AGNOSTID TRILOBITES FROM THE LOWER ORDOVICIAN KOMSTAD LIMESTONE FORMATION OF KILLERÖD, SCANIA, SWEDEN

by PER AHLBERG

ABSTRACT. *Geragnostus tullbergi* (Novák 1883), *G.* cf. *ingricus* (Schmidt 1894), *Arthrorhachis lentiformis* (Angelin 1851)?, and *Oculagnostus frici* (Holub 1908*a*) are described from the Lower Ordovician Komstad Limestone Formation at Killeröd, south-east Scania (Skåne), southern Sweden. *Geragnostella* is a subjective junior synonym of *Geragnostus*. Conodonts and associated polymerid trilobites suggest the strata yielding these agnostids correlate with the *Asaphus expansus* Zone or basal *A.* '*raniceps*' Zone of the lower Kunda Stage (uppermost Arenig or lowermost Llanvirn).

AGNOSTID trilobites ranged from late early Cambrian to late Ordovician (pre-Hirnantian Ashgill). They reached a maximum diversity during the Middle Cambrian and early Upper Cambrian, and they are among the most significant faunal elements in Cambrian biostratigraphy. Because of their abundance, wide geographic distribution, and relatively rapid evolution, they afford the best means of correlating Cambrian strata, especially sequences of oceanic and open-shelf facies (e.g. Robison *et al.* 1977; Rowell *et al.* 1982). The value of agnostids as stratigraphical indicators in the Middle Cambrian was well demonstrated by Westergård (1946), Robison (1964, 1984) and Öpik (1961, 1979). The biostratigraphical potential of Upper Cambrian agnostids was discussed by Shergold (1981).

Agnostid trilobites are frequently encountered in Ordovician rocks, and a number of species appear to have good biostratigraphic potential. In the Ordovician of Scandinavia, agnostids are generally rare, but they are known to range up to the base of the Hirnantian (see e.g. Olin 1906; Kielan 1960; Nilsson 1977; Owen 1981). In certain beds in the Scandinavian Ordovician, however, agnostids are comparatively common, notably in the Arenigian *Megistaspis planilimbata* Zone at Lanna in Närke, south-central Sweden (Wiman 1905; Tjernvik 1956) and in the Ashgillian Jonstorp Formation and correlative strata (Linnarsson 1869; Olin 1906; Kielan 1960; Bergström 1973). In addition, the late Johan Gunnar Andersson (1874–1960), a famous Swedish geologist and archaeologist, assembled a large collection of well-preserved and stratigraphically important agnostids together with a variety of other trilobites from the Lower Ordovician Komstad Limestone Formation at Killeröd, south-east Scania (Skåne), southern Sweden (text-fig. 1). The material, henceforth referred to as the J.G.A. collection, was probably collected around the turn of the century. The agnostids of the J.G.A. collection form the basis of this paper.

GEOLOGICAL SETTING

The name Komstad Limestone Formation was established by Jaanusson (1960, p. 300) for a sequence of limestones between the Arenigian Töyen Shale (formerly Lower Didymograptus Shale) and the Llanvirnian Upper Didymograptus Shale in Scania (text-fig. 2). The formation may be considered as a thin tongue of the 'orthoceratite limestone' of other Palaeozoic districts of Sweden, and it was previously called the Orthoceras, 'orthoceratite', or Limbata Limestone. It is widely distributed in Scania and on Bornholm, Denmark, and consists mainly of a grey to black calcilutite with abundant skeletal fragments (Hadding 1958, pp. 177–181).

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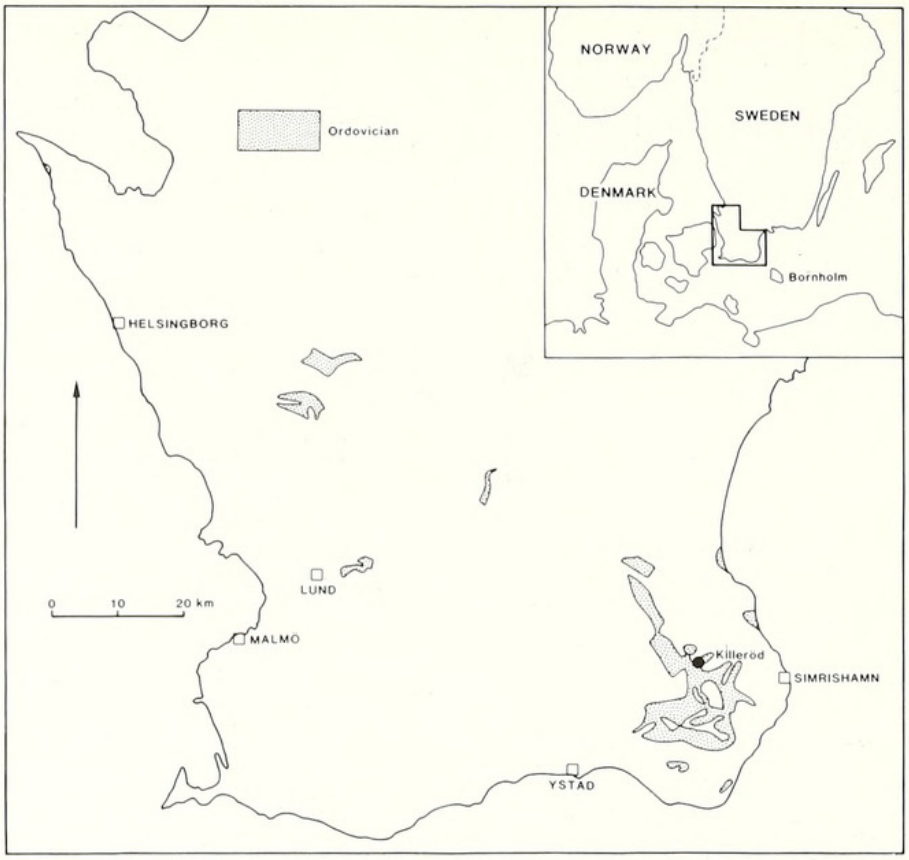
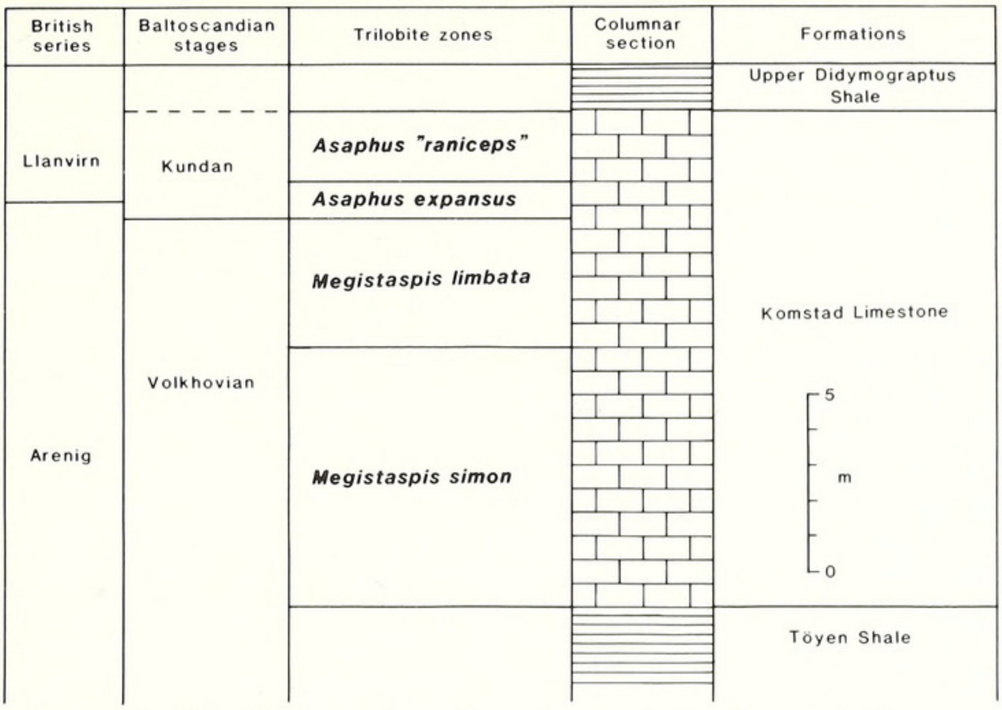


TEXT-FIG. 1. Map of Scania showing the location of Killeröd and the extent of Ordovician rocks in the bedrock surface.

The stratigraphy and faunas of the Komstad Limestone have been studied intermittently since the middle of the nineteenth century (e.g. Angelin 1851, 1854; Funkquist 1919; Ekström 1937). Regnéll (1960) and Bergström (1982) summarized the stratigraphy and palaeontological characteristics of the formation as known at the time. A recent detailed account is that of Nielsen (1985), who also reviewed the history of earlier geological work. Biostratigraphic studies have demonstrated that in Scania the Komstad Limestone can be assigned to the zones of *Megistaspis simon*, *M. limbata*, and *Asaphus expansus* of the Volkhov and basal Kunda Stages (Nielsen 1985; text-fig. 2 herein; see Jaanusson 1982, fig. 4 for stratigraphy). It must also be emphasized that a fauna suggesting a correlation with the overlying *Asaphus* '*raniceps*' Zone has recently been obtained from the uppermost beds of the formation at Killeröd, south-east Scania (Arne Thorshøj Nielsen, Copenhagen, written communication October 1986).

The agnostid trilobites described in this paper were collected near an abandoned quarry at Killeröd, about 14 km west of Simrishamn (text-fig. 1). The quarry (national grid reference X 61616 Y 13944) corresponds to locality 2 of Regnéll (1960, fig. 4) and has been briefly described by Bergström (1982, p. 193). Material was collected from a section (J.G.A. coll. *in situ*) and from seven boulders (J.G.A. coll. boulders 1–7). J.G.Andersson took great care to label the fossils according to the boulder from which they were collected. Boulders 1–6 are labelled 'Killeröd'. Outcrop material and boulder 7 are labelled 'Killeröds kanal'. Kanal is the Swedish word for drainage ditch, and it is likely that the fossils labelled Killeröds kanal were recovered from a locality adjacent to the ditch running in a NNE–SSW direction east of the quarry (see Regnéll 1960, fig. 4). No details are known as to where the fossils labelled Killeröd were found. Faunal evidence, however, indicates that all material was collected from about the same stratigraphic position in the uppermost part of the Komstad Limestone (see below).



TEXT-FIG. 2. Simplified stratigraphic column of the Komstad Limestone Formation in the Killeröd area, south-east Scania. Mainly after Nielsen (1985 and written communication October 1986).

AGE OF THE FAUNA

The agnostid trilobites include the following taxa: *Geragnostus tullbergi* (Novák 1883), *G.* cf. *ingricus* (Schmidt 1894), *Arthrorhachis lentiformis* (Angelin 1851)?, and *Oculagnostus frici* (Holub 1908*a*). The associated fauna is dominated by diverse polymerid trilobites, of which the following are common to abundant: *Pterygometopus sclerops* (Dalman 1827), *Raymondaspis limbata* (Angelin 1854), and *Celmus* cf. *granulatus* Angelin 1854. Other less common or rare trilobites are *Trinucleoides* cf. *praecursor* (Poulsen 1965), *Asaphus* sp., *Nileus* sp., *Ampyx* sp., in addition to pliomerid, remopleuridid, and cybelid trilobites. The composition of the trilobite fauna is closely comparable to that of the Volkhovian Skelbro Limestone fauna on Bornholm, Denmark (Poulsen 1965). However, the record of *Pterygometopus sclerops* and *Asaphus* sp. suggests that it is younger. In Baltoscandia, *P. sclerops* is largely restricted to the *Asaphus expansus* Zone of the basal Kunda Stage. It appears, however, to range into the overlying *Asaphus* '*raniceps*' Zone (Tjernvik and Johansson 1980, p. 195). *Asaphus* sp. is probably conspecific with a new and undescribed asaphid from the uppermost part of the Komstad Limestone. At Killeröd this new asaphid is confined to strata correlative with the *Asaphus* '*raniceps*' Zone (Arne Thorshøj Nielsen, Copenhagen, written communication October 1986). Thus, the trilobite assemblage suggests equivalence with the *Asaphus expansus* or more probably the basal *Asaphus* '*raniceps*' Zone, and it is very likely that the fauna was recovered from the uppermost part of the Komstad Limestone Formation (cf. text-fig. 2).

The trilobite-based correlation is broadly supported by conodonts recovered from outcrop material, boulder 1, and boulder 6 of the J. G. A. collection. These have been examined by Dr Anita Löfgren, Lund University. Outcrop material and boulder 6 yielded *Baltoniodus prevariabilis medius* and *Eoplacognathus*? *variabilis*. This combination is characteristic of the *E.*? *variabilis* Zone (excluding its lowermost part where *B. p. norrlandicus* prevails) in the conodont zonal scheme (Löfgren 1978, 1985). Boulder 1 yielded *Scalpellodus gracilis* which is present in beds from the *E.*? *variabilis* Zone and slightly younger beds (Löfgren 1978, 1985). Thus, the conodonts are indicative of the upper part of the *Asaphus expansus* Zone or the *A.* '*raniceps*' Zone in the trilobite zonation (see Löfgren 1985).

In conclusion, the polymerid trilobites and conodonts together indicate an early Kundan age (latest Arenig or earliest Llanvirn) for the agnostid trilobites described in this paper. The occurrence of *Geragnostus tullbergi* (Novák 1883) and *Oculagnostus frici* (Holub 1908*a*) in southern Sweden is a further indication for correlation of the Šárka Formation of Bohemia with the Kunda Stage of Baltoscandia.

The Arenigian and Llanvirnian trilobite faunas of Baltoscandia and Bohemia belong to different biogeographical provinces (Whittington 1963, 1966; Whittington and Hughes 1972; Jaanusson 1979), and polymerid trilobites of these two regions have very little in common. The occurrence of identical agnostid species in Scania and Bohemia indicates that, as in the Cambrian, distribution of Ordovician agnostids may have been largely independent of the biogeographical differentiation of the benthic faunas. In this case, agnostids may prove to represent a potentially important group for correlation between various Ordovician biogeographical provinces.

SYSTEMATIC PALAEONTOLOGY

Terminology. The morphological terms used in this paper are basically those defined by Harrington *et al.* (*in* Moore 1959, pp. O117–O126). Additional terms for agnostid features have been defined by Öpik (1963, pp. 30–32, 1967, pp. 52–62, fig. 15), Robison (1964, pp. 515–516, text-fig. 3, 1982, pp. 134–135, text-fig. 2), and Shergold (1975, pp. 39–44, figs. 14–15). Rhachis is used instead of axis and dorsal furrow instead of axial furrow. The glabella is taken to exclude the basal lobes and the occipital band. Acrolobe is used in the sense of Öpik (1967, p. 53). The terminology of the furrows and lobes on the glabella and the pygidial rhachis follows Robison (1982). Thus, the furrows are designated F1, F2, and F3, and the corresponding lobes M1, M2, and M3, counting from either the posterior of the glabella or the anterior of the pygidium. All descriptions refer to features of the external surface of the exoskeleton unless specifically stated otherwise. The symbols amplifying the information included in the synonymy lists are explained by Matthews (1973, pp. 717–718).

Measurements. Measurements were made with a micrometer eyepiece fitted in a binocular microscope. The accuracy for all measurements is to 0·05 mm. The following symbols have been used for measured parameters (cf. Shergold 1975, pp. 47–48).

Lc maximum length (sag.) of cephalon
Lbc length (sag.) of cephalic border (incl. border furrow)
Lac length (sag.) of cephalic acrolobe
G length (sag.) of glabella
N distance (sag.) from rear of glabella to high spot of median node
Wc maximum width (tr.) of cephalon
Wg maximum width (tr.) of glabella
Lp_1 maximum length (sag.) of pygidium, including articulating half-ring
Lp_2 length (sag.) of pygidium, excluding articulating half-ring
Lr length (sag.) of pygidial rhachis, excluding articulating half-ring
Lbp length (sag.) of the posterior pygidial border (incl. border furrow)
Wp maximum width (tr.) of pygidium
Wr maximum width (tr.) of pygidial rhachis

Repository. All illustrated specimens are deposited in the type collections of the Geological Survey of Sweden (*Sveriges geologiska undersökning*, SGU), Uppsala, Sweden.

Family METAGNOSTIDAE Jaekel, 1909
Genus GERAGNOSTUS Howell, 1935

Type species. *Agnostus sidenbladhi* Linnarsson 1869 (pp. 82–83, pl. 2, figs. 60–61), from the upper Tremadocian Ceratopyge Limestone (*Apatokephalus serratus* Biozone) at Mossebo, Hunneberg, Västergötland, south-central Sweden; by original designation.

Remarks. The concept of *Geragnostus* has been discussed extensively in the literature (e.g. Palmer 1954, p. 719, 1955, p. 88, 1968, p. B23; Whittington 1963, p. 28; Whittard 1966, p. 265; Dean 1966, pp. 273–274; Ross 1967, p. D8; Koroleva 1982, p. 17). Its characteristics are well shown and summarized by Fortey (1980), and his interpretation of the genus and its referral to the Metagnostidae are largely followed here. The problems of generic discrimination between *Geragnostella*, *Geragnostus*, and *Arthrorhachis* are discussed below.

Kobayashi (1939, p. 171) proposed *Geragnostella* as a new subgenus of *Geragnostus* and designated *Agnostus tullbergi* Novák, 1883 as its type species. It was established to include species without a transverse furrow on the glabella and an effaced posterior rhachial lobe on the pygidium. Subsequently, Whittard (1955, p. 7) considered *Geragnostella* as a separate genus. Since then, arguments both for (Dean 1966, p. 273; Zhou and Dean 1986, p. 748) and against (Howell *in* Moore 1959; Pek 1977, pp. 12–13) suppression of *Geragnostella* have been presented.

Pek (1977) diagnosed *Geragnostella* and noted the morphological differences between *Geragnostus sidenbladhi* and *Geragnostella tullbergi*. According to him, *G. sidenbladhi* differs from *G. tullbergi* by having a transverse glabellar furrow, a wider border, and a shorter posterior rhachial lobe on the pygidium. It is clear that the length of the posterior rhachial lobe is a variable feature in many agnostids (cf. Fortey 1980, p. 26; Hunt 1967, pl. 22, figs. 27, 29), and in *Geragnostella* it closely approaches the range of variation seen in *Geragnostus*. In addition, a short transverse furrow or depression immediately in front of the glabellar node is present in *G. tullbergi* and it corresponds to the glabellar furrow in *G. sidenbladhi*. Apparently, the differences between the two genera can only effectively be applied to the type species, and I conclude that the supposedly definitive characteristics of *Geragnostella* intergrade among the large number of species now known which have been referred to *Geragnostus*. Thus, I concur with Dean (1966) and regard *Geragnostella* as a subjective junior synonym of *Geragnostus*.

Geragnostus bears a strong similarity to *Arthrorhachis* Hawle and Corda, 1847, and obviously they are closely related. The discrimination between the two genera is a persistent problem which has been tackled by several authors over the past 30 years, in particular by Ross (1967), Dean (1966), and Fortey (1980). Species with a long pygidial rhachis and a median transglabellar furrow are generally referred to *Geragnostus*, whereas species with a short pygidial rhachis and an effaced transglabellar furrow are referred to *Arthrorhachis*. As noted by Fortey (1980, p. 26), however, these characters are variable, even within some populations, and the characteristics of the two genera intergrade. Fortey (1980) gave an extensive review of the problems involved, and suggested that forms with the terminal lobe of the pygidial rhachis exceeding the length of the postrhachial region (sag.) inside the border should be assigned to *Geragnostus*. In the type species, *G. sidenbladhi*, however, the terminal lobe of the pygidial rhachis may be shorter than the postrhachial region inside the border. This is evident in a topotype pygidium (SGU Type 25), which, according to the label, is probably one of the two syntypes figured by Linnarsson (1869, pl. 2, fig. 61; cf. Moberg and Segerberg 1906, pl. 4, fig. 1). Therefore, I conclude that the relative length of the pygidial rhachis has been accorded undue generic significance, and *Geragnostus* may eventually prove to be a junior subjective synonym of *Arthrorhachis* (cf. Dean 1966; Zhou and Dean 1986, p. 748). For the time being, however, the much-used name *Geragnostus* is retained until the type species is thoroughly redescribed.

Geragnostus is a cosmopolitan genus with a great number of named species. As noted by several authors (e.g. Zhou and Dean 1986), many of these are exceedingly alike and distinguishable only on the basis of minor characters, which may be of questionable taxonomic value. Thus, a number of species that have been assigned to *Geragnostus* may prove to be synonymous. This uncertainty affects the validity of e.g. the Llanvirnian species *G. clusus* Whittington 1963, *G. symmetricus* Zhou (*in* Zhou *et al.* 1982), and *G. hadros* Wandås 1984, all of which may be conspecific with *G. longicollis* (Raymond 1925).

Geragnostus tullbergi (Novák 1883)
Plate 61, figs. 1–15; Plate 62, figs. 1–3

*1883 *Agnostus tullbergi* Nov.; Novák, pp. 59–60, pl. 9, figs. 7–10.
v?1919 *Agnostus* cf. *lentiformis* Ang.; Funkquist, pl. 2, fig. 7.

?1972 *Geragnostus* sp.; Gil Cid, pl. 1, fig. 5.
1973*a* *Geragnostus semipolitus* Dean, pp. 287–288, pl. 1, figs. 2, 4, 5, 7–12, 14, 16, 17.
. 1977 *Geragnostella tullbergi* (Novák); Pek, pp. 13–14, text-fig. 4, pl. 2, figs. 1–4, pl. 3, figs. 1, 2, 4, 6, pl. 4, fig. 4, pl. 8, figs. 5 and 6, pl. 9, fig. 4, pl. 10, figs. 1 and 2 [further synonymy].
?1985 *Geragnostella gilcidae* Rábano *et al.*, p. 441, pl. 1, figs. 2, 6, 8, 9.

Neotype. An incomplete pygidium with two articulated thoracic tergites, figured and selected by Pek (1977, pl. 3, fig. 6). It is preserved in the type collections of the Municipal Museum of Rokycany, Czechoslovakia, as No. 1–356.

Type stratum. Šárka Formation, Llanvirn.

Type locality. Osek near Rokycany, Czechoslovakia.

Material. 27 complete or nearly complete cephala, 5 fragmentary cephala, 18 complete or nearly complete pygidia, and 6 fragmentary pygidia.

Diagnosis. A species of *Geragnostus* characterized by a wide pygidial border without postero-lateral spines, partial effacement of the posterior lobe of the pygidial rhachis, and an almost obliterated furrow in front of the median glabellar node. A secondary median node is present close to the posterior end of the pygidial rhachis.

Description. The cephalon is moderately to highly convex, subcircular, and subequal in length and width. The glabella, occupying 60–65 % of the total cephalic length, is slightly tapered forward or nearly parallel-sided, moderately rounded anteriorly, and highly convex. It is generally slightly constricted opposite the median node. The median node is usually distinct and situated at about the midpoint of the glabella. In front of the node there is a faint depression. The glabellar rear is obtusely angulate. In front of the occipital band there is a narrow median ridge. Lateral glabellar furrows are absent. The basal lobes are entire, subtriangular, and wider than long.

The acrolobe is evenly rounded and unconstricted. The genae are smooth and equal in width anteriorly and laterally. They are separated from the glabella by weakly impressed dorsal furrows, and slope most steeply laterally; less steeply in front of the glabella. The border is moderately narrow, anteriorly being 6–10 % of the total cephalic length (sag.), and slopes gently forward and laterally. It becomes narrower laterally and postero-laterally. The border furrow is weakly developed anteriorly and laterally. Postero-laterally, the border and border furrow nearly pass under the convexity (tr.) of the acrolobe. The posterior border is narrow, convex (exsag.), and defined by a deep border furrow. It is flexed down beyond the fulcrum and then curved forward to become the lateral border. The genal angles (at the fulcrum) are pointed without spines. The cephalic recess is not visible.

The pygidium is moderately to highly convex, subcircular, and subequal in length and width or slightly wider than long. The pygidial rhachis (excluding the articulating half-ring), occupying 57–62 % of the total pygidial length, is tapered backward, slightly constricted at the posterior furrow (F2), and divided into three lobes. The

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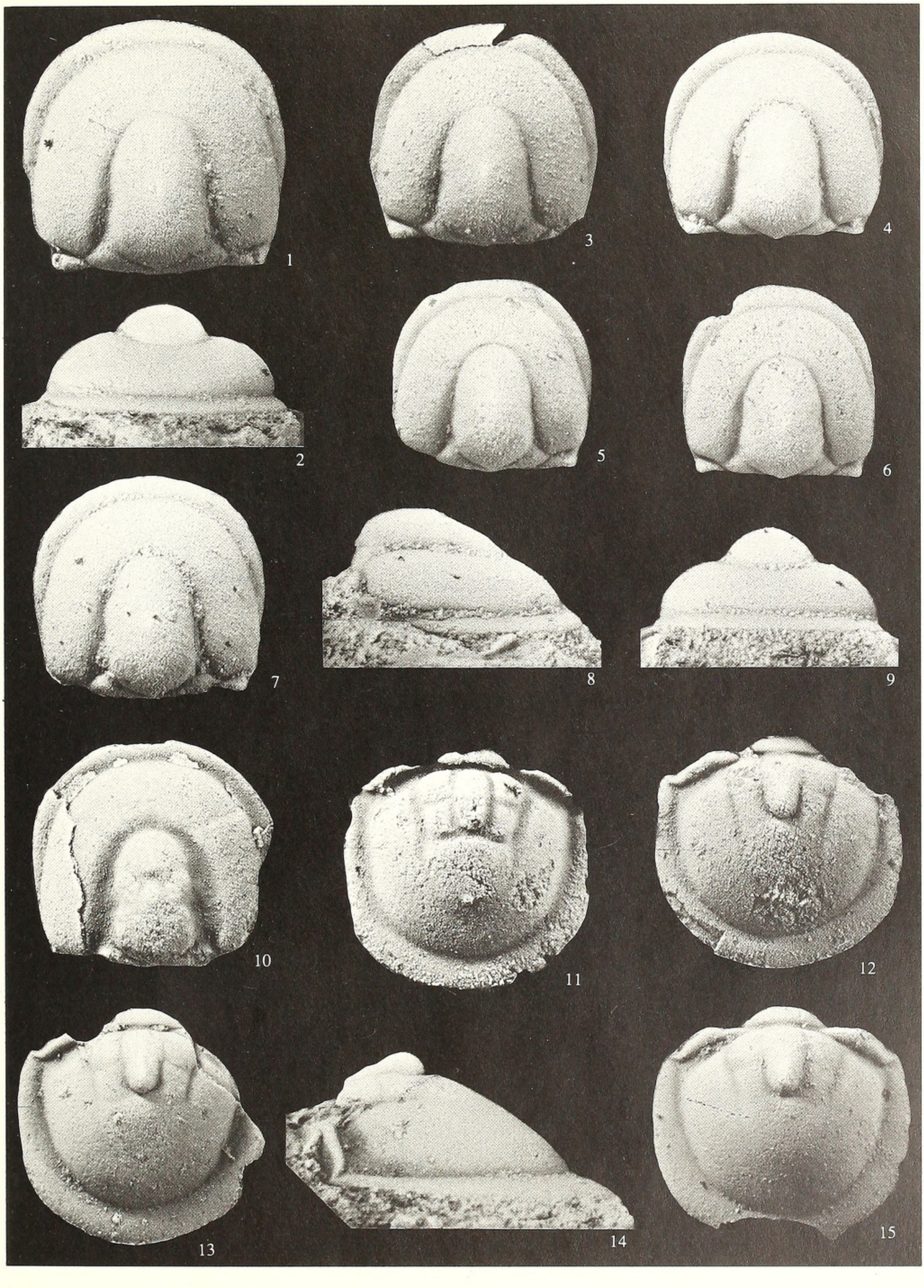
EXPLANATION OF PLATE 61

Figs. 1–15. *Geragnostus tullbergi* (Novák 1883). Upper part of Komstad Limestone Formation (Arenig-Llanvirn transition beds); J.G.A. coll. boulder 1 (1–6, 10–15), boulder 5 (7–9). Killeröd, Scania, southern Sweden. 1–2, SGU 99, dorsal and anterior views of large cephalon, × 11. 3, SGU 100, cephalon, dorsal view, × 12. 4, SGU 296, cephalon, dorsal view, × 12. 5, SGU 353, cephalon, dorsal view, × 13. 6, SGU 793, cephalon, dorsal view, × 14. 7–9, SGU 794, dorsal, right lateral, and anterior views of cephalon, × 12. 10, SGU 1233, largely exfoliated cephalon, dorsal view, × 10. 11, SGU 3311, internal mould of pygidium, × 12. 12, SGU 3312, pygidium, dorsal view, × 11. 13–14, SGU 3313, dorsal and left lateral views of pygidium, × 11 (13), × 14 (14). 15, SGU 3314, pygidium, dorsal view, × 11.

All specimens whitened with ammonium chloride sublimate, and preserved with the exoskeleton unless otherwise indicated.



AHLBERG, *Geragnostus*

articulating half-ring is about one-third of the maximum width of the pygidium. The anterior and second rhachial lobes (M1 and M2) are generally distinct, subequal in length (exsag.), and crossed by a prominent median ridge, which is highest posteriorly. M1 is widest (tr.) and occupies 41–45% of the maximum width of the pygidium. The anterior furrow (F1) is present laterally, but absent medially across the median ridge. The posterior lobe (M3) is nearly effaced and only faintly outlined. It is slightly longer (sag.) than M1 and M2 combined, and separated from M2 by a transverse furrow (F2), which is curved slightly forward medially. The posterior end of M3 is acutely rounded and bears a low secondary median node just in front of the rear of the lobe.

The acrolobe is nearly semi-circular, evenly curved and unconstricted. The pleural fields are smooth, convex, and slope appreciably laterally and posteriorly. The posterior and postero-lateral border is wide, generally attaining 12–16% of the total pygidial length (sag.), and defined by a weak border furrow and an abrupt change in the slope of the exoskeleton. It becomes narrower antero-laterally and slopes laterally and posteriorly. Postero-lateral spines are absent. The anterior border furrow is deeply incised. The articulating facets are prominent and rise adaxially to the fulcrum. The antero-lateral corners of the pygidium are angulate.

The dimensions of the species are given in Tables 1 and 2.

Remarks. The description above is based upon adult specimens preserved with the exoskeleton. In exfoliated specimens, showing the parietal morphology, the furrows and lobes tend to be more distinct (Pl. 61, fig. 10). The posterior lobe of the pygidial rhachis is well defined on small specimens (Pl. 62, fig. 3). As size increases it becomes progressively less discernible until it is nearly effaced and only faintly outlined in pygidia longer than 2·5 mm.

The material from the Komstad Limestone Formation conforms in all essential features with Novák's (1883) and Pek's (1977) description of *G. tullbergi* from Bohemia. The Bohemian specimens, however, have a slightly longer posterior rhachial lobe on the pygidium, but this can be attributed to intraspecific morphological variability.

The relatively long (sag.) pygidial rhachis, the absence of postero-lateral spines on the pygidium, the poor development of a glabellar furrow in front of the median node, partial effacement of the posterior rhachial lobe on the pygidium, and the presence of a secondary median node on the pygidial rhachis are the most distinctive characteristics of *G. tullbergi*. In addition, the glabella seems to be more convex (tr. and sag.) than in most other species of *Geragnostus*.

Funkquist's (1919, pl. 2, fig. 7) drawing of a cephalon which he ascribed to *Agnostus* cf. *lentiformis* Angelin 1851, from the Komstad Limestone Formation at Komstad, south-east Scania, strongly resembles *G. tullbergi*. Pygidia are required, however, for a confident determination.

G. semipolitus Dean 1973*a*, from strata probably corresponding to the upper Arenig in the Taurus Mountains of Turkey, is a subjective junior synonym of *G. tullbergi*, because it agrees in all essential characters with the diagnosis and description above.

Recently Rábano *et al.* (1985) described a closely comparable form, *G. gilcidae* Rábano, Pek and Vanek, 1985, from the Lower Llanvirn of Montes de Toledo and Villuercas, central Spain. According to Rábano *et al.* (1985), it differs from *G. tullbergi* mainly in having a narrower cephalic and pygidial border, and a narrower (sag.) postrhachial region. However, slight differences in the proportions of the individual parts of the exoskeleton cannot be considered as valid discriminatory characteristics. Thus, in view of the morphological variability of *G. tullbergi*, it is questionable whether the specimens recognized as *G. gilcidae* really represent a separate species.

G. explanatus Tjernvik 1956 from the lower Arenig (*Megistaspis planilimbata* Zone) of Närke, south-central Sweden, is closely comparable to *G. tullbergi* in having a partly effaced pygidial rhachis. It differs, however, in having a distinct transverse furrow on the glabella and a prominent, elongate glabellar node. In addition, the pygidium of *G. explanatus* is more elongate.

G. occitanus Howell 1935 from the lower and middle Arenig of Montagne Noire, France, corresponds fairly well with *G. tullbergi*. However, according to the detailed description given by Dean (1966) it differs in having a more quadrate cephalon, short genal spines, generally wider pygidial rhachis, and traces of pygidial marginal spines. Furthermore, the pygidial rhachis of *G. occitanus* apparently lacks a secondary median node.

TABLE 1. Dimensions (in mm) of cephala of *Geragnostus tullbergi*.

Specimen	Lc	Lbc	Lac	G	N	Wc	Wg
SGU 1419	1·60	0·15	1·50	1·05	0·50	1·60	0·70
SGU 793	2·25	0·25	2·00	1·40	0·65	2·30	0·95
SGU 353	2·30	0·20	2·10	1·40	0·70	2·40	0·90
SGU 1417	2·60	0·20	2·40	1·60	0·80	2·65	1·10
SGU 296	2·80	0·25	2·50	1·75	0·85	2·95	1·10
SGU 1418	2·85	0·25	2·60	1·75	0·85	2·85	1·10
SGU 100	3·00	0·30	2·70	1·80	0·90	3·10	1·20
SGU 794	3·00	0·25	2·70	1·85	0·90	3·10	1·20
SGU 99	3·80	0·30	3·50	2·30	1·20	3·90	1·45

TABLE 2. Dimensions (in mm) of pygidia of *Geragnostus tullbergi*.

Specimen	Lp_1	Lp_2	Lr	Lbp	Wp	Wr
SGU 3909	1·75	1·60	1·00	0·30	1·70	0·75
SGU 3315	—	2·70	1·70	0·40	3·10	1·40
SGU 3311	3·30	3·05	2·00	0·50	3·30	1·60
SGU 3313	3·40	3·10	—	0·50	3·60	1·60
SGU 3312	3·60	3·35	—	0·45	3·70	1·60
SGU 3314	3·60	3·35	2·20	0·50	3·80	1·65
SGU 3910	4·30	3·95	—	0·50	—	2·00

Occurrence. Arenig(?)-Llanvirn. Czechoslovakia, Šárka Formation; Taurus Mountains of Turkey, Sobova Formation; Scania, southern Sweden, Komstad Limestone Formation (J.G.A. coll. boulders 1, 3, and 5; *Asaphus expansus* Zone or basal *A*. '*raniceps*' Zone of the lower Kunda Stage); central Spain(?), 'Shales with *Neseuretus*'. In Czechoslovakia, the species appears to range into the Dobrotívá Formation of Llandeilo age (Pek 1977, p. 14).

Geragnostus cf. *ingricus* (Schmidt 1894)

Plate 62, figs. 4–16

cf. 1894 *Agnostus glabratus* Ang. var. *ingrica*; Schmidt, pp. 90–92, pl. 6, figs. 39–44.

Material. 24 cephala and 14 pygidia. In addition there are two small enrolled specimens and three thoracic tergites, tentatively assigned to this form.

Description. The cephalon is about as wide as long and subquadrate to subcircular in outline. The glabella, occupying 60–66% of the sagittal cephalic length, is well defined by dorsal furrows, gently tapered forward, and moderately rounded in front. It is slightly constricted at about mid-length. The low median node is situated slightly anterior to the midpoint of the glabella. Four pairs of muscle insertion areas are generally apparent on the glabella. Counting from the front, the first and second sets flank the median glabellar node. The first set is comparatively long (tr.) and directed antero-laterally from the median node end. The second set is nearly transverse. The third set is the longest (tr.) and directed postero-laterally. The fourth set consists of elliptical impressions with the long axes directed postero-laterally. The glabellar rear is obtusely angulate. In front of the occipital band there is a narrow median ridge, extending forward up the slope from the occipital furrow. The basal lobes are entire, subtriangular, wider than long, connected medially, and provided with transverse muscle impressions postero-medially.

The acrolobe is evenly rounded or slightly constricted antero-laterally. The genae are moderately convex, smooth, and equal in width anteriorly and laterally. They gently decline anteriorly, more steeply so laterally. The border is gently declined, and it is widest antero-laterally, expanding in width from the posterior border, and slightly narrowing adaxially again towards the mid-line. Sagittally it occupies 9–13% of the total cephalic length. The posterior border is narrow, convex (exsag.), and defined by a deep border furrow. It is steeply declined beyond the fulcrum and then curved forward to become the lateral border. The genal angles (at the fulcrum) are pointed without spines.

The thorax is of typical *Geragnostus/Arthrorhachis* type (e.g. Jaekel 1909; Whittington 1963, fig. 3, 1965, pl. 1, figs. 4 and 6).

The pygidium is subcircular to subquadrate, highly convex, and about as wide as long. The pygidial rhachis (excluding the articulating half-ring) is divided into three well-defined lobes and occupies 45–57% of the total pygidial length. It is generally slightly constricted at the posterior furrow (F2), tapers gently backwards, and is broadly rounded posteriorly. The anterior rhachial lobe (M1) is slightly shorter (exsag.) than M2, and both are crossed by a prominent median ridge which is highest posteriorly. They are separated from each other by a furrow (F1) which is directed inward and slightly forward from the dorsal furrow. The posterior lobe (M3) is about as long (sag.) as M1 and M2 combined, and separated from M2 by a transverse furrow which is curved slightly forward medially. In some specimens there is a minute median node on the posterior tip of the rhachis. The pleural fields are smooth, of almost constant width, and steeply downsloping. The posterior and lateral border is like that of the cephalon and generally widest postero-laterally where there is a pair of spines commencing on a transverse line well behind the rhachis. Sagittally the posterior border occupies 10–15% of the total pygidial length. The anterior border furrow is deeply incised. The articulating facets are prominent and steeply downward-sloping. The antero-lateral corners of the pygidium are obtusely angulate.

The dimensions of this form are given in Tables 3 and 4.

Remarks. In the general outline and proportions of the individual parts of the exoskeleton, the specimens from the Komstad Limestone most closely resemble those of *G. ingricus* (Schmidt 1894) from the Volkhov or Kunda Stage of the Leningrad district (Ingermanland), East Baltic area. The specimens figured by Schmidt (1894, pl. 6, figs. 39–44) seem to lack distinct muscle insertion areas, however, but this may be due to taphonomic processes. In addition, a median glabellar node on the material from the Leningrad district was not indicated by Schmidt (1894), and the identification must be tentative. It must also be emphasized that the type material of *G. ingricus* needs to be revised.

The Scanian material also shares many features with *G. clusus* Whittington 1963, from the Llanvirn of Lower Head, western Newfoundland, and other closely allied forms from Llanvirn units elsewhere in North America, Europe, and China. There are, however, minor differences in the morphological details, and the Scanian form can be differentiated *i.a.* by having a consistently shorter (sag.) pygidial rhachis and a slightly shorter (sag.) glabella.

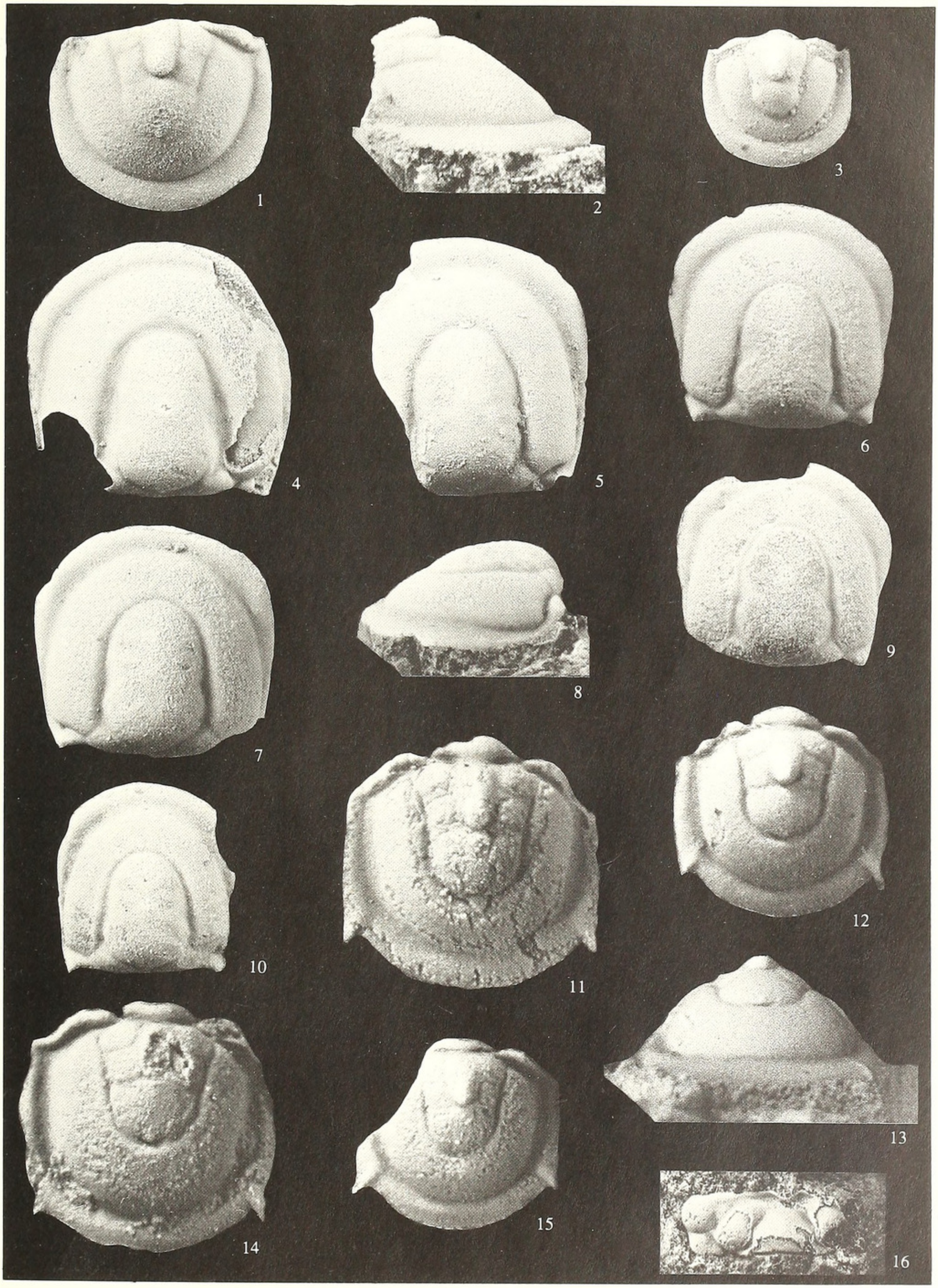
G. cf. *longicollis* of Dean (1937*b*), from the Keele Range, northwestern Yukon Territory, Canada, is broadly similar to *G.* cf. *ingricus*, but differs in having lateral genal areas, a slighty wider glabella, and a more convex posterior lobe of the pygidial rhachis.

EXPLANATION OF PLATE 62

Figs. 1–3. *Geragnostus tullbergi* (Novák 1883). Upper part of Komstad Limestone Formation (Arenig-Llanvirn transition beds); J.G.A. coll. boulder 1. Killeröd, Scania, southern Sweden. 1–2, SGU 3315, dorsal and left lateral views of pygidium, ×11 (1), ×13 (2). 3, SGU 3909, small pygidium, dorsal view, ×13.

Figs. 4–16. *Geragnostus* cf. *ingricus* (Schmidt 1894). Upper part of Komstad Limestone (Arenig-Llanvirn transition beds); J.G.A. coll. boulder 1 (6 and 9), boulder 2 (11 and 16), boulder 3 (5 and 10), boulder 5 (4), boulder 7 (7–8, 12–15). Killeröd, Scania, southern Sweden. 4, SGU 4160, large cephalon, dorsal view, ×8. 5, SGU 4620, large cephalon, dorsal view, ×9. 6, SGU 4643, cephalon, dorsal view, ×13. 7–8, SGU 4659, dorsal and left lateral views of cephalon, ×12 (7), ×10 (8). 9, SGU 4660, cephalon, dorsal view, ×12. 10, SGU 4661, cephalon, dorsal view, ×13. 11, SGU 4662, partly exfoliated pygidium, dorsal view, ×15. 12–13, SGU 4756, dorsal and posterior views of pygidium, ×14 (12), ×15 (13). 14, SGU 4869, pygidium, dorsal view, ×13. 15, SGU 5124, pygidium, dorsal view, ×16. 16, SGU 5126, anterior thoracic tergite, dorsal view, ×7.

All specimens whitened with ammonium chloride sublimate, and preserved with the exoskeleton unless otherwise indicated.



AHLBERG, *Geragnostus*

TABLE 3. Dimensions (in mm) of cephala of *Geragnostus* cf. *ingricus*.

Specimen	Lc	Lbc	Lac	G	N	Wc	Wg
SGU 4661	2·40	0·25	2·15	1·50	0·80	2·30	1·15
SGU 4643	2·75	0·35	2·40	1·70	1·00	2·80	1·20
SGU 4660	2·80	0·30	2·50	1·85	1·10	2·90	1·30
SGU 4659	3·20	0·30	2·90	2·10	1·30	3·20	1·40
SGU 4620	4·70	0·60	4·10	3·05	1·85	5·00	2·00
SGU 4160	5·10	0·50	4·60	3·30	1·70	5·20	2·25

TABLE 4. Dimensions (in mm) of pygidia of *Geragnostus* cf. *ingricus*.

Specimen	Lp_1	Lp_2	Lr	Lbp	Wp	Wr
SGU 5125	2·25	2·05	1·30	0·30	2·50	1·10
SGU 4756	2·40	2·20	1·30	0·35	2·50	1·05
SGU 4662	2·60	2·40	1·40	0·40	2·60	1·10
SGU 4869	3·20	3·00	1·50	0·50	3·20	1·40

Arthrorhachis erratica (Jaekel 1909) from glacial erratics originating from the 'Asaphus-kalk' of Scandinavia, differs from the Scanian specimens in having a slightly wider (tr.) and less tapered pygidial rhachis, and a shorter (sag.) terminal lobe on the pygidial rhachis. The cephala from Scania are generally subquadrate in outline with the maximum width at the antero-lateral corners, and they are similar to the holotype cephalon of *A. erratica*, which was refigured by Neben and Krueger (1971, pl. 11, fig. 34). The holotype cephalon, however, lacks distinct muscle insertion areas on the glabella, but as noted above this may be due to the state of preservation.

The arrangement and outline of the glabellar muscle impression areas are very similar to that of *A. elspethi* Raymond 1925 from the Middle Ordovician of North America (see Cooper 1953; Hunt 1967).

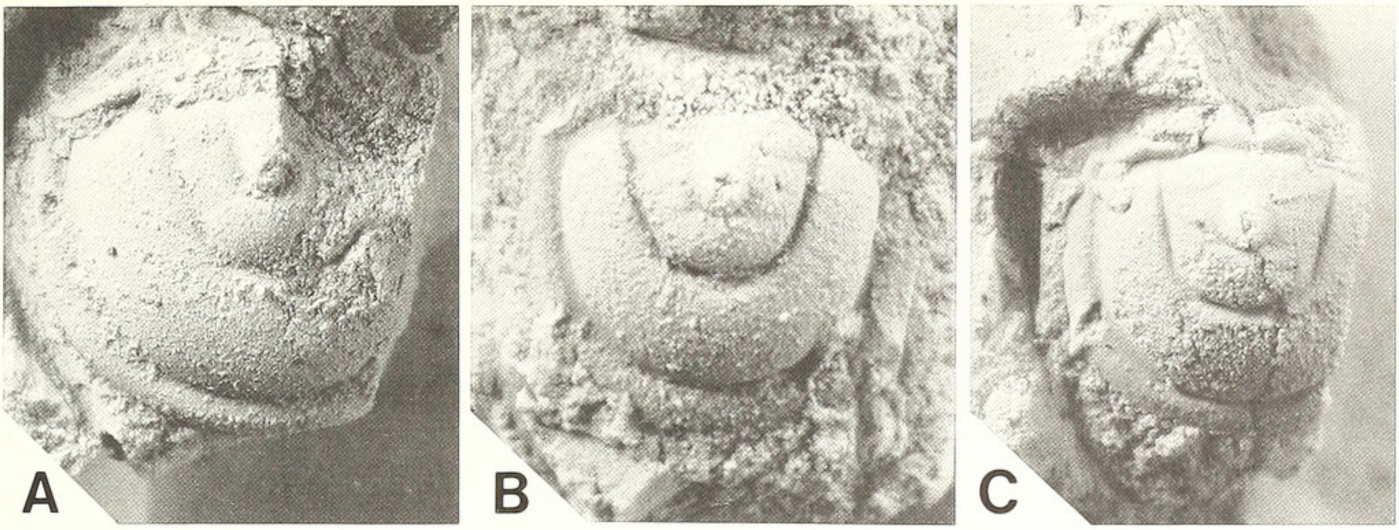
There is considerable morphological variation exhibited by the Scanian material, particularly with regard to the length and outline of the terminal lobe of the pygidial rhachis, and the general outline of the cephalon and pygidium. It is possible that more than one species is involved. I consider, however, these differences to represent minor intraspecific variation rather than specific differences.

Occurrence. Scania, southern Sweden (Komstad Limestone Formation; J.G.A. coll. *in situ* and boulders 1–3, 5–7). *Asaphus expansus* Zone or basal *A*. '*raniceps*' Zone of the lower Kunda Stage.

Genus ARTHRORHACHIS Hawle and Corda, 1847

Type species. *Battus tardus* Barrande, 1846, from the Králův Dvůr Formation (Ashgill) of Libomyšl, near Zdice, Czechoslovakia.

Remarks. I follow Fortey (1980) in restricting the genus *Trinodus* to the holotype of the type species, *T. agnostiformis* M'Coy 1846. The problems surrounding the discrimination between *Arthrorhachis* and *Geragnostus* are discussed above under *Geragnostus*.



TEXT-FIG. 3. Pygidia of *Arthrorhachis lentiformis* (Angelin 1851)?. Upper part of Komstad Limestone Formation (Arenig-Llanvirn transition beds); J.G.A. coll. *in situ* (B and C) and boulder 2 (A). Killeröd, Scania, southern Sweden. A, SGU 5127, ×9. B, SGU 5128, ×16. C, SGU 5129, ×13.

Arthrorhachis lentiformis (Angelin 1851)?
Text-fig. 3

?1851 *Agnostus lentiformis* Angelin, p. 7, pl. 6, fig. 6.
?1878 *Agnostus lentiformis* Angelin, p. 7, pl. 6, fig. 6.

Material. Three pygidia.

Dimensions (mm)

	Lp_1	Lp_2	Lr	Lbp	Wp	Wr
SGU 5129	2·60	2·40	1·30	0·30	—	1·40

Remarks. *Arthrorhachis lentiformis* (Angelin 1851) is based on material from the Komstad Limestone in the classical Fågelsång area east of Lund, Scania. The specimen(s?) figured by Angelin (1851, pl. 6, fig. 6) cannot be located, and are considered lost (cf. Wiman 1905, p. 13). No other possible syntypes can be traced. The selection of a neotype has to await a revision of the agnostids from the Komstad Limestone Formation in the Fågelsång area. Unfortunately, Angelin's description is short and his figure is vague. Thus, it is difficult to recognize diagnostic features. His figure, however, clearly shows a specimen with a short, tapered pygidial rhachis, occupying about half of the pygidial length. The terminal lobe of the pygidial rhachis appears to be very short, and spines are absent on the pygidial border. His figured cephalon is of typical *Geragnostus*/*Arthrorhachis* type with a fairly long glabella.

The three pygidia at hand have a short rhachis, occupying about 50% of the total pygidial length. In one of the pygidia the border lacks marginal spines and the rhachis tapers backward strongly (text-fig. 3A). The two other pygidia have a gently tapered rhachis and a minute pair of spines are present on the border (text-fig. 3B–C). In addition, they are more convex and the dorsal furrows are more prominent than in the specimen lacking spines. Thus, two species may be involved. For the moment, however, the three pygidia are questionably assigned to *A. lentiformis*.

A. danica (Poulsen 1965) from the lower part of the Komstad Limestone Formation at Skelbro, Bornholm, Denmark, corresponds fairly well with Angelin's (1851) figure of *A. lentiformis* and may prove eventually to be a junior subjective synonym of *A. lentiformis*. A similar uncertainty affects the validity of *A. hebetatus* (Dean 1973*a*) from the Sobova Formation of the Taurus Mountains, Turkey.

Occurrence. Scania, southern Sweden (Komstad Limestone Formation; J.G.A. coll. *in situ* and boulder 2). *Asaphus expansus* Zone or basal *A.* '*raniceps*' Zone of the lower Kunda Stage.

Genus OCULAGNOSTUS Ahlberg, 1988

Type species. Agnostus frici Holub 1908*a* (pp. 9–11, pl. 1, fig. 1a–b) from the Llanvirnian Šárka Formation at Osek near Rokycany, Czechoslovakia; by original designation.

Diagnosis. See Ahlberg (1988).

Remarks. This monotypic genus was recently erected by Ahlberg (1988) to include a rare species, *Agnostus frici* Holub 1908*a*, from the Llanvirn of Bohemia and the Arenig-Llanvirn transition beds of Scania, southern Sweden. It is unique amongst agnostid trilobites in possessing ocular structures, located at the postero-lateral part of the genae (Ahlberg 1988). In addition, the morphology of the glabella and the course of the glabellar furrows easily distinguish the genus from most other agnostid genera. In the glabellar configuration it most closely resembles species of the scrobiculate genus *Corrugatagnostus*, especially *C. fortis* (Novák 1883).

The systematic affinities of *Oculagnostus* are obscure. For the moment, however, it is questionably placed within the family Metagnostidae as defined by Fortey (1980).

Oculagnostus frici (Holub 1908*a*)
Text-fig. 4

*1908*a* *Agnostus Friči*; Holub, pp. 9–11, pl. 1, fig. 1a–b.
.1908*b* *Agnostus Fritschi*; Holub, pp. 2–3, pl. 1, fig. 1a–b.
.1977 *Segmentagnostus frici* (Holub); Pek, pp. 19–20, pl. 1, fig. 6, pl. 2, figs. 5–8.
v.1988 *Oculagnostus frici* (Holub); Ahlberg, pp. 116–118, figs. 1–3.

Neotype. An incomplete cephalon, figured and selected by Pek (1977, pl. 1, fig. 6). It is preserved in the type collections of the Municipal Museum of Rokycany, Czechoslovakia, as No. 1–361.

Type stratum. Šárka Formation, Llanvirn.

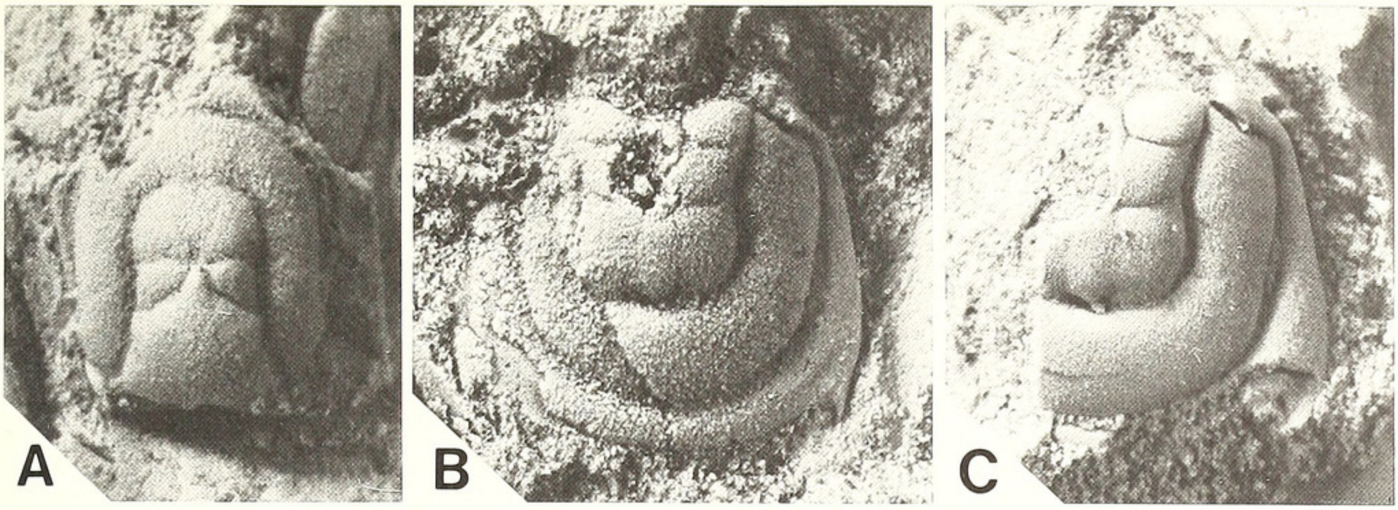
Type locality. Osek near Rokycany, Czechoslovakia.

Material. Three nearly complete cephala and two incomplete pygidia.

Diagnosis. As for the genus (see Ahlberg 1988).

Description. The cephalon is moderately convex and subquadrate in outline. The maximum width, being on a transverse line passing the preglabellar furrow, is 0·8–0·9 of the sagittal length. The glabella, occupying 65–70% of the total cephalic length, is nearly parallel-sided, 1·6–1·8 times longer than wide, truncate in front, and set off from the genae by well-developed dorsal furrows. The glabellar rear is obtusely angulate. Transversely, the glabella is highly convex; sagittally it is moderately convex. Two distinct transglabellar furrows divide the glabella into three lobes of which the middle is the shortest (sag. and exsag.). The anterior lobe (M3) is subrectangular, attaining 30–40% of the glabellar length (sag.), and separated behind by the anterior glabellar furrow (F2), which is directed inward and slightly forward from the dorsal furrows, then curved slightly backward adaxially. The posterior glabellar furrow (F1) is curved inward and forward from the dorsal furrows, making a forward-pointing V in front of the median node, which is situated slightly in front of the mid-length of the glabella. The basal lobes are large, entire, subtriangular, and separated from the glabella by a basal furrow which becomes weaker postero-medially.

The acrolobe is evenly rounded anteriorly, but laterally slightly constricted. The genae are smooth, convex, of almost constant width, and slope most steeply laterally; less steeply in front of the glabella. At the postero-lateral margin of the genae there are ocular structures (including palpebral lobes; Ahlberg 1988). The border is narrow postero-laterally, widening forward to a maximum width at the antero-lateral corners of the cephalon. The lateral border is downward-sloping distally and provided with a shallow furrow, extending from the ocular structure some distance forward parallel with the lateral margin. Anteriorly the border is convex (sag.) and moderately wide. Combined with the border furrow it occupies 6–9% of the total cephalic



TEXT-FIG. 4. *Oculagnostus frici* (Holub 1908*a*). Upper part of Komstad Limestone Formation (Arenig-Llanvirn transition beds); J. G. A. coll. *in situ* (B and C) and boulder 1 (A). Killeröd, Scania, southern Sweden. A, SGU 5130, cephalon, ×16. B, SGU 5131, pygidium, ×12. C, SGU 5635, pygidium, ×15.

length. The posterior border is convex (exsag.), defined by a deeply incised border furrow, and curved around the genal angle to meet the lateral border. There is no postero-lateral spine at this point.

The pygidium is moderately convex and subcircular in outline. The maximum width, being on a transverse line passing immediately in front of the posterolateral spines, is slightly greater than the total pygidial length. The pygidial rhachis occupies about 60% of the total pygidial length and about 40% of the maximum width of the pygidium. It is subrectangular, constricted at the middle lobe (M2), defined by well impressed dorsal furrows, and truncate behind with a median node on the posterior tip. The dorsal furrow is slightly deepened behind this node. The rhachis is divided into three lobes by two nearly transverse furrows, and crossed by a median ridge which is only faintly outlined on the posterior lobe (M3). M1 and M2 are subequal in length (exsag.). M3 is slightly less than half the length of the rhachis (excluding the articulating half-ring).

The acrolobe is laterally constricted. The pleural fields are smooth, of almost constant width, convex, and slope appreciably laterally and posteriorly; most steeply laterally. The border is convex and downward-sloping laterally. It is extremely wide posterolaterally, narrowing considerably forward and medially. Short posterolateral spines commence on a transverse line across the rear of the pygidial acrolobe. The anterior border is convex (exsag.) adaxially, faceted anterolaterally, and separated from the pleural field by a deep border furrow.

Dimensions (mm)

	Lc	Lbc	Lac	G	N	Wc	Wg
SGU 5466	3·40	0·30	3·10	2·35	1·30	3·00	1·30
SGU 5467	2·90	0·20	2·70	2·05	1·20	2·60	1·20
SGU 5130	2·15	0·20	1·95	1·40	0·80	1·80	0·90

Remarks. The specimens from the Komstad Limestone Formation are specifically indistinguishable from Holub's (1908*a*, *b*) and Pek's (1977) descriptions and illustrations of *Oculagnostus frici* from Bohemia. Although the description of Pek (1977) is adequate, a new description is presented above because additional information is now available. The ocular structures of *O. frici* were recently described by Ahlberg (1988).

Occurrence. Arenig(?)-Llanvirn. Czechoslovakia, Šárka Formation; Scania, southern Sweden, Komstad Limestone Formation (J. G. A. coll. *in situ* and boulder 1; *Asaphus expansus* Zone or basal *A.* '*raniceps*' Zone of the lower Kunda Stage).

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PER AHLBERG

Department of Historical Geology
and Palaeontology
Sölvegatan 13
S-223 62 Lund
Sweden

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