SVERIGES GEOLOGISKA UNDERSÖKNING

SER. Ca AVHANDLINGAR OCH UPPSATSER I 4:o NR 49

PER AHLBERG

AND

JAN BERGSTRÖM

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WITH FOUR PLATES

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Dedicated to
RAGNAR NILSSON
on his 75th birthday

Abstract

Ptychopariid trilobites from the Lower Cambrian of Scandinavia are described. The phylogeny and systematics are discussed. Traditionally they have been regarded as ellipsocephalids, but in this study they are all assigned to the family Solenopleuridae. Most of the material is from Scania (Skåne), south Sweden, the Mjøsa district, southern Norway, the south Bothnian area, and from three localities along the Swedish Caledonides. 16 species belonging to presumably five genera are described. The following genera are revised: *Ellipsocephalus, Strenuaeva* and *Proampyx*. New taxa: *Strenuaeva spinosa* n.sp., *Strenuaeva inflata* n.sp., *Strenuaeva? kullingi* n.sp., *Proampyx grandis* n.sp., *Proampyx sularpensis* n.sp., *Proampyx triangularis* n.sp., *Comluella? scanica* n.sp. Formerly known species are revised and the type specimens are refigured.

CONTENTS

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Introduction

Early Cambrian non-olenellid and non-agnostid trilobites are a fairly important component of the Lower Cambrian faunas in Scandinavia. Traditionally they have been regarded as ellipsocephalids. In this study they are referred to the subfamily Ellipsocephalinae of the family Solenopleuridae. They appear in the middle part of the Lower Cambrian, in Norden in the Zone of *Holmia kjerulfi* (Norway) or *Holmia sulcata* (Scania, Sweden), and it seems as if they partly succeed the olenellids (Fig. 1). The Swedish Middle Cambrian forms are comparatively well described by Westergård (1936, 1948, 1950, 1953), whereas the Early Cambrian species are poorly known. However, the latter have been treated, amongst others, by Linnarsson (1883), Wiman (1903), Moberg (1908), Thorslund & Westergård (1938), and Kautsky (1945), but usually the descriptions are inadequate and the material is often incorrectly determined, both at species and genus level. This condition is partly caused by the commonly fragmentary and poorly preserved material. The non-olenellid and non-agnostid trilo-

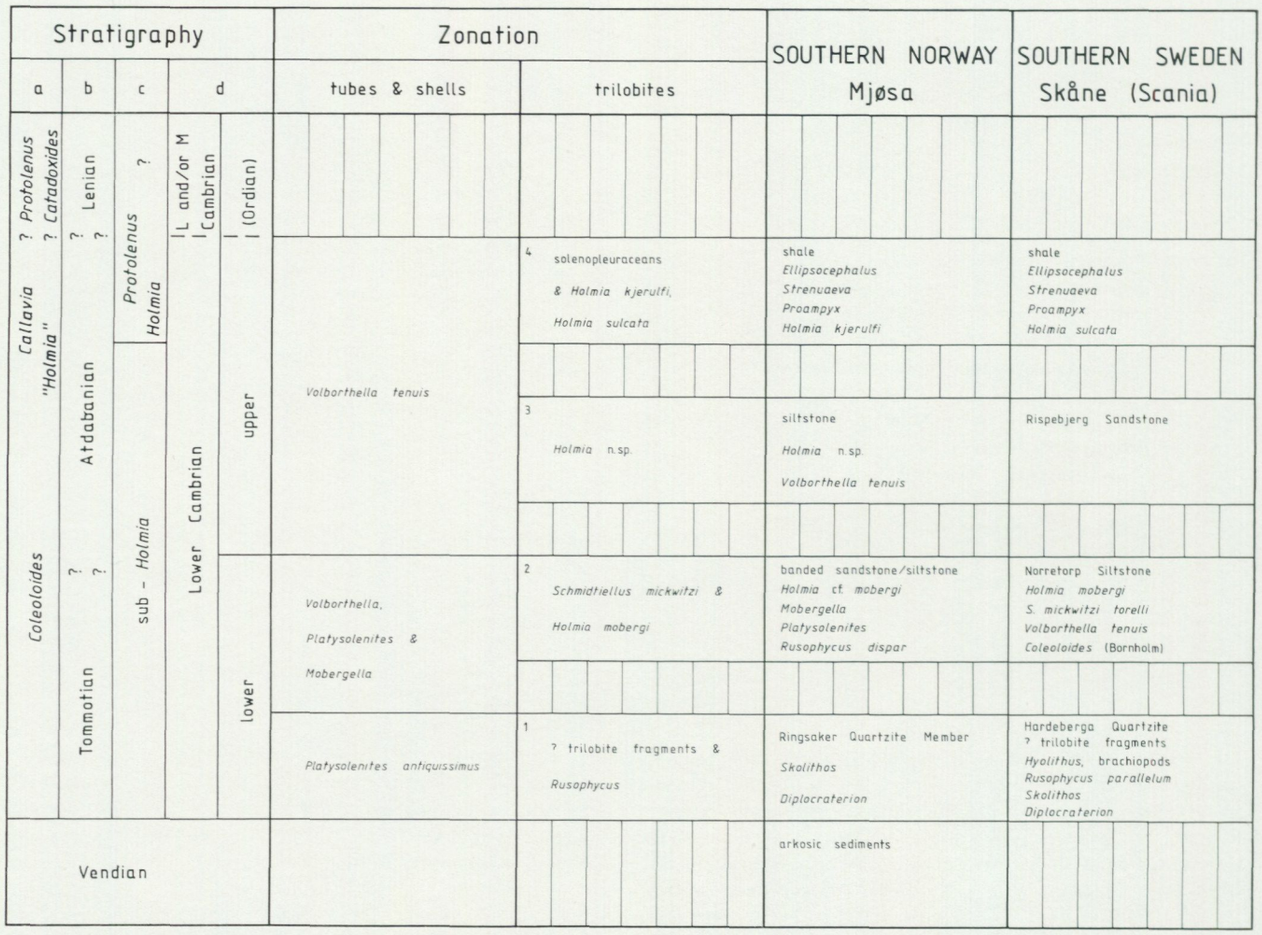


Fig. 1. Lower Cambrian stratigraphy in southern Norway (Mjøsa) and southern Sweden (Scania, Skåne). Note that the *"Strenuella" linnarssoni* Zone and the *Holmia kjerulfi* Zone are united provisionally to form a single zone (4).
a: Britain & Newfoundland
b: Siberia
c: Poland, Germany
d: Scandinavia (Öpik's term Ordian is used provisionally for the interval between the uppermost local Lower Cambrian and the *Eccaparadoxides oelandicus* beds.)

bites from the Lower Cambrian of Norway have been described mainly through the studies of Brøgger (1879), Kiær (1917) and Størmer (1925). A single species, *Proampyx? conifrons,* has been reported from Denmark (Poulsen, 1969).

New studies have led to a redescription or reconsideration of old material, and we have also found it necessary to erect seven new species, although these in some cases are based on poor material.

Although all parts of this paper have been thoroughly discussed between the authors, the bulk of it was prepared by the senior author (P. A.). Only the discussion on general phylogeny and systematics and the chapter on morphological variation was written by the junior author (J. B.). The stratigraphical table was constructed by the junior author.

Material

The trilobites treated here have been collected through almost 100 years in beds which are either fairly unfossiliferous, poorly exposed, or poor with respect to preservation. Although we have been able to collect some new material, museum collections have been a most valuable source for us. The following institutions have generously provided material as loan:

Palaeontological Department, the University of Lund, Lund, Sweden (LM).

Palaeontological Institute, the University of Uppsala, Uppsala, Sweden (PIU).

Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Stockholm, Sweden (RM).

Sveriges geologiska undersökning (Geological Survey of Sweden), Uppsala, Sweden (SGU).

Palaeontological Museum, Oslo, Norway (PMO).

In addition, Dr Stefan Bengtson of Uppsala has kindly lent us a specimen from his collection. Boliden AB, Sweden, provided us with material from Aistjakk, Lappland, northern Sweden.

Terminology

Morphologic terminology, except where specifically noted, follows that of Harrington, Moore & Stubblefield *(in* Moore 1959, pp. O117–O126). The term median keel indicates a poorly marked ridge, which extends longitudinally over the glabella and the occipital ring. Rhachis is used instead of axial lobe (axis), and dorsal furrow instead of axial furrow. The term glabella excludes the occipital ring. The abbreviations 'sag.' (sagittal), 'exsag'. (exsagittal) and 'tr.' (transverse) are used to qualify such words as 'wide', 'long', etc. where such words alone might be misleading.

Measurements

During the measurements the normal projection of the sagittal cranidial length, i. e. the straight line joining the mid-point of the anterior margin of the cranidium to the mid-point of the posterior margin of the occipital ring, was placed horizontally (cf. Temple 1975, p. 463). Subsequently the various distances were measured normal to the horizontal plane using a caliper. The measurements are given in the Appendix, which also shows the ratio of various parameters to the length of the cranidium. The measured parameters are evident from Fig. 2.

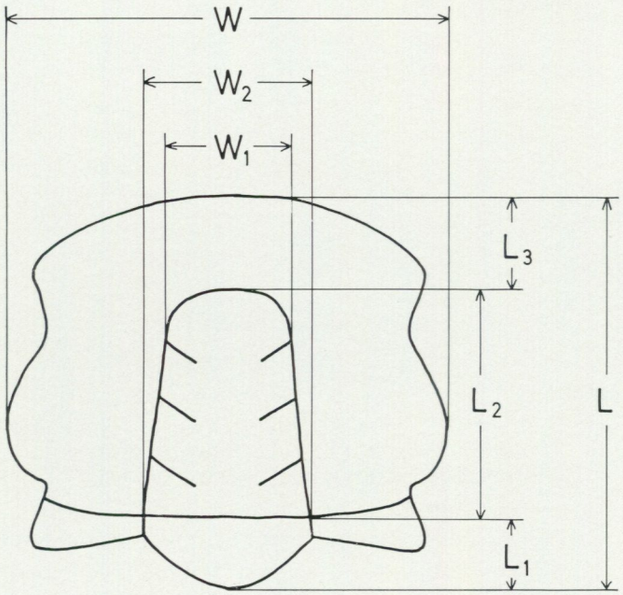


Fig. 2. Generalized ptychopariid cranidium showing the measured parameters.

- L = total length of cranidium
- L_1 = sagittal length of occipital ring
- L_2 = sagittal length of glabella
- L_3 = distance between anterior margin and glabella
- W = width of cranidium across the palpebral lobes
- W_1 = width of anterior part of glabella (at foremost furrows if present)
- W_2 = width of posterior part of glabella (at occipital furrow)

Morphological variation

As indicated by the fact that the trilobites treated here were mostly incorrectly determined in old collections, they are quite difficult to determine. There are several reasons for this, including the generalized "ptychopariod" design and the commonly distorted state of preservation. Here only the morphological variation will be treated. This variation is of two kinds. First, there is a clear phenotypic variation in supposedly adult specimens. Second, there is a pronounced shift in morphology with individual growth, even if truly larval individuals have probably not been encountered.

The general convexity is subject to much deformation and it is difficult to say anything about original variation. However, in some instances there is convincing evidence of decrease of relief with growth. This is well seen in *Strenuaeva inflata* n. sp., where a cranidium 5.0 mm long has strongly elevated fixed cheeks, whereas the corresponding elevations in a cranidium 8.7 mm long are longer but lower. A similar relative decrease in height without a corresponding lengthening of the cheek elevations is seen in a series of cranidia of *Strenuaeva? kullingi* n.sp., measuring 3.3, 4.1 and 9.0 mm in length (Pl. 2, Figs. 7–9). In this series the eye ridges are fairly strong, of intermediate strength, and absent, respectively. The glabella is notably narrower in the smallest specimen than in the others. The relatively stronger relief in the smaller specimens may induce faulty determination. Thus the lectotype cranidium of *Proampyx? balticus* is 20 mm long and has the general appearence of a *Proampyx*, whereas a cranidium 14.7 mm long and most probably belonging to the same species has more relief and may be mistaken for a *Strenuaeva*.

The general outline is deformed with the general convexity, and it is similarly difficult to judge the original variation. The outline of the glabella is less easily deformed. As seen in several species, there is a fair amount of variation in the shape. *Ellipsocephalus gripi*, known from many specimens, has a glabella which may grade from parallel-sided to one with a distinct forward taper. Another example is *Strenuaeva primaeva*, the lectotype of which has a glabella which is more tapering than in most other specimens. A similar variation is found in specimens referred to *Proampyx grandis*. However, most species are known from so few specimens that the amount of variation is not fully appreciated.

Some of the apparent variation and difference is due to the preservation with or without exoskeleton. The internal mould generally has much stronger relief than the exterior surface, as convincingly demonstrated by a specimen of *E. gripi* with one half of the specimen exfoliated (Pl. 1, Fig. 10). Ornamentation is considered an important specific characteristic. However, there is always the possibility that foliation exposes the internal surfaces of the exoskeleton with a false ornamentation.

Phylogeny and systematics

The Lower Cambrian non-olenellid and non-agnostid trilobites in Scandinavia are traditionally regarded as ellipsocephalids. This study shows that there are several distinct genera, and the question arises as to which of these are to be regarded as true ellipsocephalids and which, if any, should belong to other groups. In the latter case the problem is to find a suitable family group. The questions are not so easy to answer. If ellipsocephalids are defined generally as effaced trilobites, one will most probably arrive at a situation where the family consists of distinctly unrelated end members of stocks with parallel evolution in the particular characteristic. A stratigraphical or geographical definition is likewise not likely to be natural. What is really needed is an analysis of the phylogeny of the group(s) of trilobites which is (are) concerned. Only in this way will a natural classification be reached.

No doubt at least most of the trilobites concerned belong to the Solenopleuracea, as defined by Bergström (1973a), i.e., to the stock characterized by the spiral type of enrollment. It is not clear how early the spiral type of enrollment evolved. It was well developed in Early Cambrian *Ellipsocephalus*. The general morphology indicates that it was also developed in Early Cambrian genera like *Antatlasia, Kingaspis, Strenuella,* and *Antagmus,* each a type of a previously defined family group taxon. Spirally enrolling conocoryphids are also represented in the Lower Cambrian, as well as *Periommella,* which seems to belong to this general group.

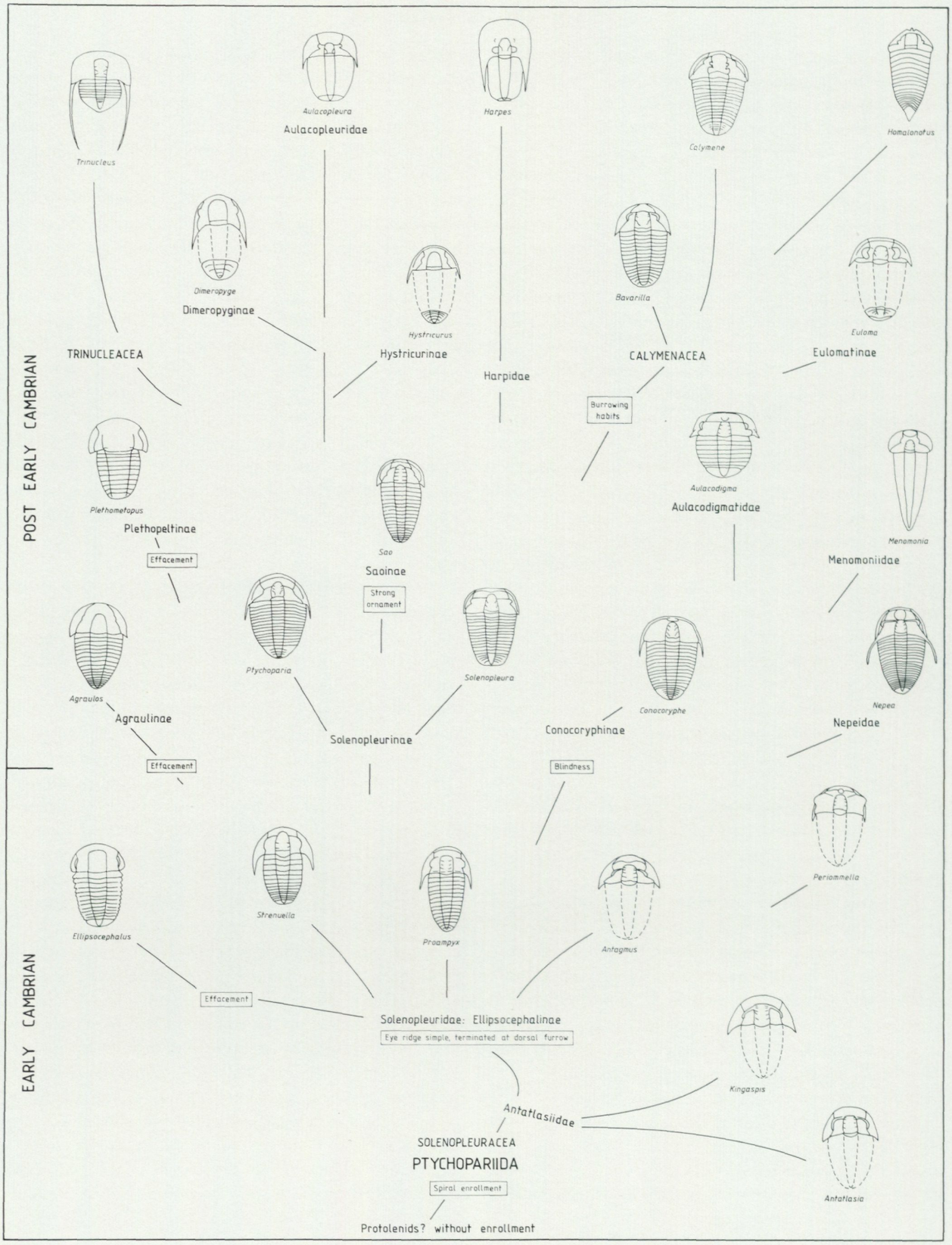
Of these forms, *Antatlasia* and *Kingaspis* have a "primitive" appearence with four to five glabellar furrows and eye ridges which merge with the glabella without being terminated by the dorsal furrows (a feature found in olenellids, redlichiids and some protolenid-type trilobites). These trilobites may have evolved from primitive protolenid-type trilobites with the same characters. However, in the construction of the thorax they are already typical members of the Solenopleuracea. It is possible to keep them in a family of their own, if this is preferrable. Antatlasiidae may be an appropriate name, as Hupé (1953) suggested this group as a family, whereas he regarded the Kingaspidinae as only of subfamily rank. This family should include the basic stock from which all later solenopleuraceans were ultimately derived.

Strenuella and *Antagmus* are spirally enrolling trilobites of the next following organizational level. The number of glabellar furrows has decreased to three pairs in general, with a fourth pair weakly developed in some genera. The dorsal furrows separate the eye ridges from the glabella. *Strenuella* is considered advanced in possessing weak glabellar furrows, and *Antagmus* is advanced in having small eyes, but they are probably sufficiently closely related to be included in the same subfamily. Strenuellinae and Antagmidae were formally erected by Hupé in 1953 and 1955, respectively. *Ellipsocephalus* may have evolved from a general *Strenuella*-like stock with effacement of facial topography. It is possible that *Ellipsocephalus*-like forms have evolved more than once, as e.g. indicated by the Late Cambrian and Early Ordovician "plethopeltids", which were included in the Ellipsocephalacea by Öpik (1967). *Ellipsocephalus* is probably quite close to the *Strenuella* group, and the Ellipsocephalinae MATTHEW, 1887, may be regarded as including *Strenuella* and *Antagmus*.

Periommella is easily derived from *Strenuella*-like forms through lateral displacement of the eyes and added relief. It may be included in the Ellipsocephalinae without inconvenience. It also shows similarities to later forms such as conocoryphids, nepeids and aulacodigmatids, possibly because of affinity.

Conocoryphids are simply blind solenopleuraceans and may have several different origins among forms with eyes. The Lower Cambrian *Atops* may have had an origin in Ellipsocephalinae of generalized appearance, while the Middle Cambrian *Ctenocephalus* and *Elyx* more likely evolved from a *Periommella*-like origin. It is highly questionable whether there is any reason to keep any family-group taxon for any of these forms.

Many Middle Cambrian forms agree closely with their probable *Strenuella* type ancestors and the most common difference lies in the pygidium which had added segments and grown larger. The general outline is maintained and it is still significantly wider than long in most instances. As noted by Westergård (1953, pp. 8–9) the family type genera *Ptychoparia* and *Solenopleura* appear to be closely related and there is probably no reason to keep them in separate subfamilies. Solenopleurinae ANGELIN, 1854, clearly has priority over Ptychopariinae MATTHEW, 1887. *Sao* seems to be closely allied but may represent a well recognizeable group with distinct ornamentation. *Nassovia* is poorly known and may be a solenopleurinid or ellipsocephalinid. Other Middle Cambrian type genera are members of allied but morphologically distinct groups. Examples are *Bolaspis, Nepea, Menomonia,* and *Aulacodigma. Agraulos* is considered primitive in that it retains a small pygidium, and it probably


POST EARLY CAMBRIAN
EARLY CAMBRIAN
Trinucleus
Aulacopleura
Aulacopleuridae
Harpes
Calymene
Homalonotus
Dimeropyge
Dimeropyginae
Hystricurus
Hystricurinae
Bavarilla
CALYMENACEA
Eloma
Eulomatinae
TRINUCLEACEA
Harpidae
Burrowing habits
Plethometopus
Plethopeltinae
Effacement
Sao
Saoinae
Strong ornament
Aulacodigma
Aulacodigmatidae
Menomonia
Menomoniidae
Ptychoparia
Solenopleura
Agraulos
Agraulinae
Solenopleurinae
Conocoryphe
Conocoryphinae
Nepea
Nepeidae
Blindness
Periommella
Ellipsocephalus
Strenuella
Proampyx
Antagmus
Solenopleuridae: Ellipsocephalinae
Eye ridge simple, terminated at dorsal furrow
Kingaspis
Antatlasiidae
SOLENOPLEURACEA
PTYCHOPARIIDA
Spiral enrollment
Antatlasia
Protolenids? without enrollment

stems directly from Early Cambrian ellipsocephalinids. It also shows at least superficial similarities with *Antatlasia*.

Two problems remain: where to place *Proampyx* and *Strenuaeva* in this plexus and where to draw boundaries between families. As to the first, the Middle Cambrian forms of *Proampyx* (synonymized with *Agraulos)* have been regarded as unquestioned solenopleurids. In the Lower Cambrian, they have been characterized as ellipsocephalids, in accordance with general practice. Actually, the morphology is closely comparable with that of several ellipsocephalinids. The similarities include a forked posterior glabellar furrow (S1), also found in, e.g. *Antagmus, Onchocephalus* and *Proliostracus* as well as in the later calymenids. This character in *Proampyx* was thought by Sdzuy (1966) to indicate relationship to olenids, but as all glabellar features it is due to occur in unrelated groups through convergent evolution. The probable derivation of separate "solenopleurid" groups directly from Early Cambrian *Strenuella*-type trilobites raises the question if the Solenopleuridae in the sense of the Treatise (Moore *et al.* 1959) are a polyphyletic assemblage; we tend to believe that this is the case. Also *Strenuaeva* may be derived from a general ellipsocephalinid stock. The origin may be close to that of *Ellipsocephalus*.

Regarding the systematics, there seem to be two main possibilities: either each subfamily may form a distinct family, or the central plexus may form a comprehensive family. At present it seems impossible to sort out the plexus around *Strenuella–Antagmus–Ellipsocephalus–Agraulos–Nassovia–Ptychoparia–Solenopleura–Conocoryphe* into natural phylogenetic units, and it may be best to include them all in one family. The oldest available names for this group are Solenopleuridae ANGELIN, 1854, and Conocoryphidae ANGELIN, 1854. As the blind *Conocoryphe* is unsuitable as a representative type and the group of blind forms obviously polyphyletic, Solenopleuridae is preferred as a name. Subfamilies based on the above-mentioned genera may be distinguished, but the later ones particularly are likely to be polyphyletic. Much work is needed to map the detailed phylogeny before any reliable systematics can be obtained.

Solenopleuraceans including the post-Cambrian aulacopleurids and hystricurids were generally conservative in cephalic configuration, i.e. they kept much of the generalized appearance found in their protolenid-type ancestors. This is the reason why "ptychopariids" are regarded as the general stock from which most later trilobites evolved. It is also the reason for the common lumping of aulacopleurids and the also generalized proetids. However, solenopleuraceans did not preserve the generalized structure of thorax and pygidium found in protolenids. Instead they show a specialized departure from the morphology and function found in other trilobite groups except for calymenaceans and trinucleaceans, and they are difficult to regard as general trilobite ancestors (Bergström 1973a, 1977).

SYSTEMATIC DESCRIPTIONS

Family *SOLENOPLEURIDAE* ANGELIN, 1854

Spirally enrolling trilobites of "ptychoparioid" design. Cephalon usually with well defined, tapering glabella and commonly with transverse eye ridges. There is a tendency to develop a preglabellar boss. Facial suture usually opisthoparian. Labral plate probably isolated from rostral plate, at least as a rule. Thorax tapering, usually with at least 10 segments and with short, blunt pleural spines. Pygidium usually small and transverse and without marginal spines.

Systematics cannot be truly "natural" as long as the evolutionary history is not known in any detail, although this is the aim. There is a certain probability or even plausibility that subdivision of the Solenopleuridae as here defined will create groups that represent evolutionary levels rather than evolutionary lineages, at least at the present level of knowledge. This is perhaps the main reason why we chose provisionally to regard the Solenopleuridae as a comprehensive family including a number of groups previously considered as indepen-

Fig. 3. Tentative phylogeny of solenopleuracean trilobites. The origin is likely to have been in protolenid-type trilobites which were similar to early solenopleuraceans in cephalic aspects but lacked enrollment adaptations. Much of the morphological uniformity is connected with functional adaptations to spiral enrollment needs. Modified types of spiral enrollment occur in members of some late groups, such as the trinucleaceans, dimeropygids and homalonotids. Dr John Shergold of Canberra (personal communication) stressed that particular morphologies (such as the effaced cephalic morphology in different trilobites) may be due to environmental factors more than to relationships. A close connection between habitat and morphological aspects such as ornamentation and glabellar morphology was exemplified by Bergström (1973b, p. 198).

dent families. A separation into subfamilies at present must be provisional but may be preferrable for practical purposes. Such a subdivision may be as follows:

Subfamily *ELLIPSOCEPHALINAE* MATTHEW, 1887 (= Antagminae, Strenuellinae)
Subfamily *CONOCORYPHINAE* ANGELIN, 1854 (probably not including all blind forms)
Subfamily *AGRAULINAE* RAYMOND, 1913
Subfamily *SOLENOPLEURINAE* ANGELIN, 1854 (= Ptychopariinae MATTHEW, 1887)
Subfamily *SAOINAE* HUPÉ, 1955
Subfamily *PLETHOPELTINAE* RAYMOND, 1924
Subfamily *EULOMATINAE* KOBAYASHI, 1955
Subfamily *DIMEROPYGINAE* HUPÉ, 1955
Subfamily *HYSTRICURINAE* HUPÉ, 1955

Groups like the Nepeidae, Aulacodigmatidae, Menomoniidae, Entomaspididae and Harpidae may be considered sufficiently distinct to be regarded as monophyletic families. The Antatlasiidae (= Kingaspidinae) differs in preserving primitive features and is separated into a distinct family.

Subfamily *ELLIPSOCEPHALINAE* MATTHEW, 1887

Early solenopleurids with a dorsal furrow separating the eye ridge from the glabella, simple or bifurcated glabellar furrows, commonly comparatively large eyes, and a small, transverse pygidium.

Genus *Ellipsocephalus* ZENKER, 1833

TYPE SPECIES. – *Trilobites hoffi* SCHLOTHEIM, 1823.

EMENDED DIAGNOSIS. – The outline of the cephalon is semicircular. The glabella is fairly wide and parallel-sided or somewhat constricted in the middle. However, in some species it slightly narrows forwards. The glabella is bluntly rounded in front or pointed to form an obtuse angle. Lateral glabellar furrows are absent or faintly marked. In some species the occipital ring joins with the glabella, in others it is separated from the glabella by an occipital furrow. The dorsal furrows and the preglabellar furrow are weakly impressed. The palpebral lobes are long, reaching back to the posterior border furrow. The anterior sections of the facial suture commonly diverge slightly forward. The posterior sections of the facial suture are shorter than the anterior sections. The anterior border is strongly downsloping. The eye ridges (if present) form a boundary between a low terrace in front (the anterior border) and a distinctly higher fixigenal terrace. Eye ridges are absent or faintly marked. The occipital ring is short (sag.) with a rounded posterior margin. Occipital spine or node absent. The fixigenae are comparatively wide (tr.) and extend almost horizontally outward. The free cheeks are narrow (tr.). Genal spines are not present in holaspidids. The number of thoracic tergites is 12–14. There is a deep pleural furrow on all pleura. A well marked fulcrum is also present in all pleura. The pygidium is very small and wide in comparison with its length (sag.). The pygidial axis tapers strongly and extends to or almost to the posterior margin of the pygidium.

INCLUDED SPECIES. – *Trilobites hoffi* SCHLOTHEIM, 1823; *Calymene lejostraca* ANGELIN, 1851; *E. polytomus* LINNARSSON, 1877; *E. nordenskioeldi* LINNARSSON, 1883; *E. galeatus* MATTHEW, 1892; *E. grandis* MATTHEW; *E. vetustus* POMPECKJ, 1896; *E. latus* WIMAN, 1903; *Strenuella (Ellipsostrenua) gripi* KAUTSKY, 1945; *E. leonicus* SDZUY, 1958; *Ellipsostrenua alanisana* SDZUY, 1961; *E. snajdri* SDZUY, 1966; *E. guerichi* ORLOWSKI, 1959; *E. puschi* ORLOWSKI, 1959; *E. sandomiri* ORLOWSKI, 1959; *E. jugoszovi* ORLOWSKI, 1959; *E. longus* ORLOWSKI, 1959.

REMARKS. – Šnajdr (1958) gave a detailed diagnosis of the genus and it agrees fairly well with that presented above. On the basis of *E. germari* BARRANDE from the Middle Cambrian of Bohemia, Šnajdr (1958) erected the genus *Germaropyge* of the family Ellipsocephalidae, thereby following Lake (1940) who excluded *E. germari* from the genus *Ellipsocephalus*. On the other hand, Richter & Richter (1940, p. 39) and Westergård (1950, p. 10) stressed that the mentioned species is a typical representative of the genus *Ellipsocephalus*. Orlowski (1975a) also maintains that *E. germari* should be retained in *Ellipsocephalus*. However, the species differs from species referred to *Ellipsocephalus* in several respects (see Šnajdr 1958, pp. 247–248) and the separation of the genus *Germaropyge* seems to be motivated.

In this study *Ellipsostrenua* is considered as a junior synonym of *Ellipsocephalus*, as the type species, *E. gripi* KAUTSKY, 1945, seems to be a typical member of the genus *Ellipsocephalus* (see p. 17).

Ellipsocephalus nordenskioeldi LINNARSSON, 1883
Pl. 1, Figs. 1–4

v 1883 *Ellipsocephalus nordenskiöldi* n.sp. – Linnarsson, pp. 20–21, Pl. 4, Figs. 1–2.

1890 *Ellipsocephalus nordenskoldi.* – Walcott, Pl. 97, Fig. 4.
v non 1908 *Ellipsocephalus Nordenskiöldi* LINRS. – Moberg, p. 27, Pl. 1, Figs. 6–7.
v non 1917 *Ellipsocephalus Nordenskiöldi* LNRS. – Kiær, pp. 41–44, Pl. 4, Figs. 7–8, Pl. 5, Figs. 11–13.
v non 1917 *Ellipsocephalus Nordenskiöldi* LNRSN. – Troedsson, pp. 617–618.
1931 *Ellipsocephalus nordenskiöldi* Linnarsson. – Cobbold, Pl. 39, Fig. 22.
?1962 *Ellipsocephalus nordenskjöeldi?* Lnr. – Samsonowicz, p. 12, Pl. 4, Fig. 1.
non 1975b *Ellipsocephalus nordenskjoeldi* Linnarsson, 1883. – Orlowski, pp. 381–382, Pl. 1, Figs. 3–4, Pl. 2, Figs. 1–4.

MATERIAL. – Apart from Linnarsson's (1883) originals, there are nine complete but somewhat flattened cranidia, the impression of an almost complete specimen lacking only the librigenae, and the posterior part of a deformed cranidium with eight articulated thoracic tergites. In addition there are about 40 more or less fragmentary and often distorted cranidia. In all specimens the exoskeleton is missing. About half of the material is deposited at the Geological Survey of Sweden. The rest is preserved in the collections of the Palaeontological Department, the University of Lund, Lund. The material is from the Lower Cambrian "greywacke shale" at Forsemölla, eastern Scania, south Sweden, and the greater part is collected by S. A. Tullberg (1878), G. von Schmalensee (1879), N. O. Holst (1889), and Tellander (1902). The other collectors are unknown.

LECTOTYPE. – The cranidium figured by Linnarsson 1883, Pl. 4, Fig. 2 (SGU Type 3); selected herein.

DISTRIBUTION. – The species is known with certainty only from the "greywacke shale" at Forsemölla in Andrarum, eastern Scania, south Sweden, where it occurs in the same horizon as *Holmia sulcata* BERGSTRÖM and *Proampyx rotundatus* (KIÆR) (for further information regarding the locality, see Regnéll 1960, pp. 38–39). This arenaceous shale is usually correlated with the Zone of *Holmia kjerulfi* in Norway, but this should not be taken for granted (cf. Bergström 1973c, p. 293). According to Westergård (1929, p. 13), *E. nordenskioeldi,* and also *Holmia kjerulfi?,* was collected by G. C. von Schmalensee from the shore line 600 m north of Gislövshammar or 1 km south of Brantevik, eastern Scania, south Sweden. Unfortunately we have not been able to confirm Westergård's determinations. Apart from Scania, south Sweden, the species is reported from Luopakte, Torneträsk, northern Sweden (Moberg 1908), Tømten, Ringsaker, Norway (Kiær 1917) and Poland (Samsonowicz 1962; Orlowski 1975b), but from the discussion below it follows that the trilobites from these localities cannot be considered identical with the Scanian species.

DIAGNOSIS. – *Ellipsocephalus* species with fairly long (exsag.), wide (tr.) and raised palpebral lobes. There are three pairs of shallow lateral glabellar furrows. The posterior border is comparatively short (tr.), and the postero-lateral corners of the cranidium are rounded.

DESCRIPTION. – The cranidium is comparatively flat, and its length is somewhat less than the maximum width (across the palpebral lobes). The anterior sections of the facial suture diverge forward. The glabella is delimited laterally by very slightly impressed dorsal furrows and is almost parallel-sided. In some specimens it is somewhat narrower between the palpebral lobes. The anterior end of the glabella is bluntly rounded or slightly pointed to form an obtuse angle. The length of the glabella is considerably larger than the width. Transversely it is moderately convex, sagittally somewhat less convex. The convexity in the sagittal line increases forwards. The anterior end of the glabella slopes fairly steeply towards the preglabellar furrow, whereas the posterior end slopes more gently towards the occipital furrow. The glabella is provided with three pairs of shallow, lateral glabellar furrows which in some specimens are hardly visible. They are directed inward-backward from the distal ends and situated at an almost equal distance from each other. The occipital furrow is deep and the course is straight or with a slight backward curvature. The occipital ring has an evenly rounded posterior margin. The length (sag.) of the occipital ring is about one-third of the width (tr.). Transversely it is moderately convex. Sagittally it slopes very gently backwards. There is no occipital spine or node.

The preglabellar furrow touches the anterior end of the glabella and from that point extends obliquely outward-backward. The furrow becomes wider laterally and extends parallel to the anterior margin. In some specimens the preglabellar furrow is almost effaced. The anterior border is strongly bent down in the anterior part. The length (sag.) of the anterior border is about one-sixth the length of the cranidium. There is no anterior border furrow. The fixigenae including the palpebral lobes are narrower (tr.) than the width of the glabella (1:1.3) and they extend almost horizontally outward. Inside the palpebral lobes the fixigenae are very slightly vaulted. The palpebral lobes are fairly long (exsag.), wide (tr.) and commonly markedly raised. Transversely they are convex. Their outer margin is slightly bent in the anterior part, becoming progressively more curved backwards until the posterior end is directed straight

inwards at the posterior border furrow. Forward they attain the height of the foremost furrows of the glabella and from that point one can usually follow a faint eye ridge extending inwards towards the frontal lobe of the glabella, but not into it. The posterior border is relatively short (tr.), somewhat more than half the length of the occipital furrow, and extends outward almost as far as the palpebral lobes. Proceeding outwards from the occipital ring it increases in width laterally, as does the limiting and well defined posterior border furrow. The posterior border is depressed below the level of the fixigena. The posterior margin is directed outwards and very slightly backwards. The postero-lateral corners of the cranidium are rounded.

The number of thoracic tergites is 14 in a complete specimen. In transverse section the rhachis is moderately convex but markedly elevated above the pleural fields. It continuously tapers backwards and the width is about one-third the width of the thorax. The adaxial half portion of the pleura is of uniform width (exsag.) and the margins are directed perpendicularly outwards from the rhachis. Distal to the fulcrum they are bent down and from that point they also diminish in width and terminate in a slender, somewhat posteriorly directed spine. The pleural furrows are wide and distinct. They commence just outside the dorsal furrows and are deepest at the fulcrum. The furrows extend outward to about midway between the fulcrum and the tip of the pleura. Each tergite in the rhachis is furnished with a deep furrow which separates the axial ring from the articulating half-ring. The pygidium is very small with a triangular rhachis which is divided into two parts (segment + telson?) by a transverse furrow. The pleural fields of the pygidium are not preserved.

DIMENSIONS. – The length of the cranidia ranges from 8.4 to 17.3 mm. The results of the other measurements are given in the Appendix.

REMARKS. – Linnarsson's (1883) description of *E. nordenskioeldi* agrees very well with the present material. However, one of his two figures (Pl. 4, Fig. 2, lectotype) is furnished with a prominent preglabellar furrow and a markedly tapering glabella. A study of his original shows that the illustration is misleading and that the preglabellar furrows is not so distinct. Nor does the glabella taper so much on the original as indicated in the figure. This was also pointed out by Kautsky (1945, p. 193). Consequently, we cannot agree with Wiman (1903, p. 44) who proposed that Linnarsson's Pl. 4, Fig. 2 might be referred to *Strenuaeva primaeva,* and Kiær (1917, pp. 40, 43) who stated that it is probably a *Strenuella* species, most closely related to his *"S." linnarssoni*. According to Linnarsson (1883), the maximum number of thoracic tergites seems to be 12. However, in an almost complete specimen preserved in the Palaeontological Department in Lund there are 14 thoracic tergites.

Troedsson (1917) has reported *E. nordenskioeldi* from the uppermost Lower Cambrian at Hardeberga, S. Sandby, east of Lund, south Sweden. However, his specimens have proved to belong to *Proampyx sularpensis* n.sp.

Kiær (1917) has reported *E. nordenskioeldi* from Tømten, Ringsaker, Norway, and according to him it occurs both in the Zone of *Holmia kjerulfi* and in the Zone of *"Strenuella" linnarssoni*. An examination of his originals shows that they are not identical with the species from southern Sweden. The most obvious difference is the absence of markedly raised and prominent palpebral lobes in the Norwegian specimens. In general, Kiær's (1917) specimens most resemble *E. gripi,* and they should preferably be referred to that species.

From Luopakte, Torneträsk, northern Sweden, Moberg (1908) has reported *E. nordenskioeldi*. We have examined his two originals and it is quite obvious that they are completely different from *E. nordenskioeldi* and cannot be referred to the species. On the cranidia of Moberg's specimens the dorsal furrows are deeply impressed and the fixigenae are highly vaulted and slope inward. Furthermore, the glabella is transversely more convex than in *E. nordenskioeldi* and a fairly well marked anterior border furrow is also present. In all probability, Moberg's two specimens do not even belong to *Ellipsocephalus*. Herein they are questionably referred to the genus *Comluella.*

Cobbold (1931, Pl. 39, Fig. 22) figured an *E. nordenskioeldi* from the "greywacke shale", Forsemölla, eastern Scania, south Sweden, which conforms in all respects with the description above. The raised palpebral lobes are well visible.

Samsonowicz' (1962, Pl. 4, Fig. 1) *E. nordenskioeldi?* from the *Protolenus* beds in the Klimontów anticlinorium, Holy Cross Mountains, Poland is restricted to a very poorly preserved cranidium which besides being poorly illustrated lacks a description. Hence, a confident determination is not possible. According to Orlowski (1975b), *E. nordenskioeldi* occurs in the Lower Cambrian of SW Poland together with *Strenuaeva primaeva* and *Schmidtiellus panowi*. However, his specimens can hardly be referred to *E. nordenskioeldi*. Judging from his figures they differ in possessing deeper dorsal furrows and a shallower occipital furrow than *E. nordenskioeldi*. Furthermore, the preglabellar furrow does not run paral-

lel with the anterior margin and the postero-lateral corners of the cranidium seem to be sharply pointed.

In the longer (exsag.), wider (tr.) and more raised palpebral lobes, *E. nordenskioeldi* differs from the Middle Cambrian *E. polytomus* and *E. lejostracus*. Besides, the cranidium of *E. nordenskioeldi* is sagittally less convex than in the two mentioned species. This condition can of course be the effect of compression. Another distinguishing feature is that the glabellar furrows commonly are not visible in *E. polytomus* and *E. lejostracus*. Furthermore, Westergård (1950, p. 13) mentioned that in *E. nordenskioeldi* the anterior corners of the cranidium are less angulate and in the thorax the pleura terminate in somewhat stronger spines than in *E. lejostracus*. The Middle Cambrian *E. hoffi* from Bohemia is easily distinguished from *E. nordenskioeldi* in the absence of glabellar furrows, less prominent palpebral lobes and in the presence of a faint anterior border furrow. In *E. hoffi* the glabella is also somewhat constricted in the middle and consequently it slightly widens at the anterior corners. This feature is less distinct in *E. nordenskioeldi*. The pleural spines are shorter in *E. hoffi* than in *E. nordenskioeldi*. The difference between *E. nordenskioeldi* and *E. latus* from the south Bothnian area are discussed under the latter.

Ellipsocephalus latus WIMAN, 1903
Pl. 1, Fig. 5

v 1903 *Ellipsocephalus latus n.sp.* – Wiman, pp. 44–45, Pl. 1, Figs. 22, 24.
v 1962 *Ellipsocephalus latus* Wim. – Kautsky, Pl. 2, Fig. 4.

MATERIAL. – Two cranidia figured by Wiman 1903, Pl. 1, Figs. 22, 24. They are almost complete and represent internal moulds with fragments of the exoskeleton retained.

LECTOTYPE. – The cranidium figured by Wiman 1903, Pl. 1, Fig. 22 (SGU Type 6); selected herein.

DISTRIBUTION. – The species is known from glacial erratics from Dorfe Öfverby in the parish of Jomala, Åland, an archipelago in the Baltic Sea.

DIAGNOSIS. – *Ellipsocephalus* species with wide (tr.) fixigenae, parallel-sided glabella, deeply impressed posterior border furrow and faintly marked occipital furrow. Lateral glabellar furrows are absent. The outer margin of the palpebral lobes are strongly curved.

DESCRIPTION. – The width (tr.) of the cranidium greatly exceeds its length. The anterior sections of the facial suture are directed forward to very slightly outward. The antero-lateral corners of the cranidium are rounded. The glabella is of high convexity both sagittally and transversely. It is parallel-sided and delimited laterally by very weakly impressed dorsal furrows. The anterior end of the glabella is bluntly rounded on the lectotype, in the other specimen it is pointed to form an obtuse angle. The length of the glabella is larger than the width. Lateral glabellar furrows are not present. The occipital furrow is faintly marked. The occipital ring is short (sag.) with a rounded posterior margin. Transversely it is highly convex.

Transversely the anterior border is moderately convex and bent down. The anterior margin is evenly rounded. In the foremost part of the anterior border there are traces of terrace lines. The fixigenae including the palpebral lobes are wide (tr.), almost as wide as the width of the glabella. They slope gently down to the palpebral lobes. The length of the palpebral lobes are somewhat less than half the length of the glabella. They are not raised. The outer margin of the palpebral lobes is strongly curved. The posterior border is depressed below the level of the fixigena. The posterior border furrow is deeply impressed. The posterior border extends outwards a bit longer than the palpebral lobes. The postero-lateral corners are pointed.

REMARKS. – The species differs from *E. nordenskioeldi* in having considerably wider (tr.) fixigenae, longer (tr.) posterior border, and in the absence of lateral glabellar furrows. Furthermore, the palpebral lobes are not distinctly raised and the occipital furrow is faint in *E. latus,* distinguishing it from *E. nordenskioeldi*. In the convexity of the cranidium, as well as in the shape of the glabella, the species resembles the Middle Cambrian *E. polytomus*. However, it differs from this species in having wider fixigenae, deeper impressed posterior border furrow and stronger curved palpebral lobes.

Ellipsocephalus gripi (KAUTSKY, 1945)
Pl. 1, Figs. 6–10

v?1917 *Ellipsocephalus Nordenskjöldi* LNRS. – Kiær, pp. 41–44, Pl. 4, Figs. 7–8, Pl. 5, Figs. 11–13.
1945 *Strenuella (Ellipsostrenua) gripi* nov. spec. – Kautsky, pp. 162–195, Pl. 11, Fig. 1, Pl. 13, Figs. 8–12, Pl. 14, Figs. 6–8, Pl. 15, Figs. 1–8, Pl. 16, Figs. 1–14, Pl. 17, Figs. 4–8, Pl. 18, Figs. 1–9.
1959 *Ellipsostrenua gripi* KAUTSKY, 1945. – Henningsmoen (*in* Moore), p. O207, Fig. 150/7.
1962 *Strenuella gripi* Kauts. – Kautsky, Pl. 1, Figs. 1–4, Pl. 3, Figs. 4–12, Pl. 4, Figs. 1–6. Pl. 5, Figs. 4–6.
?1972 *Ellipsostrenua* cf. *gripi* Kautsky. – Lendzion, p. 130, Pl. 3, Figs. 16–17.

v 1973a *Ellipsocephalus (Ellipsostrenua) gripi* Kautsky. – Bergström, p. 27, Pl. 4, Fig. 9 (shows a spirally enrolled specimen).

MATERIAL. About 70 cranidia and some disarticulated thoracic tergites (belonging to Boliden AB, Sweden), an enrolled specimen (RM Ar. 9030), a cranidium with at least 13 articulated thoracic tergites (RM Ar. 9042), and a cranidium with the right librigena and eight incomplete, articulated thoracic tergites (RM Ar. 9034). The specimens are commonly distorted though the exoskeleton is preserved in a majority of them. The above-mentioned material was collected by F. Kautsky at Assjatj (Aistjakk), Lappland, northern Sweden. Additional material includes three deformed cranidia which seem to conform with *E. gripi*. These specimens, occurring together with *Holmia kjerulfi* in the same lump of rock, were collected by Professor G. Henningsmoen in 1976 from a concretion found in situ on the shoreline of the River Glomma, Østre Åbu, south of Rena, Hedmark, Norway. The specimens from Tømten, Ringsaker, Norway, by Kiær (1917) referred to *E. nordenskioeldi,* but here considered as probably belonging to *E. gripi,* have also been examined during the present study.

LECTOTYPE. – The cephalon with eight incomplete thoracic tergites, figured by Kautsky 1945, Pl. 14, Fig. 7 (RM Ar. 9034); selected herein. The specimen is somewhat compressed laterally.

DISTRIBUTION. – The species is known from lenses of anthraconite at Assjatj (Aistjakk), about 4 km east of the village of Laisvall, Lappland, northern Sweden. Kautsky (1945) compared the bed with the Zone of *Proampyx ("Strenuella") linnarssoni* in Norway, but there is nothing to clearly indicate the correlation. There occurs an olenellid, *'Fallotaspis' ljungneri* (KAUTSKY), together with *E. gripi*.

As mentioned above, the species or a very closely related form also appears to occur in the Zone of *Holmia kjerulfi* at the River Glomma, Norway. If the specimens by Kiær (1917) assigned to *E. nordenskioeldi* are conspecific with *E. gripi,* then the species also occurs at Tømten, Ringsaker, Norway.

According to Lendzion (1972), the species or a related form designated as *E.* cf. *gripi* occurs in the *Holmia* Zone in the Podlasie area in Poland. The preservation does not allow a confident determination.

DESCRIPTION. – There is considerable variation exhibited by the material, to a great deal this is caused by deformation. It must also be observed that the relief of the cranidium is much more pronounced on internal moulds than on specimens retaining the exoskeleton, i.e. the preglabellar furrow, the dorsal furrows, the occipital furrow, etc. are more prominent on the internal moulds (see Pl. 1, Fig. 10). This is probably a feature characteristic of most or all solenopleurids, but it is particularly well seen in the good material of *E. gripi*.

The cranidial width across the palpebral lobes is somewhat larger than the cranidial length. Sagittally, the cranidium is usually rather highly convex. The exoskeleton is smooth except for terrace lines on the anterior border. In some specimens one can also observe small, closely spaced pits on and in front of the glabella and on the occipital ring. The glabella is either slightly narrowing forwards or parallel-sided. It is rounded in front. The length of the glabella is larger than its width. It is commonly moderately convex both sagittally and transversely. There are three pairs of short, lateral glabellar furrows. However, in specimens retaining the exoskeleton they are absent or hardly visible. The two posterior pairs are directed inward to slightly backward while the foremost pair generally is transverse or, as in some specimens, directed inwards to slightly forwards from the distal ends. The occipital furrow is deep and distinct on internal moulds. In specimens with the exoskeleton preserved it is considerably shallower and often ill defined. The occipital ring is of moderate length (sag.) with a rounded posterior margin. There is no indication of any occipital node or spine. The preglabellar furrow is shallow, particularly when the exoskeleton is preserved. Occasionally it is almost effaced. The dorsal furrows of the cranidium are generally rather well impressed on internal moulds.

The anterior border is strongly downsloping. The anterior sections of the facial suture diverge forward. The anterior margin is evenly rounded. The fixigenae are narrower (tr.) than the width of the glabella, and they generally slope gently outwards. On internal moulds they are slightly elevated above the dorsal furrows and the palpebral lobes. The general outline of the raised field of the fixigenae is rectangular. In specimens retaining the exoskeleton they are hardly raised above the palpebral lobes and the dorsal furrows. Eye ridges are not present. The posterior border widens outwards. The free cheeks are narrow (tr.). In holaspidids the genal spines are strongly reduced to absent. The rhachis is moderately convex (tr.), and the width is commonly somewhat larger than one-third of the width of the thorax. The pleural furrows are deep, particularly on internal moulds.

For a more detailed description we refer the reader to Kautsky (1945). The enrollment (spiral enrollment) is described by Bergström (1973a, p. 27).

REMARKS. – On the basis of *E. gripi,* Kautsky (1945) established the subgenus *Ellipsostrenua* of the genus *Strenuella* MATTHEW. However, the species differs widely from *Strenuella strenua* (BILLINGS, 1874), the type species of the genus *Strenuella,* in having the anterior border strongly downsloping, in the absence of a raised convex rim anteriorly and in the absence of eye ridges. Furthermore, the glabella is parallel-sided or just slightly narrowing forwards in *E. gripi,* distinguishing it from species referred to the genus *Strenuella* in which the glabella tapers distinctly. Also the direction of the anterior sections of the facial suture, which diverge forwards in *E. gripi,* indicates that it is not a *Strenuella* species.

Subsequent authors, Henningsmoen (*in* Moore 1959), Sdzuy (1961), Rushton (1966) and Poulsen (1969), have treated *Ellipsostrenua* as a distinct genus of the subfamily Ellipsocephalinae. However, *E. gripi* strongly resembles species of the genus *Ellipsocephalus* in the general outline, shape and relief of the cranidium, the direction of the facial suture, the convexity of the glabella, the long palpebral lobes, and in the shape of the anterior border. Also the thoracic tergites and the librigenae are very similar to those in species referred to *Ellipsocephalus*. Commonly the glabella tapers slightly in *E. gripi,* but in many specimens it is parallel-sided, and this feature can hardly serve to distinguish this species from species assigned to *Ellipsocephalus*. Consequently, *Ellipsostrenua* must be regarded as a junior synonym of *Ellipsocephalus*.

The specimens described by Kiær (1917) as *E. nordenskioeldi* from Tømten, Ringsaker, Norway, appear to be closely comparable to Aistjakk material of *E. gripi,* and they should probably be referred to this species. Kiær's specimens are generally rather poorly preserved and somewhat deformed, and hence a definite determination is hard to deliver. In one of Kiær's (1917, Pl. 5, Fig. 13) specimens the exoskeleton is preserved, and it conforms in almost all respects with *E. gripi* from the type locality. The other specimens represent internal moulds and correspondingly they show considerable similarities with internal moulds of *E. gripi* from Aistjakk, particularly when the fixigenae and the palpebral lobes are concerned.

Genus *Strenuaeva* RICHTER & RICHTER, 1940

TYPE SPECIES. – *Arionellus primaevus* BRØGGER 1879.

Richter & Richter (1940) erected *Strenuaeva* as a new subgenus of the genus *Strenuella* MATTHEW. However, in 1941 it was raised to full generic level by the same authors. A diagnosis was given by Richter & Richter (1940). The following features appear to be typical for the genus and may constitute an emended diagnosis: The dorsal furrows of the cranidium are prominent and commonly deeply impressed, as is the preglabellar furrow which extends outwards towards the sides. The anterior border and the fixigenae are inflated. The glabella is very well defined, comparatively narrow and fairly blunt in front. It narrows forwards. Lateral glabellar furrows are commonly present. The occipital furrow is well marked. The palpebral lobes are fairly long (exsag.) and the anterior sections of the facial suture diverge forward. A distinct feature in the type species is also the long (sag.) occipital ring.

Species referred to the genus *Triangulaspis* LERMONTOVA, 1940 (syn. *Angusteva* HUPÉ, 1953) share some characters with *Strenuaeva.* However, as also noted by Sdzuy (1962, p. 208), they differ from *Strenuaeva* in possessing a smaller and more pointed glabella, fainter glabellar furrows, fainter occipital furrow, and in the presence of alae on the posterior part of the fixigenae. Thus, it cannot be regarded as a synonym of *Strenuaeva,* as was stressed by Richter & Richter (1942, p. 988). The genus *Hindermeyeria* HUPÉ, 1953, on the other hand, should be regarded as a synonym of *Strenuaeva* (Henningsmoen 1957; Sdzuy 1961, 1962).

INCLUDED SPECIES. – *Arionellus primaevus* BRØGGER, 1879; *Strenuella (Strenuaeva) sampelayoi* RICHTER & RICHTER, 1940; *Strenuaeva sampelayoi moratrix* SDZUY, 1958; *Strenuaeva incondita* SDZUY, 1961; *Strenuaeva orlowinensis* SAMSONOWICZ, 1959; *Strenuaeva marocana* HUPÉ, 1953; *Strenuaeva inflata* n.sp.; *Strenuaeva spinosa* n.sp.; probably also *Strenuaeva? kullingi* n.sp.

*Strenuaeva primaev*a (BRØGGER, 1879)

Pl. 2, Figs. 1–2, Text – Fig. 4?

1873 *Arionellus* sp. – Kjerulf, p. 83, Figs. 7–9.
1879 *Arionellus primaevus*, n.sp. – Brøgger, p. 58.
v non 1883 *Arionellus primaevus* BRÖGGER. – Linnarsson, pp. 21–22. Pl. 4, Figs. 3–4.
v 1917 *Strenuella primaeva* BRØGGER. – Kiær, pp. 31–38, Pl. 4, Figs. 3–4, Pl. 5, Figs. 1–5.
v? 1917 *Strenuella primaeva* BRØGGER. – Kiær, Pl. 5, Fig. 6 (labral plate).
1940 *Strenuella (Strenuaeva) primaeva primaeva* (BRÖGGER). – Richter & Richter, p. 40, Pl. 3, Figs. 54–55.
non 1959 *Strenuaeva primaeva* (Brögger). – Samsonowicz, pp. 521–522, Pl. 1, Figs. 1–9.

1959 *Strenuaeva primaeva* (BRØGGER). – Henningsmoen *(in* Moore), p. O207, Fig. 149/3.
non 1962 *Strenuaeva primaeva* (Brögg.). – Samsonowicz, p. 11, Pl. 2, Figs. 1–7, Pl. 3, Figs. 1–5.
non 1972 *Strenuaeva primaeva* (Brögger). – Lendzion, pp. 132–133, Pl. 4, Figs. 3–11.
non 1973 *Strenuaeva primaeva* (Brögger). – Orlowski, p. 368, Pl. 1, Fig. 1.
non 1975 b *Strenuaeva primaeva* (Brögger, 1879). – Orlowski, p. 381, Pl. 1, Fig. 2.

MATERIAL. – The cranidia figured by Kiær 1917, Pl. 4, Figs. 1–4, Pl. 5, Figs. 1–5, and four cranidia collected by the authors in 1977. In addition there are two cranidia and the incomplete labral plate (hypostome) figured and described by Kiær 1917, p. 35, Pl. 5, Fig. 6. However, it is impossible to determine whether the labral plate belongs to *S. primaeva*. All cranidia represent internal or external moulds.

LECTOTYPE. – The cranidium figured by Kiær 1917, Pl. 4, Fig. 3 (PMO 73153); selected by Richter & Richter (1940, p. 40). It is an internal mould of a comparatively large, almost complete cranidium.

DISTRIBUTION. – The species is known with certainty only from the Lower Cambrian *Holmia* Shale (Zone of *Holmia kjerulfi)* at Tømten, Ringsaker, Norway.

DESCRIPTION. – The length of the cranidium is slightly less than the maximum width (across the palpebral lobes). The anterior sections of the facial suture are directed forward-outward. The glabella is delimited laterally by deeply impressed dorsal furrows. It is comparatively narrow and tapers continuously forwards. The length of the glabella is somewhat larger than the maximum width (at the occipital furrow). The anterior end is fairly bluntly rounded. In transverse section the glabella is highly convex, sagittally it is of very low convexity. There are three pairs of short lateral glabellar furrows situated at an almost equal distance from each other. The two posterior pairs are commonly distinct and directed inward-backward, whereas the foremost is shallower and runs perpendicularly to the sagittal line. The occipital furrow is fairly narrow but commonly fairly deep and distinct. The course is straight. The occipital ring is strongly extended backwards and its posterior margin forms a semicircle. The length (sag.) of the occipital ring is somewhat less than half the width (tr.). Transversely it is highly convex, sagittally it commonly slopes gently backwards. There is no indication of any occipital node.

The preglabellar furrow is wide and deep and extends in an arc in front of the glabella and laterally in an arc or almost straight outwards towards the sides in front of the eye ridges. It is deepest lateral to the anterior end of the glabella where it is united with the dorsal furrow. In front of the glabella it is shallower and somewhat narrower. The anterior border is vaulted and the length (sag.) is about two-thirds the length of the glabella. It is moderately convex both sagittally and transversely. The anterior margin is slightly pointed to form an obtuse angle and for that reason the anterior border acquires a triangular outline. The fixigenae, including the palpebral lobes, are of about the same width (tr.) as the posterior width of the glabella. They are highly vaulted and attain almost the same level as the glabella. The dorsal furrows are of uniform width and are deeply impressed. The palpebral lobes commence at the posterior border furrow and extend in an arc forward until they attain about the same height as the foremost glabellar furrow and from that point one can usually follow a faintly marked eye ridge running inward toward the frontal lobe of the glabella without passing the dorsal furrow. The posterior border furrow extends almost perpendicularly outwards from the dorsal furrow. The posterior border increases somewhat in width (exsag.) outwards and extends almost as far as the palpebral lobe. The postero-lateral corners are rounded. The posterior border is depressed below the level of the fixigena.

DIMENSIONS. – It is a fairly small species; the length of the cranidia ranges from 2.2 to 11.2 mm. There are no major morphological differences between the smaller and the larger specimens.

REMARKS. – The specimens figured by Kiær 1917, Pl. 4, Figs. 1–2, are preserved in a calcareous sandstone and they differ widely from the specimens preserved in the shale. According to Kiær (1917, p. 33), the shale specimens are considerably deformed by compression and the fixigenae and the anterior border have been pressed upwards. However, there is evidence of only moderate compression in the shale specimens and as the specimens in the calcareous sandstone apart from their

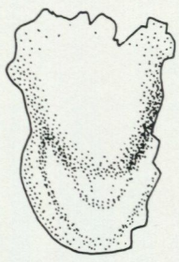


Fig. 4. Labral plate ("hypostome") from the *Holmia* Shale at Tømten, Ringsaker, Norway. Figured by Kiær 1917, Pl. 5, Fig. 6. PMO 73161. X 30.

high convexity also differ from the shale specimens in a wider (tr.) glabella, shallower dorsal furrows and a shorter (sag.) occipital ring, we can not include them in the species *S. primaeva*.

Apart from Norway, the species has been reported from Scania (Linnarsson 1883; Troedsson 1917) and Torneträsk (Moberg 1908) in Sweden and from various districts in Poland (Samsonowicz 1959, 1962; Lendzion 1972; Orlowski 1973, 1975b). The Scanian material belongs to *Strenuaeva* sp., *Proampyx rotundatus* and the new species *Proampyx grandis*. These forms are described herein. Moberg's (1908) specimens from Torneträsk, northern Sweden, have proved to be two new forms, *Proampyx triangularis* n.sp. and *Strenuaeva inflata* n.sp. The material from the Holy Cross Mountains in Poland, described and illustrated by Samsonowicz (1959, 1962), differs in several respects from *S. primaeva,* e.g. more pointed glabella, less impressed dorsal furrows, wider (sag.) occipital furrow, and a shorter (sag.) occipital ring. Neither the specimen from the Goczalkowice borehole, Upper Silesia, Poland (see Orlowski 1975b, Pl. 1, Fig. 2) can be referred to *S. primaeva*. The specimens from the Podlasie depression in Poland (see Lendzion 1972, Pl. 4, Figs. 3–11; Orlowski 1973, Pl. 1, Fig. 1) are commonly poorly preserved, but they seem to be more close to *S. primaeva*. However, they differ in possessing a less tapered glabella, shorter occipital ring and a uniformly rounded anterior margin. Unfortunately the Polish material has not been available for examination during the present study.

Strenuaeva spinosa n.sp.
Pl. 2, Figs. 3–4

HOLOTYPE. – SGU Type 8. It is an internal mould of a cranidium lacking the right fixigena. The posterior part of the occipital spine is broken off.

OTHER MATERIAL. – Internal moulds of three almost complete cranidia, belonging to the Geological Survey of Sweden. The occipital spine is complete in one specimen.

TYPE HORIZON AND LOCALITY. – The type specimen was collected by O. Kulling in 1966 from a grey "kjerulfi-shale" about 1 km WSW of the settlement known as the eastern Dellekgården, in the eastern wall of the brook Torbäcken. Dellekgårdarna (deserted) are situated about 3 km west of the southern extremity of Lake Storlaisan (about 17 km SSW of the village of Laisvall), Lappland, northern Sweden. Data according to Kulling's 1966 fieldnotes.

DISTRIBUTION. – The species is known only from the type locality and horizon.

DIAGNOSIS. – *Strenuaeva* species with a prominent occipital spine. The preglabellar furrow is as deep as the dorsal furrows.

DESCRIPTION. – The cranidial width across the palpebral lobes is larger than the total length (exclusive of the occipital spine). The anterior sections of the facial suture are directed forwards to very slightly outwards. As a whole the cranidium is comparatively flat. The glabella is delimited laterally by deeply impressed dorsal furrows. It narrows forwards and the anterior end is rounded. The posterior width of the glabella is less than its length. The length of the glabella is somewhat larger than half the cranidial length (the occipital spine excluded). It is moderately convex both ways. The anterior end slopes steeply towards the preglabellar furrow. There are three pairs of lateral glabellar furrows. The two posterior pairs are almost transverse, the foremost pair is directed inwards to slightly forwards from the distal ends. The occipital furrow is distinct and the course is straight. The occipital ring is provided with a long occipital spine. The length of the spine is almost the same as the length (exsag.) of the palpebral lobes.

The preglabellar furrow is deeply impressed throughout. It runs in front of the glabella and then outwards in an arc towards the sides. The furrow delimits a laterally somewhat narrower (exsag.) anterior border which is moderately convex sagittally. Transversely it is of low convexity. The distance between the anterior margin and the glabella is slightly less than half the length of the glabella. The fixigenae, including the palpebral lobes, are somewhat narrower (tr.) than the posterior width of the glabella. They are fairly strongly vaulted. The vaulted field of the fixigena extends forward until it attains the height of the frontal lobe of the glabella. The palpebral lobes commence at the posterior border furrow and extend in a uniform arc forwards. They are slightly raised and set off from the fixigenae by a palpebral furrow. Faint eye ridges are present. The posterior border furrow is wide and deep. The posterior border slightly widens outwards and is depressed below the level of the fixigenae. The postero-lateral corners are rounded and slightly downsloping.

REMARKS. – The most striking difference between this form and *S. primaeva,* as well as other species referred to the genus *Strenuaeva,* is in the presence of an occipital spine in the former. Furthermore, it differs significantly from *S. primaeva* in its deeper preglabellar furrow and in the shape of the glabella and the fixigenae.

Strenuaeva inflata n.sp.
Pl. 2, Figs. 5–6

v 1908 *Arionellus primaevus* BRÖGG. – Moberg, p. 26, Pl. 1, Fig. 3.

HOLOTYPE. – LO 5330 T, preserved in the Palaeontological Department, the University of Lund, Lund. It is an internal mould of an almost complete cranidium, collected by J. Bergström in 1977.

OTHER MATERIAL. – An internal mould of a cranidium, figured by Moberg 1908, Pl. 1, Fig. 3 (LM LO 2103 t), and a laterally compressed, almost complete cranidium. These two cranidia were collected by J. C. Moberg in 1908.

TYPE HORIZON AND LOCALITY. – Layer 23, profile II, Luopakte, Torneträsk, northern Sweden (Moberg 1908).

DISTRIBUTION. – The species is known only from the type locality and horizon.

DIAGNOSIS. – *Strenuaeva* species with strongly inflated fixigenae and deeply impressed dorsal furrows of the cranidium. Also the anterior border is strongly inflated. The occipital ring is fairly long (sag.) with a rounded posterior margin.

DESCRIPTION. – The length of the cranidium is less than its maximum width. The glabella is delimited laterally by deeply impressed dorsal furrows. It tapers forward and the anterior end is rounded. Three pairs of short lateral glabellar furrows are slightly indicated. The occipital ring is comparatively long (sag.) and separated from the glabella by a well marked occipital furrow. The posterior margin of the occipital ring is rounded. The preglabellar furrow is well impressed and extends outwards towards the sides in front of the fixigenae where it is deeper. The anterior border is strongly inflated. Transversely, it is highly convex. The dorsal furrows are deeper than the preglabellar furrow. The fixigenae are very strongly inflated, especially in the smallest specimen, and they almost attain the same level as the glabella. Eye ridges are present but faintly marked. The palpebral lobes and the posterior border is depressed below the level of the fixigenae. The anterior sections of the facial suture diverge slightly forward.

REMARKS. – The species differs from other known species of *Strenuaeva* in having much deeper dorsal furrows and more inflated fixigenae. The occipital ring is fairly similar to that of *S. primaeva*. The glabellar furrows and the eye ridges are less distinct than in *S. primaeva*, but this can be due to the poor state of preservation. The convexity (sag.) of the glabella is higher than in *S. primaeva*.

Strenuaeva? kullingi n.sp.
Pl. 2, Figs. 7–9, Text – Fig. 5

HOLOTYPE. – SGU Type 10. It is an internal mould of a complete, slightly flattened cranidium.

OTHER MATERIAL. – Internal moulds of three complete cranidia, which are considerably smaller than the holotype. Collected by O. Kulling in 1966.

TYPE HORIZON AND LOCALITY. – Same as for *Strenuaeva spinosa* n.sp., i.e. from a grey "kjerulfi-shale" about 4 km west of the southern extremity of Lake Storlaisan (about 17 km SSW of the village of Laisvall), Lappland, northern Sweden.

DISTRIBUTION. – The species is known with certainty only from the type locality and horizon.

DESCRIPTION. – The cranidial width across the palpebral lobes is slightly larger than the length. The glabella is delimited by well or comparatively well impressed dorsal furrows. It narrows forwards and is either rounded in front or forms an obtuse angle. The width of the glabella at the occipital furrow is less than the length. The length of the glabella is larger than half the cranidial length. Transversely, it is moderately to highly convex. The anterior end slopes steeply towards the preglabellar furrow. There are three pairs of distinct lateral glabellar furrows. The posterior is directed inwards to slightly backwards from the distal ends, whereas the two anterior pairs are approximately transverse. The occipital furrow is wide and deeply cut. The length (sag.) of the occipital ring is about one-third of its width. It is comparatively longer (sag.) in the small specimens. The posterior margin of the occipital ring is evenly rounded.

The preglabellar furrow is slightly impressed but distinct. Transversely, the anterior border is moderately convex and it is downsloping. There is a faint anterior border furrow which extends parallel with the anterior margin. However, this is not visible in the holotype. The distance from the anterior margin to the glabella is about one-fifth the length of the cranidium. The anterior margin is very slightly pointed to form an obtuse angle. The anterior sections of the facial suture diverge forwards. The fixigenae, including the palpebral lobes, are narrower (tr.) than the posterior width of the glabella (1:1.5). They are slightly to moderately vaulted. The palpebral lobes are flat, as in the holotype, or slightly

raised. They are depressed below the level of the fixigenae. They commence at the posterior border furrow and extend in an arc forwards until they attain the height of the foremost glabellar furrow. Eye ridges, extending from the anterior end of the palpebral lobes towards the frontal lobe of the glabella, are well visible in the small specimens. They are not present in the holotype. The posterior border widens outwards. It is depressed below the level of the fixigena. The posterolateral corners of the cranidium are rounded.

ONTOGENY. – In the available material there are considerable differences between the small specimens and the largest (holotype). These differences are presumedly the result of morphological differences between the various growth stages. It appears as if the eye ridges become weaker with the enlargement of the exoskeleton and are absent in the largest cranidium. There is also a decrease in depth of the dorsal furrows and elevation of the fixigenae with growth. In the small specimens there is a faint anterior border furrow which is not present in the largest cranidium. The glabella is markedly narrow in the smallest specimen.

REMARKS. – This species seems to be intermediate between *Ellipsocephalus* and *Strenuaeva*. The relief of the cranidium is not as pronounced, especially in the holotype, as in species referred to *Strenuaeva*. In the convexity of the cranidium, this form shows similarities to *Ellipsocephalus nordenskioeldi*. However, the small specimens actually have many characters in common with *Strenuaeva* and we questionably refer it to that genus.

Strenuaeva sp.
Pl. 2, Fig. 10

v 1883 *Arionellus primaevus* BRÖGGER. – Linnarsson, p. 21, Pl. 4, Fig. 3.

MATERIAL. – An internal mould of an almost complete cranidium, figured by Linnarsson 1883, Pl. 4, Fig. 3. The specimen belongs to the Geological Survey of Sweden.

LOCALITY AND HORIZON. – The Lower Cambrian "greywacke shale" at Forsemölla in Andrarum, eastern Scania, south Sweden.

DESCRIPTION. – The length of the cranidium is less than its maximum width (across the palpebral lobes). The anterior sections of the facial suture are directed forwards to slightly outwards. The glabella is prominent and raised above the fixed cheeks. It is tapered forwards and the length is somewhat larger than its posterior width. The anterior end is rounded. Transversely, the glabella is highly convex, sagittally it is of low convexity. It is provided with three pairs of short lateral glabellar furrows. The foremost is almost effaced, whereas the two posterior pairs are distinct. They are directed medially and very slightly backwards from the distal ends. The straight occipital furrow is wide (sag.) and deep, with the deepest part in the middle. The occipital ring is strongly extended backwards and its posterior margin is rounded. Transversely, it is highly convex. The length (sag.) of the occipital ring is about half its maximum width. There is no indication of any occipital spine or node.

The anterior border is partly destroyed, but evidently it has been highly vaulted. It descends steeply outwards

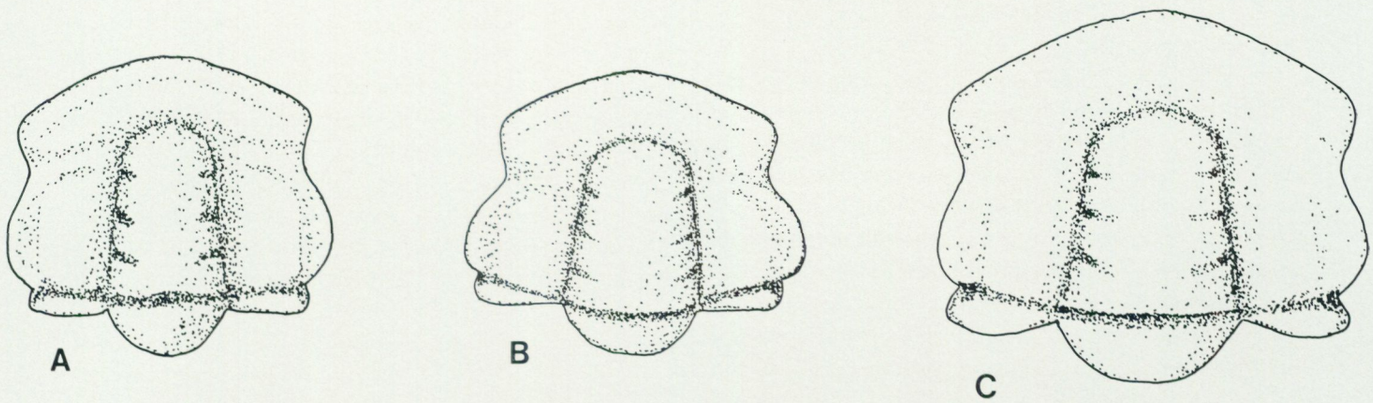


Fig. 5. *Strenuaeva? kullingi* n.sp. Drawings based on the three specimens figured on Pl. 2, Figs. 7–9. Note the presence of eye ridges in the two smaller specimens (A & B). A: SGU Type 12. X 13. B: SGU Type 11. X 10. C: Holotype, SGU Type 10. X 5.

and forwards and is posteriorly separated by a furrow running from the glabella outwards in front of the fixigenae. The furrow widens laterally. In front of the glabella it is shallow and consequently the glabella appears to continue into the vaulted anterior border. The fixigenae, including the palpebral lobes, are narrower (tr.) than the glabella. They are slightly vaulted and the vaulted portion of the fixigenae extends like a ridge inwards-forwards from behind. Distinct dorsal furrows are absent. The palpebral lobes are depressed below the level of the fixigenae. Their outer margin is slowly bent anteriorly, becoming progressively more curved backwards, until the posterior end is directed straight inwards at the posterior border furrow. The posterior border widens laterally and is delimited by a distinct posterior border furrow. It is depressed below the level of the fixigena.

REMARKS. – This form differs from the type species, *S. primaeva,* in having less vaulted fixigenae and in the absence of defined dorsal furrows.

Genus *Proampyx* FRECH, 1897

TYPE SPECIES. – *Proetus? difformis* var. *acuminatus* ANGELIN, 1851.

EMENDED DIAGNOSIS. – The relief of the cranidium in general is moderate and all its furrows tend to be effaced on the exterior surface of the exoskeleton. The glabella is slightly tapered forwards and commonly truncated or rounded in front. Three, exceptionally four, pairs of shallow lateral glabellar furrows are mostly present on internal moulds. The posterior glabellar furrow (S1) is bifurcated in some species. The glabella is commonly provided with a faintly marked median keel. The occipital ring is usually fairly long (sag.) and in some species provided with an occipital node. The posterior margin of the occipital ring is evenly rounded or obtusely pointed, exceptionally extended into a spine. An occipital furrow is present.

Eye ridges are commonly well marked on internal moulds. In front of the glabella and the eye ridges there is typically a wide, comparatively shallow furrow. The anterior border is long (sag.) and it commonly protrudes forward. The anterior border is not strongly bent down anteriorly. Transversely, it is convex. The anterior margin is uniformly rounded or pointed to an angle. The palpebral lobes are comparatively long (exsag.). The anterior sections of the facial suture typically diverge slightly forwards. The fixigenae and the posterior border usually slope gently outwards. The dorsal furrows of the cranidium are shallow, almost effaced in specimens of Middle Cambrian forms retaining the exoskeleton.

INCLUDED SPECIES. – *Proetus? difformis* var. *acuminatus* ANGELIN, 1851; *Proetus? difformis* ANGELIN, 1851; *Proetus? difformis* var. *aculeatus* ANGELIN, 1851; *Agraulos anceps* WESTERGÅRD, 1953; *Strenuella primaeva* var. *rotundata* KIÆR, 1917; *Strenuella linnarssoni* KIÆR, 1917; *Proampyx agra* ÖPIK, 1961; *Proampyx grandis* n.sp.; *P. sularpensis* n.sp.; *P. triangularis* n.sp.; probably also *Arionellus balticus* WIMAN, 1903 and *Ellipsostrenua conifrons* POULSEN, 1969.

REMARKS. – On the basis of *Proampyx acuminatus,* in which the cranidial front is prolonged into a cusp, Frech (1897, p. 66) erected the genus *Proampyx,* as he incorrectly believed it to be a forerunner of the genus *Ampyx*. The Middle Cambrian forms from Scandinavia, *P. difformis, P. aculeatus, P. acuminatus* and *P. anceps,* were assigned to the genus *Agraulos* by Westergård (1953). Šnajdr (1958, p. 174) questionably placed *P. acuminatus* and *P. anceps* in the genus *Agraulos,* while *P. difformis* and *P. aculeatus* were positively referred to *Agraulos*. However, the four species are apparently closely related and the differences between them are essentially confined to the presence or absence of a frontal cusp or an occipital spine. The cranidial front is quite variable and in cases it can be difficult to separate the species. It is also worth noting that the species occur together in the same zone at the same locality, and from a strict biological point of view they may be varieties of a single species.

Öpik (1961) concluded that the differences between *Agraulos ceticephalus* (type species for the genus *Agraulos)* and the species mentioned above are so striking that he found it reasonable to place them in a distinct genus, *Proampyx*. As noted by Öpik (1961), the palpebral lobes are considerably longer (exsag.) in *Proampyx* than in *Agraulos,* and in *Proampyx* the anterior sections of the facial suture diverge slightly forward, whereas they converge in the genus *Agraulos*. Furthermore, the pygidium is larger, at least in some species referred to *Proampyx*. A median keel is present in most species referred to the genus *Proampyx*. This feature is not as distinct in *Agraulos*. In our opinion, the separation of *Proampyx* as a distinct genus seems to be motivated. The general morphology of the genus is similar to ellipsocephalinids such as *Antagmus, Onchocephalus* and *Proliostracus*.

Proampyx rotundatus (KIÆR, 1917)
Pl. 3, Figs. 1–2

v 1883 *Arionellus primaevus* BRÖGGER. – Linnarsson, p. 22, Pl. 4, Fig. 4.
v 1917 *Strenuella primaeva* var. *rotundata* nov.var. – Kiær, p. 38.
? 1929 *Strenuella primaeva rotundata* KIÆR. – Westergård, p. 13.

MATERIAL. – The flattened cranidium figured by Linnarsson 1883, Pl. 4, Fig. 4 (holotype, SGU Type 14). Further, there is a complete cranidium with the anterior part of the right librigena and its counterpart, two complete cranidia and three fragmentary cranidia. All specimens represent internal moulds and come from the type locality and horizon.

TYPE LOCALITY AND HORIZON. – The Lower Cambrian "greywacke shale" at Forsemölla in Andrarum, eastern Scania, south Sweden.

DISTRIBUTION. – The species is known with certainty only from the type locality and horizon where it occurs in the same horizon as *Ellipsocephalus nordenskioeldi*. If the form designated by Westergård 1929, p. 13, as *Strenuella primaeva rotundata,* is identical with the specimens from the type locality, then it is also known from an unnamed formation above the Rispebjerg Sandstone on the shore line 600 m north of Gislövshammar or about 1 km south of Brantevik, eastern Scania, south Sweden. Unfortunately, we have not been able to confirm Westergård's determination.

DIAGNOSIS. – A species of *Proampyx* with a tapered glabella, rounded in front. The length of the glabella is equal to its posterior width. The occipital ring is fairly long (sag.) and its posterior margin is uniformly rounded. The postero-lateral corners of the cranidium are rounded. Occipital node, occipital spine, median keel and eye ridges are absent.

DESCRIPTION. – The width of the cranidium across the palpebral lobes is somewhat larger than the total length. The anterior sections of the facial suture are directed forwards to very slightly outwards. The cranidium as a whole is of comparatively low convexity which partly can be due to compression. The glabella is delimited laterally by faintly marked, weakly impressed dorsal furrows. It diminishes in width forward and the anterior end is rather bluntly rounded. The maximum width at the occipital furrow is equal to its length. The length of the glabella is half the total cranidial length. Sagittally it is of low convexity, transversely it is moderately convex. Three pairs of straight glabellar furrows, directed medially and slightly backwards from the distal ends, are barely observable in two specimens. The posterior of these is most distinct. In the other specimens the glabellar furrows are effaced. The occipital furrow is comparatively deep, possibly deepest laterally, and is transverse or with only an indication of a backward curvature (this feature can be the effect of compression). The occipital ring is fairly long (sag.), and its posterior margin is uniformly rounded. The length (sag.) of the occipital ring is somewhat less than half its width. Transversely it is moderately convex, sagittally it slopes gently backwards. There is no indication of any occipital node or median keel.

In front of the glabella there runs a rather broad, shallow furrow outwards-backwards towards the sides. It becomes shallower and wider laterally and delimits a wide (sag.), laterally, only somewhat narrower, anterior border, which is of low convexity sagittally. The anterior border is moderately convex transversely. The width (sag.) of the anterior border is about one-fourth the length of the cranidium. The anterior margin is evenly rounded. In one specimen (LM LO 5331 t), the doublure is visible along the anterior margin and its width (sag.) is about one-third of the width (sag.) of the anterior border. Its posterior margin is complete and there is no indication ot any attachment of a labral plate ("hypostome"). The fixigenae, including the palpebral lobes, are considerably narrower (tr.) than the posterior width of the glabella (1:1.4). They are very slightly vaulted and slope gently towards the sides. Distinct eye ridges are absent. The palpebral lobes are not raised and are fairly short (exsag.), about half the length of the glabella. Their outer margin is slowly curved anteriorly, becoming progressively more curved backwards until the posterior end is directed straight inwards at the posterior border furrow. The posterior border is short (tr.), almost half the length of the occipital furrow, and laterally it is slightly downsloping. It widens laterally, as does the delimiting posterior border furrow. The postero-lateral corners are rounded and depressed below the level of the fixigenae.

REMARKS. – This species was originally described by Linnarsson (1883, p. 22, Pl. 4, Fig. 4) as an *Arionellus primaevus* BRØGGER (= *Strenuaeva primaeva).* However, he noted that it differed widely from *S. primaeva,* but believed it to be an old individual. Subsequently, Kiær (1917, p. 38) designated Linnarsson's specimen as a new variety, *S. primaeva* var. *rotundata.* However, apart from its larger size the species is easily distinguished from *S. primaeva* in the shallower dorsal furrows, wider glabella and less vaulted fixigenae and anterior border. We do not believe that these differences can be due to

the age. On the other hand, the species shows considerable similarities to species referred to the genus *Proampyx*. These similarities include, i.a., the shape of the anterior border and the morphology of the glabella and, therefore, we assign the species to this genus.

It differs from the Middle Cambrian *P. difformis, P. aculeatus, P. acuminatus* and *P. anceps,* in having a stronger tapering and anteriorly less truncate glabella, shorter (sag.) anterior border and in the absence of an occipital node, median keel and distinct eye ridges. Furthermore, in *P. rotundatus* the anterior margin is evenly rounded, whereas it is pointed to an angle or prolonged into a cusp in the species mentioned above. The Lower Cambrian *P. grandis* n.sp. is distinguished from *P. rotundatus* in having a subtriangular occipital ring and a longer, more convex and more pointed glabella. In *P. grandis* there are also distinct eye ridges, a median keel and a small occipital node, distinguishing it from *P. rotundatus*. *P. linnarssoni* (KIÆR, 1917) from Norway is provided with more distinct eye ridges and lateral glabellar furrows, and a shorter (sag.) occipital ring than the present species. The Lower Cambrian *P.? conifrons* (POULSEN, 1969) from the boring Slagelse no. 1, Western Sealand, Denmark, is perhaps of about the same age as *P. rotundatus* and shows some similarities with the latter in the general outline and shape of the cranidium. However, it differs in possessing a narrow (sag.), slightly marked and raised rim anteriorly, and a longer glabella. *P. agra* ÖPIK from the Middle Cambrian of Queensland, Australia, differs from *P. rotundatus* in the parallel-sided glabella, longer and more diverging posterior sections of the facial suture, pointed postero-lateral corners, and longer (tr.) posterior border. Moreover, there is a vestigial median keel in *P. agra.*

Proampyx grandis n.sp.
Pl. 3, Figs. 7–8

v 1917 *Arionellus primaevus* BRÖGGER. – Troedsson, p. 617.
? 1929 *Strenuella* aff. *linnarssoni* KIÆR. – Westergård, p. 14 (at the very top of the page).
? 1944 *Strenuella* aff. *linnarssoni* KIÆR. – Westergård, pp. 26, 29.

HOLOTYPE. – LO 5336 T, preserved in the Palaeontological Department, the University of Lund, Lund.

OTHER MATERIAL. – 18 more or less complete cranidia. The exoskeleton is partly preserved in seven of these. None of the cranidia is entirely complete. Additional material includes 12 cranidial fragments. The above-mentioned material was collected by G. T. Troedsson at the type locality. Included in the species are also about ten imperfect and poorly preserved cranidia in loose boulders collected by J. C. Moberg in 1892, J. Bergström in 1972 and the present authors in 1976, from the shoreline between Brantevik and Gislövshammar, eastern Scania, south Sweden. There are also four cranidia from "Gislöv", which probably means the Brantevik-Gislövshammar region, collected by G. C. v. Schmalensee in 1877.

TYPE HORIZON AND LOCALITY. – The type specimen was collected by G. T. Troedsson in the uppermost Lower Cambrian (the fragment limestone in Troedsson's 1917, section II) at Hardeberga, S. Sandby, east of Lund, Scania, south Sweden.

DISTRIBUTION. – The species is known from the type locality and horizon. Moreover it is known from loose boulders ("greywacke shale") on the shoreline between Brantevik and Gislövshammar, eastern Scania, south Sweden. These boulders, which consists of a grey shale with interstratified calcareous layers, belong to an unnamed formation above the Rispebjerg Sandstone. Probably it is also the same species that Westergård (1944, pp. 26, 29) designated as *Strenuella* aff. *linnarssoni* KIÆR in a drilling core from Gislövshammar, where, according to Westergård, it occurs in the same horizon as *Hyolithellus* cf. *micans* BILLINGS.

DIAGNOSIS. – *Proampyx* species with a subtriangular occipital ring and a markedly tapering glabella which is highly convex in transverse section. The eye ridges and the median keel are commonly prominent. The exoskeleton is finely pitted.

DESCRIPTION. – The cranidial width across the palpebral lobes is about the same as the sagittal cranidial length. The sculpture of the exoskeleton consists, at least on the fixigenae where it is best preserved, of fine pits. The anterior sections of the facial suture are directed forward and slightly outward. The glabella is surrounded laterally by weakly impressed dorsal furrows or it is set off from the fixed cheeks by its convexity alone. It is markedly tapered forwards, especially in the frontal lobe and the anterior end is acutely rounded or angulate. The maximum width of the glabella at the occipital furrow is somewhat less than its length (1:1.2). The length of the glabella is larger than half the total cranidial length (1:1.8). Transversely it is highly convex and markedly raised above the fixigenae. Sagittally it is moderately convex, but in the anterior end it usually slopes steeply towards the preglabellar furrow. There are three pairs of lateral glabellar furrows, directed inwards-backwards from the distal ends. They are shallow and in some spe-

cimens hardly visible. Particularly the foremost furrow is faint. In the sagittal line a characteristic median keel extends across the glabella. In poorly preserved specimens this is almost effaced.

The occipital furrow is very broad and deep on internal moulds. If the exoskeleton is retained it is only faintly marked. The course of the furrow is straight. The occipital ring is strongly extended backwards and its margins runs in a faint arc until they are united into a point. Thus, in dorsal view, the occipital ring is subtriangular. The length (sag.) of the occipital ring is about half its width. In transverse section it is highly convex, sagittally it slopes gently backwards. The median keel of the glabella continues on the occipital ring and it is particularly prominent on the posterior end. In the sagittal line, quite inside the posterior margin of the occipital ring, there is commonly a small occipital node.

The preglabellar furrow touches the anterior end of the glabella, and extends outwards-backwards from that point. It is very shallow and becomes even fainter laterally. In front of the preglabellar furrow there is a laterally somewhat narrower (exsag.) anterior border, which sagittally is of very low convexity and only slightly curved down anteriorly. Transversely, the anterior border is moderately convex. The distance between the anterior margin and the glabella is about one-fifth the length of the cranidium. On the anterior portion of the anterior border there are terrace lines. The anterior margin is slightly pointed to form an obtuse angle.

The fixigenae including the palpebral lobes are considerably narrower (tr.) than the posterior width of the glabella and they slope gently towards the sides. Inside the palpebral lobes they are slightly vaulted. The palpebral lobes are narrow (tr.) and very slightly raised. They commence at the posterior border furrow and extend forwards in an arc until they attain the same height as the middle glabellar furrow. A distinct eye ridge runs from this point in an arc inwards-forwards towards the foremost glabellar furrow or towards the frontal lobe of the glabella. The eye ridges do not reach the glabella, and they are most prominent on internal moulds. In one specimen there extends a broad and rather deep furrow inwards-forwards towards the frontal lobe of the glabella from the midpont of the palpebral lobe. This feature has not been observed in any of the other cranidia. The posterior border increases in width (exsag.) outwards and the postero-lateral portion is markedly downsloping distal to the fulcrum. Also the posterior border furrow increases in width laterally.

REMARKS. – In the highly convex (tr.) glabella, the subtriangular occipital ring and the anteriorly rather pointed glabella, *P. grandis* is distinguished from other known species of *Proampyx*. The general shape of the anterior border and the occipital ring, as well as the median keel and the eye ridges, indicates that it is a species of *Proampyx*.

Proampyx sularpensis n.sp.
Pl. 3, Fig. 6, Pl. 4, Fig. 5

v 1917 *Ellipsocephalus Nordenskiöldi* LNRSN. – Troedsson,, pp. 617–618.

v ?1917 *Arionellus primaevus* BRÖGGER. – Troedsson, p. 617. It is possible that Troedsson referred some specimens to this species.

HOLOTYPE. – LO 5334 T, preserved in the Palaeontological Department, the University of Lund, Lund.

OTHER MATERIAL. – 30 mostly incomplete cranidia. Moreover, there are some cranidial impressions and fragments. Many specimens retain the exoskeleton. The material was collected by G. T. Troedsson at the type locality.

TYPE HORIZON AND LOCALITY. – The uppermost Lower Cambrian (layer 4 and 5, section II, Troedsson 1917) at Hardeberga, S. Sandby, east of Lund, Scania, south Sweden.

DISTRIBUTION. – The species is known with certainty only from the type locality and horizon.

DIAGNOSIS. – *Proampyx* species with a downsloping anterior border, both anteriorly and laterally. The glabella is tapered forwards. The eye ridges are commonly distinct and the occipital ring is comparatively short (sag.). The surface of the exoskeleton is finely nodose.

DESCRIPTION. – The cranidial width across the palpebral lobes is somewhat larger than the total length. The anterior sections of the facial suture diverge slightly forwards. The sculpture of the exoskeleton is finely nodose, i.e. it consists of small, closely spaced knobs (see Pl. 4, Fig. 5). The glabella is laterally surrounded by faintly marked, weakly impressed dorsal furrows. It tapers forwards, particularly in the frontal lobe, and the anterior end is commonly pointed to form an obtuse angle. The maximum width of the glabella, at the occipital furrow, is less than its length (1:1.3). The length of the glabella is somewhat more than half the cranidial length (1:1.6). Transversely, the glabella is highly convex, sagittally it is moderately convex. The anterior end slopes comparatively steeply toward the preglabellar furrow, but this is variable. In some specimens there is a faint indication of a median keel along the glabella. There are three pairs of lateral glabellar furrows. The

foremost pair is faintly marked and directed inwards to slightly backwards or almost perpendicularly to the sagittal line. The two posterior pairs are well marked and are directed inward-backward from the distal ends. The occipital furrow is prominent and it is deepest laterally. The furrow is deeper and wider on internal moulds. The course is straight. The posterior margin of the occipital rings is rounded, but commonly pointed to a faintly marked angle. The length (sag.) of the occipital ring is about one-third its width (tr.). Transversely, the occipital ring is highly convex. Sagittally, it is of low convexity. There is no occipital node.

The preglabellar furrow is faint and extends from the anterior end of the glabella backward-outward in front of the eye ridges. It delimits a laterally only somewhat narrower (exsag.) anterior border which is bent down both in front and laterally. In transverse section the anterior border is highly convex. The width (sag.) of the anterior border is one-third to one-fourth the total cranidial length. On the anterior portion of the anterior border there are terrace lines and laterally on the same border there is a faint anterior border furrow in some specimens. The fixigenae, including the palpebral lobes, are considerably narrower (tr.) than the posterior width of the glabella (0.6:1). They are slightly vaulted, but nevertheless distinctly raised above the dorsal and palpebral furrows. The fixigenae commonly slope gently or very gently toward the sides. The palpebral lobes are well marked and commence at the posterior border furrow. They extend in an arc forward until they attain the same height as the foremost or middle glabellar furrow. They are slightly raised and separated from the fixigenae by a palpebral furrow. The curvature of their outer margin increases backwards. The eye ridges run in an arc inward-forward from the anterior end of the palpebral lobes toward the frontal lobe of the glabella. They do not reach the glabella. In some specimens they are comparatively poorly defined. The posterior border increases in width laterally, as well as the posterior border furrow. Laterally, the posterior border extends as far as the palpebral lobe. Distal to the fulcrum it is bent down. The posterior border is depressed below the level of the fixigena.

DIMENSIONS. – It is a fairly small species; the length of the cranidia mostly ranges from 5 to 7 mm.

REMARKS. – The species seems to be fairly closely related to *Proampyx linnarssoni* (KIÆR, 1917), but differs in the following characters: the anterior border is anteriorly and laterally more bent down, the glabella is transversely of higher convexity, less well marked preglabellar furrow, comparatively longer (sag.) occipital ring, and in the commonly angulate anterior end of the glabella. Besides, the sculpture of the exoskeleton in *Proampyx linnarssoni* consists of fine pits (see Pl. 4, Fig. 4) whereas in *P. sularpensis* it is usually seen as small, closely spaced knobs (see Pl. 4, Fig. 5).

In the shorter (sag.) occipital ring, the downsloping anterior border and the comparatively blunt-ended glabella, *P. sularpensis* is easily distinguished from *P. grandis*, which is known from the same locality and horizon. Furthermore, the sculpture of the exoskeleton in the latter species is clearly distinguished as pitted.

Proampyx cf. *sularpensis* n.sp.
Pl. 3, Fig. 5

MATERIAL. – An almost complete cranidium with the greater part of the exoskeleton preserved (LM LO 5333 t). Additional material includes some flattened and poorly preserved cranidia, representing internal moulds and questionably referred to this form.

LOCALITY AND HORIZON. – The specimen retaining the exoskeleton was collected by G. T. Troedsson from layer 4, section II, at Hardeberga, S. Sandby, east of Lund, Scania, south Sweden (Troedsson 1917). The rest was collected by the authors in 1976 and 1977 from loose boulders of "greywacke shale" about 1 km south of Brantevik, eastern Scania, south Sweden.

DESCRIPTION (based on the specimen from Hardeberga). – The cranidial width across the palpebral lobes is greater than the total length. The external surface of the exoskeleton is granular on the glabella and on the anterior border. The sculpture on the fixigenae should rather be designated as pitted. The glabella considerably narrows forwards and the anterior end is rounded. It is set off from the fixigenae by its convexity alone. The maximum width of the glabella, at the occipital furrow, is somewhat less than the length. The length of the glabella is greater than half the length of the cranidium. Transversely, it is highly convex, sagittally, it is moderately convex. There is an indication of three pairs of lateral glabellar furrows. The occipital furrow is deep on the internal mould. It is considerably shallower where the exoskeleton is retained. The course is straight. The posterior margin of the occipital ring is uniformly rounded. The length (sag.) of the occipital ring is less than half of its width (tr.). Transversely, it is highly convex. There is no indication of any occipital node or median keel.

The preglabellar furrow is weakly developed. The anterior border strongly slopes down both forwards and

laterally. In transverse section the anterior border is highly convex. Anteriorly, on the anterior border, there are 4–7, well marked terrace lines. An anterior border furrow is not present. The fixigenae, including the palpebral lobes, are considerably narrower (tr.) than the posterior width of the glabella. They slope very gently towards the sides. The eye ridges are fairly well marked and extend from the sides inward-forward toward the frontal lobe of the glabella, but not into it. The palpebral lobes are not preserved. The posterior border furrow is distinct.

REMARKS. – From *P. sularpensis* this form differs essentially in its larger size and in the rounded anterior end of the glabella.

Proampyx triangularis n.sp.
Pl. 4, Fig. 3

v 1908 *Arionellus primaevus* BRÖGG. – Moberg, p. 26, Pl. 1, Figs. 1–2.

HOLOTYPE. – LO 2101 T, preserved in the Palaeontological Department, the University of Lund, Lund. It is an internal mould of a complete cranidium, figured by Moberg 1908, Pl. 1, Fig. 1.

OTHER MATERIAL. – An internal mould of a flattened and probably laterally compressed cranidium, figured by Moberg 1908, Pl. 1, Fig. 2 (LM LO 2102 t). However, the specimen is questionably referred to the species.

TYPE HORIZON AND LOCALITY. – The type specimen was collected by J. C. Moberg from layer 23, profile II, Luopakte, Torneträsk, northern Sweden (Moberg 1908).

DISTRIBUTION. – The species is only known from the type horizon and locality. According to Moberg (1908, p. 25), the fauna in the type horizon indicates the Zone of *Holmia kjerulfi,* but as his material is largely incorrectly determined this should not be taken for granted.

DIAGNOSIS. – *Proampyx* species with a triangular occipital ring. The glabella is slightly wider than long, tapers forward, and is bluntly rounded in front. Distinct lateral glabellar furrows are absent. The preglabellar furrow is deep, as are the dorsal furrows, and extends straight outward towards the sides.

DESCRIPTION. – The cranidial width across the palpebral lobes is slightly larger than the total length. The anterior sections of the facial suture are directed almost straight forward. As a whole, the cranidium is of low convexity both transversely and sagittally. The glabella is surrounded laterally by deep and wide dorsal furrows. It narrows forward and the anterior end is bluntly rounded. The length of the glabella is somewhat less than its maximum width at the occipital furrow. The length of the glabella is almost half the cranidial length. The glabella is moderately convex, both sagittally and transversely. Distinct lateral glabellar furrows are absent. The occipital furrow is shallow, but distinct, and extends in a faint arc backwards. The occipital ring is strongly extended backwards and it is provided with almost straight margins. Thus, in dorsal view the occipital ring is triangular. The length (sag.) of the occipital ring is about half its width. Transversely, it is moderately convex. Sagittally, it slopes gently backwards.

The preglabellar furrow is deep and extends straight outward towards the sides. It becomes wider and shallower laterally, and does not extend parallel with the anterior margin. In front of the preglabellar furrow there is a wide (sag.), vaulted and laterally narrower anterior border. It is moderately convex both ways. It attains almost the same level as the glabella and does not slope down anteriorly. The distance between the anterior margin and the glabella is larger than half the length of the glabella. The doublure is not visible. The fixigenae including the palpebral lobes are much narrower (tr.) than the posterior width of the glabella (1:1.5). They are highly vaulted and delimited from the glabella by deeply impressed dorsal furrows. The palpebral lobes are comparatively short (exsag.) and are about half the length of the glabella. Their outer margin is anteriorly slightly curved, becoming progressively more curved backwards until the posterior end is directed straight inwards at the posterior border furrow. There are no palpebral furrows. From the anterior end of the palpebral lobe, one can follow a faint, hardly visible eye ridge, running inwards-forwards towards the anterior end of the glabella. The posterior border is fairly short (tr.), somewhat more than half the length of the occipital furrow. It increases in width (exsag.) laterally, as well as the delimiting posterior border furrow. The posterior margin is directed outwards to very slightly backwards. The postero-lateral corners are poorly preserved, but they appear to be pointed.

REMARKS. – The two cranidia were described by Moberg (1908) as *Arionellus primaevus (= Strenuaeva primaeva),* together with a third cranidium from the same locality and horizon (here referred to *S. inflata* n.sp.). However, the three specimens most likely represent two different species, and neither of the two is *S. primaeva.* It is worth noting that Moberg's illustration of the present holotype (Moberg 1908, Pl. 1, Fig. 1) is not correct

in detail. The original is provided with a shorter and anteriorly less rounded glabella. Kiær (1917, p. 37) states that Moberg's (1908) Pl. 1, Fig. 1 (= *Proampyx triangularis* n.sp.) most likely conforms with *S. primaeva* from Tømten, Ringsaker, Norway. However, the species is easily distinguished from *S. primaeva* in the triangular occipital ring, the shorter and wider glabella, and the absence of distinct glabellar furrows. The species only resembles species of *Strenuaeva* in the deep preglabellar furrow and the deep dorsal furrows, but it is certainly not a species of *Strenuaeva*. In the long (sag.) and triangular occipital ring, and in the shape of the glabella and the anterior border, the species is reminiscent of *Proampyx*, and we prefer to refer it to that genus.

Proampyx linnarssoni (KIÆR, 1917)
Pl. 3, Fig. 10, Pl. 4, Fig. 4

v 1917 *Strenuella Linnarssoni* nov.sp. – Kiær, pp. 38–40, Pl. 4, Figs. 5–6, Pl. 5, Figs. 7–10.
? 1925 *Strenuella Linnarssoni*, Kiær. – Størmer, p. 14, Pl. 1, Fig. 1.
v 1962 *Strenuella linnarssoni* Kiær. – Kautsky, Pl. 1, Figs. 5–6.

LECTOTYPE. – The cranidium figured by Kiær 1917, Pl. 4, Fig. 5 (PMO 61373); selected herein. It is an internal mould of a complete cranidium with small parts of the exoskeleton retained. The specimen is slightly compressed longitudinally.

DESCRIPTION. – See Kiær 1917, pp. 38–39.

REMARKS. – The cranidium from the Lower Cambrian at Ustaoset, Norway, described and figured by Størmer 1925, p. 14, Pl. 1, Fig. 1, is very poorly preserved, but resembles *P. linnarssoni* in the general outline and shape. However, a safe assignment to the species is hard to deliver.

During an excursion to the Mjøsa district, Norway, in 1977, Dr. J. P. Nystuen kindly showed us a small road-cutting at Skyberg, about 3.5 km east of the classical locality at Tømten, Ringsaker. The exposure can be located on the topographical map sheet Hamar (1:50 000) and the UTM grid reference is 597050-6755750. There we found a mostly strongly weathered fragment limestone about 50 cm thick, containing numerous trilobite fragments. From this limestone we also succeeded in collecting some complete cranidia which in almost every respect agree with *P. linnarssoni*. However, it is remarkable that the limestone also contained a large olenellid, probably *Kjerulfia lata*. Kiær (1917, p. 96) emphasized the absence of olenellids in the Zone of *"Strenuella" linnarssoni*. Maybe this zone represents a calcareous horizon in the *Holmia* Shale (Zone of *Holmia kjerulfi)*, and can be included in the same (see Fig. 1).

In the collection of the Geological Survey of Sweden there is a complete cranidium which seems to be identical with *P. linnarssoni* (see Pl. 3, Fig. 9). However, it is provided with a comparatively longer (sag). occipital ring than the Norwegian specimens. It was collected from a boulder by A. E. Nordenskiöld, and the locality is given as Simrishamn, a small town in eastern Scania, south Sweden. Some poorly preserved cranidia from the uppermost Lower Cambrian in the Brantevik-Gislövshammar region, eastern Scania, can questionably be referred to the species.

The species was included in the genus *Strenuella* MATTHEW by Kiær (1917), but it strongly resembles species referred to the genus *Proampyx*, and we tentatively refer it to that genus.

Proampyx? balticus (WIMAN, 1903)
Pl. 4, Figs. 1–2

v 1903 *Arionellus balticus n.sp.* – Wiman, p. 44, Pl. 1, Figs. 17–21.

MATERIAL. – The cranidia figured by Wiman 1903, Pl. 1, Figs. 17–21. The material is housed in the Palaeontological Institute, the University of Uppsala, Uppsala, Sweden.

LECTOTYPE. – The complete cranidium figured by Wiman 1903, Pl. 1, Figs. 18–20 (PIU ar. 1098); selected herein.

DISTRIBUTION. – The species is known only from erratic material (bituminous sandstone) at Biludden, Limön and Skälstenarne, in the Bay of Gävle, South Bothnian area, Sweden. This bituminous sandstone has also yielded olenellid fragments and *Torellella laevigata* (LINNARSSON) and it is regarded as Lower Cambrian.

DESCRIPTION. – The cranidium is comparatively flat, and its maximum width (across the palpebral lobes) slightly exceeds the total length. The anterior sections of the facial suture diverge forward. The glabella is delimited laterally by impressed dorsal furrows. It is fairly narrow and tapers forward. The length of the glabella is somewhat larger than its posterior width. The anterior end is bluntly rounded. Sagittally, it is of low convexity, while transversely, it is moderately convex. On a latex mould one can see three pairs of very faintly marked lateral glabellar furrows. The foremost is transverse, whereas the two posterior pairs are directed medially

and slightly backwards. The glabellar furrows are effaced on the other specimens. The occipital furrow is distinct with an indication of a backward curvature. The occipital ring is of moderate length (sag.), and its posterior margin is evenly rounded. The length (sag.) of the occipital ring is one-fourth to one-third its width. Transversely, it is moderately convex. There is no indication of any occipital node.

The preglabellar furrow is distinct and impressed. It extends in an arc towards the sides from the anterior end of the glabella. It delimits a wide (sag.), laterally somewhat narrower, anterior border which is slightly bent down. Transversely, the anterior border is moderately convex. The length (sag.) of the anterior border is about half the length of the glabella. The fixigenae including the palpebral lobes are narrower (tr.) than the posterior width of the glabella. They are slightly vaulted. The palpebral lobes are fairly short (exsag.), about half the length of the glabella. They do not reach the posterior border furrow. On the latex cast, the palpebral lobes are slightly raised and set off from the fixigenae by a shallow palpebral furrow. However, on the lectotype they are not elevated, and they slope gently outward. Eye ridges are absent. The posterior border increases slightly in width (exsag.) outwards. It is depressed below the level of the fixigena. The postero-lateral corners are not visible.

REMARKS. – The species has the general appearance of a *Proampyx*. However, it is provided with deeper dorsal furrows, a deeper preglabellar furrow, and a comparatively narrower glabella than in most species referred to *Proampyx*. Also, because of the absence of eye ridges, we questionably refer it to the genus *Proampyx*. In the fairly strong relief of the cranidium, especially in the small specimens, the species is reminiscent of the genus *Strenuaeva*.

Proampyx? conifrons (POULSEN, 1969)

1969 *Ellipsostrenua conifrons* n.sp. – Poulsen, pp. 17–18, Pl. (without number), Figs. 6–7.

REMARKS. – This species is based on a poorly preserved cranidium from the boring Slagelse no. 1, Western Sealand, Denmark, and Poulsen (1969) referred it to the genus *Ellipsostrenua* KAUTSKY. However, as mentioned above, *Ellipsostrenua* is here regarded as a junior synonym of *Ellipsocephalus*. A detailed description was given by Poulsen (1969, pp. 17–18) and it is not repeated here. The species is provided with a considerably tapering glabella and an almost horizontal anterior border, and thus it cannot be referred to the genus *Ellipsocephalus*. However, in the general shape of the glabella and the anterior border, it shows similarities to species referred to the genus *Proampyx*. On the other hand, in the narrow (sag.), slightly marked and raised rim anteriorly it differs from *Proampyx*, and for that reason the assignment to this genus is uncertain. Furthermore, the poor preservation does not seem to allow a safe assignment to any established genus.

Genus *Comluella* HUPÉ, 1953

Comluella? scanica n.sp.
Pl. 4, Figs. 9–10

v 1929 *Strenuella* aff. *linnarssoni* KIÆR. – Westergård, p. 14 (line 11).

HOLOTYPE. – SGU Type 19. It is an internal mould of an almost complete, comparatively small cranidium.

OTHER MATERIAL. – About 20 commonly incomplete or fragmentary cranidia, collected by A. H. Westergård in 1924 and 1937, and a single cranidium collected by Dr. S. Bengtson (Uppsala). All cranidia represent internal moulds. However, in some specimens the exoskeleton is partly preserved.

DISTRIBUTION. – The species is known only from an impure limestone, belonging to an unnamed formation above the Rispebjerg Sandstone in the Brantevik-Gislövshammar region, eastern Scania, south Sweden.

DESCRIPTION. – The cranidial width across the palpebral lobes is considerably greater than the length. The anterior sections of the facial suture are directed forward and slightly outward. The sculpture of the exoskeleton consists of fine pits. The glabella is surrounded laterally by weakly impressed dorsal furrows. It slightly narrows forwards, in some specimens it is almost parallel-sided. The anterior end of the glabella is rounded. The width of the glabella at the occipital furrow is less than its length. The length of the glabella is larger than half the total cranidial length. Transversely, it is highly convex. There are three pairs of distinct, almost transverse lateral glabellar furrows. The posterior pair are commonly directed inward to slightly backward from the distal ends. The occipital furrow is deeply cut and the course is straight. The posterior margin of the occipital ring is rounded.

The preglabellar furrow touches the anterior end of the glabella and extends outwards from that point. In

front of the preglabellar furrow there is a short (sag.), slightly raised anterior border or rim. A typical feature of the species is the short distance between the anterior margin and the glabella, about one-seventh the length of the cranidium. On the anterior part of the border there are terrace lines. The fixigenae including the palpebral lobes are narrower (tr.) than the posterior width of the glabella. They slope gently outward. The palpebral lobes are delimited from the fixigenae by a shallow palpebral furrow. However, this furrow as well as the dorsal furrows and the preglabellar furrow is almost effaced if the exoskeleton is retained. A distinct eye ridge extends from the palpebral lobe in an arc towards the frontal lobe of the glabella. It is terminated by the dorsal furrow.

Comluella? sp.
Pl. 4, Figs. 11–12

v 1908 *Ellipsocephalus Nordenskiöldi* LINRS. – Moberg, p. 27, Pl. 1, Figs. 6–7.

MATERIAL. – Internal moulds of three incomplete cranidia, collected by J. C. Moberg in 1908. They are preserved in the Palaeontological Department, the University of Lund, Lund as LO 2106 t, LO 2107 t and LO 5338 t.

LOCALITY AND HORIZON. – Layer 23, profile II, Luopakte, Torneträsk, northern Sweden (Moberg 1908).

DESCRIPTION. – The glabella is delimited laterally by deeply impressed dorsal furrows. It is rounded in front and provided with three pairs of lateral glabellar furrows. The foremost pair is almost effaced. The fixigenae are raised and they slope inward toward the dorsal furrow. Distinct eye ridges, terminated by the dorsal furrows, are present. Parallel with the anterior margin there extends a shallow anterior border furrow, delimiting a uniformly wide anterior border.

REMARKS. – Due to the poor and fragmentary material, this form is left under open nomenclature. In the shape of the anterior border and the glabella, this form is reminiscent of the genus *Comluella,* but differs in having fixigenae sloping toward the glabella. However, we questionably refer it to that genus. The fixigenae resemble those of species referred to the genus *Proliostracus* POULSEN, 1932, but this genus typically has bifurcated glabellar furrows, distinguishing it from the present cranidia.

Genus *Strenuella* MATTHEW, 1887

"Strenuella" obscura THORSLUND & WESTERGÅRD, 1938
Text – Fig. 6

v 1938 *Strenuella obscura* sp.n. – Thorslund & Westergård, p. 22, Pl. 1, Fig. 3.

MATERIAL. – The cranidium figured by Thorslund & Westergård 1938, Pl. 1, Fig. 3 (lectotype, selected herein, the only syntype figured. SGU Type 21). It is incomplete and represents an internal mould. The preservation is poor.

DISTRIBUTION. – The species is known only from the File Haidar boring core (level: 393.9–394.25 m), Gotland, Sweden.

REMARKS. – Due to the poor preservation it is hard to give a detailed description, and, for the same reason, the assignment to the genus *Strenuella* is only provisional. However, it is worth noting that the fixigenae are comparatively narrow (tr), the dorsal furrows are well impressed, the anterior border is weakly convex (sag.) and is not sloping down, and the occipital furrow is well marked. Furthermore, the glabella tapers forward and it is rounded in front. There are three pairs of faint lateral glabellar furrows directed inward and slightly backward from the distal ends.

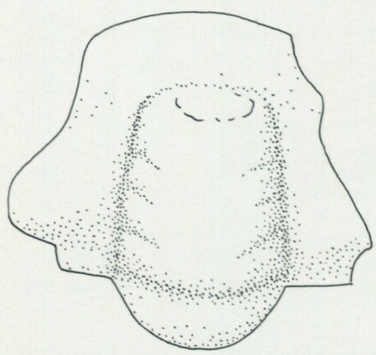


Fig. 6. *"Strenuella" obscura* THORSLUND & WESTERGÅRD, 1938. Lectotype, SGU Type 21. Figured by Thorslund & Westergård 1938, Pl. 1, Fig. 3. The anterior part of the glabella is damaged. X 4.0.

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APPENDIX. Table showing the results of the measurements (in mm). The numbers in italics show the ratio of the parameters to the length of the cranidium (L). The measured parameters are evident from Fig. 2.
In S. spinosa n.sp. the measured specimen is provided with a complete occipital spine which is included in the values.

Species	Specimen	L	L_1	L_2	L_3	W	W_1	W_2
Ellipsocephalus nordenskioeldi	lectotype	12.9 *1.00*	2.2 *0.17*	8.1 *0.63*	2.6 *0.20*	16.0 *1.24*	5.5 *0.43*	6.1 *0.47*
	SGU Type 5	17.3 *1.00*	2.7 *0.16*	11.0 *0.64*	3.6 *0.21*	22.5 *1.30*	8.2 *0.47*	8.8 *0.51*
	LM LR 1	14.2 *1.00*	2.2 *0.16*	9.5 *0.67*	2.5 *0.18*	19.2? *1.35*	6.4 *0.45*	6.9 *0.49*
	LM LR 2	13.7 *1.00*	2.0 *0.15*	9.1 *0.66*	2.6 *0.19*	16.9? *1.23*	6.6 *0.48*	6.8 *0.50*
	LM LR 3	15.2 *1.00*	2.5 *0.16*	9.8 *0.65*	2.9 *0.19*	19.6? *1.29*	7.0 *0.46*	7.8 *0.51*
	LM LR 4	11.3 *1.00*	1.8 *0.16*	7.0 *0.62*	2.5 *0.22*	13.2? *1.17*	5.7 *0.50*	5.9 *0.52*
	LM LR 5	13.0 *1.00*	1.9 *0.14*	8.4 *0.64*	2.7 *0.20*	16.2? *1.24*	5.8 *0.45*	6.1 *0.46*
Ellipsocephalus latus	lectotype	13.4 *1.00*	1.7 *0.13*	9.2 *0.69*	2.5 *0.19*	20.5 *1.53*	7.1 *0.53*	7.0 *0.52*
Ellipsocephalus gripi	Boliden AB 39	17.2 *1.00*	2.2 *0.13*	10.9 *0.63*	4.1 *0.24*	———	7.0 *0.41*	8.1 *0.47*
	Boliden AB 106	15.5 *1.00*	1.9 *0.12*	9.7 *0.63*	3.9 *0.25*	16.3 *1.05*	6.7 *0.43*	7.0 *0.45*
	Boliden AB 112	14.1 *1.00*	1.6 *0.11*	8.7 *0.62*	3.8 *0.27*	14.5 *1.03*	5.8 *0.41*	6.2 *0.44*
Strenuaeva primaeva	lectotype	10.3 *1.00*	2.0 *0.19*	4.9 *0.48*	3.4 *0.33*	11.5? *1.12*	3.3 *0.32*	4.2 *0.41*
	PMO 73158	7.2 *1.00*	1.3 *0.18*	3.6 *0.50*	2.3 *0.32*	8.3 *1.15*	2.4 *0.33*	2.8 *0.39*
Strenuaeva spinosa	SGU coll.	11.0 *1.00*	3.6 *0.33*	5.1 *0.46*	2.3 *0.21*	———	2.9 *0.26*	4.0 *0.36*
Strenuaeva inflata	holotype	8.7 *1.00*	1.3 *0.15*	4.8 *0.55*	2.6 *0.30*	10.8 *1.24*	3.1 *0.36*	3.9 *0.45*
	LM LO 2103 †	5.0 *1.00*	0.9 *0.18*	2.7 *0.54*	1.4 *0.28*	6.2? *1.24*	1.5 *0.30*	2.1 *0.42*
Strenuaeva? kullingi	holotype	9.0 *1.00*	1.4 *0.16*	5.5 *0.61*	2.1 *0.23*	10.3 *1.14*	3.5 *0.39*	4.5 *0.50*
Strenuaeva sp.	SGU Type 13	4.9 *1.00*	0.9 *0.18*	2.5 *0.51*	1.5 *0.31*	6.0 *1.22*	1.7 *0.35*	2.3 *0.47*
Proampyx rotundatus	holotype	16.1 *1.00*	3.0 *0.19*	8.1 *0.50*	5.0 *0.31*	17.2 *1.07*	6.0 *0.37*	7.8 *0.48*
	LM LO 5331 †	14.9 *1.00*	2.8 *0.19*	7.5 *0.50*	4.6 *0.31*	16.0 *1.07*	5.5 *0.37*	7.3 *0.49*
Proampyx grandis	holotype	18.9? *1.00*	4.1 *0.22*	11.5 *0.61*	3.3? *0.18*	19.0? *1.01*	———	8.8 *0.47*
	LM LO 5335 †	15.7 *1.00*	3.4 *0.22*	8.7 *0.55*	3.6 *0.23*	———	———	6.9 *0.44*
	LM LR 6	14.0 *1.00*	3.3 *0.24*	7.5 *0.54*	3.2 *0.23*	13.8 *0.99*	———	6.3 *0.45*
	LM LR 7	22.8 *1.00*	4.8 *0.21*	13.3 *0.58*	4.7 *0.21*	———	———	10.2 *0.45*
	LM LR 8	21.8 *1.00*	5.5 *0.25*	11.8 *0.54*	4.5 *0.21*	———	———	9.8 *0.45*
	LM LR 9	19.7 *1.00*	3.9 *0.20*	11.5 *0.58*	4.3 *0.22*	———	———	9.3 *0.47*
	LM LR 10	15.0? *1.00*	3.4 *0.23*	8.6 *0.57*	3.0 *0.20*	———	———	6.6 *0.44*
Proampyx sularpensis	holotype	5.9 *1.00*	0.9 *0.15*	3.7 *0.63*	1.3 *0.22*	6.7? *1.14*	2.2 *0.37*	2.7 *0.46*
	LM LO 5337 †	7.2 *1.00*	1.3 *0.18*	4.2 *0.58*	1.7 *0.24*	7.6? *1.06*	3.1 *0.43*	3.5 *0.49*
	LM LR 11	7.2 *1.00*	1.3 *0.18*	4.3 *0.60*	1.6 *0.22*	7.7? *1.07*	3.0 *0.42*	3.4 *0.47*
	LM LR 12	5.7 *1.00*	0.9 *0.16*	3.5 *0.61*	1.3 *0.23*	6.2 *1.09*	2.3 *0.40*	2.6 *0.46*
	LM LR 13	6.9 *1.00*	1.2 *0.17*	4.3 *0.62*	1.5 *0.22*	7.4 *1.07*	2.6 *0.38*	3.2 *0.46*
Proampyx cf. *sularpensis*	LM LO 5333 †	16.0 *1.00*	3.1 *0.19*	9.7 *0.61*	3.2 *0.20*	———	6.8 *0.43*	8.6 *0.54*
Proampyx triangularis	holotype	15.3 *1.00*	3.2 *0.21*	6.8 *0.44*	5.3 *0.35*	17.0 *1.11*	5.5 *0.36*	7.5 *0.49*
Proampyx? balticus	lectotype	20.1 *1.00*	2.5 *0.12*	11.1 *0.55*	6.5 *0.32*	23.5 *1.17*	7.3 *0.36*	9.2 *0.46*
Comluella? scanica	holotype	6.0 *1.00*	1.2 *0.20*	4.0 *0.67*	0.8 *0.13*	8.7 *1.45*	2.7 *0.45*	2.9 *0.48*
	SGU coll.	8.7 *1.00*	1.7 *0.20*	5.7 *0.66*	1.3 *0.15*	11.0 *1.26*	4.5 *0.52*	4.9 *0.56*
	SGU coll.	12.3 *1.00*	2.5 *0.20*	8.1? *0.66*	1.7? *0.14*	16.2 *1.32*	6.2 *0.50*	7.0 *0.57*

PLATES 1—4

The photos were made by Mr Sven Stridsberg at the Palaeontological Department, the University of Lund, Lund. Before photographing all material, if not otherwise stated, was whitened with ammonium chloride or magnesium oxide.

PLATE 1

Figs. 1—4: *Ellipsocephalus nordenskioeldi* LINNARSSON, 1883. "Greywacke shale", Forsemölla, Andrarum, eastern Scania, south Sweden. — 1: Lectotype, internal mould of an almost complete cranidium. Coll. G. C. von Schmalensee, 1877. Figured by Linnarsson 1883, Pl. 4, Fig. 2. SGU Type 3. X 3.3. — 2: Internal mould of a complete cranidium. Stereo pair. Coll. N. O. Holst, 1889. SGU Type 5. X 2.1. — 3: Internal mould of a cranidium with ten articulated thoracic tergites. Coll. G. C. von Schmalensee, 1879. Figured by Linnarsson 1883, Pl. 4, Fig. 1. SGU Type 4. X 1.9 — 4: Incomplete cranidium with 14 thoracic tergites and the pygidial axis. Flattened. Latex cast of external mould. LM LO 5329 t. X 2.8.

Fig. 5: *Ellipsocephalus latus* WIMAN, 1903. Lectotype, internal mould of a complete cranidium with fragments of the exoskeleton preserved. Stereo pair. Erratic boulder, Dorfe Öfverby, Jomala, Åland, an archipelago in the Baltic Sea. Coll. G. C. von Schmalensee. Figured by Wiman 1903, Pl. 1, Fig. 22. SGU Type 6. X 2.3.

Figs. 6—7: *Ellipsocephalus gripi* (KAUTSKY, 1945). — 6: Almost complete cranidium with the exoskeleton. Stereo pair. Aistjakk, 4 km east of the village of Laisvall, Lappland, northern Sweden. Boliden AB, no. 106. X 3.0 — 7: Lateral view of same specimen. X 3.6.

Fig. 8: *Ellipsocephalus gripi* (KAUTSKY, 1945)?. Internal mould of a deformed cranidium. Stereo pair. Tømten, Ringsaker, Norway. Figured by Kiær 1917, Pl. 4, Fig. 8. PMO 73155. X 3.7.

Fig. 9: *Ellipsocephalus* cf. *gripi* (KAUTSKY, 1945). Incomplete and deformed cranidium. The shoreline of the River Glomma, Østre Åbu, south of Rena, Hedmark, Norway. Coll. G. Henningsmoen, 1976. Plastiform cast of external mould. PMO 98116. X 3.2.

Fig. 10: *Ellipsocephalus gripi* (KAUTSKY, 1945). Cranidium with one half exfoliated. Aistjakk, 4 km east of the village of Laisvall, Lappland, northern Sweden. Boliden AB, no. 39. X 3.0.

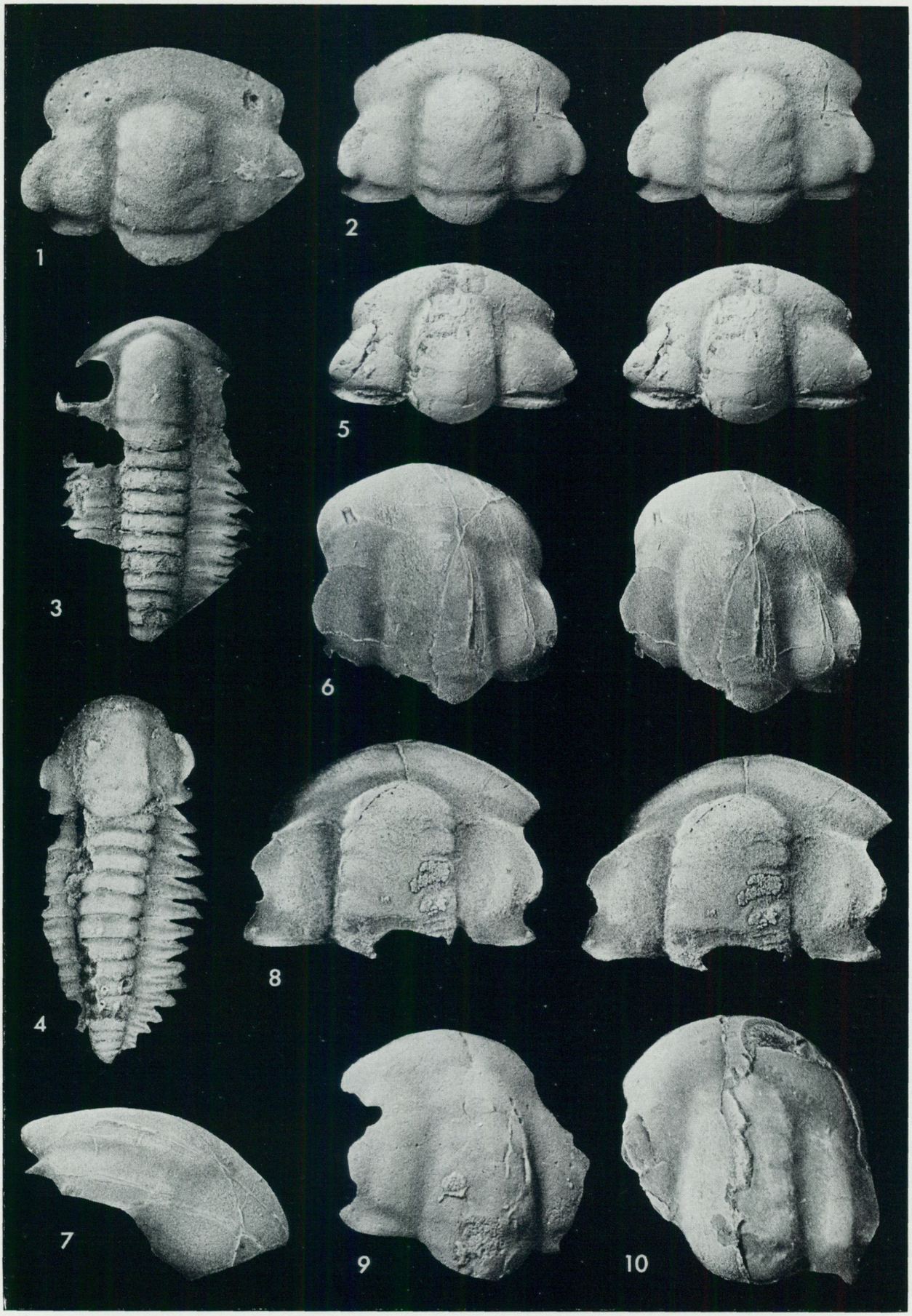
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PLATE 2

Figs. 1–2: *Strenuaeva primaeva* (BRØGGER, 1879). – 1: Internal mould of a cranidium. Stereo pair. Tømten, Ringsaker. Norway. Coll. J. Braastad, 1912. Figured by Kiær 1917, Pl. 5, Fig. 3. PMO 73158. X 5.3. – 2: Lectotype, internal mould of a cranidium. Tømten, Ringsaker, Norway. Figured by Kiær 1917, Pl. 4, Fig. 3. PMO 73153. Not whitened. X 4.9.

Figs. 3–4: *Strenuaeva spinosa* n.sp. – 3: Internal mould of a cranidium lacking the occipital spine and a great deal of the occipital ring. Stereo pair. Grey "kjerulfi-shale" about 4 km west of the southern extremity of Lake Storlaisan (about 17 km SSW of the village of Laisvall), Lappland, northern Sweden. Coll. O. Kulling, 1966. SGU Type 9. X 4.6. – 4: Holotype, internal mould of a cranidium lacking the right fixigena. Part of the occipital spine is broken off. Grey "kjerulfi-shale" about 4 km west of the southern extremity of Lake Storlaisan, northern Sweden. Coll. O. Kulling, 1966. SGU Type 8. X 5.8.

Figs. 5–6: *Strenuaeva inflata* n.sp. – 5: Holotype, internal mould of an almost complete cranidium. Stereo pair. Layer 23, profile II, Luopakte, Torneträsk, northern Sweden (Moberg 1908). Coll. J. Bergström, 1977. LM LO 5330 T. X 4.9. – 6: Internal mould of the smallest cranidium. Layer 23, profile II, Luopakte, Torneträsk, northern Sweden (Moberg 1908). Coll. J. C. Moberg, 1908. Figured by Moberg 1908, Pl. 1, Fig. 3. LM LO 2103 t. X 8.1.

Figs. 7–9: *Strenuaeva? kullingi* n.sp. Internal moulds of three complete cranidia measuring 9.0, 4.1 and 3.3 mm in length, respectively. They all come from a grey "kjerulfi-shale" about 4 km west of the southern extremity of Lake Storlaisan (about 17 km SSW of the village of Laisvall), Lappland, northern Sweden. Coll. O. Kulling, 1966. – 7: Holotype. Stereo pair. SGU Type 10. X 4.9. – 8: SGU Type 11. X 9.9. – 9: SGU Type 12. X 12.8.

Fig. 10: *Strenuaeva* sp. Internal mould of an almost complete cranidium. Stereo pair. "Greywacke shale", Forsemölla, Andrarum, eastern Scania, south Sweden. Coll. A. G. Nathorst. Figured by Linnarsson 1883, Pl. 4, Fig. 3. SGU Type 13. X 8.4.


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PLATE 3

Figs. 1–2: *Proampyx rotundatus* (KIÆR, 1917). "Greywacke shale", Forsemölla, Andrarum, eastern Scania, south Sweden. – 1: Holotype, internal mould of a complete, flattened cranidium. Coll. G. C. von Schmalensee, 1879. Figured by Linnarsson 1883, Pl. 4, Fig. 4. SGU Type 14. X 3.0. – 2: Internal mould of a complete cranidium with the anterior part of the right librigena. Stereo pair. Coll. S. A. Tullberg, 1878. LM LO 5331 t. X 3.0.

Fig. 3: *Proampyx acuminatus* (ANGELIN, 1851). Internal mould of an almost complete cranidium. Middle Cambrian Zone of *Jincella brachymetopa* (Andrarum Limestone), Andrarum, eastern Scania, south Sweden. Figured by Westergård 1953, Pl. 1, Fig. 14. LM LO 3538 t. X 3.8.

Fig. 4: *Proampyx difformis* (ANGELIN, 1851). Cranidium with the greater part of the exoskeleton preserved. Middle Cambrian Zone of *Jincella brachymetopa,* Andrarum, eastern Scania, south Sweden. Coll C. Sjöblom, 1961. LM LO 5332 t. X 2.8.

Fig. 5: *Proampyx* cf. *sularpensis* n.sp. Incomplete cranidium with the main part of the exoskeleton. Layer 4 (fragment limestone), section II, at Hardeberga, S. Sandby, east of Lund, south Sweden (Troedsson 1917). Coll. G. T. Troedsson. LM LO 5333 t. X 2.6.

Fig. 6: *Proampyx sularpensis* n.sp. Holotype, cranidium with the exoskeleton. Stereo pair. Layer 4 (fragment limestone), section II, at Hardeberga, S. Sandby, east of Lund, south Sweden (Troedsson 1917). Coll. G. T. Troedsson. LM LO 5334 T. X 7.6.

Figs. 7–8: *Proampyx grandis* n.sp. Layer 4 (fragment limestone), section II, at Hardeberga, S. Sandby, east of Lund, south Sweden (Troedsson 1917). – 7: Internal mould of an incomplete cranidium. Coll. G. T. Troedsson. LM LO 5335 t. X 3.1. – 8: Holotype, incomplete cranidium partly exfoliated. Stereo pair. Coll. G. T. Troedsson. LM LO 5336 T. X 2.3.

Fig. 9: *Proampyx* cf. *linnarssoni* (KIÆR, 1917). Internal mould of an almost complete cranidium. Boulder at Simrishamn, eastern Scania, south Sweden. Coll. A. E. Nordenskiöld. SGU Type 15. X 3.5.

Fig. 10: *Proampyx linnarssoni* (KIÆR, 1917). Lectotype, internal mould of a complete cranidium with small portions of the exoskeleton preserved. Stereo pair. Tømten, Ringsaker, Norway. Figured by Kiær 1917, Pl. 4, Fig. 5 and Kautsky 1962, Pl. 1, Fig. 6. PMO 61373. X 3.7.

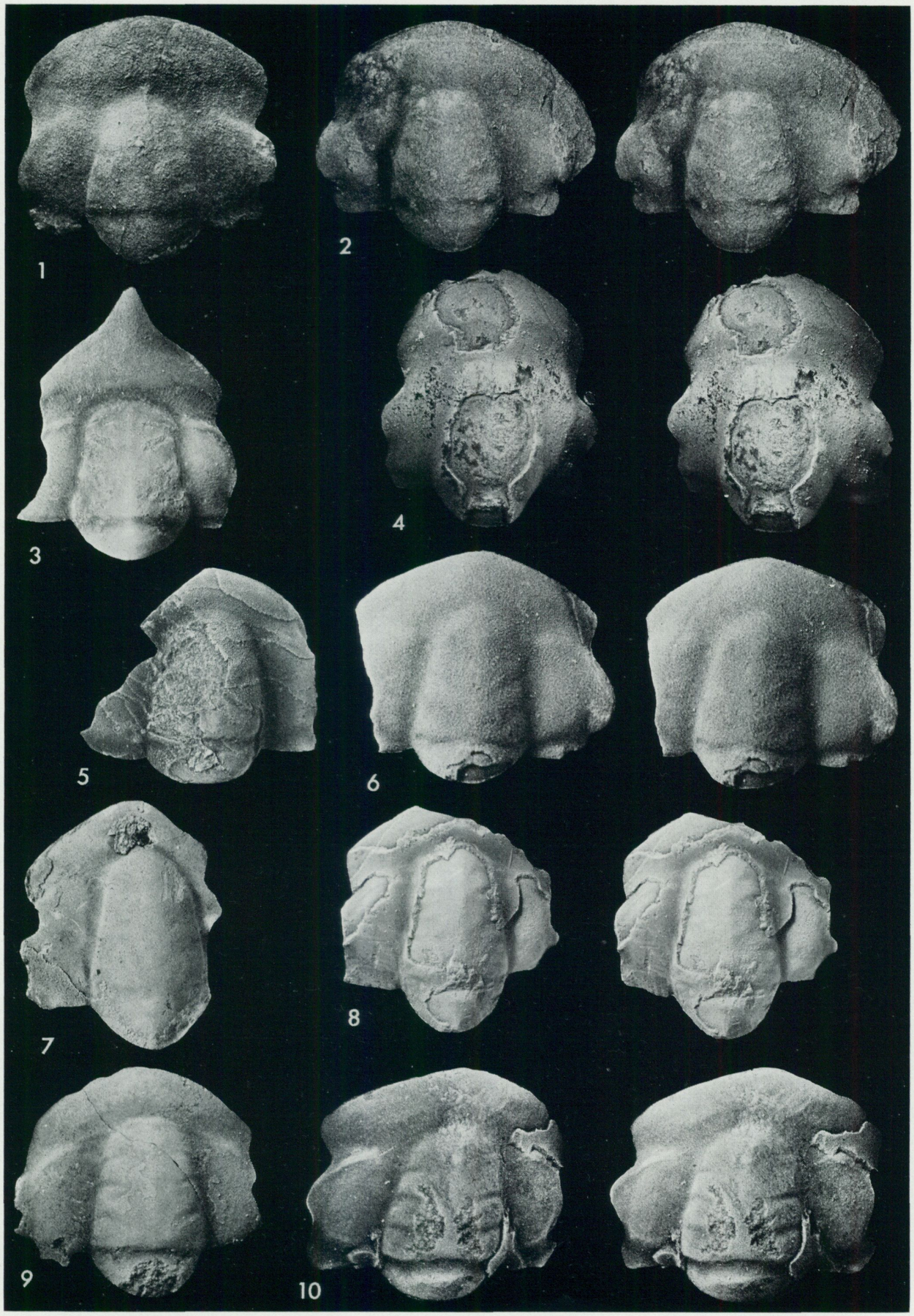
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PLATE 4

Figs. 1—2: *Proampyx? balticus* (WIMAN, 1903). — 1: Incomplete cranidium. Erratic material, Skälstenarne, in the Bay of Gävle, south Bothnian area, Sweden. Coll. C. Wiman, 1902. Figured by Wiman 1903, Pl. 1, Fig. 21. Latex cast of external mould. PIU ar. 1100 (counterpart to PIU ar. 1099). X 2.8. — 2: Lectotype, internal mould of an almost complete cranidium. Erratic material, Limön, in the Bay of Gävle, south Bothnian area, Sweden. Coll. C. Wiman, 1893. Figured by Wiman 1903, Pl. 1, Fig. 18. PIU ar. 1098. X 2.2.

Fig. 3: *Proampyx triangularis* n.sp. Holotype, internal mould of a complete cranidium. Layer 23, profile II, Luopakte, Torneträsk, northern Sweden (Moberg 1908). Coll. J. C. Moberg, 1908. Figured by Moberg 1908, Pl. 1, Fig. 1. LM LO 2101 T. X 3.3.

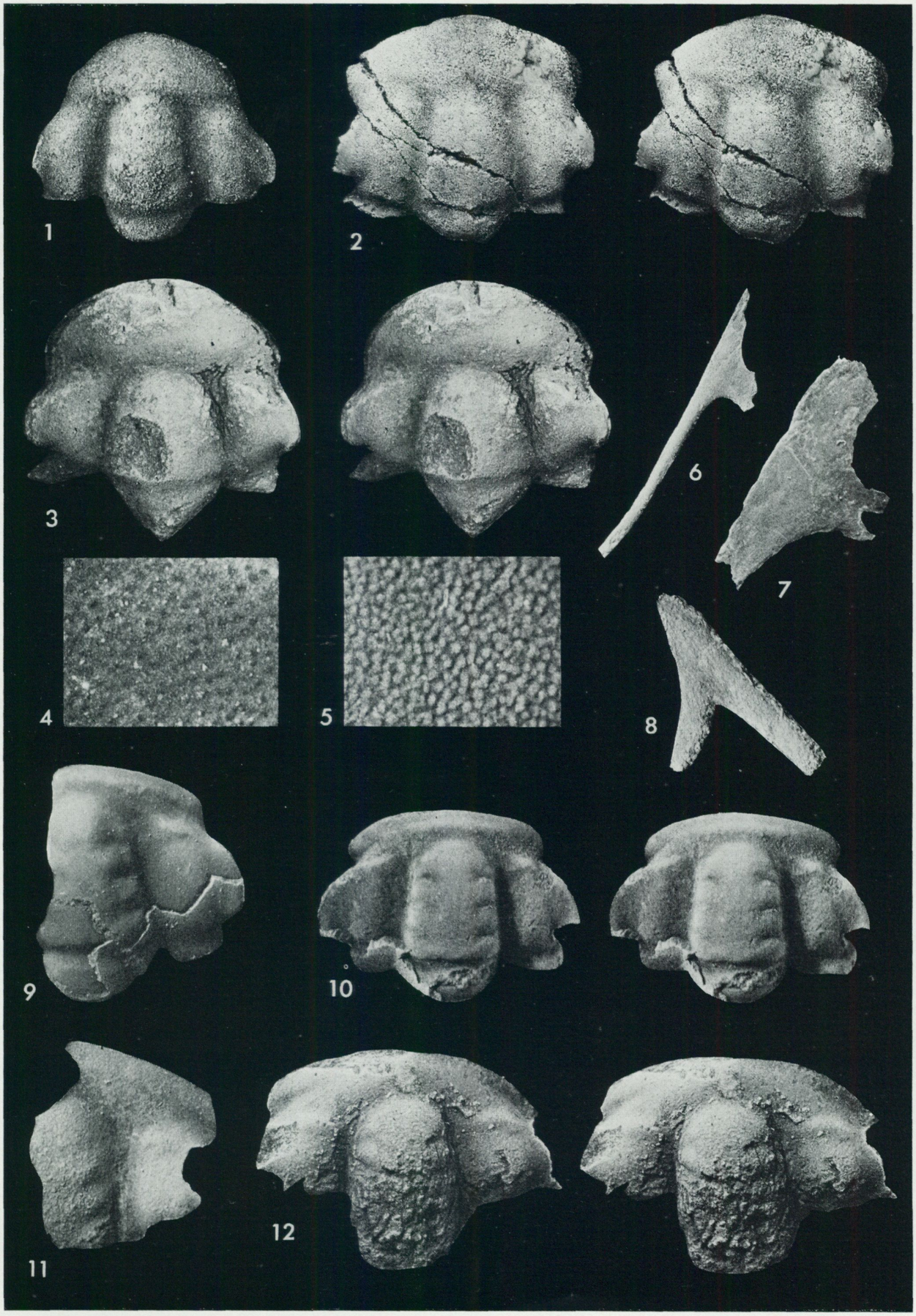
Fig. 4: *Proampyx linnarssoni* (KIÆR, 1917). Close-up of area on the right antero-lateral corner of lectotype cranidium showing details of ornamentation. PMO 61373. X 30.

Fig. 5: *Proampyx sularpensis* n.sp. Enlargement of area on the left fixigena showing details of ornamentation. Layer 4 (fragment limestone), section II, at Hardeberga, S. Sandby, east of Lund, south Sweden (Troedsson 1917). Coll. G. T. Troedsson. LM LO 5337 t. X 40.

Figs. 6—8: Three incomplete librigenae belonging to three different species. From limestone lenses in the thrusted sediments lying above the autochthonous sequence, Luopakte, Torneträsk, northern Sweden. Coll. G. Bexell, 1950. — 6: SGU Type 16. X 2.8. — 7: SGU Type 17. X 4.6. — 8: SGU Type 18. X 3.5.

Figs. 9—10: *Comluella? scanica* n.sp. — 9: Internal mould of an incomplete cranidium with a part of the exoskeleton preserved. Unnamed formation above the Rispebjerg Sandstone at Gislövshammar, eastern Scania, south Sweden. Coll. A. H. Westergård, 1937. SGU Type 20. X 3.4. — 10: Holotype, internal mould of an almost complete cranidium with a small portion of the exoskeleton preserved. Stereo pair. Unnamed formation above the Rispebjerg Sandstone at Gislövshammar, eastern Scania, south Sweden. Coll. A. H. Westergård, 1937. SGU Type 19. X 5.9.

Figs. 11—12: *Comluella?* sp. Layer 23, profile II, Luopakte, Torneträsk, northern Sweden (Moberg 1908). Coll. J. C. Moberg, 1908. — 11: Internal mould of an incomplete cranidium. LM LO 5338 t. X 4.0. — 12: Internal mould of an incomplete cranidium. Stereo pair. Figured by Moberg 1908, Pl. 1, Fig. 6. LM LO 2106 t. X 4.7.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