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Two early cheirurine trilobites and their later relatives in the Ordovician of Baltoscandia

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Highlights:
Two of the earliest Cheirurinae trilobite species in Baltoscandia are re-described
They are historically among the first cheirurine described from Baltoscandia
This is the first revision since they were described more than 100 years ago
An overview of 30 Baltoscandian cheirurine taxa is given

Ceraurinella ornata (Dalman, 1828) and *Laneites ingricus* (Schmidt, 1881) are two early representatives of the subfamily Cheirurinae in Baltoscandia. Neither species has been revised since their original description but type and new material provide additional insights into their morphology and spatial and temporal distribution. They occur in the Middle Ordovician (Volkhovian–Kundan) succession across the Baltoscandian platform, from the St. Petersburg area in Russia, through northern Estonia and central Sweden, Bornholm (Denmark) and the Oslo Region of Norway. *Laneites ingricus* ranges from the Volkhovian (BIIγ) *Megistaspis limbata* Zone through the lower Kundan (BIIIα) *Asaphus expanus* Zone. Specimens of *L.* cf. *ingricus* are known from the older Volkhovian (BIIβ) *Megistaspis simon* Zone and *L.* aff. *L. ingricus* (Schmidt) *sensu* Männil (1958) has been recorded from the lowermost Volkhovian (BIIα) *Megistaspis polyphemus* Zone in Estonia. *Ceraurinella ornata* occurs in the *A. expansus* Zone in Sweden and in the *A. raniceps* (BIIIβ) to *M. gigas* (BIIIγ) zones in Estonia. A total of 30 cheirurine taxa are known from the Middle and Upper Ordovician of Baltoscandia. Species diversity (including both formally described species and forms treated under open nomenclature) is greatest in Sweden with 14 occurrences, followed by Estonia (11), Norway (7), the St. Petersburg area (5), Denmark (Bornholm) with two and Finland with a single occurrence. Six genera are recorded: *Ceraurinella* Cooper, 1953; *Ceraurinium* Přibyl & Vaněk in Přibyl et al., 1985; *Hadromeros* Lane, 1971; *Laneites* Přibyl & Vaněk in Přibyl et al., 1985; *Paraceraurus* Männil, 1958; and *Xylabion* Lane, 1971. In Sweden, nearly half of the recorded occurrences are due to *Hadromeros* spp. in the Upper Ordovician, whereas *Paraceraurus* accounts for nearly half of the occurrences in the Middle Ordovician of Estonia. A gap in the occurrence of cheirurinae is seen across Baltoscandia between the Kukruse/Dalbyan and the Oandu/Moldåan stages.

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Introduction

Trilobites of the family Cheiruridae Hawle & Corda, 1847 were widespread and abundant during the Ordovician, with particularly high diversity in Laurentia and Baltica (Adrain, 2013). Lane's (1971) monographic treatment remains the single most comprehensive study of the family, with significant supplementary contributions made by Přibyl et al. (1985). In addition to a large number of studies on genus- and species-level taxa since then, more recent research has focused on individual subfamilies and their constituent taxa (Gapp et al., 2012; Adrain, 2013 and references therein).

Cheirurids originated in the latest Cambrian (Furongian; Pérez-Peris et al., 2021 and references therein), but the first representatives of the group in Baltoscandia appear with the widespread deposition of carbonates in the Early Ordovician (Ottenbyan Stage), assigned to the Bjørkåsholmen Formation (Ebbestad, 1999; Pärnaste et al., 2013). Several subfamilies of the Cheiruridae proliferated during the succeeding Hunneberg/Ottenbyan–Kundan stage interval, with more than 53 species recorded in the so-called Asaphid fauna (Pärnaste et al., 2013). Some of the earliest representatives of the Baltic Cyrtometopinae, as well as the Cheirurinae, appeared at this time (Pärnaste, 2003, 2004, 2007, 2008).

The present study revises and redescribes two of the earliest cheirurine species in Baltoscandia, listed in stratigraphical order of appearance: *Laneites ingricus* (Schmidt, 1881) and *Ceraurinella ornata* (Dalman, 1828). The latter was among the first cheirurine trilobites described from Scandinavia, where it is relatively rare, but additional material is known from the east Baltic. Both species are frequently mentioned in the literature but have not been revised since their original descriptions. Exquisite specimens of cheirurids from the St. Petersburg area, including *Laneites ingricus*, have been showcased for commercial sale (see Klikushin et al., 2009), but such material has not been studied here due to uncertainties regarding provenance and authenticity. However, new well-preserved material of *Laneites ingricus* from Sweden and Norway has recently been made available for study, providing new insights into the morphology, spatial, and stratigraphical range of the species. The new material also facilitates improved comparison with *Ceraurinella ornata*, which is known from a limited number of specimens in Sweden and Estonia. An overview of cheirurine occurrences across Baltoscandia is provided below (see also Electronic Supplement 1).

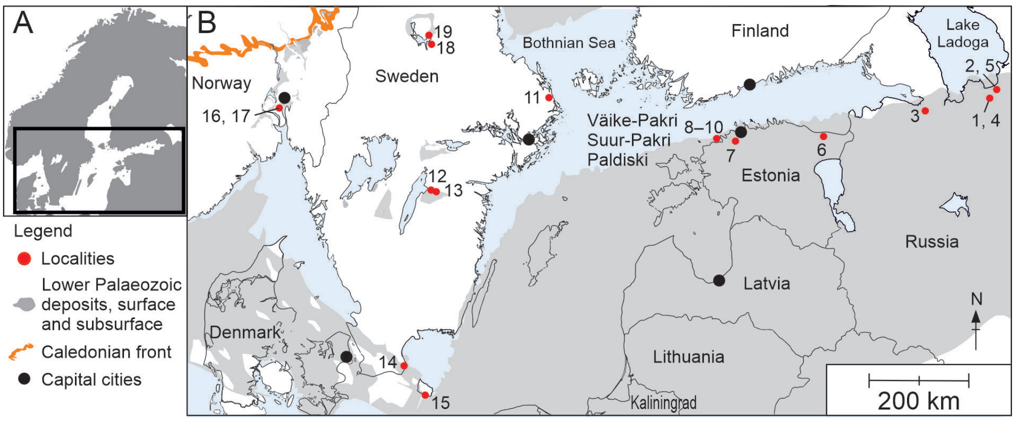

Figure 1. (A, B). Map of southern Baltoscandia (inset in A) showing geology and localities of specimens discussed in this study. Localities: 1-5 St. Petersburg area, 6–10 Estonia, 11–14 & 18–19 Sweden, 15 Denmark, and 16–17 Norway. 1) Izvoz near the village Plekhanovo; 2) Kolchanovo; 3) Popovka River area near the village Pavlovsk; 4) Obuchovo; 5) Eastern outcrop area at Lynna river. 6) Pühajõe, Ida-Virumaa county; 7) Mäeküla, Tallinn; 8) Väike-Pakri Island, Harju county; 9) Suur-Pakri Island, Harju county; 10) Paldiski, Harju county; 11) Trästa, Uppland; 12) Västanå, Östergötland; 13) Ljungsbro, Östergötland; 14) Flagabro, Skåne; 15) Skelbro, Bornholm; 16) Edelvoldveien at Vollen near Slemmestad, Asker; 17) Djuptrekkodden, Slemmestad, Asker; 18) Lindgården at Utby, Dalarna; 19) Vikarbyn, Dalarna.

Taxonomy of the Cheiruridae

Adrain (2013) recognised eight subfamilies within the Cheiruridae, ranging from the uppermost Cambrian (Furongian) to the Middle Devonian. These include the Acanthoparyphinae Whittington & Evitt, 1954; Cheirurinae Hawle & Corda, 1847; Cyrtometopinae Öpik, 1937; Deiphoninae Raymond, 1913; Eccoptochilinae Lane, 1971; Heliomerinae Evitt, 1951; Pilekiinae Sdzuy, 1955; and the Sphaerexochinae Öpik, 1937. This classification is broadly similar to that of Lane (1971) who recognised seven subfamilies, including Areiinae Prantl & Přibyl, 1947, but not the Cyrtometopinae or Heliomerinae. The Areiinae, according to Přibyl et al. (1985), includes *Areiaspis, Areia* (*Areia*) and *Areia* (*Turantyx*). They disagreed with Lane's (1971) assignment of *Areiaspis* to the Eccoptochilinae, retaining only *Areia* within the Areiinae. The subfamily Areiinae was not discussed by Adrain (1998, 2013).

Lane (1971), following Whittington (1965), assigned *Heliomera* and *Heliomeroides* – the two genera originally placed in Heliomerinae Evitt, 1951 – to the Sphaerexochinae, whereas Chatterton & Ludvigsen (1976) placed these genera within the Acanthoparyphinae. Adrain (1998) pointed out that, under the rules of priority, this assignment would make Heliomerinae the valid subfamily name, and he retained *Heliomera* and *Heliomeroides* within the Heliomerinae.

Adrain & Pérez-Peris (2021) reviewed several subfamilies – Cheirurinae, Pilekiinae Acanthoparyphinae, Deiphoninae and Sphaerexochinae – and provided a detailed assessment of the current status of the last three. Of particular relevance to the present study is their detailed redescription of *Laneites polydorus* (Billings, 1865). Adrain & Pérez-Peris (2021) further restricted the Sphaerexochinae to only include *Sphaerexochus* and, tentatively, their new genus *Newfoundlandops*, whereas several sphaerexocine genera were transferred to the Acanthoparyphinae. Although often ranked as a family, the Pilekiinae was considered by Adrain & Karim (2019) and Adrain & Pérez-Peris (2021) as a basal cheirurid subfamily. They demonstrated that differences in ventral morphology provide a better basis for distinguishing these early cheirurids from members of the Pliomeridae Raymond, 1913.

The subfamily Cheirurinae is one of the largest within the Cheiruridae, comprising approximately 270 species ranging in age from the Early Ordovician (Floian) to the Mid Devonian (Givetian) (Adrain, 2013; Pérez-Peris et al., 2024). The subfamily is considered monophyletic. Its members exhibit a fairly conservative morphology throughout their evolutionary history, with most of the variation seen in the shape of the glabella, the nature of the pygidial spines, and the surface sculpture (Pérez-Peris et al., 2024). Lane (1971) provided a comprehensive diagnosis of the group, emphasising the importance of thoracic characters in defining subfamilies. Key characters include the constricted pleurae adjacent to the convex adaxial region, the articulating flanges with fulcral processes and sockets, and the reduction of the second and third pygidial spines. Pérez-Peris et al. (2024) noted that these traits are synapomorphies shared by Cheirurinae, Cyrtometopinae and Deiphoninae. Lane (1971) considered the Cyrtometopinae as a junior synonym of the Cheirurinae, whereas Přibyl et al. (1985) maintained it is a valid group, a view subsequently supported and expanded by Pärnaste (2001, 2003). Adrain & Pérez-Peris (2021) proposed that, pending further revisions, basal cyrtometopines might be more appropriately placed within the Deiphoninae. Pérez-Peris et al. (2024) later formalised this suggestion by treating Cyrtometopinae as a junior synonym of Deiphoninae. In their phylogenetic analysis, Pérez-Peris et al. (2024) identified two lineages within the Cheirurinae: a *Ceraurus*-like and a *Ceraurinella*-like group, distinguished by synapomorphies related to the hypostomal morphology and the development of spines and surface sculpture.

Baltoscandian distribution of cheirurines. – The number of described cheirurines (including material treated in open nomenclature) is greatest in Sweden, with 14 occurrences, followed by Estonia with 11, Norway with seven, the St. Petersburg area with five, Denmark (Bornholm) with two and Finland (Åland) with one, comprising a total of 30 taxa (Electronic Supplement 1, Figs 1 & 2).

These are assigned to six genera: *Ceraurinella* Cooper, 1953: *Ceraurinium* Přibyl & Vaněk in Přibyl et al., 1985; *Hadromeros* Lane, 1971; *Laneites* Přibyl & Vaněk in Přibyl et al., 1985; *Paraceraurus* Männil, 1958; and *Xylabion* Lane, 1971 (see Electronic Supplement 1).

Half of the cheirurine occurrences in Sweden are represented by the numerous species of *Hadromeros* from the Upper Ordovician, while *Paraceraurus* accounts for nearly half of the occurrences in the Middle Ordovician of Estonia. A gap in the occurrence of Cheirurinae is observed across Baltoscandia between the Kukruse/Dalbyan and the Oandu/Moldåan stages (Fig. 2). In Norway, cheirurines are absent from the upper Kundan to Dalbyan, a prolonger gap that may reflect the development of deeper-water facies in western Scandinavia during this time.

The oldest known members of the Cheirurinae in Baltoscandia are represented by the *Laneites* species discussed in this study (see below). Slightly younger taxa include three species identified as *Ceraurinella*, among them the two taxa referred to as *Osekaspis?* spp. A & B by Hansen & Nielsen (2003), in addition to Dalman's *C. ornata* (Pärnaste et al., 2013). This species-rich group is otherwise typical of the late Early to Late Ordovician of Laurentia and its margins, where one of the earliest species – *Ceraurinella* sp. *sensu* Adrain & Fortey (1997) – has been recorded from the Tourmakeady Formation of County Mayo, Ireland (see discussion in Adrain & Pérez-Peris, 2021). The Baltoscandian Volkhovian (Dapingian) record of *Ceraurinella* sp. from the St. Petersburg area (Pärnaste et al., 2013) thus appears to be only slightly younger than the oldest Laurentian occurrences. *Ceraurinella ornata* (Dalman, 1828) is known from Sweden and Estonia (Pärnaste, 2008; Pärnaste et al., 2013) as well as from erratics (Geschiebe) found in Germany, although some of these records may be related to other taxa (see synonymy list). The specimen from the Pakri Formation in Estonia identified as *C. ornata* by Männil (1958, p. 173; pl. 3, Fig. 10) was reassigned to *Reraspis* Öpik, 1937 by Pärnaste (2004). The Norwegian specimen of *Ceraurinella* originates from the Upper Allochthon Otta Conglomerate, the age of which remains uncertain (≈Middle Ordovician). Furthermore, the Otta area is thought to have originated from somewhere in the Iapetus Ocean (Bruton & Harper, 1981; Harper et al., 2008), so strictly speaking, this occurrence should not be considered Baltoscandian. Pärnaste (2008) discussed morphological variations in species of *Ceraurinella* across Laurentia and its margins, and suggested that some of the geographical variations reflect adaptations to local environmental conditions.

Species of *Hadromeros* are mostly restricted, within Baltica, to the Jerrestadian and Tommarpian (Fig. 2) and are found in the central and western parts of the Baltoscandian region (Pärnaste, 2011). An older Moldåan occurrence, referred to as *Hadromeros* sp. by Bruton in Neuman et al. (1997), was described from the Trondheim area in Norway. It may be better placed with *Ceraurinus* sp. However, as the deposits in this area are of Laurentian origin, this occurrence is not considered as a Baltoscandian record. Like the *Ceraurinella* material from Otta, this occurrence is included in Electronic Supplement 1 and Fig. 2 for completeness.

Several species of *Hadromeros* are recorded from the mud mound limestone facies of the Jerrestadian Boda Limestone in central Sweden, as well as from the coeval limestone and mudstone facies in Norway (Warburg, 1925; Owen, 1981; Suzuki et al., 2009). A possible occurrence is recorded from the Hirnantian of Latvia (Hints et al., 2012). The genus appears to have a wide global distribution, but some identifications remain uncertain (Pärnaste, 2011). The three pairs of pygidial spines in *Hadromeros* resemble those of *Xylabion*, but *Hadromeros* is distinguished from other cheirurines by its broad (tr.) glabellar furrows, a medially effaced anterior border furrow, and a pronounced inflation of the pleurae just distal to the transverse exsagittal furrow that separates the inner part from the pleural spine (Lane, 1971; Kielan-Jaworowska et al., 1991; Pärnaste, 2011). Lane (1971) suggested that *Hadromeros* was derived from *Xylabion*, whereas Přibyl et al. (1985) suggested that it was derived from *Paraceraurus.*

Ceraurinium, established by Přibyl & Vaněk in Přibyl et al. (1985), with *Ceraurinium intermedium* (Kielan, 1955) as the type species, was diagnosed by its slightly widening glabella, very wide (tr.)

pleural spines of the thoracic segments, and a pygidium having only one pair of long pleural spines. The species was originally placed in *Ceraurinella* by Kielan (1960) but later excluded from that genus by Chatterton & Ludvigsen (1976), who noted that the absence of multiple pygidial spines resembles the condition seen in some species of *Ceraurus.* Subsequently, Kielan-Jaworowska et al. (1991), without referring to the work of Přibyl et al. (1985) —and possibly unaware of it — reinstated the assignment of *intermedium* to *Ceraurinella*. They argued that the lack of additional pairs of pygidial spines, which are typically present in species of *Ceraurinella*, simply reflects a common trend in cheirurids towards reduction in such spines. The other diagnostic characters in the original definition of *Ceraurinum* were thus not addressed by Kielan-Jaworowska et al. (1991). Three specimens of this genus in the NRM collections (NRM Ar60127–Ar60129), closely resembling the Polish species, have been identified from the Lower Jonstorp Mudstone at Mösseberg, Västergötland (H. Pärnaste personal observation).

Two Late Ordovician species from Sweden were treated as *Ceraurinium glabrum* (Angelin, 1854) and *C.*? *latifrons* (Warburg, 1925) by Přibyl & Vaněk in Přibyl et al. (1985), the first from the Jerrestadian Boda Limestone and the second from the Dalbyan Kullsberg Limestone. The latter species was tentatively assigned to *Paraceraurus* by Ludvigsen (1979), and later to the cyrtometopine *Reraspis* by Pärnaste (2004). *Ceraurinium glabrum*, which Pärnaste (2004) placed optionally in *Xylabion*, *Hadromeros* or *Ceraurinella*, is here questionably reassigned to *Ceraurinum* (Electronic Supplement 1), although it has the glabellar anterior border furrow effaced medially, similar to representatives of *Hadromeros* and some *Ceraurinella.*

Přibyl & Vaněk in Přibyl et al. (1985, p. 143) referred *Cheirurus* cf. *glaber sensu* Schmidt (1881, p. 151) to *Ceraurinium*? sp., but inconsistently cited the same specimen as *Paraceraurus* sp. (ibid. p. 146). This specimen was subsequently discussed by Pärnaste (2004, 2008), who identified it as *Xylabion* n. sp. In addition, Pärnaste (2004, 2008) described *X. sexermis* (Öpik, 1937) from Estonia and Norway, and demonstrated that the Norwegian *Paraceraurus helgoeyense* (Nikolaisen, 1961) is a junior synonym. The late Darriwilian *X. kirkdandiensis* Tripp, 1979 from Girvan, Scotland, was reassigned without discussion to *Hadromeros* by Přibyl & Vaněk in Přibyl et al. (1985). *Xylabion* is therefore currently known from nine species occurring in Laurentia, marginal Laurentia, marginal Siberia, and Baltica. They are all restricted to the Katian except for the Sandbian *X. gelasinosum* (Portlock, 1843) from Ireland (Lane, 1971; Pärnaste, 2004, 2008; Ebbestad & Fortey, 2020). Based on specimens of *Xylabion*, Pärnaste (2008) further established that the pygidial apodemes in the Cheirurinae are low and blunt-ended, in contrast to the sharper, thin, ridge-like apodemes found in cyrtometopines, which arise from large triangular structures.

Paraceraurus is typically restricted to the East Baltic region, with only one record from Norway and two from Sweden. The sole fragmentary cranidium of *P. perlongus* (Brøgger, 1882) from Norway consists primarily of the glabella. It was assigned to *Paraceraurus* by Nikolaisen (1961), although the age probably is much younger than other *Paraceraurus* species. Without additional parts preserved, the affinity remains uncertain, as the glabella could equally well belong to a species of *Xylabion*. Nonetheless, the tentative determination is retained for now due to the lack of additional material. Jaanusson (1960) and Jaanusson et al. (1982) reported *P.* cf. *exsul* (Beyrich, 1846) from the Segerstadian 'Folkeslunda Limestone' on Öland and in Jämtland (Fig. 2). Karis (1982) also reported *Paraceraurus exsul* from the uppermost part of the Isö Limestone (now recognised as the Stein Formation, see Rasmussen & Bruton 1994) in Jämtland and correlated it with the 'Folkeslunda Limestone' of Sweden. Based on findings of the conodont *Eoplacognathus suecicus,* Rasmussen & Bruton (1994) assigned the Stein Formation to the Kundan; in modern terms, the *E. suecicus* Zone corresponds to the lower Segerstadian (S.M. Bergström, 2007; Hints et al., 2012). Hadding (1913) reported *P. exsul* from the lowermost part of the Andersön Shale, which overlies the Isö Limestone in the same section in Jämtland. It is unclear if this is the specimen referred to by Karis (1982). Hadding's specimen was re-illustrated in Pålsson et al. (2002, Fig. 9K) as *Paraceraurus* sp., and these authors also reported the genus from slightly higher in the same succession.

Six East Baltic species were attributed to *Paraceraurus* by Männil (1958), mostly known from well-preserved material of Aseri to Kukruse age (Fig. 2 & Electronic Supplement 1). The genus is especially common in northeastern Estonia, where the Kukruse oil shale is quarried. Commercially available, complete specimens may be prone to falsification, and are best avoided, but although incomplete, comparatively well-preserved museum material of cranidia, thoracic elements and pygidia is available for study. *Paraceraurus* morphology appears fairly consistent and is characterised by a forward-projecting rostral plate, and a pygidium with four axial segments and three pairs of spines, as well as a median projection or spine. A species originally described as *Cheirurus elatifrons* by Krause (1895) from Haljala-age erratics in Germany, was later attributed to *Paraceraurus* by Neben & Krueger (1971, 1979) and van Keulen & Rhebergen (2017). It was tentatively assigned to *Reraspis* by Přibyl et al. (1985), and this assignment is confirmed here after reexamination of the specimen (H. Pärnaste, personal observation).

Paraceraurus is endemic to Baltica. *Paraceraurus ruedemanni* (Raymond, 1916) from Laurentia, reported by Shaw (1968), was designated as the type species of *Cerauropeltis* Přibyl & Vaněk in Přibyl et al. (1985). A specimen referred to as *Paraceraurus* sp., by Harper & Rast (1964) from the Darriwilian (upper Llanvirn) in Bellewstown (Co. Dublin, Ireland), was later referred to *Ceraurinella* by Dean (1966). Zhou & Zhou (2008) assigned several Katian species from China previously attributed to *Paraceraurus* to *Parisoceraurus*. The species of *Paraceraurus* described by Lu (1975) were synonymised by Fortey (1997) with *Hadromeros xiushanensis* Sheng, 1964.

Laneites Přibyl & Vaněk in Přibyl et al. (1985) is discussed in detail below.

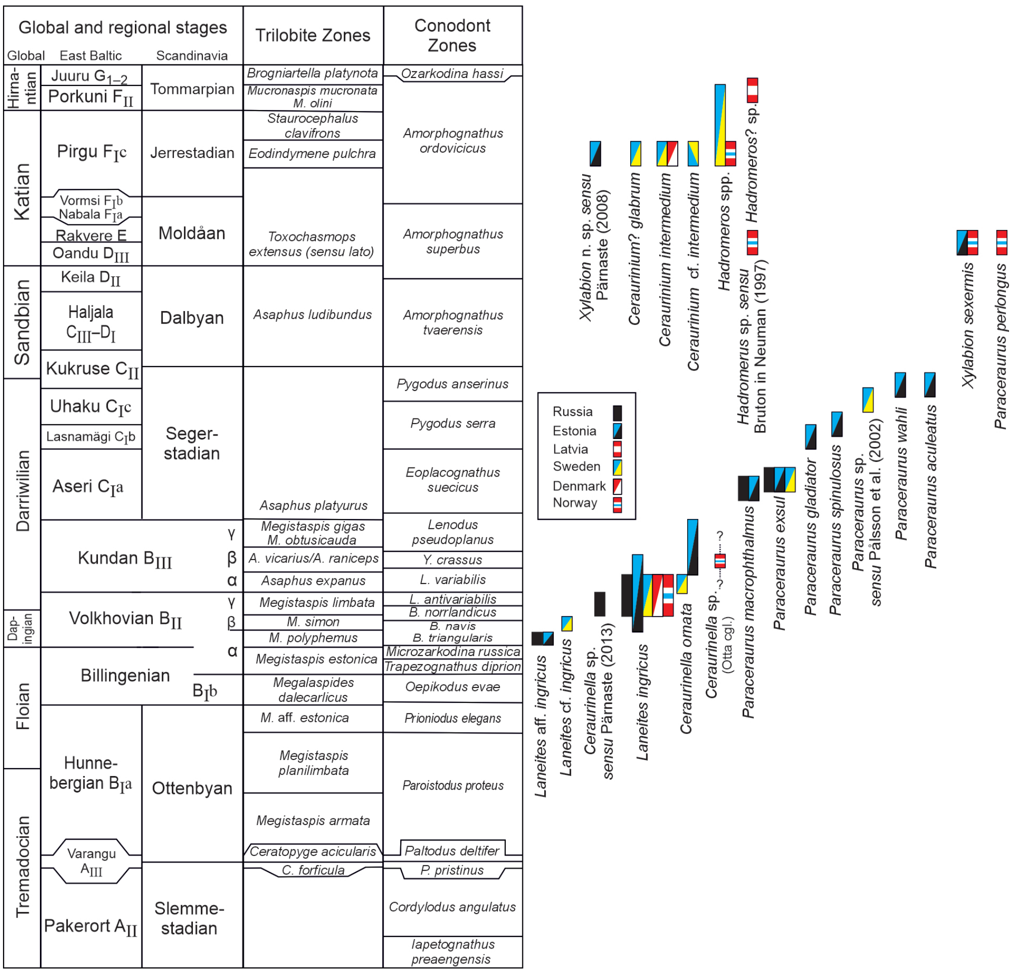

Figure 2. Stratigraphy and distribution of cheirurine trilobite taxa in Baltoscandia. The stratigraphic framework is based on Nielsen et al. (2023).

Geological setting and biostratigraphy

The two cheirurine species discussed herein come from the Volkhovian–Kundan limestone successions across the Baltoscandian platform, including the St. Petersburg area (Russia), northern Estonia, south-central Sweden, Bornholm (Denmark), and the Oslo Region of Norway (Fig. 1). The Middle Ordovician Volkhovian–Kundan limestones in Sweden and eastwards are extremely condensed, with numerous hardground omission surfaces, some of which can be traced for several hundred kilometres (Jaanusson, 1961). Although the carbonate platform appears to have been laterally fairly uniform at this time, the distribution of trilobite, brachiopod and cephalopod faunas varies across the region. These variations form distinct biofacies that reflect differences in depth and bottom conditions (Nielsen, 1995; Rasmussen et al., 2009; Pärnaste & Bergström, 2013; Kröger & Rasmussen, 2014). Following the Kundan, the facies distribution developed into spatial zones (confacies belts of Jaanusson, 1976) in which lithology and associated faunal assemblages remained fairly stable throughout the remainder of the Ordovician.

The Russian type material of *Laneites ingricus* derives from the Volkhov and Lynna formations, which are exposed along the extensive Baltic-Ladoga Glint. The oldest occurrence is in the ~3.5 m-thick Frizy Member of the Volkhov Formation, composed largely of nodular and glauconitic limestone (Ivantsov, 2003; Dronov, 2005; Dronov & Mikuláš, 2010). The Volkhov Formation itself is 6.5–6.9 m thick and is subdivided, in ascending order, into the Dikari, Zheltiaki, Frizy and Khamontovo members (Ivantsov, 2003). These correspond to the *Megistaspis polyphemus* to *Asaphus lepidurus* zones (Fig. 2), of which the Frizy Member correlates with the latter (= upper part of the *M. limbata* Zone in Scandinavia) (Hansen & Nielsen, 2003; Dronov, 2005; Dronov & Mikuláš, 2010). Hansen & Nielsen (2003, fig. 3) found *L. ingricus* in the Volkhov Formation at Lynna River, in the uppermost Zheltiaki Member (probably equivalent to the basal part of the *M. limbata* Zone) and through the overlying Frizy Member (upper part of the *M. limbata* Zone). The 3.5 m-thick, bioclastic limestone of the Lynna Formation occurs in the eastern part of the outcrop area and wedges out towards the west, where the Sillaoru Formation is developed (Ivantsov, 2003). The Lynna Formation is the lowermost unit of the Kundan Stage, with the *A. expansus* Zone marking its base (Ivantsov, 2003; Dronov, 2005).

Laneites was listed from the upper Volkhovian to middle Kundan (*A. lepidurus* to *A. raniceps* zones) of Estonia by Pärnaste et al. (2013). One specimen attributed to *L. ingricus* derives from the 0.6 m-thick iron ooid-rich limestone of the upper Sillaoru Formation (Voka Member), representing the *Asaphus expansus* Zone in northeastern Estonia. A second specimen from Estonia, treated as *L.* aff. *L. ingricus,* is from the up to 1.2 m-thick lowermost Volkhovian Saka Member of the Toila Formation (*Megistaspis polyphemus* Zone), near Tallinn in northern Estonia. *Ceraurinella ornata* has been recorded from the Kundan *A. raniceps* and *Megistaspis gigas* zones (Pärnaste et al., 2013). The material studied here is from the 4.5 m-thick brownish-grey arenaceous limestone of the Kundan Pakri Formation in northwestern Estonia. This unit represents nearshore facies (Hints in Hints & Toom, 2023).

In Sweden, the traditional 'orthoceras limestone' includes the 'Latorp', 'Lanna', 'Holen', 'Segerstad', 'Skärlöv', 'Seby' and 'Folkeslunda' limestones. These are defined as topostratigraphic units, where one boundary was placed at a level of a recognisable faunal shift and the other boundary was defined based on lithological features (Jaanusson, 1960). These units are now considered obsolete and in need of revision; to signal this, they are referred to in quotation marks following Nielsen et al. (2023; see that paper for a more detailed discussion on topoformations).

Both *Laneites ingricus* and *Ceraurinella ornata* occur within the *Asaphus expansus* Zone in the lower part of the 'Holen limestone'. This unit is ~7 m thick in Dalarna and ~15 m thick in Västergötland (Ebbestad & Högström, 2007; Lindskog & Eriksson, 2017). It is a massive reddish-brown, marly limestone with frequent limonitic hardgrounds, although fewer than in the underlying ´Lanna limestone´ (Lindskog et al., 2014). The earliest Kundan is characterised by relatively deep-water facies that becomes progressively shallower upwards (Lindskog & Eriksson, 2017). In Västergötland and on Öland, a distinct 1.5 m-thick grey interval, known as the Täljsten/Sphaeronites bed, is developed at the *A. expansus*–*A. raniceps* transition (Fig. 2) in the lower part of the otherwise reddish-brown limestone (Lindskog & Eriksson, 2017). The Täljsten interval represents a shallow-water facies and contains a distinctive fauna.

Along the western margin of the Baltoscandian platform, from Jämtland in the north, through the Oslo Region, to Skåne and Bornholm in the south, the Volkhovian and Kundan limestone interval is sandwiched by shale-dominated units. The limestone facies migrated westwards into these areas during a period of sea level lowstand, peaking in the middle of the *Leonodus variabilis* conodont Zone (Fig. 2), which corresponds to the *Asaphus expansus*–*A. ranicep*s trilobite zonal boundary (Nielsen, 2004; Rasmussen & Bruton, 1994; Nielsen et al., 2023). Cheirurids have not been recorded in the northwestern allochthonous facies of the Stein Formation in Norway, nor in the 'Lanna' and 'Holen' limestones of the autochthonous platform deposits, for example in Jämtland. However, *Paraceraurus exsul* was reported from the allochthonous Stein Formation (= Isö Limestone) in Jämtland by Larsson (1973) and Karis (1982).

In the Oslo Region, *Laneites ingricus* occurs in the Lysaker Member of the Huk Formation (~6–11 m thick). The Huk Formation is subdivided, in ascending order, into the Hukodden, Lysaker and Svartodden members (Owen et al., 1990). The Lysaker Member is 1.5–4.5 m thick in the central Oslo-Asker district and is developed as nodular limestone embedded in calcareous mudstone. It spans the upper part of the *Megistaspis limbata* Zone and the entire *Asaphus expansus* Zone (Nielsen, 1995).

In SE Skåne and on Bornholm, the Volkhovian–Kundan limestone interval is developed as the Komstad Limestone. This unit is at least some 16 m thick in parts of southernmost Sweden but varies considerably in thickness and wedges out towards both northwest and southeast, with a thickness of 0.1–4.7 m on Bornholm (Nielsen, 1995, 2004; Nielsen et al. 2018). Here the Komstad Limestone represents the *M. polyphemus* Zone to the lowermost *A. expansus* Zone (Fig. 2). *Laneites ingricus* occurs in the upper part of the c. 4 m-thick Komstad Limestone section at Skelbro on Bornholm, within the lower *Asaphus expansus* Zone. The cranidia described herein as *L.* cf. *ingricus* derive from the lower part of the c. 16 m-thick Komstad Limestone at Flagabro in SE Skåne (*Megistaspis simon* Zone).

Material and methods

Terminology and subdivisions of the Ordovician succession in the St. Petersburg area in Russia follow Dronov & Mikuláš (2010), whereas those for Estonia follow Meidla et al. (2014). The regional biostratigraphical zonation adopted here follows Pärnaste et al. (2013) and Nielsen et al. (2023). Specimens discussed in this paper are housed in the following palaeontological collections: the Natural History Museum in Oslo, Norway (specimen numbers prefixed PMO), the Swedish Museum of Natural History, Stockholm (NRM), the Palaeontological collections, Museum of Evolution, Uppsala University (PMU), the department of Lithosphere and Biosphere Science, Institute of Geology, Lund University (LO), the Natural History Museum of Denmark (MGUH), the Department of Geology, Tallinn University of Technology (GIT), the Museum of Paleontology and Stratigraphy, University of St. Petersburg (PSM), the Paleontological Institute of the Russian Academy of Sciences in Moscow (PIN), and the Museum für Naturkunde Berlin, Germany (MB).

Systematic palaeontology

Suborder Cheirurina Hawle & Corda, 1847
Family Cheiruridae Hawle & Corda, 1847
Subfamily Cheirurinae Hawle & Corda, 1847
Genus *Laneites* Přibyl & Vaněk in Přibyl et al., 1985

Type species. – Original designation by Přibyl & Vaněk in Přibyl et al. (1985, p. 162): *Ceraurus polydorus* Billings, 1865, p. 286, fig. 274, from the Middle Ordovician (Darriwilian, Dw2) Table Cove Formation, *Cybelurus mirus* Zone, at Portland Creek, Newfoundland, Canada.

Diagnostic characters. – (Modified from Přibyl & Vaněk in Přibyl et al., 1985 and Adrain & Pérez-Peris, 2021). Glabella broad, subtetragonal, narrowing rearwards, with three lateral glabellar furrows; S2 and S3 with marked posteromedian deflection. Fixigenae broad, markedly divergent, and genal angle extended into stout and long genal spine. Elongate palpebral lobes located opposite L2. Palpebro-ocular ridge marked adaxially with deep furrow. On either side of occipital ring is a small occipital lobe. Librigenae with short (exsag.) but wide (tr.) fields. Genal spine with large base and apparently directed laterally. Hypostome with relatively weak middle furrow. Anterior pair of pygidial spines is the longest and most robust and diverges obliquely rearwards and upwards. The second pleural spine pair is short and runs rearwards parallel to the pygidial axis. Third pair is developed as small knobs or completely reduced. Axis with three rings and terminal piece. No independently inflated pygidial terminal piece developed.

Remarks. – In addition to the type species *L. polydorus* (Billings) from the Darriwilian of Newfoundland (Whittington, 1965; Boyce, 2015), Přibyl & Vaněk in Přibyl et al. (1985) assigned two East Baltic forms to *Laneites*: *L.*? *ingricus* (Schmidt) from the uppermost Volkhovian and lowermost Kundan near St. Petersburg, Russia, and *L.* sp. aff. *L. ingricus* (Schmidt) *sensu* Männil (1958, p. 175, pl. 1, fig. 7), based on a partial cranidium from the lowermost Volkhovian Saka Member of the Toila Formation (*Megistaspis polyphemus* Zone) in Estonia. Herta Schmidt (1935, p. 111) considered [modern names applied here] *Paraceraurus exsul, P. macrophthalmus, Laneites*? *ingricus* and *C. ornata* to be closely related. Shared features include a small distance between the palpebral lobes and the glabella (less than half of the glabellar width), a steep profile (sag.) of the anterior glabellar lobe (as opposed to a more gently sloping lobe), and long anterior pleural spines on the pygidium.

Whittington (1965, p. 410) remarked that the Newfoundland species was most similar to Friedrich Schmidt's *ingrica*, particularly regarding the orientation of the broad-based fixigenal spines and the position of the eyes.

Adrain & Pérez-Peris (2021) cautiously accepted that the characters listed for *Laneites* by Přibyl & Vaněk in Přibyl et al. (1985) appear valid for distinguishing the type species from early representatives of *Ceraurinella*. These include the posterior curvature of S2 and S3, the divergent fixgenal spines, and the long anterior pygidial spines, which project up- and outward. Earlier, Ludvigsen (1979, p. 20) had already observed that *C. polydorus* has a distinctive cranidial morphology not seen in younger species of *Ceraurinella*, such as a barrel-shaped glabella, short anterior glabellar lobes, markedly curved and deep lateral glabellar furrows, deep and long palpebral furrows, erect and widely divergent first pygidial spines, and widely spaced third spines. The last feature is expressed as mere knobs in *L. polydorus* and is barely discernible in *L. ingricus.* Adrain & Pérez-Peris (2021) pointed out that poor knowledge of early *Ceraurinella* species hinders a more detailed phylogenetic assessment of the relationship between *Laneites* and *Ceraurinella*.

Laneites ingricus (Schmidt, 1881)

Non 1859 *Cheirurus ornatus* Dahn. [sic] sp.: Nieszkowski, p. 374, pl. 2, figs 4 & 5. [description, = *Paraceraurus macrophthalmus*]

1861 *Ceraurus ornatus*: Roemer, p. 78, pl. 8, fig. 9. [comparative discussion]

1881 *Cheirurus* (*Cheirurus*) *ingricus* n. sp., Schmidt, pp. 135, 136, pl. 6, figs 1 & 2, text-fig. 9. [description]

1883 *Chirurus ingricus* Schmidt: Törnquist, p. 16. [listed]

1884 *Chirurus ingricus* Schmidt: Törnquist, pp. 14, 94, pl. 1, fig. 10. [description, listed]

1888 *Chirurus ingricus* Fr. Schmidt: Lindström, p. 8. [listed]

1896 *Ch.* [*Cheirurus*] *engricus* [sic] Fr. Schmidt: Wysogórski, p. 410. [comparative discussion]

1896 *Cheirurus sadewitzensis* n. sp., Wysogórski, p. 410. [description of specimen illustrated in Roemer (1861)]

1896 *Cheirurus* (*Cheirurus*, sens. stri.) *ingricus* (Schmidt): Reed, p. 165. [listed]

1901 *Chirurus ornatus* Dalman: Lindström, p. 50, pl. 3, figs 12–14. [description of eyes]

1905 *Cheirurus ingricus* Dalm.: Lamansky, pp. 68, 169. [listed, distribution]

1907 *Cheirurus ingricus* Schmidt: Schmidt, p. 8, pl. 1, fig. 4. [description, distribution]

1908 *Chirurus ingricus* Fr. Schm.: Wiman, p. 86, and table 2. [listed, distribution]

1911 *Cheirurus ingricus* Schmidt: Bassler, p. 23. [faunal list]

1913 *Ceraurinus ingricus* Schmidt: Barton, pp. 547–549, 553. [comparative discussion]

1915 *Ceraurinus*: *Cheirurus ingricus* Schmidt, 1881: Barton, p. 134. [listed, distribution]

1925 *Ceraurus ingricus* Schmidt: Raymond, p. 141. [comparative discussion]

1927 *Cheirurus ingricus* F. Schmidt: Kummerow, p. 18. [listed: distribution]

1928 *Cheirurus ingricus* Schmidt: Troedsson, p. 73. [listed under species of Ceraurinus]

1928 *Cheir. ingricus* F. Schm.: Patrunky, pp. 33, 34. [comparative discussion]

1934 *Cheirurus ingricus* Fr. Schm.: Rüger, p. 17. [listed]

1935 *C.* [*Ceraurus*] *ingricus* (Schmidt): Schmidt, pp. 110, 111. [distribution, comparative discussion]

1949 Ceraurus ingricus F. S.: Bohlin, table p. 566. [listed: distribution]

1951 *Cheirurus* (= *Ceraurinus*) *ingricus:* Jaanusson & Mutvei, p. 635. [listed]

1958 *Ch.* [*Cheirurus*] *ingricus* (Schmidt): Männil, p. 173. [comparative discussion as tentative species of *Ceraurinella*]

1965 [no taxon name given]: Whittington, pp. 410, 411. [comparative discussion with reference to Schmidt's 1881 description of *ingricus*]

1971 *Paraceraurus ingricus* (Schmidt, 1901): Neben & Krueger, pl. 2, figs 16 & 17. [stratigraphy]

1971 *Ceraurinella ingrica* Schmidt, 1881: Lane, p. 18, text-fig. 10 (pars) on p. 74, 75. [comparative discussion]

1973 *Ceraurinella ingricus* (Schmidt): Chugaeva, p. 76. [listed: taxonomy & distribution]

1976 *Cheirurus ingricus* (Schmidt): Chatterton & Ludvigsen, p. 52. [listed as a species of *Ceraurinella*]

1977 *Ceraurinus ingricus* (Schmidt): Ludvigsen, p. 960. [comparative discussion]

1979 *Ceraurinella*? *ingrica* (Schmidt): Ludvigsen, p. 28. [comparative discussion]

1981 *C. ingricus* Schmidt 1881: Bruton & Harper, p. 171. [comparative discussion]

1985 *Laneites*? *ingricus* (Schmidt): Přibyl et al., p. 146. [listed: taxonomy]

1997 *Ceraurinella*? *ingrica*: Bruton et al., p. 25. [listed: taxonomy]

2003 *Laneites*? *ingrica*: Hansen & Nielsen, pp. 109–111. [stratigraphy]

2009 *Paraceraurus ingricus* (Schmidt 1881): Klikushin et al., pp. 336, 337, figs 530–533. [description, synonymy list]

2013 *Laneites*? *ingrica* (Schmidt): Pärnaste et al., no. 294 in table S5, no. 445 in table S6, nos 294, 445 in table S8. [listed: distribution]

2015 *Paraceraurus ingricus* Schmidt 1881: Corbacho et al., p. 22 & fig. 1E on p. 25. [falsifications discussed; caption wrongly indicates fig. 1B]

2021 *Cheirurus* (*Cheirurus*) *ingricus* Schmidt, 1881: Adrain & Pérez-Peris, p. 6. [listed in connection with *Laneites*]
2022 *Paraceraurus ingricus* (Schmidt, 1881): Secher, figure p. 151. [illustration with stratigraphical information]

Lectotype. – Selected here. A partial specimen (PSM 149/2) preserving the cranidium and nine thoracic segments, originally described by Schmidt (1881, p. 135, pl. 6, fig. 1). It derives from the uppermost part of the 'glauconite limestone' (B2) at the locality Izvoz (Iswos) near the village Plekhanovo on the bank of Volkhov River, St. Petersburg area, Russia (loc. 1, Fig. 1). The beds at this locality are no younger than the *Asaphus raniceps* Zone (Pedersen & Rasmussen, 2019, p. 3). Thus, the lectotype most likely originates from the glauconite-rich Frizy Member of the Volkhov Formation (uppermost Volkhovian Stage (BIIγ), upper *Megistaspis limbata* Zone; see Dronov & Mikuláš, 2010). The specimen is refigured here in Fig. 3A.

Paralectotypes. – Only two additional specimens from the St. Petersburg area were described and figured by Schmidt (1881), and these are here considered as paralectotypes. Neither specimen was located in the museum collection by Bruton et al. (1997). 1) A partial cephalon with some thoracic segments, recorded by Schmidt (1881, p. 135, text-fig. 9) from the village Kolchanovo on the Syas river (loc. 2, Fig. 1), corresponding to the Lynna Formation (Kundan Stage, *Asaphus expansus* Zone (BIIIα); see also Schmidt, 1907, p. 8 regarding stratigraphy), and 2) a partial cranidium, which according to Schmidt (1881, p. 135, pl. 6, fig. 2) was collected by H.C. Pander in the Popovka River area near the village Pavlovsk (loc. 3, Fig. 1). This specimen is possibly from the Kundan Stage, *Asaphus expansus* Zone.

Other Russian material. – One partial cranidium (PIN 4248/48), described by Schmidt (1907, p. 8, pl. 1, fig. 4), originates from the village Obukhovo (Obuchovo), St. Petersburg area (loc. 4, Fig. 1), and was attributed to the '*expanus* level' by Schmidt. It is refigured here in Fig. 3B–C. A partially complete enrolled specimen (GIT 448-26, Fig. 4A–E) and a large partial cranidium (GIT 448-28, Fig. 4F, G) both come from the Lynna River (loc. 5, Fig. 1). The first occurs together with *Asaphus lepidurus* (BIIγ, Volkhovian Stage) at the level corresponding to L25i in fig. 3 of Hansen & Nielsen (2003); the second was found at the top of the bank, corresponding to level L31c (BIIIα, Kundan Stage), within the *Asaphus expansus* Zone. Hansen & Nielsen (2003, fig. 3) otherwise recorded *L. ingrica* throughout the Volkhovian, including zones BIIß and BIIγ, in a ~4 m-thick section in the eastern outcrop area at the Lynna River (loc. 5, Fig. 1). These zones are equivalent to the uppermost *M. simon* and *M. limbata* zones in Scandinavia.

Estonian material. – A partial cranidium (GIT 448-25-1, Fig. 4H) from Pühajõe, Ida-Virumaa County, northeastern Estonia (loc. 6, Fig. 1), is likely from the upper Sillaoru Formation (Kundan Stage), *Asaphus expansus* Zone (BIIIα), as suggested by the presence of the nominal species and by the abundance of iron ooids in the sample.

Swedish material. – Twenty-one specimens have been studied, most of which originate from the *Asaphus expansus* Zone, although only four have precise stratigraphical control (i.e., collected from measured sections). The matrix of the host rock of the *Laneites ingricus* (as well as *Ceraurinella ornata*) specimens discussed herein is grey, but this does not necessarily indicate that they derive from the grey Täljsten interval developed in parts of Västergötland, as the colour of the 'orthoceras limestone' is not stratigraphically consistent from area to area and the Täljsten interval cannot readily be recognised outside Västergötland and Öland (Lindskog et al., 2014).

Most specimens show signs of compaction, typically causing splaying of the pleural fields and fixigena whereas the axial part retains its convexity. Some specimens also exhibit anterior-posterior shortening, as seen in PMU 18190 (Fig. 5D).

One specimen (PMU ar 1176, cranidium in grey limestone, Fig. 6A–C) originates from a glacial erratic at Trästa in Uppland (loc. 11 in Fig. 1). Wiman (1908, p. 86) attributed it to the upper part of the 'Limbata limestone' (*Megistaspis limbata/Asaphus expansus* transition).

Seven specimens, mostly incompletely preserved, are from the *Asaphus expansus* Zone at the classic Västanå (Husbyfjöl) locality at Borensberg in Östergötland (see Linnarsson & Tullberg, 1882; Tjernvik, 1956; Bergström et al., 2003 for details on this site; loc. 12 in Fig. 1): NRM Ar 17837 (cephalothorax, not figured), NRM Ar 17838 (cranidium, not figured), NRM Ar 17840 (complete, not figured), NRM Ar 17843 (cephalon with hypostome, Fig. 12C–F), NRM Ar 17844 (cephalon, not figured), NRM Ar 17846 (complete, Figs 10E, 11H & 12A, B), NRM Ar 55494 (cephalothorax, not figured).

Nine additional specimens collected from loose blocks at Ljungsbro near Västanå in Östergötland (loc. 13), originate from the *Asaphus expansus* or *Asaphus raniceps* zones (see Johansson et al., 1972 and Bergström et al., 2003 for details on this site; loc. 12 in Fig. 1): PMO 234.663 (complete, Figs 5A, B, 10D & 11D), NRM Ar 62114–62116 (all partial cephalothoraxes, not figured). PMU 18187 (complete, Figs 7 & 11A–C), PMU 18188 (cephalothorax, Figs 5E–G & 6G, H), PMU 18189 (nearly complete, Figs 10B & 11F, G), PMU 18190 (cephalon with four thoracic segments, Fig. 5C, D), PMU 18191/1 (complete, Figs 8A–D, 10A & 11I).

Two specimens come from the Siljan Ring, Dalarna: LO 570T (cranidium, Fig. 6D–F) was collected from a loose block at Lindgården, Utby, south of Rättvik (loc. 18 in Fig. 1). It was described by Törnquist (1884, pp. 14, 94, pl. 1, fig. 10) who attributed it to the 'lower grey orthoceras limestone' (= *Asaphus expansus* Zone; see Ebbestad & Högström, 2007 for details on the stratigraphy). A second partial cranidium (NRM Ar 54313, not figured), from the Vikarbyn section (see Jaanusson, 1963 for details on this site; loc. 19 in Fig. 1), derives from the *Asaphus raniceps* level.

Norwegian material. – One nearly complete dorsal shield (PMO 234.525, Figs 9, 10C, F & 11E), lacking only the right librigena, found in the hillock just north of Edelvoldveien at Vollen near Slemmestad (loc. 16, Fig. 1). The specimen comes from the Lysaker Member of the Huk Formation, about 2.5 m above its base, which is just above bed level 29 of Nielsen (1995, fig. 28) that represents the basal *Asaphus expansus* Zone. A partial cranidium (MGUH 34999, sample no. A694, Fig. 8E) from Djuptrekkodden, Slemmestad, Asker (loc. 17, Fig. 1), originates from layer M14 of Nielsen (1995, fig. 36), the uppermost limestone bed of the Hukodden Member, Huk Formation, lower *Megistaspis limbata* Zone.

Danish material. – A partial cranidium (MGUH 35000, sample no. S1733, Fig. 8F–H) from the Skelbro quarry, Bornholm (loc. 15, Fig. 1), was collected from layer +13 of Nielsen (1995, fig. 33) within the Komstad Limestone, lower *Asaphus expansus* Zone.

Diagnosis. – A species of *Laneites* with a proportionally long and narrow glabella, occipital ring long (sag.), about 1/5 of glabellar length in dorsal view with a distinct sub-trapezoidal outline. L1 as long (exsag.) as occipital ring (sag.), longer than L2 and L3. S3 having a weak and uniform posterior curvature, the frontal glabellar lobe being proportionally long (sag.) relative to total glabellar length and rounded at front. Third pygidial spine pair is completely reduced.

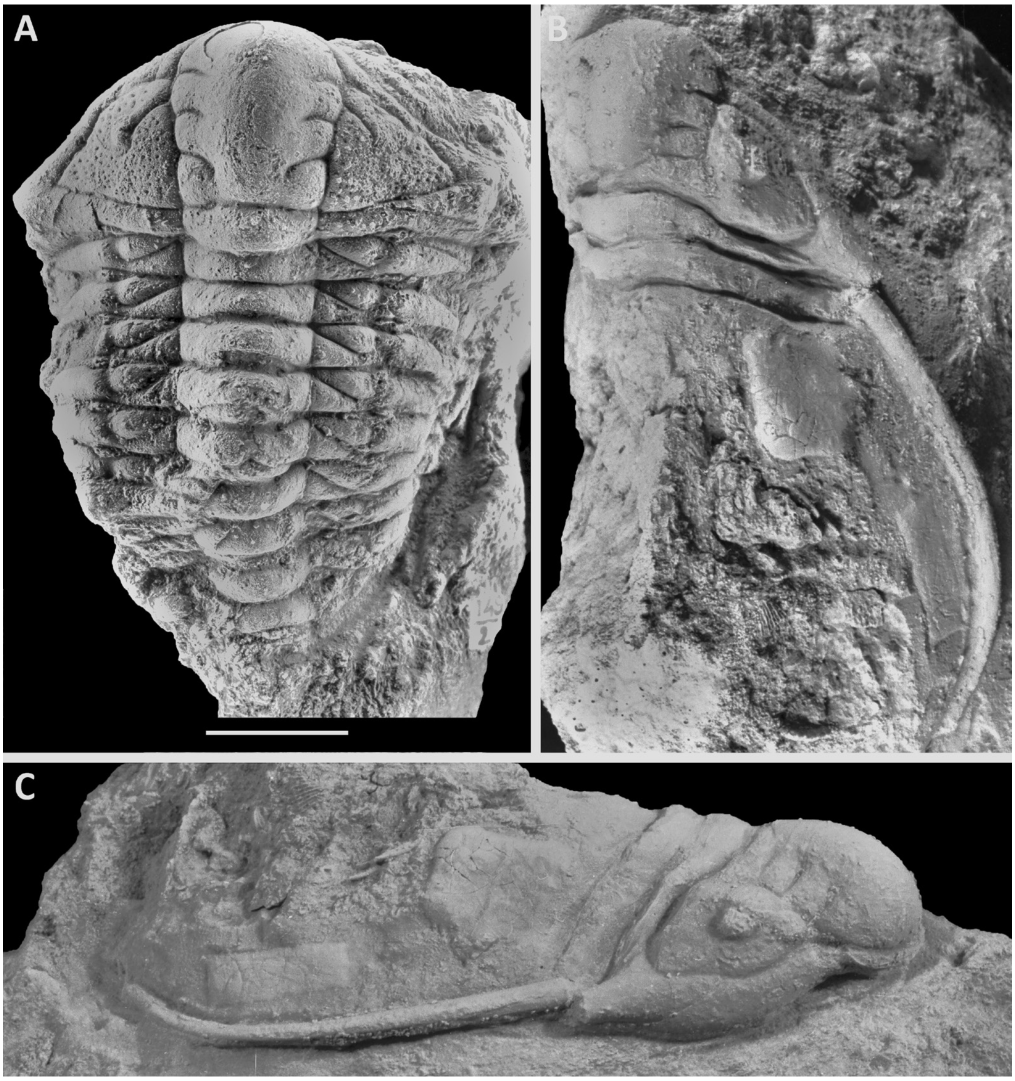

Figure 3. Laneites ingricus *(Schmidt, 1881). (A) Dorsal view of the lectotype (PSM 149/2) from Izvoz, near the village Plekhanovo (Volkhov Formation, Volkhovian Stage (BIIγ), upper* Megistaspis limbata *Zone), described by Schmidt (1881, p. 135, pl. 6, fig. 1). (B, C) Dorsal and lateral views of cranidium (PIN 4248/48) from Obuchovo, St. Petersburg area (Kundan Stage (BIIIα),* Asaphus expansus *Zone), described by Schmidt (1907, p. 8, pl. 1, fig. 4). Scale bar in A = 1 cm (applies to all).*

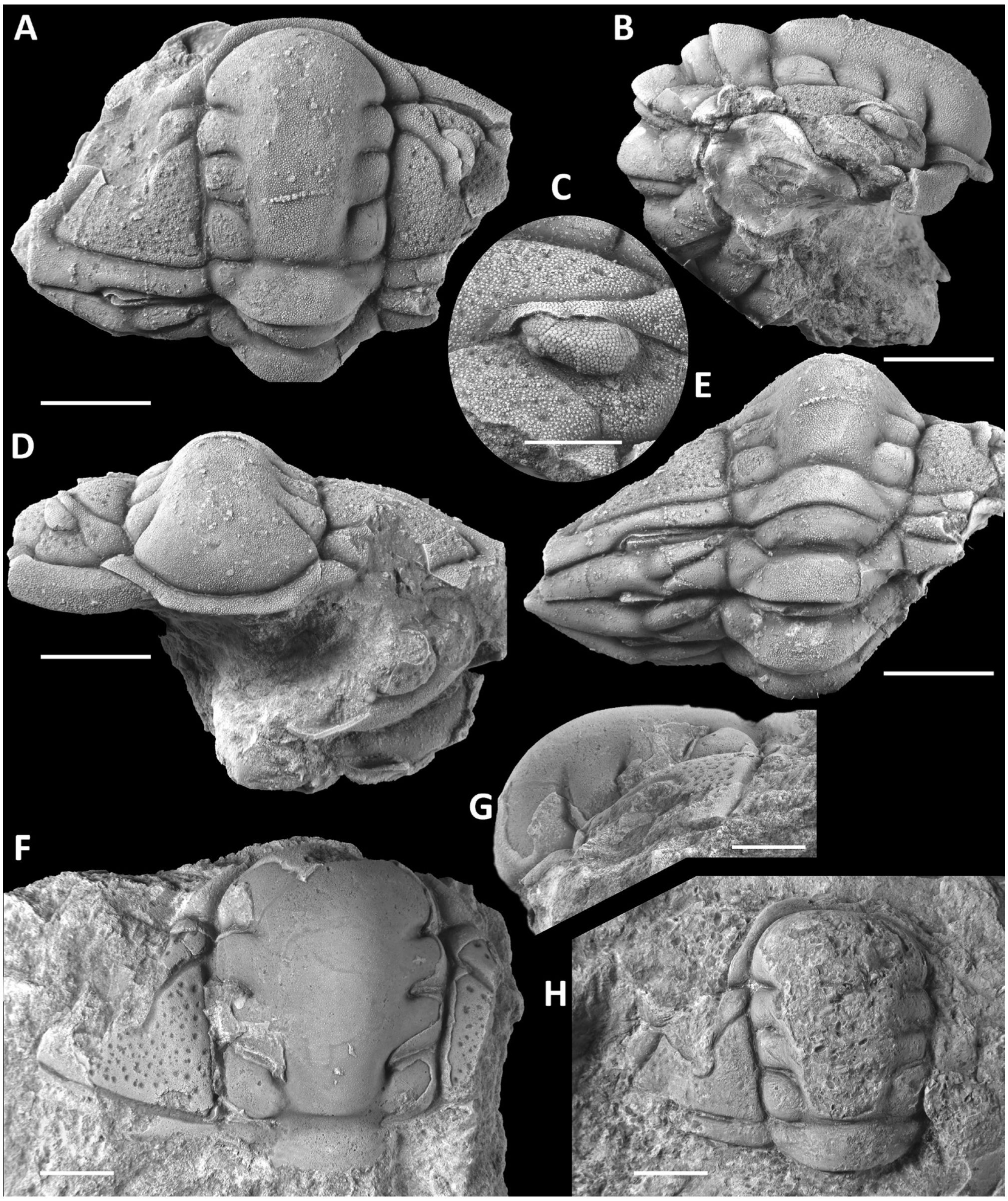

Figure 4. Laneites ingricus *(Schmidt, 1881). (A–E) Complete enrolled specimen (GIT 448-26) from the Lynna River, St. Peterburg area (Kundan Stage (BIIIα),* Asaphus expansus *Zone) shown in dorsal, right-lateral, detail of ocular field, anterior, and dorsal views. (F, G) Large cranidium (GIT 448-28) from the Lynna River, St. Petersburg area, in dorsal and left-lateral views. (H) Dorsal view of a partial cranidium (GIT 448-25-1) from Pühajõe, Ida-Virumaa county (Sillaoru Formation, Kundan Stage (BIIIα),* Asaphus expansus *Zone). Coll. R. Männil. Scale bar = 0.5 cm (applies to all).*

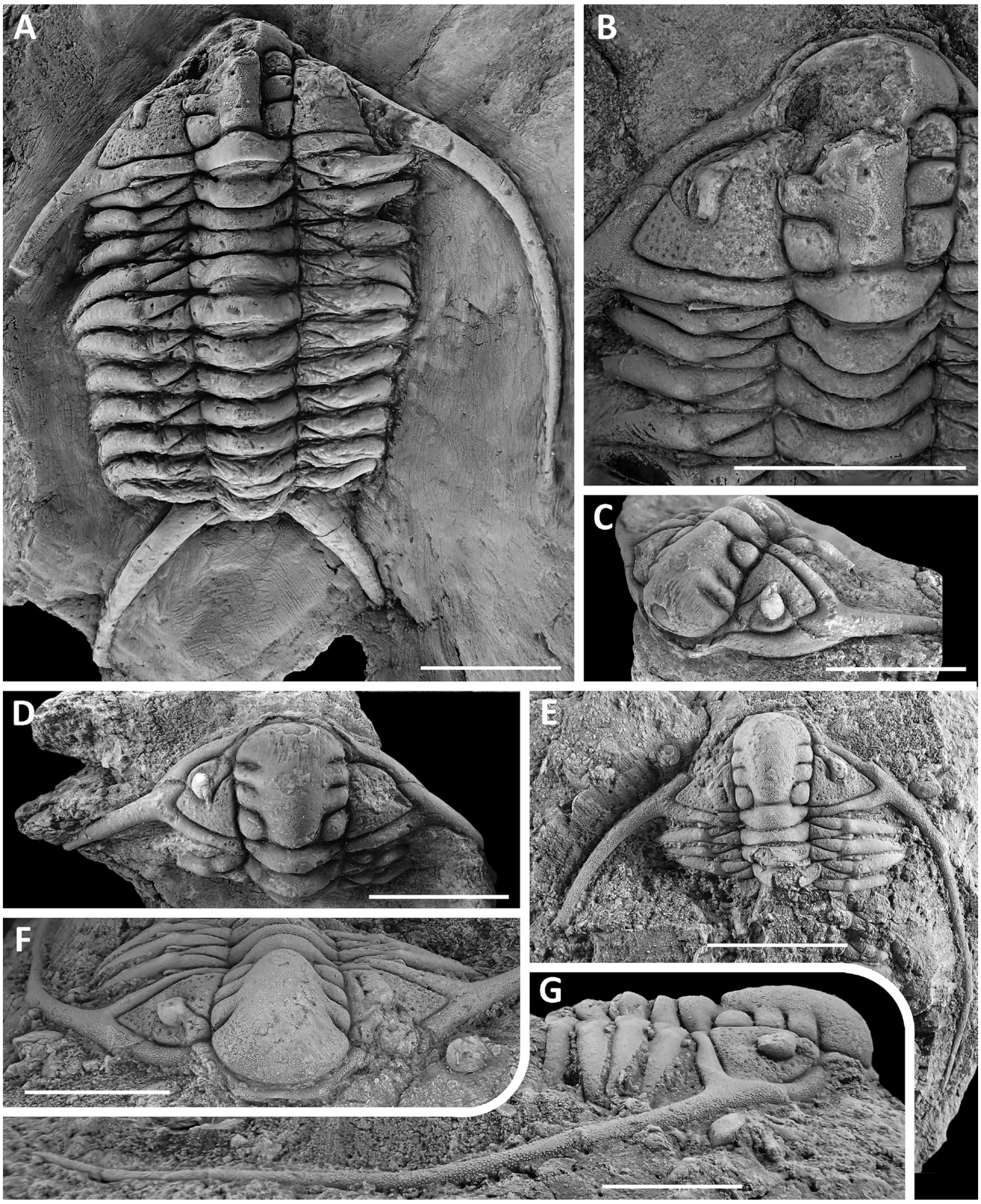

Figure 5. Laneites ingricus *(Schmidt, 1881) from Ljungsbro, Östergötland ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone). (A, B) Complete specimen (PMO 234.663) in dorsal view. Coll. R. Weiss. Also illustrated in Figs 10D & 11D. (C, D) Cephalon, slightly anterio-posteriorly compressed (PMU 18190), anterodorsal and dorsal views. (E–G) Cephalothorax with long genal spines (PMU 18188), shown in dorsal, anterior and right-lateral views. Coll. J. Johansson. Also illustrated in Fig. 6G, H. Scale bar = 1 cm (applies to all).*

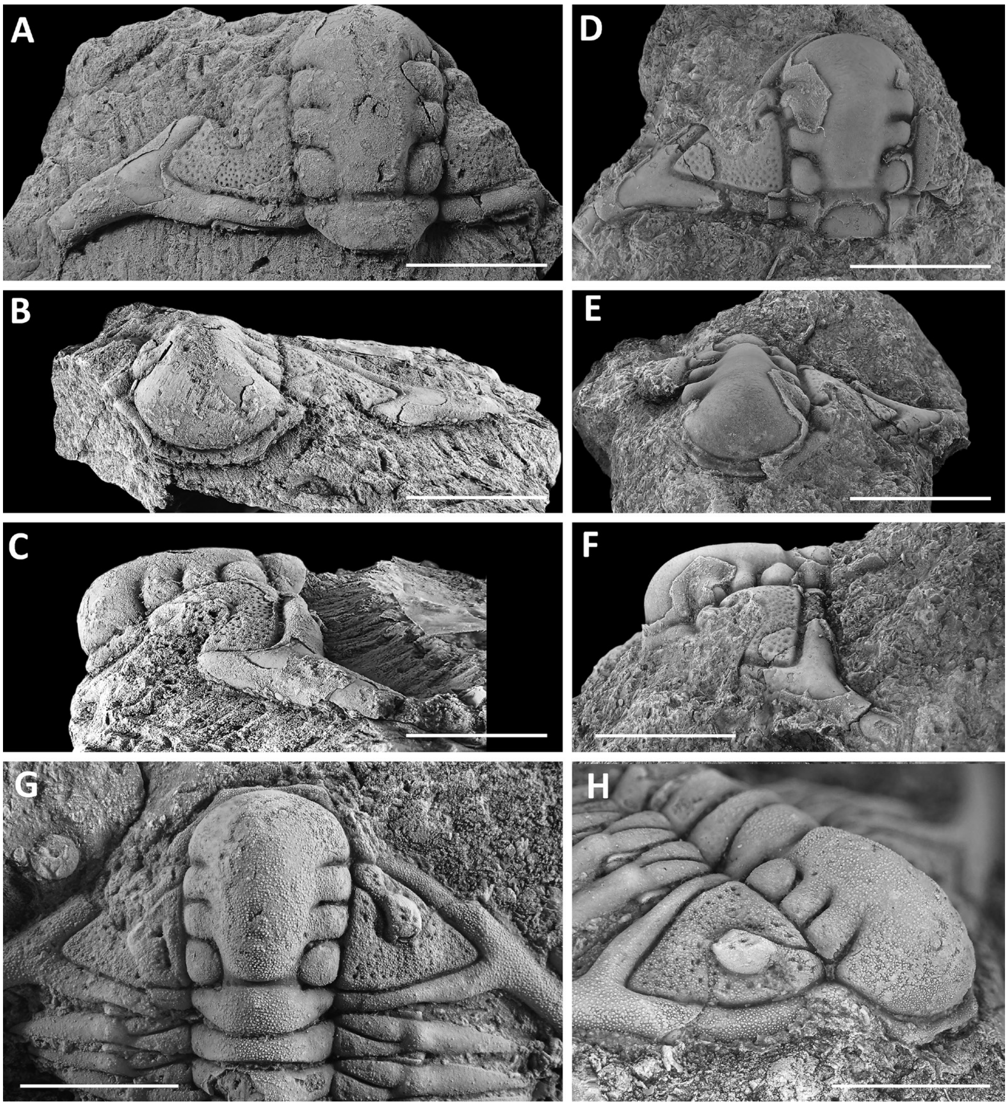

Figure 6. Laneites ingricus *(Schmidt, 1881). (A–C) Cranidium (PMU ar 1176) from Trästa, Uppland (Volkhovian Stage,* Megistaspis limbata/Asaphus expansus *transition), mentioned by Wiman (1908, p. 86). Shown in dorsal, anterior oblique and left-lateral views. (D–F) Cranidium (LO 570T) from a loose block at Lindgården, Utby, Dalarna ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone), described by Törnquist (1884, pp. 14, 94, pl. 1, fig. 10). Shown in dorsal, anterior oblique and left-lateral views. (G, H) Small cranidium (PMU 18188) from Ljungsbro, for comparison ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone). Shown in dorsal and left-anterodorsal views. Also illustrated in Fig. 5E–G. Scale bars: A–F = 1 cm; G & H = 0.5 cm.*

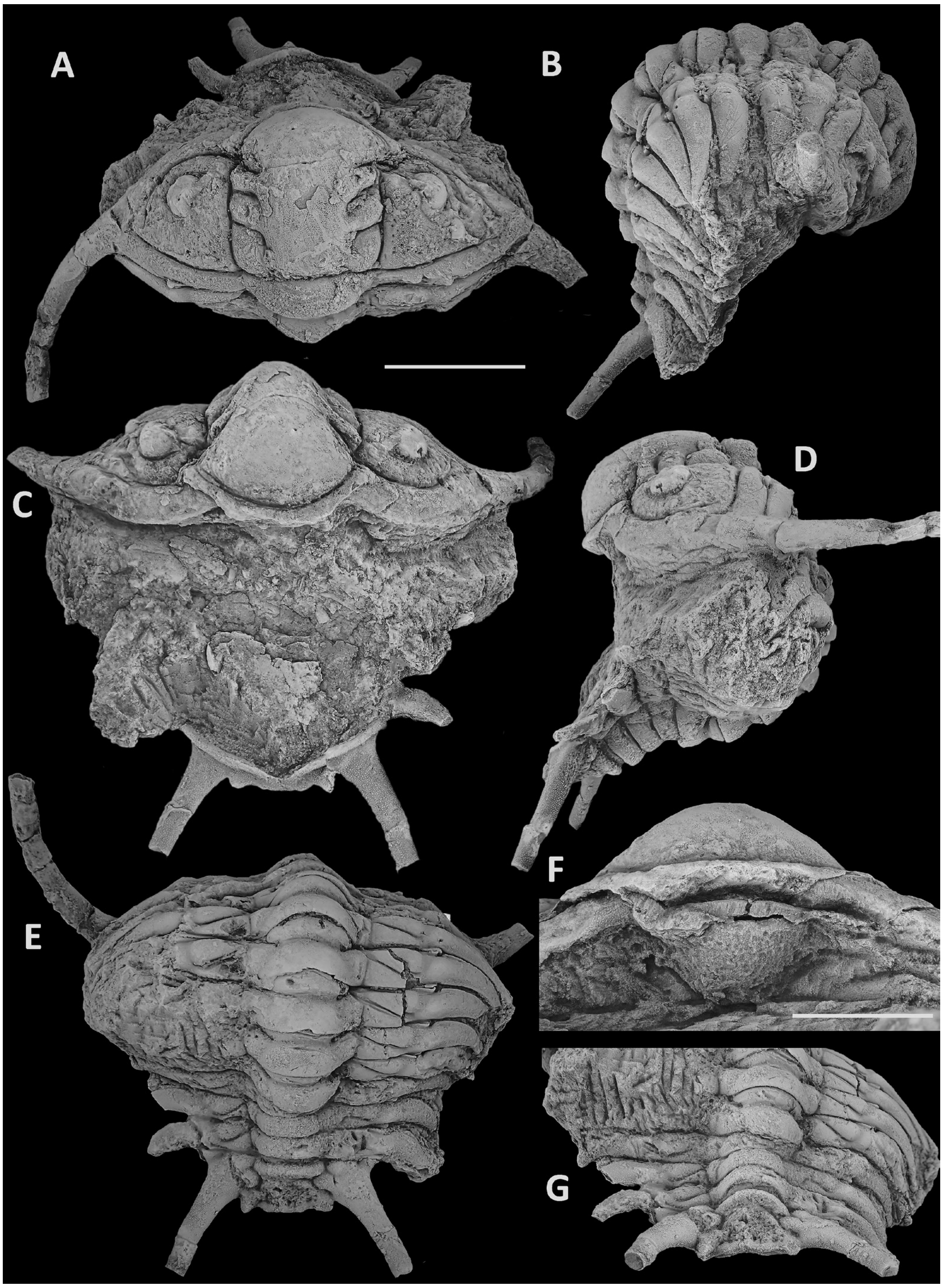

Figure 7. Laneites ingricus *(Schmidt, 1881). Complete specimen from Ljungsbro, Östergötland (PMU 18187) ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone). Shown in dorsal, right-lateral, anterior, left-lateral, and dorsal views, with close-ups of the hypostome with rostral plate and the pygidium. Also illustrated in Fig. 11A–C. Coll. J. Johansson. Scale bar = 1 cm for all.*

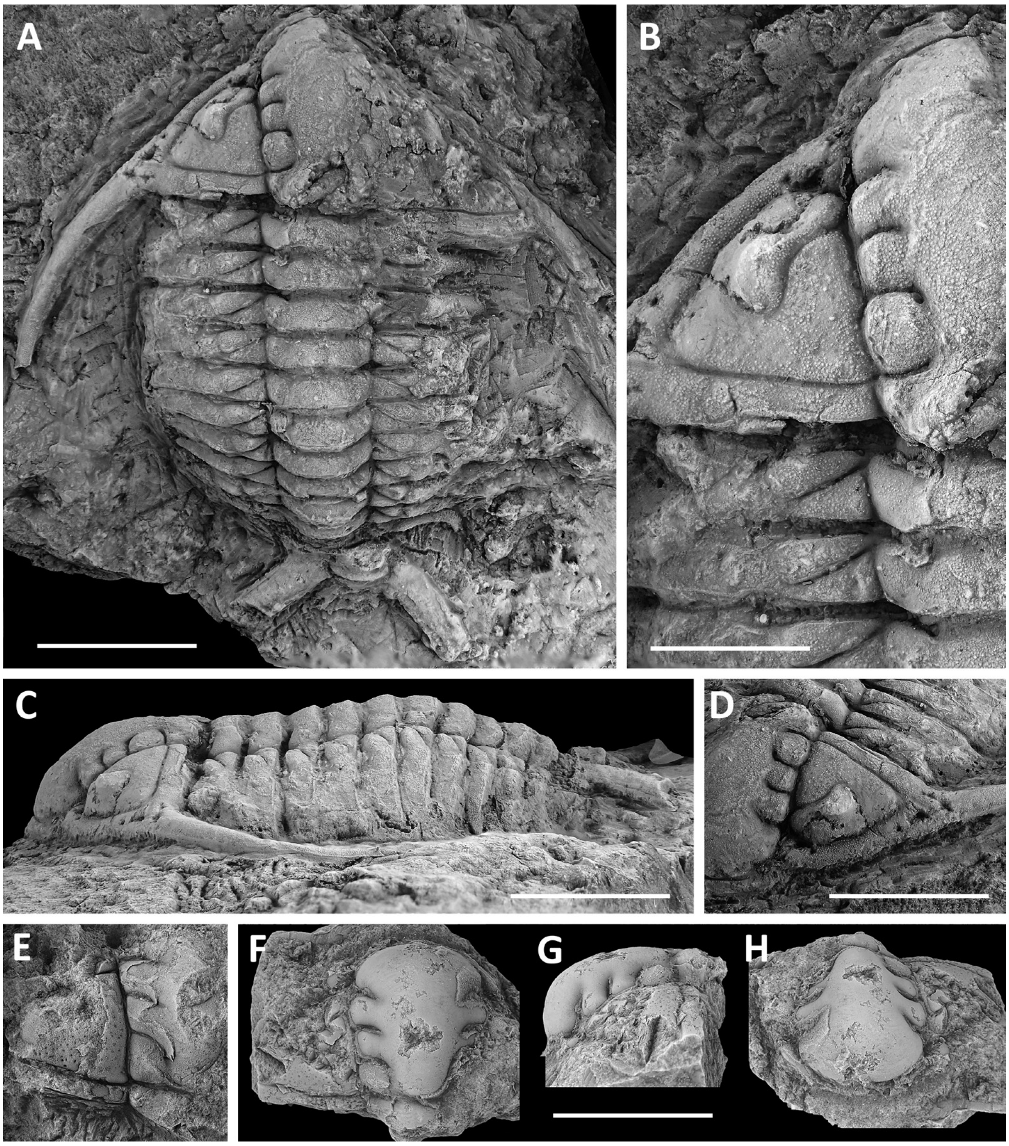

Figure 8. Laneites ingricus *(Schmidt, 1881). (A–D) Complete specimen (PMU 18191/1) with stout pygidial spines, from Ljungsbro, Östergötland ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone). Shown in dorsal view, detail of cephalon, lateral view, and anterior oblique view, respectively. Also illustrated in Figs 10A & 11I. Coll. M. Tassinari. (E) Partial cranidium (MGUH 34999, sample no. A694) from Djuptrekkodden, Slemmestad (Huk Formation, Kundan Stage,* Asaphus expansus *Zone). Dorsal view. (F–H) Partial cranidium (MGUH 35000, sample no. S1733) from Skelbro, Bornholm (Komstad Limestone, Kundan Stage, lower* Asaphus expansus *Zone. Shown in dorsal, lateral and anterior oblique views. E–H coll. A.T. Nielsen. Scale bar = 1 cm (applies to all).*

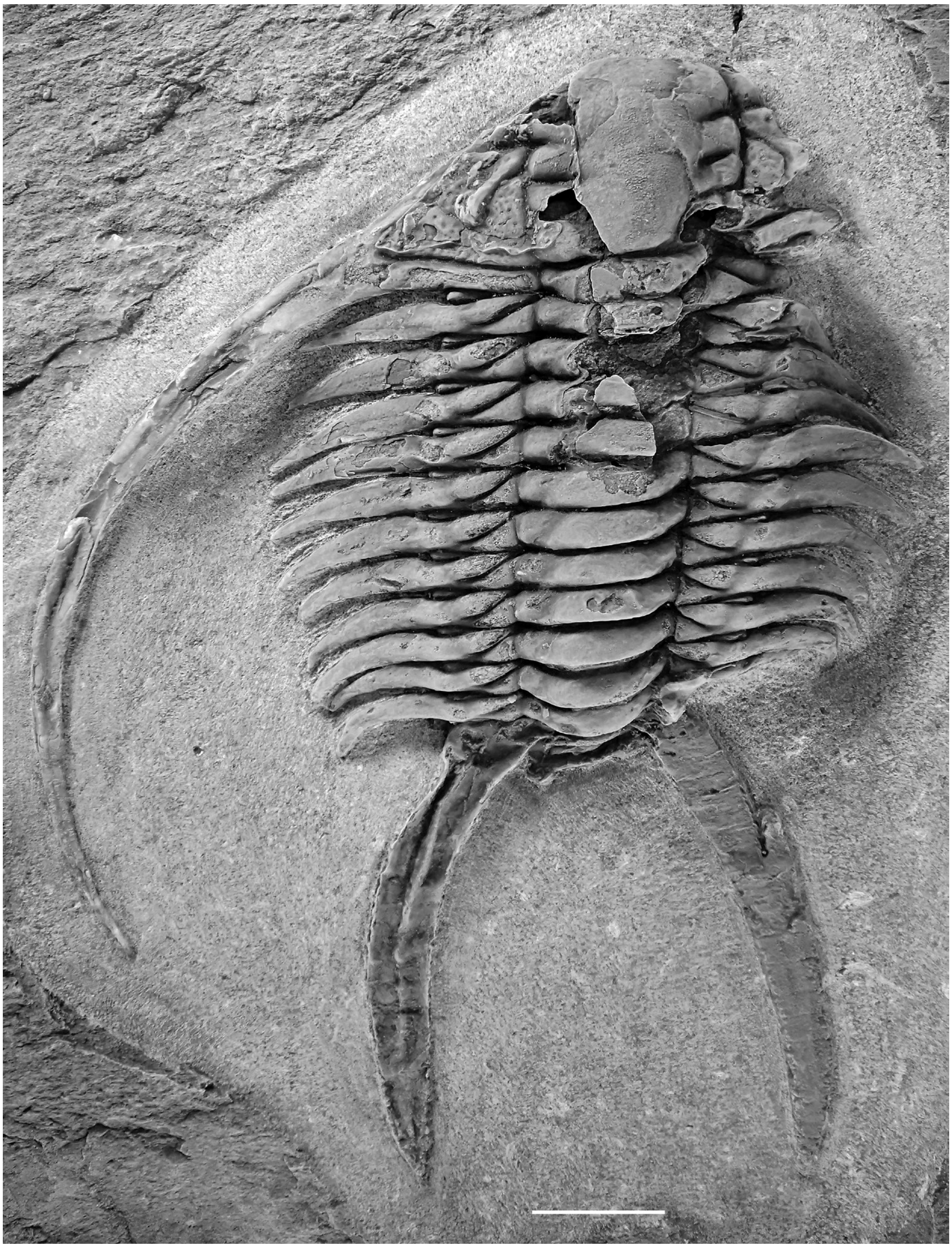

Figure 9. Laneites ingricus *(Schmidt, 1881). Dorsal view of complete specimen (PMO 234.525) from Edelvoldveien at Vollen near Slemmestad (Huk Formation, Kundan Stage,* Asaphus expansus *Zone). Also illustrated in Figs 10C, F & 11E. Coll. M. Alfonso Rojo. Scale bar = 1 cm.*

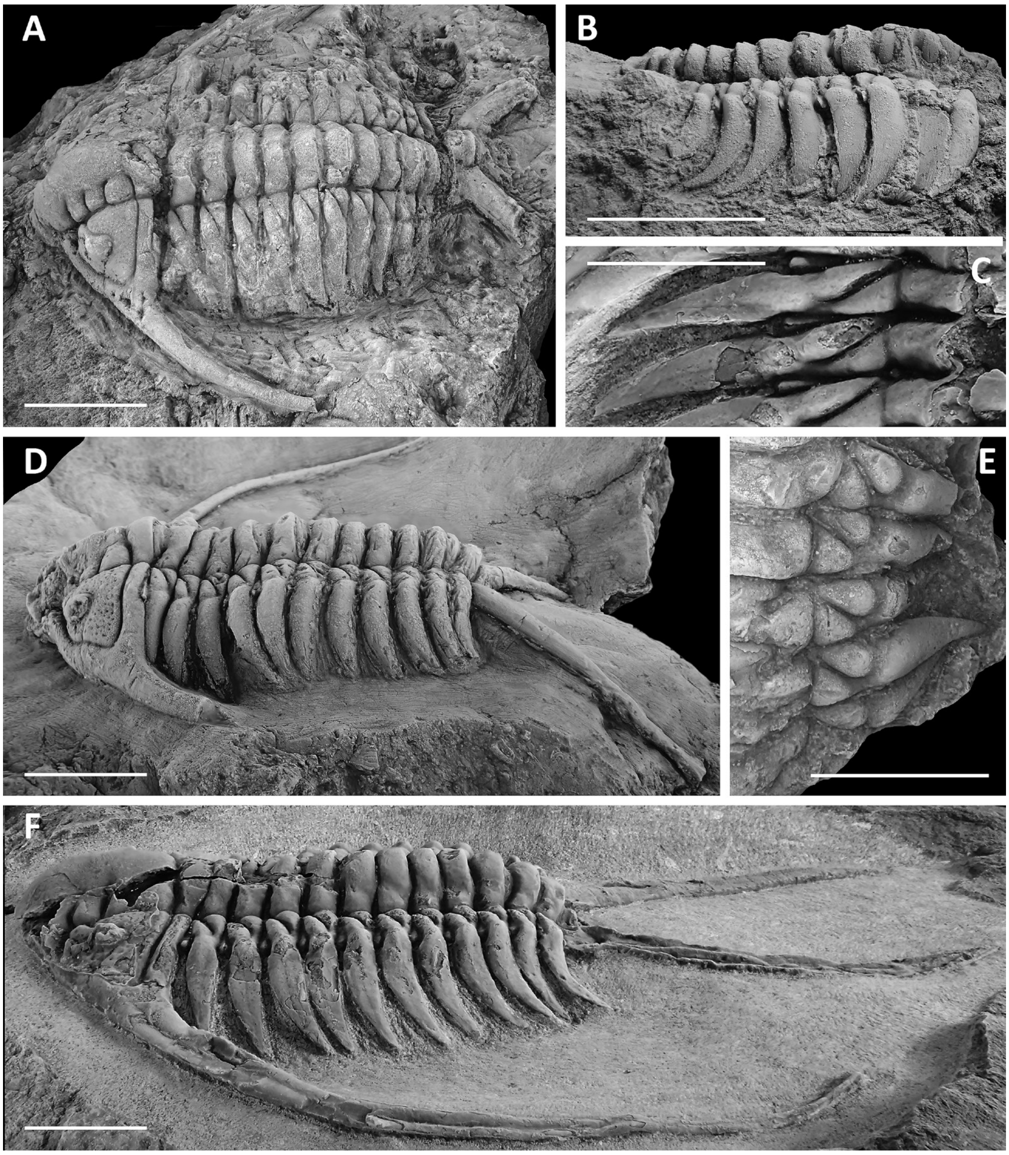

Figure 10. Laneites ingricus *(Schmidt, 1881). (A) Lateral oblique view of complete specimen (PMU 18191/1) from Ljungsbro, Östergötland. Also illustrated in Figs 8A–D & 11I. (B) Thoracopygidium, lateral view (PMU 18189), from Ljungsbro, Östergötland. Also shown in Fig. 11F, G. (C, F) Detail of pleural field and lateral oblique view, respectively, of nearly complete specimen (PMO 234.525), from Edelvoldveien at Vollen near Slemmestad (Huk Formation, Kundan Stage,* Asaphus expansus *Zone). Also illustrated in Figs 9 & 11E. (D) Lateral oblique view of complete specimen (PMO 234.663) from Ljungsbro, Östergötland. Also illustrated in Figs 5A, B & 11D. (E) Detail of pleural field in complete specimen (NRM Ar 17846) from Västanå, Östergötland. Note the short, bulbous, and rounded adaxial swellings on the pleurae in contrast to e.g., Fig. 10C. Also illustrated in Figs 11H & 12A, B. The specimens from Ljungsbro and Västanå are from the 'Holen limestone', Kundan Stage,* Asaphus expansus *Zone. Scale bar = 1 cm (applies to all).*

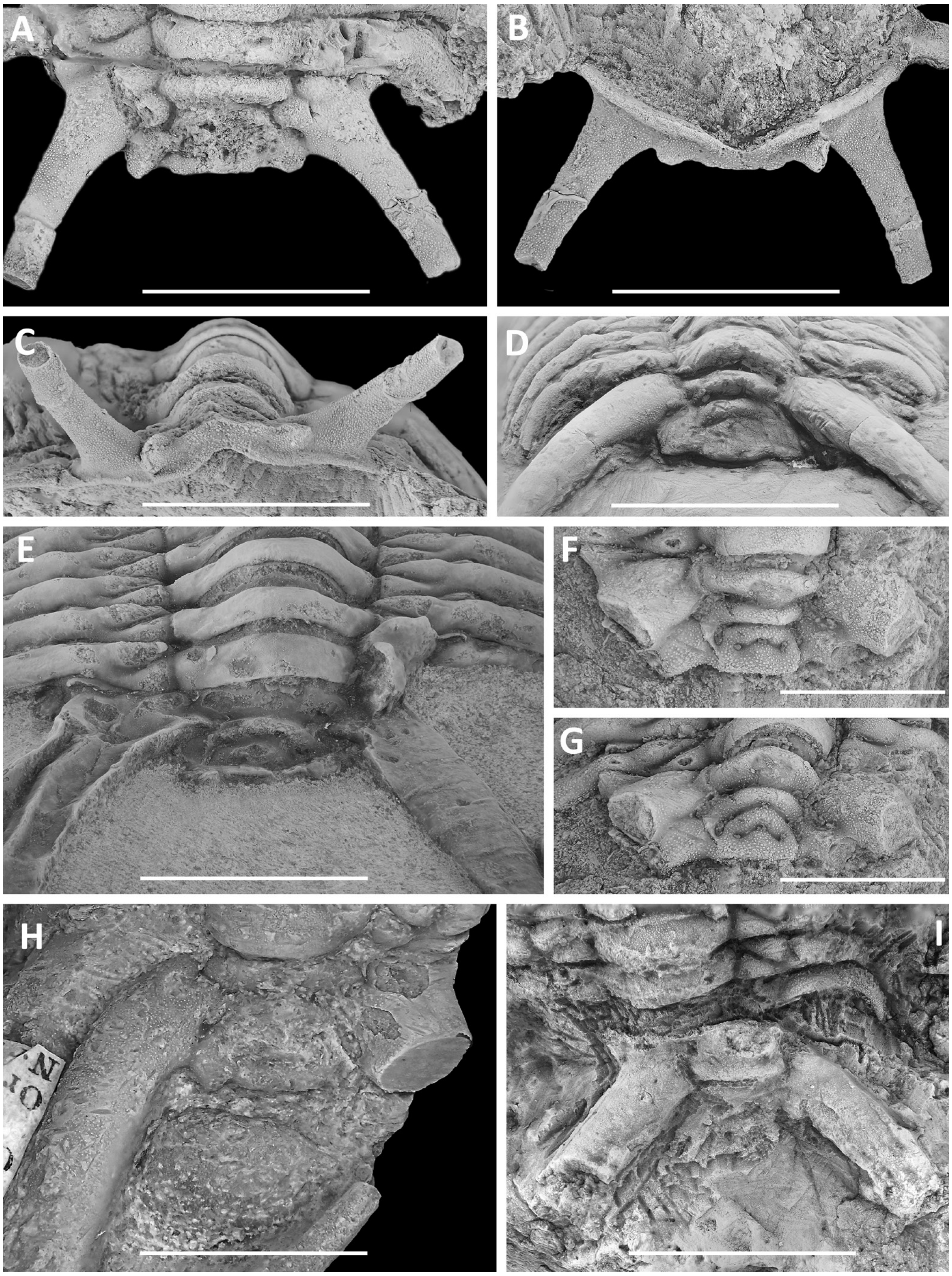

Figure 11. Laneites ingricus *(Schmidt, 1881), pygidia. (A–C) Dorsal, ventral and posterior views of specimen PMU 18187 from Ljungsbro, Östergötland. Also illustrated in Fig. 7. (D) Posterior view of specimen PMO 234.663 from Ljungsbro, Östergötland. Also shown in Figs 5A, B & 10D). (E) Dorsal view of specimen PMO 234.525 from Edelvoldveien at Vollen near Slemmestad (Huk Formation, Kundan Stage,* Asaphus expansus *Zone). Also illustrated in Figs 9 & 10C, F. (F, G) Dorsal and posterior views of small specimen (PMU 18189) from Ljungsbro, Östergötland. Also shown in Fig. 10B. (H) Dorsal view of specimen NRM Ar 17846 from Västanå, Östergötland. Note stout lateral spines. Also illustrated in Figs 10E & 12A, B. (I) Dorsal view of specimen PMU 18191/1 from Ljungsbro, Östergötland. Note stout lateral spines. Also shown in Fig. 8A–D. Specimens from Ljungsbro and Västanå are from the 'Holen limestone', Kundan Stage,* Asaphus expansus *Zone. Scale bars: A–E, H & I = 1 cm; F & G = 0.5 cm.*

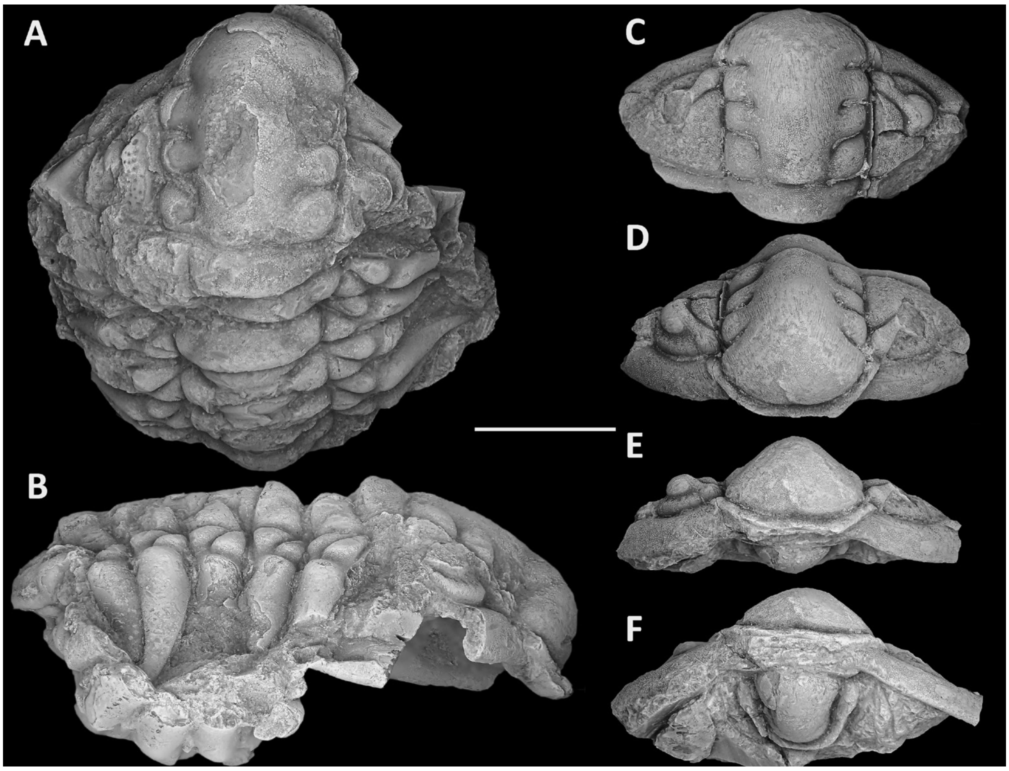

Figure 12. Laneites ingricus *(Schmidt, 1881) from Västanå, Östergötland ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone). (A, B) Large, partially complete enrolled specimen (NRM Ar 17846), shown in dorsal and right-lateral views. Also illustrated in Figs 10E & 11H. (C–F) Cephalon with hypostome (NRM Ar 17843), shown in dorsal, anterior oblique, anterior, and ventral views. Scale bar = 1 cm (applies to all).*

Description. – Cephalon subtrapezoidal in outline, widest across the genal angles. Length of cranidium corresponds to ~55% of the width (measured between border furrows at genal angle) in splayed specimens, and ~60–66% in specimens with convexity preserved (Figs 5A, 6A, B & 9 vs. Figs 4A, 5E, 6G & 7A). Glabella expanding slightly forwards from the occipital ring, which is 90% as wide (tr.) as the frontal glabellar lobe (Figs 5B, 6A, D, G & 9); in the lectotype it only corresponds to 80% (Fig. 3A). Frontal glabellar lobe accounts for about 25% of glabellar length (sag.). Length (sag.) of occipital ring about 20% of cranidial length. Occipital ring sub-trapezoidal, delimited anteriorly by a deep, straight and wide occipital furrow, whereas the lateral sides extend adaxially obliquely rearwards from dorsal furrow to straight and narrow (tr.) posterior margin. The posterior margin is of the same width (tr.) as the mid-section of the glabella (Figs 4A, 5B & 6A, G). Small occipital lobes present at the base of the occipital ring, and their faint anterior adaxial demarcations align with the continuation of the posterior part of S1 (Figs 3A, 4A, 5B, 6G & 7A). Occipital ring has the same convexity (tr.) as the glabella, whereas lateral lobes have a different convexity. Posterior part of glabella between L1 lobes clearly set off from the lateral lobes and occipital furrow. Central glabella is thus raised above the lateral lobes when viewed laterally (Figs 3C, 4B, 5G, 6C, F, 7D & 8C). Central part of glabella nearly flat or weakly convex in side view, while the anterior glabellar lobe is weakly inflated in lateral view, rounded and extends to, or slightly overhanging, anterior cranidial margin. Glabellar lobes sub-quadrate, L1 isolated adaxially and longer (exsag.) than the equally sized L2 and L3. These are less inflated than the more domed L1. Glabellar lateral furrows deeply incised, shallowing in their very adaxial part, with nearly equal length corresponding to only about one fifth of glabellar width. S1 transversely directed near axial furrow from where it runs at a slight angle rearward then curves sharply posteriorly towards the occipital furrow. Expression and depth of adaxial part of S1 is variable. S2 nearly straight with increased posterior curvature in the adaxial end. S3 slightly shorter than the other furrows, with weak and even rearwards curvature. Glabellar, axial and preglabellar furrows of similar depth. Posterior border furrow and lateral border furrow of similar depth.

Fixed cheek triangular in outline, slightly convex, with small irregularly spaced pits on the palpebral area and posterior field (Figs 3A, 4A, 5B & 6A, D, G). Intersection between posterior and lateral border furrows is located opposite mid part of L1. Abaxial part of posterior branch of suture, where it meets lateral border, is opposite S2. Palpebral lobe positioned near the middle (tr.) of the fixigena, opposite L2 and the posteriormost part of L3, with its posterior end level with or slightly posterior to anterior part of S1. Adaxial margin of palpebral lobe and eye ridge marked by a deeply incised furrow. Palpebral lobe continuous with well-developed eye ridge running forward and adaxially terminating in a slightly bulbous end at the axial furrow opposite S3. Preocular fixigena small and triangular, being delimited by the anterior branch of the facial suture; axial furrow and anterior border furrow meets slightly anterior to the junction to S3 and separate S3 from eye ridge. Anterior branch of facial suture is gently arched and directed downward in lateral view, extending obliquely forward to anterolateral corner of glabella where it meets squared-off corner of anterior margin. The intersection level with the inner part of S3 (if an imaginary exsagittal line is extended posteriorly). The median segment of the rounded (sag.) anterior margin is slightly concave. Posterior border weakly convex (exsag.), running slightly anteriorly from axial furrow to fulcrum and widening into broad genal angles. These extend into genal spines with round cross-section projecting outward at about 60° relative to the axis and extending in a wide recurved bow posteriorly to well behind pygidium (excluding pygidial spines) (Figs 3C, 5G & 9). Librigena sub-trapezoidal in outline; librigenal field with small pits and about the distance between eye socle and border furrow is equal to the width of the border (Figs 6H & 8D). Eye bulbous, slightly wider than high, tilted forward and defined below by shallow furrow (Figs 4B–D, 5C, 6H & 7C, D). More than 25 dorsoventral lens-files present with at least 15 lenses in each file (Fig. 4C). Entire cephalon covered by minute densely spaced granules, except in furrows (Figs 4A, 6G & 8B). Rostral plate poorly preserved but seemingly trapezoidal in shape, gently convex anteriorly, short (sag.).

Anterior part of hypostome sub-rectangular (not seen on figure), but the hypostome is sub-trapezoidal in shape with gently rounded anterior edge (Fig. 12F). Middle body moderately convex, bounded by well incised lateral and posterior furrows. Anterior lobe accounts for 80–85% of total length (sag.) with poor distinction from posterior lobe. Middle furrow shallow and macula weakly indicated. Shoulder slightly wider (tr.) than lateral border, both convex, only weakly tapering posteriorly. Posterior border as broad (tr.) as the lateral border, weakly curved. Surface covered by minute densely spaced granules. Thorax with 11 segments, narrowing very slightly rearwards (Figs 5A, 8A, 9 & 10A, D, F). Axial part evenly curved and convex (sag. and tr.). Convexity of axial rings separated from convexity of lateral axial lobes, as seen in occipital lobe. Axial furrow shallow but distinct. Articulating half ring well developed and accounts for about 60% of the length (sag.) of the axial ring. Width (tr.) of pleurae relative to width (tr.) of axial ring difficult to estimate due to flattening, but proximal part from axial furrow to end of connective flange about half as wide (tr.) as the axial ring, whereas the distal spine is about of the same width (tr.) as the axial ring. The proximal part of the pleurae extends horizontally to abaxial end of well-developed flanges, continuing distally into falcate spines (Fig. 10B, C, E). These extend nearly horizontally laterally in splayed specimens, but sharply downwards in non-splayed specimens (Fig. 10C vs. 10E). Tips of spines on anterior thoracic segments gently curved rearwards, whereas spines on posterior thoracic segments curve more strongly. Both anterior and posterior band of pleurae with marked elongated triangular swellings bifurcated by deep oblique pleural furrow. This extends posteriorly from axial furrow but fades out at the abaxial posterior margin of the pleurae where instead there is a space posterior to the anterior swelling. Pleural furrow extends for about 2/3 of the inner portion of pleura. Abaxially, another weaker swelling is seen at the proximal part of the falcate spines, separated from the anterior swelling by a broad shallow depression. Surface covered by minute densely spaced granules.

Pygidium transversely rectangular, length (sag.), excluding articulating half-ring and spines, is equivalent to 30% of anterior width (Fig. 11). Axis triangular in outline with three convex (sag.) rings and a terminal piece. Axial furrow shallow next to anterior ring, and effaced adjacent to posterior rings and terminal piece. Axis tapers rearwards such that the posterior ring is about half as wide (tr.) as the anterior ring. Two anterior-most rings transverse. Anterior margin of third axial ring transverse, posterior margin convex medially and constricting the length (sag.) of the axial ring. Terminal piece is seen as a small swelling, only well-defined anteriorly (Fig. 11F, G). Inter-ring furrows are transverse medially, bending sharply rearwards at axial margin and leading into interpleural furrows. These end in deep pits adjacent to the posterior end of the next axial ring. Post-axial field short (sag.) and slightly inflated, posterior margin transverse. Pleural field otherwise narrow (tr.). Anterior pleural rib inflated adjacent to anterior axial ring, with short and shallow pleural furrow. Each rib develops into a broad and stout pygidial spine, rounded in cross-section, extending out and upwards in a bow outside the edge of the thorax, length possibly as long as the thorax (Figs 5A, 7E, G, 9 & 11C). Second pleural rib flat, without pleural furrow, but with short, triangular and blunt marginal spine. At its adaxial base a small indentation is observed. The third pleural rib develops knob-like spines at the margin, that may be completely reduced. Ventrally, the pygidial border forms a narrow edge that medially forms an arch between the second pleural spines (Fig. 11B, C). Surface of pygidium and spines covered by tiny granules.

Remarks. – Laneites ingricus sensu stricto ranges from the Volkhovian (BIIγ) *Megistaspis limbata* Zone through the lower Kundan (BIIIα) *Asaphus expanus* Zone. The slightly older *L.* cf. *ingricus* occurs in the Volkhovian (BIIγ) *Megistaspis simon* Zone, whereas the oldest taxon *L.* aff. *L. ingricus* is from the Volkhovian (BIIα) *Megistaspis polyphemus* Zone. Together, these three Baltoscandian *Laneites* representatives span the mid Dapingian to early Darriwilian interval (see Fig. 2 & Electronic Supplement 1) and are thus slightly older than the type species *L. polydorus* from the Table Cove Formation. The latter occurs within the late Darriwilian (mid Kundan) *Holmograptus lentus* Graptolite Zone (Albani et al., 2001). The type species was redescribed by Whittington (1965) and Adrian & Pérez-Peris (2021). *Laneites ingricus* differs from *L. polydorus* in having a proportionally longer glabella with a longer and more inflated anterior glabellar. The L1 lobes are longer relative to L2 and L3, and the curvature of the S3 furrow is markedly less pronounced. Additionally, the basal occipital lobes of *L. ingricus* are larger, the sagittal length of the lateral occipital lobe is proportionally greater, and its sub-trapezoidal shape is more pronounced. The posterior branch of the facial suture in *L. ingricus* reaches the lateral margin opposite the anteriormost part of L2, whereas in *L. polydorus* it terminates opposite the posteriormost part of L3. The lateral projection of the fixigena in *L. polydorus* is therefore proportionally longer (exsag.), and the base of the genal spine is broader than in *L. ingricus*. The librigena of *L. ingricus* is proportionally wider and lower, and the eye is larger. The pygidia also differ: in *L. ingricus*, the pleural furrow on the anterior plaural rib is shorter and shallower, and the third pygidial segment lacks prominent marginal spines. In *L. polydorus,* the third pygidial spine pair is reduced to small and knob-like structures, whereas in *L. ingricus* they are completely absent (see modified diagnosis).

The complete specimen from the Huk Formation (basal *Asaphus expansus* Zone) at Slemmestad in Norway (Fig. 9) is among the largest in the present material and is comparable in size to GIT 448-25-1 from Pühajõe (Fig. 4H), GIT 448-28 from Lynna River (Fig. 4F), and NRM Ar 17846 from Västanå (Fig. 12A, B). Note that the elongated triangular swellings on the pleurae are unusually bulbous and rounded in the latter specimen (Fig. 10E), making comparison with other figured thoraces difficult. The Swedish and Norwegian specimens are also similar in possessing very broad-based outer pygidial spines (Fig. 11E, H). A smaller specimen from the 'Holen Limestone' (*Asaphus expansus* Zone) at Ljungsbro (PMU 18191/1) likewise shows proportionally broad-based pygidial spines (Fig. 11I); see Fig. 10A, D, F for size comparisons between complete specimens. Other specimens, also from the 'Holen Limestone' at Ljungsbro and Västanå, display relatively slender outer pygidial spines (Figs 5A, 7, 10D). These differences do not appear to be size-related, and may instead reflect sexual dimorphism, eco-morphotypes, stratigraphic differences or intraspecific variability. At present, the observed variation does not warrant taxonomic separation, as the overall morphological range, despite differences in preservation, is considered consistent. However, future discoveries of additional material may lead to a reassessment.

Wysogórski (1896) described *Cheirurus sadewitzensis* based on a cranidium found in glacial erratics near Wrocław, Poland. The specimen had previously been figured by Roemer (1861, pl. 8, fig. 9), who compared it to *C. ornatus*, collected by himself at Västanå, the type locality for both *Laneites ingricus* and *Ceraurinella ornata*. However, Roemer's illustration, it suggests that the specimen likely represents *L. ingricus.* Wysogórski (1896) considered it intermediate between *ingricus* and *ornata.* The specimen was housed in the collections at the Institute of Geology at the University of Wrocław, which was bombed during WWII, destroying most of the collections. The specimen is therefore presumed lost.

Hansen & Nielsen (2003) found that the lower part of BIIIα may mark the upper range of *L. ingricus,* although the higher interval has not been sufficiently studied. They also recorded the species in the uppermost Zheltiaki Member (BIIß) of the Volkhov Formation at Lynna, in the St. Petersburg area, which may represent the basal *M. limbata* Zone.

Laneites cf. *ingricus* (Schmidt, 1881)

Material. – Two partial cranidia from Flagabro, Skåne (loc. 14 in Fig. 1), MGUH 34997 (sample no. B355) from layer Å11 and MGUH 34998 (sample no. B526) from layer Å13, Komstad Limestone (*Megistaspis simon* Zone), and a partial cranidium (GIT 448-27) from a loose boulder at Simankovo, St. Petersburg area (Fig. 13A–H).

Remarks. The two Swedish specimens (Fig. 13A–D) and the partial Russian specimen (Fig. 13E–H) are assigned to *Laneites* cf. *ingricus.* They differ slightly from coeval to younger specimens of *L. ingricus* in that the glabella is more inflated and expands more markedly forward; the anterior glabellar lobe is proportionally shorter (sag.); S3 curves more evenly and more strongly rearward and extending further adaxially, which also results in a more elongated (tr.) basal occipital lobe.

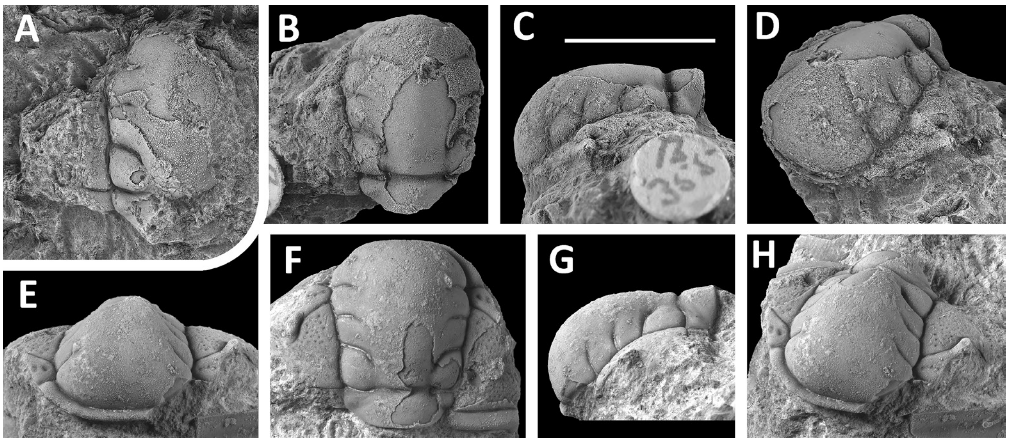

Figure 13. Laneites *cf.* ingricus *(Schmidt, 1881). (A) Partial cranidium (MGUH 34998, sample no. B526) from Flagabro, Skåne. Dorsal view. (B–D) Partial cranidium (MGUH 34997, sample no. B355) from Flagabro, Skåne, shown in dorsal, lateral and anterior oblique views. (E–H) Partial cranidium (GIT 448-27) from a loose boulder at Simankovo, St. Petersburg area (unknown stratigraphical horizon), shown in anterior, dorsal, lateral, and dorsoanterior oblique views. Specimens in A–D coll. A.T. Nielsen. The Flagabro specimens are from the Komstad Limestone, Volkhovian Stage,* Megistaspis simon *Zone. Scale bar in C = 1 cm (applies to all).*

Laneites aff. *L. ingricus* (Schmidt, 1881)

1958 *Ceraurinella*? aff. *ingrica* (Schmidt, 1881): Männil, p. 175, pl. 1, fig. 7.
1985 *Laneites*? sp.: Pribyl et al., p. 146.
2013 *Laneites*? aff. *ingrica* (Schmidt, 1881): Pärnaste et al., table S5.

Material. – A partial cranidium (GIT 103-7, Fig. 14) from the Toila Formation (Volkhovian Stage, *Megistaspis polyphemus* Zone) at Mäeküla, west of Tallinn, Estonia (loc. 7, Fig. 1).

Remarks. – The partial cranidium (GIT 103-7) described as *Ceraurinella*? aff. *ingrica* by Männil (1958, p. 175) was subsequently listed as *Laneites*? sp. by Pribyl et al. (1985, p. 146) and as *Laneites*? aff. *ingrica* by Pärnaste et al. (2013, table S5). It is re-illustrated here in Fig. 14. As it derives from the *Megistaspis polyphemus* Zone, it may be the oldest known representative of *Laneites*. The cranidium of this specimen is relatively large (c. 2 cm long) and is characterised by a broad (tr.) and short (sag.) glabella, with a very short (sag.) and rectangular anterior glabellar lobe that resembles that of the type species, *L. polydorus*. S3 has a distinct posteriorly directed curvature (Fig. 14A). As with the Flagabro and Simankovo specimens, the glabella expands more markedly forwards compared with the younger *L. ingricus.*

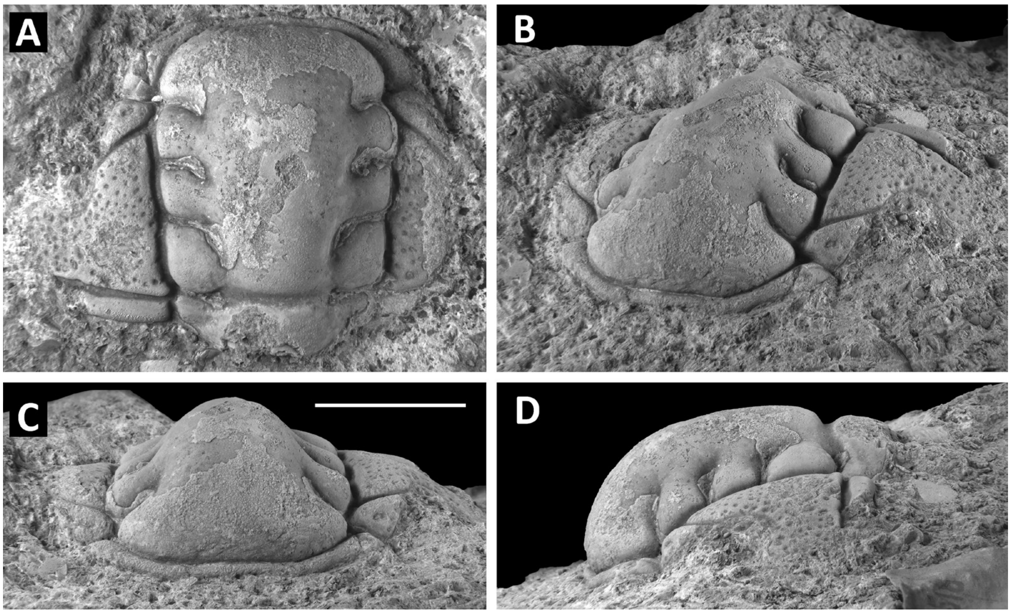

Figure 14. Laneites *aff.* L. ingricus *(Schmidt, 1881). Partial cranidium (GIT 103-7) shown in dorsal, anterior oblique, anterior, and left-lateral views. Previously figured by Männil (1958, pl. 1, fig. 7). The specimen is from Mäeküla (Toila Formation, Volkhovian Stage,* Megistaspis polyphemus *Zone), Tallinn. Coll. R. Männil. Scale bar = 1 cm (applies to all).*

Genus *Ceraurinella* Cooper, 1953

Type species. – *Ceraurinella typa* Cooper, 1953, by original designation of Cooper (1953, p. 29, pl. 12, figs 1–5, 7, 8, 15 & 16), from the Upper Ordovician (Turinian, Sa2) Edinburg Formation, Strasburg Junction, Virginia, USA.

Diagnosis. – (From Lane 1971, p. 18) Cheirurinae with a glabella that is parallel-sided or expands very slightly forward. Anterior border and border furrow either very narrow or interrupted mesially by the frontal lobe of the glabella. Thorax of 11 segments. Pygidium with anterior pair of spines well developed and long; posterior to this the pygidium has either two very short pairs of spines or spines are absent, in which case the posterior margin forms a nearly transverse gentle curve.

Remarks. – The taxonomy of the genus *Ceraurinella* has been reviewed by Männil (1958), Lane (1971), Chatterton & Ludvigsen (1976), Ludvigsen (1977, 1979), Pärnaste (2008) and Adrain & Pérez-Peris (2021).

Ceraurinella ornata (Dalman, 1828)

1828 *Calymene ornata* n. sp., Dalman, p. 134. [description]
1828 *Calymene ornata* Dalm.: Hisinger, p. 235. [listed: stratigraphy]
1832 *Calymene ornata* Dalman: De La Beche, p. 449. [listed]
1837 *Calymene ornata*: Hisinger, p. 11. [description]
1839 *Calymene ornata*. (Dalman): Huot, p. 578. [listed]
1840 *Calymene ornata* Dalman: Milne-Edwards, p. 319. [comparative discussion]
1843 *Calymene ornata* Dalm.: Burmeister, p. 129 [listed]
1844 *Calymene ornata* Dalm.: Lovén, p. 39. [comparative discussion]
1845 *Calymene ornata* Dlm.: Lovén, pp. 63, 64. [description]
1845 *Calymene ornata* Dalm.: Murchison, p. 492, table 1. [listed]
1845 *Calymene ornata*: Beyrich, p. 18. [comparative discussion]
Non 1846 *Cheirurus ornatus:* Beyrich, p. 5, pl. 4, fig. 7. [description, cf. *Reraspis*? *elatifrons* (Krause, 1895)]
1846 *Chirurus ornata* Dalm.: Burmeister, p. 71. [English edition; footnote, listed under species of *Chirurus* [sic.]]
1846 *Calymene ornata* Dalm.: Burmeister, p. 112. [English edition; listed]
1848 *Calymene ornata* Dalm.: Bronn, p. 286. [listed under species of *Cheirurus*]
1851 *Cheirurus ornatus* Beyrich: Sjögren, table p. 41. [listed]
1852 *Cheirurus ornatus* Dalman: Barrande, pp. 753, 754, 756, 764, 770 table, 786. [comparative discussion, literature references, distribution, stratigraphy]
1853 *Cheir.* [*Cheirurus*] *ornatus* (Dalm.): Salter, pp. 1, 12. [comparative discussion]
1854 *Chirurus ornatus* Dalm.: Angelin, p. 31, pl. 21, fig. 1a, b. [description; text on p. 31 wrongly indicates plate 20]
Non 1859 *Cheirurus ornatus* Dalm. sp.: Nieszkowski, p. 374, pl. 2, figs 4 & 5. [= *Paraceraurus macrophthalmus*]
Non 1861 *Ceraurus ornatus:* Roemer, p. 78, pl. 8, fig. 9. [= *L. ingricus*]
1864 *Ch.* [*Cheirurus*] (*Calymene*) *ornatus* Dalman: Salter, p. 67. [comparative discussion]
1868 *Cheirurus ornatus* Angel.: Bigsby, p. 45. [listed]
1874 *Ceraurus ornatus* Beyrich: Steinhardt, p. 56. [comparative discussion]
?1875 *Chirurus ornatus* Dalm.: Linnarsson, p. 38. [listed]
1878 *Chirurus ornatus* Dalm.: Angelin, p. 31, pl. 21, fig. 1a, b. [reproduction of 1854 work]
1878 *C.* [*Cheirurus*] *ornatus* Dalman: Nicholson & Etheridge, p. 106. [comparative discussion]

1881 *Cheirurus* (*Cheirurus*) *ornatus* Dalm.: Schmidt, pp. 126, 131 (table), 133, 134, 145, pl. 6, figs 3 & 4; pl. 16, fig. 1. [description, comparative discussion, distribution]
1882 *Cheirurus ornatus* Dalm.: Schmidt, p. 519, 533 table. [listed]
?1885 *Ceraurus ornatus* Ferd. Roem.: Roemer, p. 316. [listed]
1888 [*Chirurus*] *ornatus* Dm: Lindström, p. 8. [listed]
1896 *Cheirurus* (*Cheirurus,* sens. stri.) ornatus (Dalman): Reed, p. 165. [listed]
1896 *Ch.* [*Cheirurus*] *ornatus* Ang.: Wysogórski, p. 410. [comparative discussion]
Non 1901 *Chirurus ornatus* Dalman: Lindström, p. 50, pl. 3, figs 12–14. [description of eyes; = *L. ingricus*]
1905 *Cheirurus ornatus* Dalm.: Lamansky, pp. 68, 169. [listed]
1907 *Cheirurus ornatus* Dalm.: Schmidt, pp. 7, 8. [distribution]
1910 *Chirurus ornatus* Dalm.: Westergård, p. 22. [listed]
1911 *Cheirurus ornatus* Dalman: Bassler, p. 23. [faunal list]
1912 *Ch.* [*Cheirurus*] *ornatus* Dalman: Reed, p. 109. [comparative discussion]
1913 *Ceraurinus*: *Cheirurus ornatus* Dalman: Barton, pp. 547–549, 553. [comparative discussion]
1915 *Calymene ornatus* Dalman, 1828: Barton, p. 134. [listed under species of *Cheirurus*]
1922 *Cheirurus ornatus* Dalman: Winkler, pp. 52, 60. [listed]
1925 *Cheirurus ornatus* Dalm.: Öpik, p. 2. [distribution]
1927 *Cheirurus ornatus* Dalman: Öpik, pp. 52, 53. [listed]
1928 *Cheirurus ornatus* Dalman: Troedsson, p. 73. [listed under species of *Ceraurinus*]
1934 *Cheirurus ornatus* Dalman: Rüger, pp. 18, 19. [listed]
1935 *Ceraurus ornatus* (Dalman): Schmidt, pp. 110, 111. [distribution, comparative discussion]
1949 *Cheirurus ornatus* Dalm.: Alikhova et al., p. 9. [distribution]
1949 *Ceraurus ornatus* Dalm.: Bohlin, p. 566 table. [listed]
1952 *Ceraurus ornatus*: Öpik in Bubnoff, p. 122. [listed]
Pars. 1958 *Ceraurinella*? *ornata* (Dalman): Männil, pp. 173, 174. [comparative discussion], non pl. 3, fig. 10. [= *Reraspis orvikui*, see Pärnaste, 2004]
1960 *Ceraurinus ornatus* (Dalman): Rõõmusoks, pp. 73, 74. [listed]
1967 *Ceraurinella*? *ornata* (Dalman): Tripp, p. 63. [comparative discussion]
?1971 *Paraceraurus* sp.: Neben & Krueger, pl. 10, fig. 9. [figure only]
?1971 *Paraceraurus* cf. *perlongus*: Neben & Krueger, pl. 12, fig. 10. [figure only]
1977 *Ceraurinus ornatus* (Dalman): Ludvigsen, pp. 959, 960. [history of nomenclature]
1985 *C.* (*C.*) [*Ceraurinella* (*Ceraurinella*)] *ornata* (Dalman, 1828): Přibyl et al., p. 143. [listed: taxonomy]
1997 *"Ceraurinella" ornata* (Schmidt, 1881): Bruton et al., p. 26. [listed: taxonomy]
2003 *Ceraurinella ornatus* (Dalman, 1827): Hansen & Nielsen, p. 110. [stratigraphy]
2004 *Ceraurinella ornata* (Dalman, 1827): Pärnaste, fig. 1 (pars) on p. 126, pp. 127, 132. [comparative discussion]
2008 *Ceraurinella ornata* (Angelin): Pärnaste, p. 309, fig. 1A. [comparative discussion]
2009 *Paraceraurus*? *ornatus* (Dalman 1828): Klikushin et al., p. 340, fig. 537. [description, synonymy list]
2013 *Ceraurinella ornata* (Dalman, 1827): Pärnaste et al., table S6. Interval 8. [listed]

Lectotype. – Selected here. Cephalothorax (NRM Ar 53339) with 10 thoracic segments and vestiges of an 11th segment. Originally described by Dalman (1827, p. 134) from 'grey limestone at Husbyfjöl' [Västanå], at Borensberg in Östergötland, and originating from the *Asaphus expansus* Zone. Refigured here in Fig. 15C–H.

Paralectotype. – Selected here. Worn specimen (NRM Ar 17865) consisting of seven thoracic segments and a pygidium lacking the anterior pair of spines. Described by Dalman (1827, p. 134), from the same locality and level as the lectotype. Refigured here in Fig. 15A, B.

Other material. – Additional specimens from the same locality and stratigraphic level as the lectotype include: a well-preserved enrolled specimen (NRM Ar 17853/54, Fig. 16A–H); a cranidium with only the glabellar part preserved (NRM Ar 17851, Fig. 16I, J); a small partial cranidium (NRM Ar 17857, Fig. 16K); and an incomplete cephalothorax with 11 segments (NRM Ar 17850, Fig. 16L). Estonian material is from the *Asaphus raniceps* (BIIIβ) to *Megistaspis gigas* (BIIIγ) zones, and includes: a partial cranidium (GIT 319-14, Fig. 17A–D) from Mäeküla; a partial cranidium (GIT 319-11, Fig. 17E–H) from Väike-Pakri Island (loc. 9 in Fig. 1); two large, partial cranidia (GIT 319-9-1, Fig. 17I; GIT 319-8-1, Fig. 17J, K) from Suur-Pakri Island (loc. 10 in Fig. 1); a partial pygidium (GIT 319-6, Fig. 17L, M) from Paldiski (Loc. 11 in Fig. 1); and a hypostome (GIT 319-8-2, Fig. 17N) from Suur-Pakri Island.

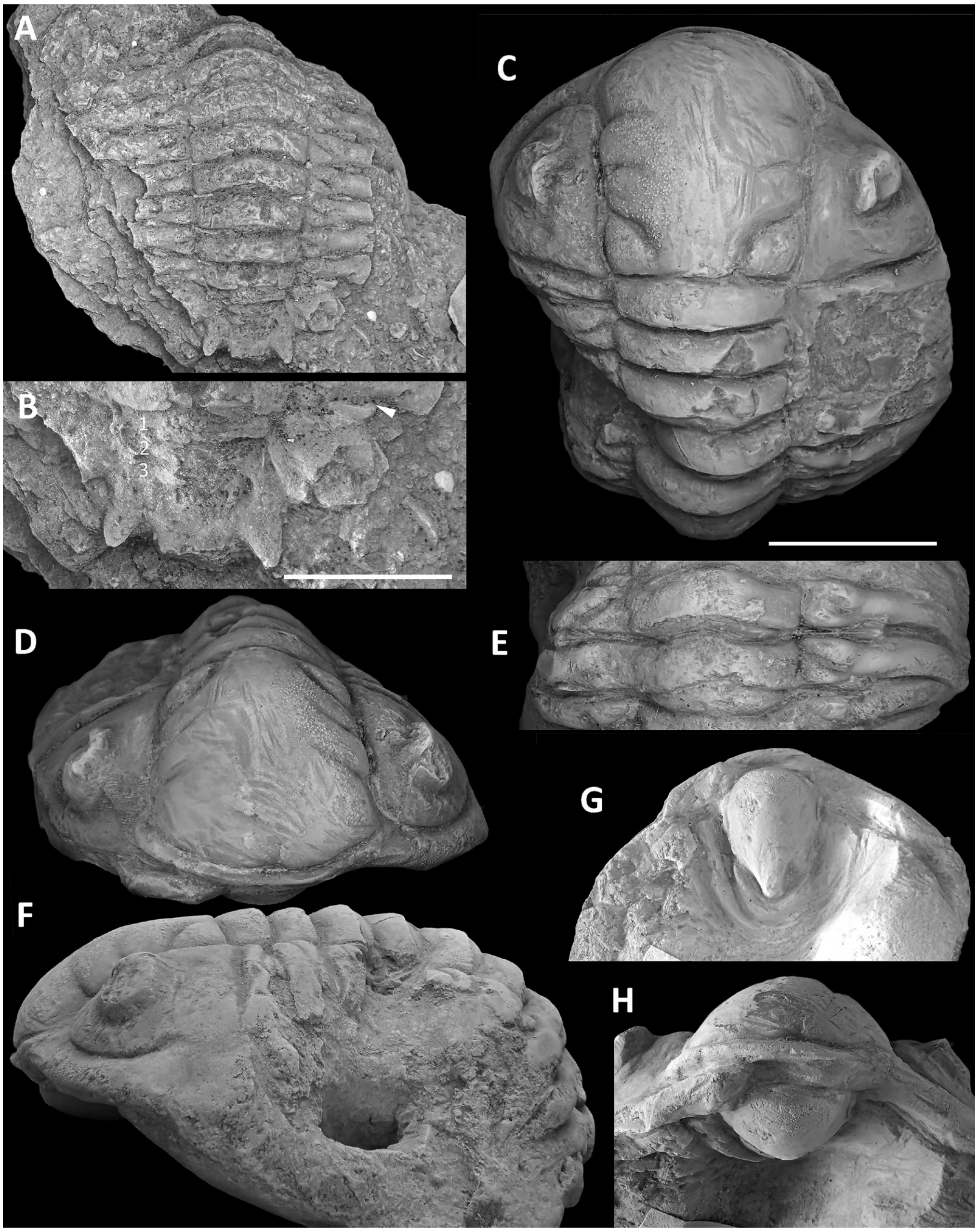

Figure 15. Ceraurinella ornata *(Dalman, 1828) from Västanå, Östergötland ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone). (A, B) Paralectotype (NRM Ar 17865), described by Dalman (1827, p. 134). Arrow in B points to pygidial fulcrum. Numbers 1–3 indicate pleural segments. Shown in dorsal view and close-up of pygidium. (C–H) Lectotype cephalothorax (NRM Ar 53339) with 10 thoracic segments and vestiges of an 11th segment. Described by Dalman (1827, p. 134) and figured by Angelin (1878, pl. 21, figs 1, 1a, 1b). Shown in dorsal and anterior oblique views, detail of thorax, lateral, ventral view hypostome and anterior view. Coll. J.W. Dalman. Scale bar in C = 1 cm (applies to A & C–H); scale bar in B = 0.5 cm.*

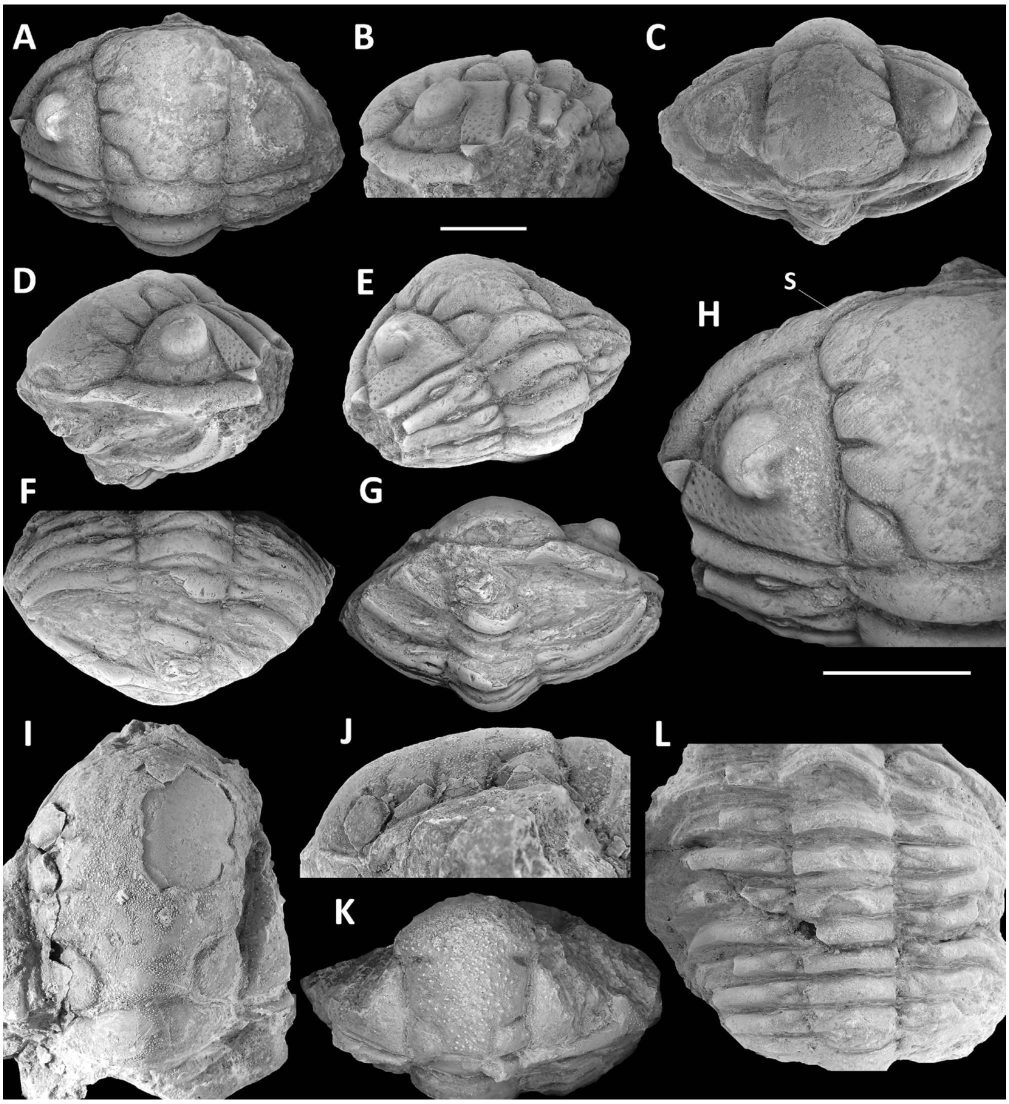

Figure 16. Ceraurinella ornata *(Dalman, 1828) from Västanå, Östergötland ('Holen limestone', Kundan Stage,* Asaphus expansus *Zone). (A–H) Nearly complete enrolled specimen (NRM Ar 17853). The 's' in fig. H indicates the anterior facial suture. Views: Dorsal (A), lateral (B), anterior oblique (C), lateral oblique (D), dorsal oblique (E), detail of thorax (F), detail of pygidium (G) and detail of left half of cephalon (H). (I, J) Large partial cranidium (NRM Ar17851), dorsal and lateral views. (K) Small cranidium (NRM Ar 17857) with nearly effaced S2 (considered an artefact of preservation), dorsal view. (L) Thoracic region of incomplete cephalothorax (NRM Ar 17850), dorsal view. Scale bars: A–G & I–L = 1 cm; H = 0.5 cm.*

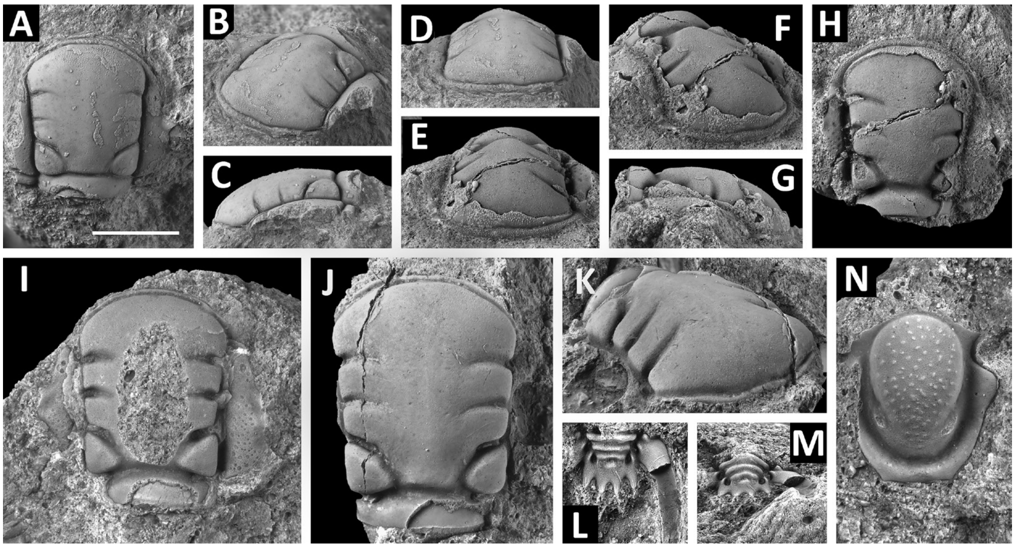

Figure 17. Ceraurinella ornata *(Dalman, 1828) from the* Asaphus raniceps *(BIIIβ) to* Megistaspis gigas *(BIIIγ) zones. (A–D) Partial cranidium (GIT 319-14) from Mäeküla, Tallinn. Shown in dorsal, dorsoanterior oblique, lateral and anterior oblique views. Coll. V. Jaanusson. (E–H) Partial cranidium (GIT 319-11) from Väike-Pakri Island. Shown in anterior oblique, dorsoanterior oblique, lateral and dorsal views. Coll. K. Orviku. (I) Dorsal view of partial cranidium (GIT 319-9-1) from Suur-Pakri Island. Coll. K. Orviku. (J, K) Partial cranidium (GIT 319-8-1) from Suur-Pakri Island. Dorsal and dorsoanterior oblique views. Coll. K. Orviku. (L, M) Latex cast of pygidium (GIT 319-6), previously figured by Pärnaste (2008, p. 309, Fig. 1A), from Paldiski. Dorsal and posterior views. Coll. K. Orviku. (N) Hypostome (GIT 319-8-2) from Suur-Pakri Island, ventral view. Coll. K. Orviku. Scale bar in A = 0.5 cm (applies to all).*

Diagnosis. – A species of *Ceraurinella* with an evenly vaulted cephalon, occipital ring shorter (sag.) than sagittal length of L1, triangular L1 isolated adaxially, longer than sub-quadrate L2 and L3, S2 and S3 nearly straight and narrow (tr.), reaching adaxially only about 1/6 of glabellar width, and relatively wide (tr.) palpebral area.

Description. – Cephalon almost semi-circular in outline, evenly vaulted (tr. and sag.), length (sag.) equivalent to ~66% of maximum width (tr.; excluding the genal spines) (Figs 15C & 16A). Shape and size of genal spines unknown. Glabella sub-rectangular in outline, about 70% as wide as long (sag.), expanding slightly anteriorly, width of occipital ring in lectotype is 82% of width of anterior glabellar lobe (Fig. 15C). Glabella gently convex transversely and with low sagittal profile, in lateral view sloping evenly and gently forwards (15F, 16B, J & 17C, G). Occipital ring slightly shorter (sag.) than length (exsag.) of L1, evenly convex posteriorly, narrowing laterally towards axial furrow, delimited anteriorly by well-defined occipital furrow that laterally follows the gentle posterior curvature of L1, while the axial part is straight. L1 triangular, isolated adaxially. They are somewhat longer (exsag.) than the equally sized and sub-quadrate L2 and L3. S1 straight and directed obliquely rearwards-inwards from axial furrow, adaxially becoming shallow and more posteriorly directed. Both S2 and S3 are narrow (tr.), with only a weak posterior curvature adaxially; length corresponds to only about 1/6 of glabellar width. Anterior border short (sag.) throughout, little inflated, straight medially with gently rounded corners laterally (Figs 15D, 16C & 17A, H–J). Anterior border furrow well incised, narrow. Posterior branch of facial suture directed outward and only slightly forward to lateral border where it turns outward and obliquely rearwards (Fig. 16D). The suture meets the lateral border slightly behind level of S2. Anterior branch of facial suture poorly preserved, but seemingly straight, running forward and adaxially to rounded anterolateral corner of anterior border. Outline of rostral plate unknown. Palpebral lobe small, triangular, placed slightly posterior to middle (tr.) of fixigena (Figs 15C & 16H). Palpebral area broad (tr.) placing the eye close to lateral border (when viewed dorsally) (Figs 15C & 16A).

Posterior end of palpebral lobe located slightly behind level of anteriormost part of S1, anterior end slightly anterior to S2. Palpebral furrow indistinct, shallowing anteriorly. Eye ridge poorly defined. Preocular field small and triangular, being delimited by anterior branch of facial suture, axial furrow and pre-fixigenal furrow that extends from axial furrow opposite the middle of the anterior glabellar lobe (Fig. 16D, H). Posterior and lateral borders evenly convex, of similar width. Adaxial part of posterior border slightly narrower (exsag.) along the part corresponding to the articulating flange of the anteriormost segment. Posterior and lateral border furrows of similar depth, well-defined and broad. Librigena sub-trapezoidal, twice as wide as high with height of librigenal field slightly less than height of lateral border. Eye large, extending for the length of L2 and half of L3, bulbous and placed on low socle (Fig. 16D, H). Entire cephalon covered by minute, densely spaced granules, except in furrows (Fig. 16H, I).

Hypostome in lectotype poorly preserved (Fig. 15G, H), but the Estonian specimen (Fig. 17N) has a sub-quadrate outline, narrowing slightly rearwards. Middle body globose, sub-oval, with short (sag.) posterior lobe. Maculae small, raised and located in posterior third of hypostome. Shoulder wide. Lateral and posterior border furrow distinct, moderately deep and with a broad U-shape. Borders wide and of equal width posteriorly and laterally. Posterior margin straight (tr.) with faintly pointed posterolateral corners. Posterior border as wide as the width between adaxial parts of the maculae. Surface of middle body covered by minute, densely spaced granules and wider spaced tubercles.

Thorax with 11 segments, tapering (tr.) only slightly rearwards. Axial part evenly arched and weakly convex (sag. and tr.). Axial ring short (sag.), its width about 20–25% of thoracic width (tr.). Axial furrow shallow, but clearly incised. Inner portion of pleura narrow (tr.), no more than about 40% of pleural width, with prominent flanges. Distal parts extend into thin falcate spines. Anterior and posterior band of pleura with elongate triangular swellings bifurcated by shallow pleural furrow directed obliquely rearwards. Pleural furrow narrow (tr.), extending only about half of inner portion of pleura. Surface covered by minute densely spaced granules.

Pygidium (Figs 15A, B & 17L, M) excluding spines semi-circular in outline, length (sag.) 1/3 of anterior width (tr.). Axis sub-trapezoidal in overall outline, tapering rearwards; it accounts for about 40% of the anterior pygidial width (tr.) and consists of three convex (sag.) axial rings and a small terminal piece seen as a small swelling (Fig. 17L, M). Third axial ring about 80% as wide (tr.) as anterior ring, with transverse anterior margin and a slight median constriction at posterior margin constricting the length (sag.) of the axial ring. Second and third axial rings with deep apodemal pits at their ends. Post-axial field accounts for about 30% of the pygidial length (sag.). Anterior pleural rib developed into broad-based spine, directed slightly outwards and rearwards. Width of preserved part of spine narrows only slightly, suggesting that it is approximately three times as long as the middle part of pygidium. Anterior pleural field incised by a short but prominent pleural furrow; the anterior portion is larger and bulbous, the posterior part ridge-like. Adaxial part of spine base extends from margin opposite third axial ring. Spine of second pleural rib short and blunt, directed slightly outward, outer margin in line with abaxial edge of first axial ring. Marginal spines of third pleural rib directed rearwards; they are similar in size and shape to the previous pair but extend a little more posteriorly. Outer margin nearly in line with abaxial edge of third axial ring.

Remarks. – Dalman (1828, p. 134) discussed two specimens of his new species from Västanå, collected during an excursion in 1826 (J. Bergström, 2007). One was compared to *Calymene blumenbachii* and distinguished by the adaxial swellings on the inner portion of the pleurae. This specimen is designated here as the lectotype of *C. ornata* (NRM Ar 53339, Fig. 15C–H). The second specimen, showing the pygidium with marginal spines, is designated here as the paralectotype (NRM Ar 17865, Fig. 15A, B). A brief description, comparable to that provided by Dalman, was given by Hisinger (1837). The species was eventually described in more detail by Lovén (1845, p. 63), based on Dalman's original specimens.

Lovén (1845) assigned the thorax with pygidium (paralectotype) to *Cyrtometopus clavifrons* (Dalman, 1827), a cheirurid commonly found at Västanå and Ljungsbro (for a revision of this species, see Hansen 2010). However, the specimen neither represents *C. clavifrons* nor *L. ingricus*. It differs from *Cyrtometopus clavifrons* in several respects by having 1) a higher length/width pygidial ratio compared with the more rectangular shape in *C. clavifrons*, 2) a longer (sag.) postaxial field, and 3) a shorter transverse distance between the marginal spines of the second pleural field relative to the length (sag.) of the pygidium. The same differences apply when compared to the pygidium of *L. ingricus*, which additionally has barely distinguishable marginal spines inside the stout anterior spines.

Angelin (1854) also provided a brief description and illustrated a cephalothorax based on the specimen here designated as lectotype. However, Angelin's illustration differs significantly from the actual specimen — Westergård (1910, p. 3) noted that Angelin's illustrations were 'badly drawn'. The illustrated cephalothorax shows features not preserved in the lectotype, including genal spines, small eyes, a narrow palpebral field, subquadratic L1, and an anteriorly expanding glabella in lateral view. It also depicts the occipital ring with basal nodes (Angelin, 1854, pl. 21, fig. 1a). Nonetheless, Angelin correctly illustrated the number of thoracic segments and the hypostome, and especially the latter matches well with the actual specimen, particularly the very deep furrow drawn at the maculae, which is a result of unfortunate preparation (see also Fig. 15C–H). It is possible that Angelin took a liberal approach in his interpretation of the species and incorporated elements from specimens of *Laneites ingricus*. Many cheirurid specimens from Västanå in the historical collections at NRM are labelled as '*Chirurus ornatus*' but can readily be distinguished as *L. ingricus* (e.g., NRM Ar 17840, Ar 17843, Ar 17844, Ar 17846, Ar 17848–Ar 17860).

Schmidt (1881) provided a detailed description of *Ceraurinella ornata* (as *Cheirurus ornatus*), based on an unpublished drawing by Lovén of Dalman's original (Schmidt indicated only one specimen), along with a nearly complete specimen supplied by Gustaf Lindström at the Swedish Museum of Natural History (NRM). Schmidt did not comment on Angelin's illustration, nor did he mention his new species *Cheirurus ingricus* in this context.

A total of 10 specimens of Estonian *Ceraurinella ornata* are registered in the collections of the Department of Geology at Tallinn University of Technology, one each from Jägala, Leetse, Mäekul, Paldiski and Väike-Pakri Island and five from Suur-Pakri Island. Of these, the seven best-preserved have been studied here. None of the cranidia are complete, whereas one pygidium is well-preserved (part and counterpart). A single hypostome is attributed, by association, to *C. ornata*. The Estonian specimens are younger than the Swedish, occurring in the *Asaphus raniceps* Zone (Leetse) but mainly in the *Megistaspis gigas* Zone (Jägala, Paldiski and Pakri islands and not the *Asaphus expansus* Zone.

There are subtle differences between the two sets of specimens. In the Estonian material, S2 and S3 are deeper (tr.) adaxially and show a more clearly defined curvature. Additionally, the anterior corner of the palpebral lobe is opposite S2, whereas in the Swedish specimens it appears to be positioned slightly more anteriorly, opposite the posterior part of L2 (compare Figs 16H & 17A, I). The only pygidium at hand from Sweden is poorly preserved but closely resembles the only known Estonian specimen (see Figs 15B vs. 17L, M). Better preserved material may eventually reveal further differences between these two sets of specimens, but for the time being they are here treated as conspecific.

Beyrich (1846) illustrated a worn cranidium from glacial erratics near Berlin (MB.T.7487), attributed to Dalman's species. Schmidt (1881) noted that the glabella differs from that of *C. ornata* but was unable to determine the species more precisely. The cranidium differs from *C. ornata* in having a proportionally squarer glabella with larger L1 lobes, a shorter occipital ring (sag.), and a well-developed eye ridge. The glabella does not seem to expand forward. New photographs of the Beyrich specimen show that it is comparable to the specimen described as *Paraceraurus elatifrons* (Krause, 1895) by Neben & Krueger (1971, 1979), which possibly can be assigned to *Reraspis* (see discussion on

Paraceraurus species). However, two fragmentary cephala from upper Kundan Geschiebe in Germany figured by Neben & Krueger (1971, pl. 10, fig. 9; pl. 12, fig. 10) as *Paraceraurus* sp. and *Paraceraurus* cf. *perlongus* may represent *C. ornata*.

Ceraurinella ornata differs from the type species *C. typa* in several respects: it has a shorter (sag.) anterior glabellar lobe, shorter (exsag.) and less robust palpebral lobes, an indistinct eye ridge, and a broader (tr.) palpebral area. Additionally, the surface texture consists of much finer granules. The poorly preserved pygidium of *C. ornata* seems to be proportionally wider than that of the type species. Dalman's species resembles the Late Ordovician (Sandbian) *C. kingstoni* Chatterton & Ludvigsen, 1976 in the shape and proportions of the glabella and the convexity of the cephalon. However, they differ in curvature and depth of the glabellar furrows, where S1 is narrow (tr.) in *C. kingstoni* and relatively wide in *C. ornata.* In *C. ornata*, L1 is also smaller and more triangular and the palpebral area is wider. The first pair of pygidial spines is much shorter in *C. kingstoni*, and the third pair is far less developed than in *C. ornata*. Tripp (1967) compared the Darriwilian *Ceraurinella magnilobata* to *C. ornata* as figured by Männil (1958, pl. 3, fig. 10) but that particular specimen was transferred to *Reraspis orvikui* by Pärnaste (2004). *Ceraurinella magnilobata* is quite similar to *C. ornata* in the expression of the glabellar lobes and furrows but has a narrower fixigenal field. Its pygidium bears stout first pygidial spines, similar to those of *C. ornata*, but the second and third pygidial spines are reduced and blunt compared with the well-developed spines in *C. ornata*.

Conclusions

· *Laneites ingricus* (Schmidt, 1881) and *Ceraurinella ornata* (Dalman, 1828) are among the earliest cheirurine species recorded in Baltoscandia, occurring in the Volkhovian–Kundan stages.
· Both species have been frequently cited in the literature, and our review clarifies their synonyms.
· *Ceraurinella ornata* was one of the first cheirurine trilobites described from Scandinavia, but it has not been revised since its original description, and the morphology as well as the spatial and temporal distribution remain poorly documented.
· *Laneites ingricus* occurs in the Volkhovian–Kundan limestone succession across the Baltoscandian platform, from the St. Petersburg area of Russia, through central Sweden and Bornholm (Denmark), to the Oslo Region of Norway.
· *Laneites ingricus* ranges from the Volkhovian (BIIγ) *Megistaspis limbata* Zone through the lower Kundan (BIIIα) *Asaphus expanus* Zone. A form identified as *L.* cf. *ingricus* occurs in the older Volkhovian (BIIβ) *Megistaspis simon* Zone.
· *Laneites* aff. *L. ingricus* (Schmidt) from the lowermost Volkhovian (BIIα) *Megistaspis polyphemus* Zone in Estonia represents the oldest known cheirurine species in Baltoscandia.
· *Ceraurinella ornata* is known from the *Asaphus expansus* Zone in Västergötland, Sweden, where it is comparatively rare, and from several specimens found in the younger *Asaphus raniceps* to *Megistaspis gigas* zones
in Estonia.
· Slight differences in the cranidial morphology are evident between the Swedish and Estonian specimens of *C. ornata*, but these are not currently considered sufficient to warrant taxonomic separation.
· In total, 30 cheirurines taxa are known from the Ordovician of Baltoscandia. Species diversity (including both formally described species and material treated in open nomenclature) is greatest in Sweden with 14 occurrences, followed by Estonia with 11, Norway with seven, the St. Petersburg area with five, Denmark (Bornholm) with two, and Finland (Åland) with one. It should be noted that two of the Norwegian taxa occur in allochthonous strata derived from Laurentia. No representatives of the subfamily Cheirurinae are recorded from Baltoscandia in the interval between the Kukruse/Dalbyan stages and the Oandu/Moldåan stages.

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