nielsen (1995, p. 80) to be typical of *A. fallax*, are not so impressive in the lectotype (Nielsen 1995, fig. 62B), and are seen occasionally in specimens from Ljungsbro, and occur in individuals of other *Asaphus* species as well. For in-

stance, they are seen in some specimens of *Asaphus raniceps* (see Fig. 4G), and they are strongly developed in the lectotype of *Asaphus striatus* (see Størmer 1940, pl. 3, fig. 12). Obviously it is not a reliable species character. There is also individual variation in the development of the posterior border furrow. It can have an almost V-shaped cross section, but can also have a more rounded bottom as in *Asaphus expansus*. The pygidium of *A. fallax* is indistinguishable from that of *A. raniceps* in the sense of Tjernvik & Johansson (1980), and the same is the case with the moderately vaulted axial rings, which are in turn different from the highly vaulted rings of *A. expansus* and the flat rings of *A. raniceps* in the sense of Angelin (1854).

Asaphus raniceps in the sense of Dalman 1827

Dalman's (1827) plate 3 includes drawings of *Asaphus expansus* (his fig. 3a–d; Fig. 2D herein is the cephalon of Dalman's fig. 3d) and of his *Asaphus expansus* β *raniceps* (his pl. 3, fig. 4; Fig. 2E herein). Although the drawings are schematic, it can be stated that the characters are accurately illustrated in the case of *A. expansus*. Thus, the outlines of the cephalon, thorax and pygidium are quite realistic. The genal corners are characteristically rounded, the eyes have a more forward position than in most other species of the subgenus, the glabella is shaped as in a typical *A. expansus* and reaches the anterior margin.

There is therefore reason to also treat his illustration of *A. raniceps* as reliable. Although only the cephalon is shown, it is clear that Dalman wished to illustrate a species that is different from *Asaphus expansus* in some important respects. Thus, the cephalic outline is more triangular, with distinctly more angular genal corners. The glabella is notably longer and angular in front, and the eyes are placed much farther away from the anterior end. The cranium reaches the anterior margin only at the midline, and the facial sutures approach this point well off the cephalic margin.

Jaanusson (1953, p. 394) argued that Dalman's figure can not represent the same species as that of Angelin because it shows an occipital furrow and because the eyes are placed farther back. However, with respect to the first point, not only Dalman but also Angelin drew a complete occipital furrow. This is not remarkable, since there is a faint furrow on individual specimens. As to the second point it can be said that compared with Angelin's drawing and type specimen, Dalman's picture has the eyes farther back, but *A. raniceps* in the sense of Tjernvik and Johansson

(and Nielsen) has its eyes farther forward. Dalman's drawing therefore cannot possibly show *Asaphus raniceps* in the sense of Tjernvik & Johansson (1980). The latter is identical to *Asaphus expansus* in all characters mentioned except that the facial sutures and the glabella reach the margin only medially, leaving the cranidium with a short anterior tip unseen in *A. expansus*. On the other hand, Dalman's figure conforms well to Angelin's (1854, pl. 28, figs 2, 2a) illustrations of *Asaphus raniceps* in all the respects mentioned above.

Further arguments of Jaanusson's (1953, p. 395) are that *Asaphus raniceps* in the sense of Angelin is rare in Östergötland, and at least occurs usually higher in the sequence than *A. expansus*. Determinations of material in the Pihl collection, and redetermination of the old collections, show that the species is not that rare but fairly common. According to Nielsen (1995) there is a partial overlap in range of the two species, but the fact that specimens of Angelin's *A. raniceps* are commonly more compressed and distorted (even though it appears to have had a thinner exoskeleton and a larger maximum size) indicates that the species may largely come from another level than *A. expansus*.

It is worth mentioning that there are extant museum specimens collected by Dalman, Berzelius and Olivecrona in 1826. These, labelled "*Asaphus expansus*, β , *raniceps*" by Dalman, were certainly available to Angelin, who occasionally added a label reading "*Asaphus raniceps*. Dalm. Boeck". There is therefore reason to believe that Angelin had hard evidence in support of Dalman's species concept from Dalman's actual specimens and knew what he was doing.

In the case of *Asaphus fallax* Angelin, 1854, Angelin mentioned it as "*Asaphus fallax* DALM.", indicating that one or more specimens in the collection had been labelled with this name by Dalman. Angelin otherwise used to add 'n. sp.' to those species he regarded as being erected by himself. One such label of Dalman's is still with specimen Ar. 16626 (which unfortunately appears to be a small *A. raniceps*). It reads: "*Asaphus fallax* n. sp.? ... intermedius inter *expansus* & (*r*)*raniceps* ...". Angelin's label to the same specimen reads: "547 *Asaphus fallax*. Dalm. Östergötland". Dalman must have been aware of the difficulty of distinguishing this species, particularly on small specimens: he refrained from describing it, and his label name *fallax* means 'false', 'deceitful'.

Dalman, in his 1827 publication, recognized two species of *Asaphus*. His labelling appears consequent. Specimens of '*A. raniceps* in the sense of Angelin' were labelled "*Asaphus expansus* var. β *raniceps*" by Dalman, whereas specimens of *A. expansus* and '*A. raniceps* in the sense of Tjernvik & Johansson' were labelled "*Asaphus expansus* Lin."

The only reasonable conclusion is that Angelin was correct in identifying Wahlenberg's and Dalman's species of *Asaphus*. The species *Asaphus raniceps* in the sense of Angelin 1854 is indeed identical to *Asaphus expansus* var. β *raniceps* Dalman, 1827. As a consequence, we can again use terms such as the '*Asaphus raniceps* Zone' without quotation marks. It also means that the *A. raniceps* Zone, previously reported as being absent in Östergötland (Gorbatshev *et al.* 1976), is present, after all.

The situation can be summarised as follows:

name in current use	correct name
<i>A. expansus</i> Wahlenberg	<i>A. expansus</i> Wahlenberg
<i>A. fallax</i> Angelin	<i>A. fallax</i> Angelin
<i>A. raniceps sensu</i> Dalman	<i>A. raniceps</i> Dalman
<i>A. "raniceps" sensu</i> Angelin	<i>A. raniceps</i> Dalman

Systematic Palaeontology

Genus *Asaphus* Brongniart, in Brongniart and Desmarest, 1822

Asaphus (*Asaphus*) *expansus* (Wahlenberg, 1818)
Figs 2A, D, 3A, 4A

1818 *Entomostracites expansus* Wahlenberg, pp. 25–27; not illustrated (preprint).

1821 *Entomostracites expansus* Wahlenberg, pp. 25–27; not illustrated.

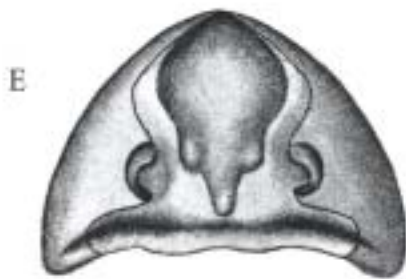
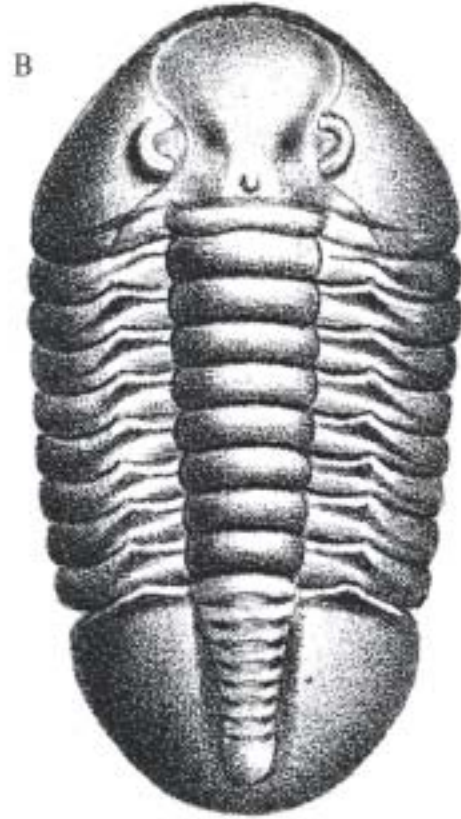
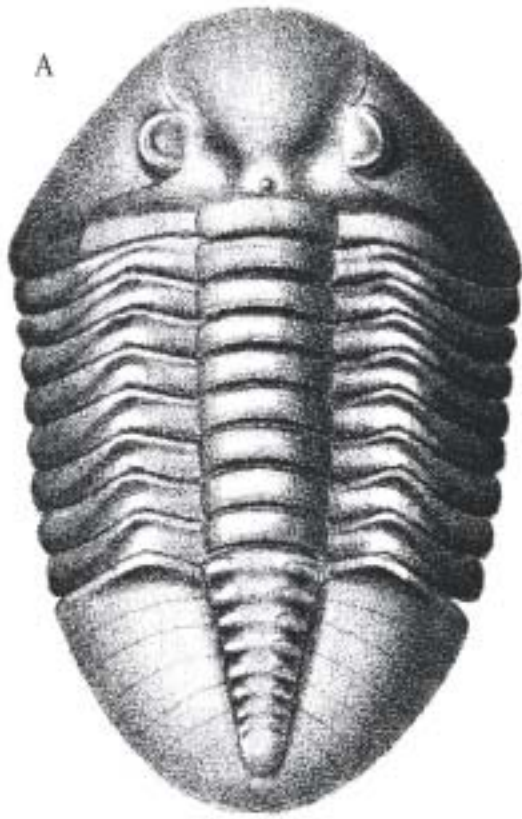
1827 *Asaphus expansus* Dalman, pp. 55–57, pl. 3, figs 3a–d.

1854 *Asaphus expansus* Linn. ex. p. – Angelin, pp. 52–53, pl. 28, fig. 1, fig. 1a–b.

1995 *Asaphus* (*Asaphus*) *expansus* (Wahlenberg, 1821) – Nielsen, pp. 77–80 (*cum. syn.*).

Remarks. A preprint of Wahlenberg's 1821 paper distributed in 1818 was considered taxonomically invalid

Fig. 2. A–C Angelin's (1854) illustrations of: A. *Asaphus expansus*, B. *A. fallax*, and C. *A. raniceps*. D–E. Dalman's (1827) illustrations of the cephalo of D. *Asaphus expansus*, and E. *A. raniceps*. The maximum sizes of *A. expansus*, *A. fallax* and *A. raniceps* are approximately 7, 6 and 10 cms, respectively.



by Jaanusson (1956), when selecting a lectotype for *Asaphus expansus*. However, Reyment (1976) stated that the preprint was widely distributed in 1818, which at that time perhaps would make it a valid publication.

Lectotype. Specimen Ög. 23 in the collections of the Palaeontological Department, Uppsala University, designated and figured by Jaanusson (1956, pl. 1, figs 1–5).

Holger Pihl collection. 265 specimens, most of which are complete and 83 rolled up.

Brief description. Body parallel-sided, with short, evenly rounded cephalon and pygidium. Length commonly up to 60–80 mm, exceptionally up to 90 mm. The facial suture joins (or comes extremely close to) the anterior margin far from the midline, with the result that the cranidium is truncated in front, devoid of a median spine projection. The angle between the two branches is notably blunt (exact measures depend on projection angle and the length of suture included, and are difficult to define). The ratio between cranial length and maximum width in front of the eyes is about 1 (0.9–1.1). Cephalic relief comparatively strong, with a vaulted glabella, a prominent axial node, fairly prominent eyes, wide and deep axial furrows and a wide posterior border furrow with rounded bottom profile. Occipital furrow well developed and complete. In the present material, terrace lines are rarely seen on the cephalon, but occasionally are well developed and preserved on the occipital ring of large specimens. A sagittal profile through the thoracic axial ring is usually strongly vaulted and commonly shorter than a more lateral profile. The pleural tips are rounded in the anterior part of the thorax. Pygidium little vaulted, smooth or with short, weakly developed segmentally arranged terrace lines on and close to axis. Pygidial doublure with 9–14 terrace lines.

Distribution. The distribution outside Östergötland apparently needs to be restudied. For instance, all the specimens from Dalarna in the Riksmuseum collections determined as *Asaphus expansus* appear to be *Asaphus fallax*. From the material available to us we can state that it occurs with certainty in Öland, Närke and Jämtland. It is also reported from Norway and the eastern Baltic area (see Nielsen 1995, p. 77). At least some specimens from Norway have a facial suture which is *fallax*-like in reaching the midline, and have a *fallax*-like low relief (Nielsen 1975, fig. 60). Other reports need substantiation.

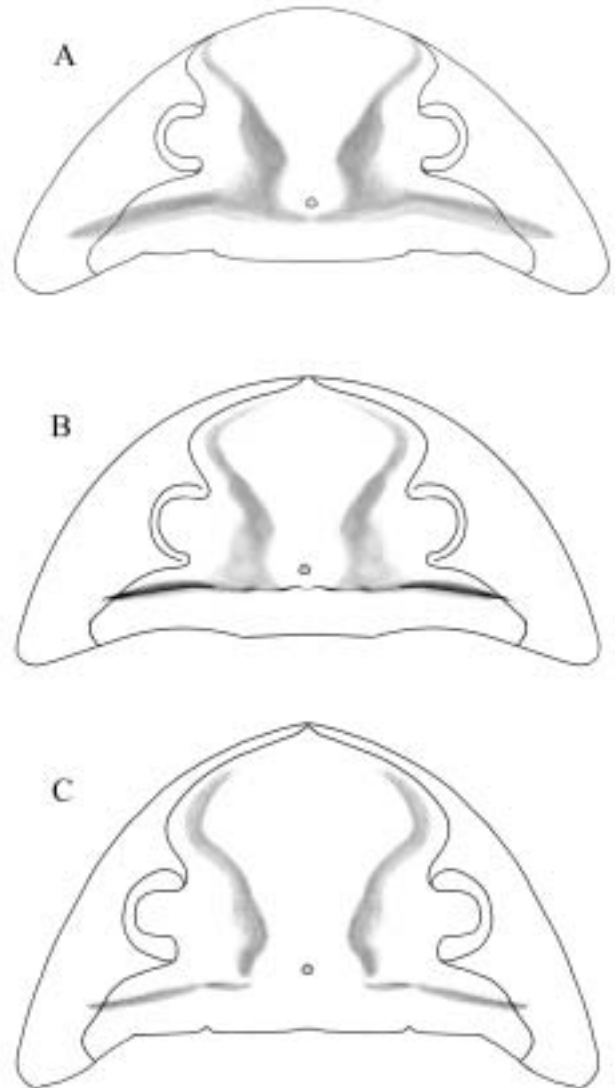


Fig. 3. Drawings of the cephalon of A. *Asaphus expansus*, B. *A. fallax*, and C. *A. raniceps*, all based on specimens from Östergötland. Note the similarity in outline between *A. expansus* and *A. fallax* and the comparatively longer cephalon of a fully grown *A. raniceps*. *A. expansus* is unique among these three in having a cranidium reaching the margin as a broad front rather than as a median tip. Drawings are approximately $\times 3$ natural size.

Comments. Typical specimens are easily distinguished from *A. fallax*. However, some specimens (for instance, from Norway) are more or less intermediate in having a lower relief and facial sutures extending further inwards before they meet the margin in front of the glabella. The lack of stratigraphic control makes it impossible to know if these specimens are from lower levels than others or if they revive atavistic features similar to those of *A. fallax* and the older *A. lepidurus*.

Asaphus (Asaphus) fallax Angelin, 1854
Figs 2B, 3B, 4B, C, E

- 1854 *Asaphus fallax* Dalm. – Angelin, p. 53, pl. 28, figs 1e?, 3, 3a–c.
1980 *Asaphus raniceps* Dalman – Tjernvik & Johansson, p. 190, fig. 10A.
1995 *Asaphus (Asaphus) fallax* Angelin, 1854 – Nielsen, pp. 80–81, fig. 62 (*cum. syn.*).
1995 *Asaphus (A.) raniceps* (Dalman, 1827) (*s. str.*) – Nielsen, p. 97, fig. 75A–D.

Lectotype. Ar.16515, from Västana (Husbyfjöl), Östergötland, selected by Jaanusson (1953), illustrated by Brögger (1886) and Nielsen (1995, Fig. 62B–D).

Holger Pihl collection. 83 reasonably complete specimens, of which 30 are rolled up.

Brief description. Body parallel-sided, with short, evenly rounded cephalon and pygidium. Length commonly up to 50–70 mm, not more as far as is known. The facial suture meets the anterior margin at the midline, leaving a short median spine on the cranidium. The angle between the two branches is blunt, similar to that in *A. expansus*. The relation between cranidial length and maximum width in front of the eyes is about 1.0 (0.9–1.1). Cephalic relief comparatively weak, with a low glabella and shallow furrows. Two pairs of glabellar muscle scars are commonly deep and are occasionally revealed by corresponding bulges on the outside. The posterior border furrow is narrower than in *A. expansus*, commonly with a V-shaped cross section. Occipital furrow weak in the middle, but complete. A sagittal profile through the thoracic axial ring is moderately vaulted. The pleural tips are rounded in the anterior part of the thorax. Pygidium lowly vaulted, commonly with short, weakly developed segmentally arranged terrace lines on and close to axis. Pygidial doublure with 10–14 terrace lines.

Distribution. Far from being a rare species restricted to one quarry, as previously reported, it is a common species in Östergötland, Öland, Dalarna and Jämtland.

Affinities. The concept of the two groups typified by *A. expansus* and *A. raniceps*, respectively, was based on plesiomorphic characters in the former and derived characters (such as loss of occipital furrow and narrower Panderian fissure) in the latter. The grouping therefore has no phylogenetic significance. *A. fallax* is close to *A. expansus*, and both may be derived from the older *A. lepidurus*. *A. fallax* may have given rise to the younger and very similar *A. striatus* (Boeck, 1838).

Nielsen (1995) stated that the pygidial axis of *A. lepidurus* is characterized by curved terrace lines, so this would seem to be a difference between that species and *A. fallax*. However, this seems to be an oversimplified view. Curved terrace lines are common in *A. lepidurus* from the Oslo area and in *A. fallax* from Dalarna. They are typically not present in *A. fallax* from Östergötland. They are stated to be typical of *A. lepidurus* from the East Baltic (Schmidt 1901, pp. 30–31; Balashova 1953, p. 300), but not visible in published illustrations. The character apparently is subject to geographic and population variation within the two species and does not characterise the species as such.

Asaphus (Asaphus) raniceps Dalman, 1827
Figs 2C, E, 3C, 4D, F, G

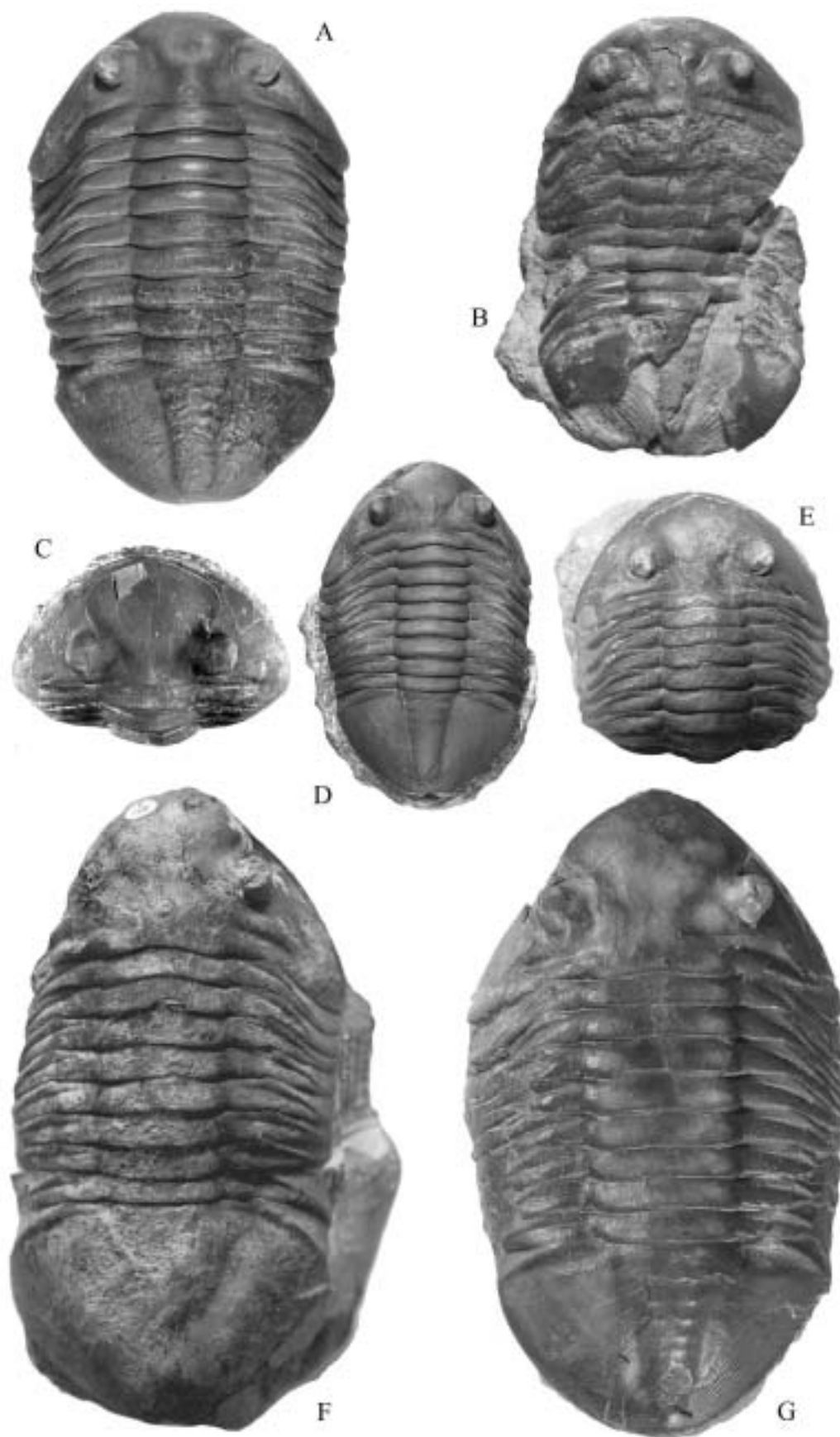
- 1827 *Asaphus expansus* var. β *raniceps* Dalman, p. 108, pl. 3, fig. 4.
1854 *Asaphus raniceps*; Dalm. – Angelin, p. 53, pl. 28, fig. 2, fig. 2a–2c. (Angelin's types: Ar.16629–30).
?1980 *Asaphus "raniceps"* – Tjernvik & Johansson, p. 190, fig. 10B.
?1995 *Asaphus (Asaphus) 'raniceps' sensu* Angelin, 1854 – Nielsen, pp. 96–98, fig. 75E–F, fig. 76.

Lectotype selected herein. Ar. 16531 (Fig. 4F), collected at Husbyfjöl by Dalman in 1826. This is not the best specimen in the collections made in 1826, but the only one with Dalman's label attached.

Syntypes. 1. Collected at Husbyfjöl by Dalman in 1826: 16363, 16379, 16410, 16531, 16632, 51808, 51809, 51810, 51811, 51820, 52047, 52066, 52573; 2. Collected at Husbyfjöl by Berzelius in 1826: 16414, 51814, 51818; 3. Probably also specimens collected at Skarpåsen some 12 km southeast of Husbyfjöl by Olivecrona in 1826: Ar. 16664, 16680.

Holger Pihl collection. 49 reasonably complete specimens, of which 15 are rolled up, and 3 cephalata.

Brief description. Body parallel-sided, with roundly triangular cephalon and pygidium. This species appears to have been 'thin-shelled', but grew to a comparatively large size. Length commonly up to 90–110 mm. The facial suture meets the anterior margin at the midline, leaving a short median spine on the cranidium (which is more prolonged than in *A. fallax*). The angle between the two branches is notably narrower than in the other two species. The ratio between cranidial length and maximum width in front of the eyes is about 1.3 (1.15–1.50). Cephalic relief is fairly



strong. The sagittal profile of the long glabella is fairly strongly vaulted, but the anterior delimitation indistinct since there is no flattened border. The axial node is small. The posterior border furrow is wide and deep. Occipital furrow poorly developed, incomplete. The eyes appear to be further back from the anterior end of the cephalon than in *A. expansus* and *A. fallax*. A sagittal profile through the thoracic axial ring is completely flat. The pleural tips are rounded in front and have a characteristic angular corner in the rear. Pygidium moderately vaulted. Widest part of pygidial doublure with 10–13 (–18?) terrace lines. The differences from *A. raniceps* and *A. expansus* become more pronounced with size, and small specimens are more difficult to determine.

Distribution. The typical form occurs at least in Östergötland and Öland. Nielsen (1995, p. 97) reported it from Scania, the Oslo area and the East Baltic. This distribution should be checked. Nielsen's (1995, fig. 76) determination of the Scanian material is unconvincing – the pygidia appear to be shorter than in the Östergötland specimens.

Affinities. Whereas *A. expansus* and *A. fallax* have a notably shortened cephalon and pygidium in comparison with *A. lepidurus*, *A. raniceps* is at least as long. It may represent a second lineage stemming from *A. lepidurus*, and it may have given rise to similar younger *Asaphus* species. Its glabella is almost not delimited in front, which differentiates it from such broadly similar forms as *A. acuminatus* (Boeck, 1838) and *A. incertus* Brögger, 1882 (cf. Nielsen 1995, figs 66A–D, F–I and 74A–B, respectively).

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Fig. 4. Photographs of the three species at roughly the same scale. A. *Asaphus expansus*, a specimen (RM Ar. 51076 from Husbyfjöl = Västanå, length 70 mm) used by Dalman (1827, pl. 3, fig. 3a, 3d) for his illustration of this species. B, C, E. *Asaphus fallax*. B. Angelin's (1854, pl. 28, fig. 3c) type specimen (RM Ar. 16575 from Husbyfjöl, length 60 mm). Anterior part of facial suture not seen because of tilt, but the course is identical to that of fig. 4C. C. Specimen nicely exposing the facial suture which is clearly separated from the anterior margin until the midline. Collected after name change of collecting site to Västanå (Ar.17532, length of cephalon 17 mm). E. Specimen from the Holger Pihl collection from Ljungsbro (Ar. 55637, length of cephalon 18 mm). D, F, G. *A. raniceps*. D. Small specimen from Västanå (Ar.16681, length 53 mm) apparently belonging to this species. It could easily be mistaken for *A. fallax*, but the cephalon is more elongated and triangular. F. Specimen collected by Dalman at Husbyfjöl in 1826, here selected as lectotype (Ar.16531, length 79 mm). G. Large specimen in the Holger Pihl collection from Ljungsbro (Ar.55636, length 88 mm).

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