

THE TRILOBITE FAMILY OLENIDAE

WITH DESCRIPTION OF NORWEGIAN MATERIAL
AND REMARKS ON THE OLENID AND
TREMADOCIAN SERIES

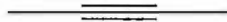
BY

GUNNAR HENNINGSMOEN

PALEONTOLOGISK MUSEUM, UNIVERSITETET I OSLO

WITH 19 FIGURES IN THE TEXT AND 31 PLATES

SKRIFTER UTGITT AV DET NORSKE VIDENSKAPS-AKADEMI I OSLO
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I KOMMISJON HOS H. ASCHEHOUG & CO. (W. NYGAARD)

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A. W. BRØGGERS BOKTRYKKERI A/S

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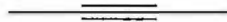
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¹ The species are treated in alphabetical order within each genus, except doubtful species, which are treated after the others.

Abstract

A few new terms are introduced for the description of trilobite shields (cf. text-figs. 1—2).

Earlier classifications of the family Olenidae are reviewed. In the classification proposed here (p. 17), three subfamilies are recognized (Oleninae, Leptoplastinae, Pelturinae), thus reviving the tripartition of the family proposed by Persson (1904). The subfamily Triarthrinae is included in the Oleninae, and the Jujuyaspidinae in the Pelturinae. The subfamily Papyriaspidinae is considered as not belonging to the Olenidae. Several genera and species previously assigned to the Olenidae have also been removed, and a number of doubtful members are discussed.

The Olenidae may have developed from the Andrarinidae, which again may be related to the Elviniidae and, more remotely, to the Anomocaridae, Ceratopygidae, Asaphidae, and Richardsonellidae.

The geographic, stratigraphic, and lithologic occurrence of the olenids is discussed. They are especially characteristic of the Upper Cambrian Olenid Series and the Lowermost Ordovician Tremadocian Series in the Acado-Baltic province, and very often occur in a black shale facies.

Several new subfaunizones are erected for the Olenid Series in Norway, which is divided into 8 faunizones comprising 29 subfaunizones. Most of these are also known in Sweden, as well as three other subfaunizones, so that the total number of subfaunizones recognized in the Olenid Series in Scandinavia amounts to 32. The 8 faunizones are proposed to be used for the whole of the Acado-Baltic province, and are given the symbols I-IV, Va, Vb, Vc, VI.

Faunal lists from outside Scandinavia have sometimes suggested the association of Upper Cambrian olenid species which occur in separate subzones in Scandinavia. Re-examinations of such faunas (e.g. the Dryton Brook olenid fauna from Shropshire, England) have shown that this is not the case, and that either fossils from different horizons have been mixed together, or some of the fossils have been incorrectly determined. So far there is thus no evidence of the Upper Cambrian olenid species not occurring in the same order of appearance in the whole of the Acado-Baltic province. On the contrary, whenever it can be controlled, they seem to do so. Further-

more, the olenid faunas in the various areas of the Acado-Baltic province seem to be much more similar than it appeared from earlier lists of species, since the same species often was given different names in the different areas. It seems impossible to distinguish any olenid subprovinces in the Upper Cambrian of the Acado-Baltic province.

There is a marked difference between the olenid faunas in the various areas of the Acado-Baltic province in Tremadocian times, and it does not seem possible to establish any standard scheme of olenid zones for the Tremadocian of the whole of the province, although local zones may be recognized. The genus *Jujuyaspis*, previously known only from South America, has been found in the Lower Tremadocian Dictyonema Shales in Norway.

At present, Upper Cambrian and Tremadocian olenids outside the Acado-Baltic province are known with certainty only from isolated occurrences in North America, Siberia, Central Asia and South Korea, and possibly also in Australia. The Tremadocian olenids in South America are regarded as belonging to an extension of the Acado-Baltic province.

Olenids are rather scarce in post-Tremadocian beds, and *Triarthrus*, which extends through the whole of the Middle Ordovician, appears to be the last olenid genus.

Little new has been added to solve the problems of correlation between the Upper Cambrian and Lowermost Ordovician zones in the Acado-Baltic and North American provinces. A new fossiliferous section in Norway supports Wilson's view (1954) that there is no gap between the Olenid Series and the Tremadocian Series, in contrast to what was suggested in many earlier correlation tables. However, it is still uncertain where the boundary between these series lies in correlation with the North American standard scheme — probably not too far from the boundary between the Franconian and Trempealeauian. The lower boundary of the Olenid Series apparently corresponds more or less closely to the boundary between the *Crepicephalus* and *Aphelaspis* zones of the Dresbachian.

Conditions in the Olenid Sea (where the Olenid Series was deposited) often tended to be stagnant, at least near the sea floor. Its fauna was characterized by the dominance of Olenidae and the scarcity or absence of many groups of invertebrates, as far as can be judged from the fossils. Thus no benthonic sessile or sedentary forms are known, with the exception of a few brachiopods. The few non-olenid trilobites seem to be accidental invaders, except for some agnostids, which may be regarded as remnants of the earlier *Paradoxides* fauna.

Conditions in the Tremadoc Sea (where the Tremadocian Series was deposited) were at first rather like those of the Olenid Sea, but gradually became much more variegated, as is shown by the greater variety of sediments. The Tremadoc Sea transgressed over areas apparently never covered by the Olenid Sea. Faunal interchange with other seas became easier, and the olenids even spread to areas outside the Acado-Baltic province. On the

other hand, the Acado-Baltic province was invaded by a number of trilobite families and other invertebrates. At least the greater part of this new faunal element came from the west, i. e. the North American province. In accordance with the various ecological habitats, the new forms invaded the different areas of the Acado-Baltic province at different times. The local variations of the olenid faunas in Tremadocian times may perhaps have been caused by the olenids being restricted to the more or less isolated areas with a stagnant sea floor.

A find of specimens of *Acerocare ecorne* apparently in moulting position is of considerable interest, both in showing how the ecdysis took place, and in suggesting that the olenids actually could sojourn in the stagnant bottom waters of the Olenid Sea, at least for shorter periods.

One may distinguish between three different morphological types of shields in the Olenidae. Those with the *Peltura* type of shield probably were vigorous animals and may have been good swimmers. Those with the *Olenus* type probably also swam well, although perhaps not so fast and vigorously. Those belonging to the *Ctenopyge* type have been more adapted to floating.

For several reasons the dominance of the Olenidae in the Olenid Sea may be explained as a result of their adaptation to stagnant waters. The rather rapid decline of the olenids in the Tremadocian epoch probably was caused by the decrease and splitting up of areas with stagnant conditions and the invasion of the Acado-Baltic province by other trilobites and invertebrates, some no doubt competing with them, and some perhaps preying upon them.

The phylogeny of the Olenidae is discussed. Within a phylogenetic trend the number of thoracic segments may increase or decrease, the size of the trilobite may increase or decrease, and likewise the length of the pygidium in relation to the length of the cranidium. Features that may seem to be lost in a phylogenetic lineage, at least in the adults, may reappear later in the lineage. Features that for a long time remain stable, may later be subject to great variation. The in general opisthoparian family Olenidae gave rise to various proparian off-shoots.

In the remarks on the ontogeny it is stressed that there may be marked differences in proportions also between later stages.

Glabellar muscle marks, previously not observed in olenids, are described in *Acerocare ecorne*, and a new type of an olenid pygidium has been found, belonging to *Ctenopyge* (*Mesoctenopyge*) *erecta*.

Since it was unknown whether the olenids had a median suture, a pair of connective sutures, or no sutures crossing the cranidial doublure, evidence for this was specially sought for. It was ascertained that *Parabolina spinulosa*, *Parabolina lobata*, and most probably *Olenus attenuatus* had no sutures crossing the cranidial doublure, i. e. their free cheeks were fused. This may be the case of other olenids as well, although the long and narrow doublure between the free cheeks apparently easily broke, which would explain why the free cheeks usually are found separated.

Descriptions of Norwegian olenids are included in the Systematic Descriptions, which treat all known olenid genera and species, except post-Tremadocian species of *Triarthrus*, which only are listed. New are the genera *Parabolinites*, *Peltocare*, and *Pelturina*, the subgenera *Eoctenopyge* and *Mesoctenopyge*, and the species and subspecies *Olenus alpha*, *Olenus? wilsoni*, *Parabolina kinnekullensis*, *Parabolina? quadrisulcata*, *Parabolinella lata*, *Bienwillia tetragonalis broeggeri*, *Ctenopyge (Eoctenopyge) modesta*, *Ctenopyge (Mesoctenopyge) similis*, *Ctenopyge (Mesoctenopyge) tumidoides*, *Ctenopyge (Ctenopyge) affinis gracilis*, *Protopeltura holtedahli*, *Peltura scarabaeoides westergårði*, *Pelturina punctifera*, *Jujuyaspis angusta*, and *Jujuyaspis keideli norvegica*.

A number of synonyms have been detected. A re-examination of the type material of *Sphaerophthalmus alatus* (Boeck 1838) has most unfortunately shown that it is specifically distinct from the *Sphaerophthalmus* species referred to *Sph. alatus* by most subsequent authors, but is conspecific with the species referred to *Sph. major* Lake 1913 by Scandinavian authors. The name *Sph. humilis* (Phillips 1848) may be revived for *Sph. alatus* auctorum, non Boeck.

Introduction

The Upper Cambrian alum shales of the Oslo region with their stink-stone concretions yielding incredible numbers of trilobites early attracted my interest, and I eventually decided to study this so-called Olenid Series and its trilobite faunas. My attention was drawn more and more to the olenids, which constitute by far the greater number of trilobites in this series and on which a detailed biostratigraphic division could be based. The palaeontological part of the research finally became restricted to the family Olenidae, but a new section through passage beds with olenids between the Olenid Series and the overlying Ceratopyge Series (Tremadocian) led me into including later olenids as well. For taxonomic reasons it was necessary to compare the Norwegian olenids with foreign material, and as most of the genera and almost half the number of the known species of olenids occur in the Norwegian succession, I was tempted to include the remaining forms in my research. In addition there seemed to be justification for a general revision of the whole family. The present paper thus became a monograph on the family Olenidae.

There already exists an extensive literature on the olenids, but in most papers only a restricted number of species are treated. Exceptions are "A Monograph on the British Cambrian Trilobites" by Lake (1906—1946) and the excellent monograph on the Olenid Series of Sweden ("Sveriges Olenidskiffer") by Westergård (1922). However, the olenids described in these papers are confined to the Upper Cambrian and Tremadocian forms of Great Britain and the Upper Cambrian forms of Sweden, respectively. Contributions on the olenids of Norway have been given i. a. by Boeck (1838), Brøgger (1882), Høltedahl (1910), Størmer (1920, 1922a), and Strand (1927, 1929).

I have restricted my study of the morphology of the olenids to the dorsal shields and hypostomae, especially as I have no new material of specimens showing e. g. the extremities. Although an account of the phylogeny and taxonomy of the olenids forms the main aim of the present paper, I have tried to discuss biological problems, more or less along the lines recommended by Weller (1952, p. 146). As one approach to the understanding of the

ecology of the olenids, I have compiled data on their bed rocks and discussed the possible conditions of deposition of the sediments, primarily of the black alum shales. Since the olenids are especially characteristic of the Upper Cambrian Olenid Series, and to some degree also of the Tremadocian Series,¹ I have concentrated on the stratigraphy and lithology of these series. The olenids appear to be good index fossils, often having a short stratigraphic and a great geographic range, and the study of the olenids has yielded information of interest to the stratigraphy of the beds in question.

I hope that the present paper may form a useful basis for further studies on the Olenidae and also be of use to students of Upper Cambrian and Tremadocian stratigraphy. I believe that statistical analyses of populations, phylogenetic trends, and ontogenetic development of olenids are promising fields for research, and may lead to interesting results on trilobites in general.

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For the loan of material used in this study I am greatly indebted to Professor E. Stensiö and Dr. Tor Ørvig (both of the Paleozoological Department of the Swedish State Museum of Natural History), Professor P. Thorslund, Dr. T. Tjernvik, and Dr. V. Jaanusson (of the Palaeontological Museum of the University of Uppsala), the late Professor G. Troedsson (of the Palaeontological Museum of the University of Lund), Dr. G. Regnéll (of the same Museum), Dr. F. Brotzen (Geological Survey of Sweden), Professor Chr. Poulsen (Mineralogical Museum of the University of Copenhagen), Dr. C. J. Stubblefield (Geological Survey and Museum, London), Professor

¹ Regarded here as forming the base of the Ordovician.

O. M. B. Bulman and Mr. A. G. Brighton (both of the Sedgwick Museum, Cambridge), and Dr. J. M. Edmonds (Department of Geology and Mineralogy, University Museum, Oxford). I am also very grateful to Dr. Madeleine A. Fritz (of the Royal Ontario Museum of Zoology and Palaeontology) for sending me casts of Canadian olenids.

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Palaeontological Museum, University of Oslo, June 1956.

Abbreviations

The following abbreviations are used in connection with particular specimens:

- G.S.M. Geological Survey and Museum, London.
- P.I.L. Museum of the Palaeontological Institute, University of Lund.
- P.M.O. Palaeontological Museum, University of Oslo.
- R.O.M.P. Royal Ontario Museum of Palaeontology.
- R.M. Palaeontological Department, State Museum of Natural History, Stockholm (Naturhistoriska Riksmuseet).
- S.G.U. Museum of the Geological Survey of Sweden, Stockholm (Sveriges Geologiska Undersökning).

Terminology

Different authors often use different terms for the same features of the trilobite shield, and sometimes the same terms are given different meanings. This is especially true of the terms for the cephalon. To avoid misunderstanding, some of the terms used here are shown on text-figures 1 and 2.

Cranidium. I have found it useful to introduce a new term, *eye line*, for a line through the centres of the eyes normal to the axial (sagittal) plane. The fixed cheeks are divided into four areas: the postocular, interocular, preocular part of the fixed cheek (abbr.: *postocular*, *interocular*, and *preocular cheek*), and the palpebral lobe. The postocular cheek is separated from the interocular cheek by an imaginary line normal to the axial plane immediately behind the eyes, and the interocular cheek is separated from the preocular cheek by the eye ridge, or, when no eye ridges are present, by an imaginary line from the anterior end of the palpebral lobe to the anterior corner of the glabella. When the two preocular cheeks are joined in front of the glabella, they together form the preglabellar field. The facial sutures are divided in four: the *postocular*, *ocular*, *preocular*, and *anterior* (part of the facial) *sutures*. Similarly, the terms postocular, ocular, preocular, and anterior margins may be used for the corresponding parts of the lateral margin of the cranidium and the inner lateral margin of the free cheeks. Some terms for describing different courses of the preocular and postocular margins of the cranidium are shown in text-figure 2.

The glabellar furrows (sulci) are counted from the rear and given the symbols *S1*—*S4* (cf. text-fig. 1).¹ The occipital furrow is given the symbol *SO* (sulcus occipitalis). Similarly, the glabellar lobes may be referred to as *L1*, *L2*, etc., counted from the rear, the anterior lobe as *LA*, and the occipital ring as *LO* (lobus occipitalis). Some terms for describing different types of occipital and glabellar furrows are shown in text-figure 2.

Free cheeks. The angle between the outer lateral and the posterior margin is called the *corner angle*. In opisthoparian trilobites this angle is also the

¹ Cf. postscript.

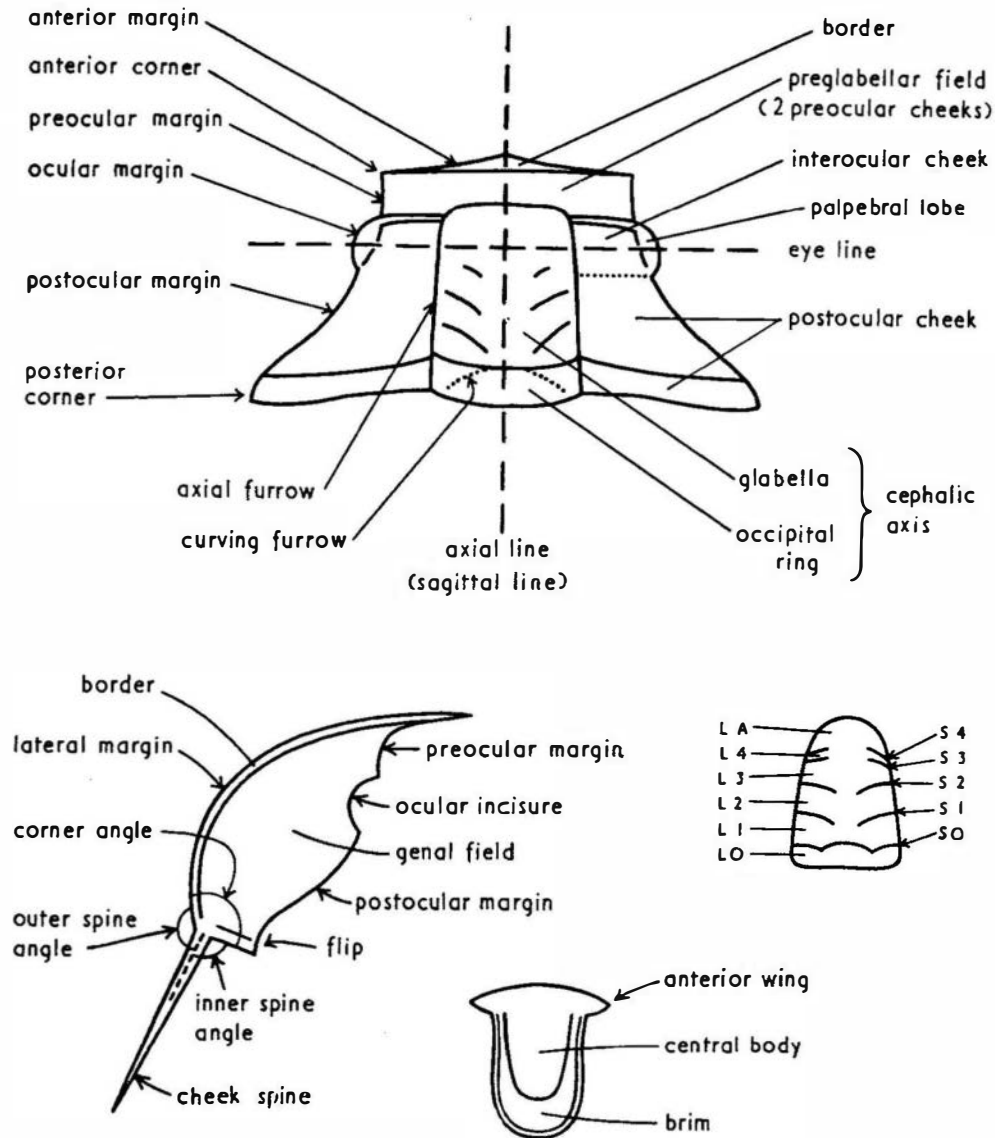


Fig. 1. Terminology for features of the cephalon and hypostoma.

genal angle. The angle between the outer lateral margin and the median line of the cheek spine is called the *outer spine angle*, and the angle between the posterior margin and the median line of the spine is called the *inner spine angle*. The three angles together amount to 360° . When the outer lateral margin and the posterior margin form an even curve, the cheeks are said to be *pelturoid*. The corner area between the posterior margin and the postocular margin is called the *flip*.

Hypostoma. The area between the central body and the marginal border is referred to as the *brim*.

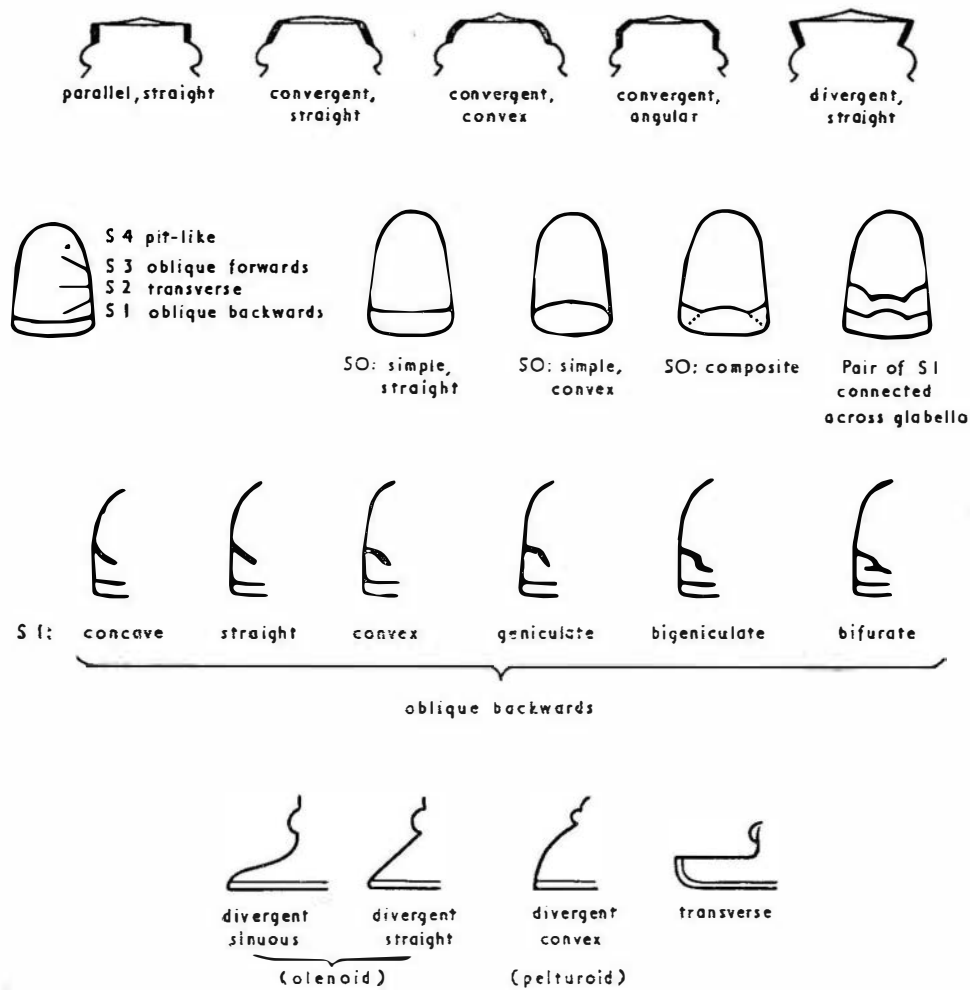


Fig. 2. Some qualifying terms for the preocular margins (or preocular facial sutures), the occipital and glabellar furrows, and the postocular margins (or postocular facial sutures).

Axial shield. This term is introduced for a dorsal shield without free cheeks, i. e. the axis and all parts of the dorsal shield connected with the axis (cranidium + thorax + pygidium).

Length and width. As is now the general practice, "length" refers to the sagittal (sag.) or exsagittal (exsag.) extension, "width" to the transverse (tr.) extension of the shield, or parts of the shield, thus also in the preocular, interocular, and postocular cheeks, occipital ring, and preglabellar field. Exceptions are borders, spines, and furrows, whose lengths are always measured along the longest extension.

Classification, affinities, and origin of olenids

Previous classifications

When Burmeister (1843) erected the family Olenidae, he assigned to it the two genera *Paradoxides* and *Olenus*. It should be remembered, however, that at that time *Parabolina* species were still assigned to *Paradoxides*, and that *Olenus* included species now assigned to other genera, olenid and non-olenid (*Sphaerophthalmus*, *Eurycare*, *Peltura*, *Parabolina*, *Triarthrus*, *Ctenopyge* a. o.).

Angelin (1854) erected a family Leptoplastidae, which only included genera which are still considered as olenid genera: *Olenus*, *Peltura*, *Parabolina*, *Acerocare*, *Leptoplastus*, *Eurycare*, *Sphaerophthalmus* (including species later assigned to *Ctenopyge*), and *Anopocare* (based on the head of *Sphaerophthalmus humilis* and the tail of *Peltura scarabaeoides*).

In his Monograph of British Trilobites Salter (1864) took the family Olenidae more in the sense of Burmeister, and listed the following genera: *Olenus*, *Sphaerophthalmus*, *Paradoxides*, *Anopolenus*, *Remopleurides*, *Triarthrus*, *Tiresias*, *Cyphoniscus*, and *Hydrocephalus*.

Brøgger (1882) again restricted the concept of the family. As can be inferred from his remarks on the Olenidae (p. 164) and his descriptions, he referred the following genera to it: *Olenus* (subgenera *Olenus*, *Parabolina*, *Parabolinella*), *Peltura* (subg. *Peltura*, *Protopeltura*, *Cyclognathus*, *Acerocare*), *Triarthrus* (or subgenus?), *Leptoplastus* (subg. *Leptoplastus*, *Eurycare*, *Sphaerophthalmus*, *Ctenopyge*), *Boeckia*. This division of the Olenidae approaches that accepted now, except that his subgenera are now considered genera, and three of his genera are treated as subfamilies.

Beecher (1897) brought confusion into the classification of Olenidae Salter (sic!), which he took in a very wide sense. He recognized four groups (subfamilies), *Paradoxinae*, *Oryctocephalinae*, *Oleninae*, and *Dikelocephalinae*. Only two of these subfamilies included genera that we now assign to the Olenidae (as well as non-olenid genera), these being *Oryctocephalinae* and *Oleninae*. Looking apart from all the non-olenids in these groups, *Oryctocephalinae* embraced *Ctenopyge*, *Parabolina*, *Eurycare*, *Angelina*, *Peltura*, and *Protopeltura*, while *Oleninae* included *Olenus*, *Acerocare*, *Leptoplastus*, *Sphaerophthalmus*, *Parabolinella*, *Boeckia*, and *Triarthrus*. This grouping of the olenids is quite unsatisfactory.

Persson (1904) again restricted the Olenidae, developed Brøgger's scheme and divided the olenid genera into three groups: Continuæ (*Olenus*, *Parabolina*), Abruptæ (*Eurycare*, *Leptoplastus*, *Ctenopyge*, *Sphaerophthalmus*), and Inermes (*Peltura*, *Acerocare*). This grouping was based on the position or absence of the genal spine, and was also adopted by Lake (1908), who added *Parabolinella* to the Continuæ.

Westergård (1922) in his monograph on the Olenid Shale in Sweden added important knowledge on the Cambrian Olenidae, and gave a "phylogenetic tree" for the Upper Cambrian genera in Scandinavia.

Ulrich (1931) erected a new family Triarthridae for *Triarthrus*, *Parabolinella*, *Peltura*, *Protopeltura*, *Acerocare*, and, doubtfully, *Triarthropsis* and *Stenochilina*.

This family was later incorporated in the Olenidae again by Kobayashi (1935c, p. 256), who divided the Olenidae into subfamilies in the following way: Subfamily Oleninae nov. (sic.!) (*Olenus*, *Parabolina*, *Parabolinella*, *Parabolinopsis*, *Beltella*, *Angelina*), Subfamily Leptoplastinae Angelin (*Leptoplastus*, *Eurycare*, *Ctenopyge*, *Sphaerophthalmus*), Subfamily Triarthrinae Ulrich (*Protopeltura*, *Peltura*, *Acerocare*, *Cyclognathus*, *Westergardia*, *Boeckia*, *Triarthrus*).

In 1936 Kobayashi added a new genus, *Jujuyaspis*, to the Leptoplastinae, and in 1937 Troedsson added two new genera, *Hedinia* and *Westergårdites*, to the Oleninae and Triarthrinae respectively. *Hedinia* (i. e. *Hedinaspis* Troedsson 1951) is removed here from the Olenidae (cf. p. 20).

Whitehouse (1939) added a new subfamily, Papyriaspinae, comprising *Pianaspis*, *Papyriaspis*, *Rhodonaspis*, and *Hedinia*. For reasons discussed below (p. 21) this subfamily is removed from the Olenidae.

Harrington & Leanza (1952) divided the Olenidae into four subfamilies: Oleninae, Triarthrinae, Leptoplastinae, and Pelturinae. The latter was erected as a new subfamily, but as Corda (in Hawle & Corda, 1847) erected a family Pelturides, the subfamily should be referred to as Pelturinae Corda 1847. Harrington & Leanza furthermore gave a "phylogenetic tree" of the olenids, which is based on Westergård's, but is important as it also included non-Scandinavian and Tremadocian genera.

Hupé (1953) recognized six olenid subfamilies: Papyriaspinae, Oleninae, Leptoplastinae, Triarthrinae, Jujuyaspinae, and Aulacopleurinae. The Papyriaspinae and Aulacopleurinae are not regarded as olenids here (pp. 20, 21). The Jujuyaspinae (recte: Jujuyaspidinae) was erected for the genus *Jujuyaspis* and should be characterized by a proparian suture. However, as shown by Harrington & Leanza (1952), *Jujuyaspis* does not have a proparian suture (cf. postscript).

Tjernvik (1955) published a phylogenetic tree suggesting the relationships of the new genus *Nericiaspis* and another proparian genus, *Saltaspis*, to other pelturines.

Proposed classification

I suggest dividing the family Olenidae into three subfamilies, thus reviving the tripartition of the family proposed by Persson (1904).

I have preferred to include the subfamily Triarthrinae in the subfamily Oleninae because the subfamily Oleninae would otherwise include only two or three genera, and because it is uncertain whether all the genera assigned to the Triarthrinae form a group which developed monophyletically from the Oleninae s. s. Apart from this, the classification adopted here on the whole agrees with that proposed by Harrington & Leanza (1952), but differs in the following items:

To the Oleninae (including Triarthrinae) I have added *Westergårdites* (not mentioned by Harrington & Leanza), *Parabolinites* n. gen., and, with doubt, *Leiobienvillia* and *Moxomia*. I have removed *Plesioparabolina*, which probably is not an olenid (cf. below), and which Harrington & Leanza only tentatively assigned to this subfamily.

From the Leptoplastinae I have removed *Mekynophrys* and *Pyraustocranium*, which I doubt should be assigned to the Olenidae (cf. below), and which Harrington & Leanza only hesitatingly included in this subfamily.

To the Pelturinae I have added *Sphaerophthalmoides* Hutchinson 1952 (which I consider to be a synonym of *Westergårdia*), *Nericiaspis* Tjernvik 1955, *Sphaerophthalmella* Kobayashi 1955 (cf. postscript), and the two new genera *Pelturina* and *Peltocare*. *Leptoplastides*, *Beltella* and *Paenebeltella* are included with some doubt.

Like many earlier classifications, the present one is based on the assumed phylogeny (cf. p. 82 and chart 6).

Family *Olenidae* Burmeister 1843.

Subfamily *Oleninae* Burmeister 1843

(including *Triarthridae* Ulrich 1931).

Olenus Dalman 1827.

Parabolina Salter 1849.

Parabolinites n. gen.

Parabolinella Brøgger 1882.

Bienvillia Clark 1924 (synonym: *Diatemnus* Raymond 1937).

Triarthrus Green 1832.

Porterfieldia Cooper 1953.

Westergårdites Troedsson 1937.

Plicatolina Shaw 1951.

Angelina Salter 1864 (synonym: *Keidelaspis* Harrington 1937).

? *Leiobienvillia* Rasetti 1954.

? *Moxomia* Walcott 1924.

Subfamily *Leptoplastinae* Angelin 1854.*Leptoplastus* Angelin 1854.*Eurycare* Angelin 1854.*Ctenopyge* Linnarsson 1880.Subgenus *Ctenopyge* Linnarsson 1880.» *Eoctenopyge* n. subgen.» *Mesoctenopyge* n. subgen.*Sphaerophthalmus* Angelin 1854.Subfamily *Pelturinae* Corda 1847(including *Jujuyaspidinae* Hupé 1953).*Protopeltura* Brøgger 1882.*Peltura* Milne Edwards 1840 (synonym: *Anthes* Goldfuss 1843).*Pelturina* n. gen.*Acerocarina* Poulsen 1951 (= *Cyclognathus* Linnarsson 1875 non St. Hillaire 1833).*Acerocare* Angelin 1885.*Nericiaspis* Tjernvik 1955.*Saltaspis* Harrington & Leanza 1952.*Peltocare* n. gen.*Westergårdia* Raymond 1927 (synonym: *Sphaerophthalmoides* Hutchinson 1952).*Boeckaspis* Henningsmoen 1955 (= *Boeckia* Brøgger 1882 non B. Brady 1871).*Sphaerophthalmella* Kobayashi 1955 (cf. postscript).*Jujuyaspis* Kobayashi 1936.? *Leptoplastides* Raw 1919 (synonyms: *Parabolinopsis* Hoek 1912, *Andesaspis* Kobayashi 1935).? *Beltella* Lake 1919.? *Paenebeltella* Ross 1951.**Trilobites doubtfully belonging to or excluded
from the Olenidae***Doubtful genera.*

In a discussion of some genera possibly belonging to the Olenidae, Kobayashi (1936a, p. 98) concluded that "It is yet uncertain that *Andesaspis*, *Moxomia*, *Tostonia*, *Moosia*, *Triarthropsis* and *Stenochilina* belong to the Olenidae". Since then, *Andesaspis* has been shown to be a true olenid, and *Moosia* Walcott 1924 is now regarded as a synonym of *Elvinia*, and is thus an elviniid. *Triarthropsis* and *Stenochilina* are now regarded as members of

the Catillicephalidae (cf. Rasetti, 1954b). *Moxomia* is discussed below as a possible member of the Olenidae.

Tostonia Walcott 1924 (type species: *Dicellosephalus iole* Walcott 1884) is rather olenid-like, but may equally well belong to some other family. However, as long as the type species is not better known, it is difficult to trace its relationships. *Tostonia duplicata* and *T. unidulcata* (both Raymond 1937) have rather wide anterior border and are not olenids, but it is possible that they are not congeneric with the type species of *Tostonia*.

Since the appearance of the above-cited paper by Kobayashi, some more genera have been described, which have been assigned to the Olenidae, but whose reference to this family is doubtful, namely;

Mekynophrys Harrington 1938 (type species: *M. nanna*) from the Upper Tremadocian of Argentina, originally assigned to the Leptoplastinae, but only tentatively included in this subfamily by Harrington & Leanza (1952). It is certainly not a leptoplastine. If it is an olenid, it may possibly be related to genera like *Beltella*, but its olenid affinities seem doubtful.

Mendoparabolina Rusconi 1951 (type species: *M. pirquinenis*) was described as an olenid by Rusconi (1951), but probably does not belong to this family (cf. p. 25).

Plesioparabolina Harrington & Leanza 1942 (type species: *P. proparia*) was originally assigned to the Olenidae, and doubtfully included in the Oleninae by Harrington & Leanza in 1952. It may possibly be an olenid, but its reference is perhaps best regarded as doubtful.

Pyraustocranium Ross 1951 (type species: *P. vultulata*) from zone F of the Garden City formation was suggested by Ross to be closely related to such forms as *Parabolina*, *Leptoplastus*, and *Ctenopyge*. It is not a leptoplastine, and its reference to the Olenidae is at least doubtful, although it might be related to *Pacnebeltella*.

Triarthroides Raymond 1937 (type species: *T. cyclas*) was erected as a genus of the Triarthridae. Only the cranium is known, and it is safest to regard its reference to the Olenidae as uncertain.

Genera excluded from the Olenidae.

The family Olenidae was previously often taken in a very wide sense, and e. g. Beecher (1897) included in this family a number of genera (such as *Olenellus*, *Paradoxides*, *Ptychoparia*, *Zacanthoides*) which are now assigned to other families or even superfamilies. It is hardly necessary to discuss here the removal of all these non-olenid genera, and I shall only discuss the genera which more recently have been assigned to the Olenidae, but which I believe are not olenids.

Aulacopleura Corda 1847 (type species: *Arethusina konincki* Barrande) from the Ordovician and Silurian of Bohemia, has often been assigned to the Olenidae (e. g. by Richter, 1932, p. 854; cf. also under *Proaulacopleura*).

Příbyl (1947) for good reasons assigned *Aulacopleura* and the Aulacopleurinae to the Otarionidae R. & E. Richter 1926. He did not deny the possibility of *Aulacopleura* together with *Otarion* and *Proetus* being derived from the Olenidae, but considered such a relationship to be completely illogical. *Aulacopleura* should undoubtedly not be assigned to the Olenidae (as also maintained by Warburg, 1925, and Poulsen, 1927, 1934), and I believe it is highly improbable that it (and the Aulacopleurinae) should have descended from, or be closely related to the Olenidae, since *Aulacopleura* differs from the Olenidae in many important features, such as type of glabella, type of thoracic segments, and in not having the facial sutures united in front.

Bavarilla Barrande 1868 (type species: *B. hofensis*) from the Tremadocian of Bavaria and eastern Bohemia has sometimes been assigned to the Olenidae, recently by Příbyl (1953, p. 16). The type species differs from the Olenidae in several respects (see illustrations of it in Prantl & Ružička, 1941, pl. II). The cranium is of the ptychoparoid type, but with rather wide border. The preglabellar field and thorax are unlike those of olenids. The thoracic segments are more like those of *Ptychoparia* and allies, and I confidently exclude *Bavarilla* from the Olenidae. It is included in the Calymenidae by Sdzuy (1955).

Bernia Frederickson 1949 (type species: *B. obtusa*). See under *Parabolinoidea*.

Euloma Angelin 1854 was earlier often assigned to the Olenidae, and recently also by Příbyl (1953) and Sdzuy (1955). Its type species, *E. laeve* from the Tremadocian of Sweden, unfortunately is poorly known, but if *E. ornatum* is congeneric, *Euloma* differs from the Olenidae i. a. in the type of glabella, type of glabellar furrows, in the palpebral lobes, and in the type of pleurae, and cannot be closely related to the olenids, although its relationships are uncertain (cf. Henningsmoen, 1951, p. 202).

Eulomia Ružička 1931 (type species: *E. mitratum*) from the Tremadocian in Bohemia was assigned to the Olenidae by Příbyl (1953). Its wide and thickened border excludes it from the Olenidae, and the outline of its glabella is furthermore different from that found in any olenids.

Hedinaspis Troedsson 1951 (= *Hedinia* Troedsson 1937, type species *Hedinia regalis*). Troedsson (1937) described the two genera *Hedinia* and *Westergårdites* from black limestone beds in eastern T'ien-Shan, Central Asia, and referred them to the Oleninae and Triarthrinae, respectively. *Westergårdites* no doubt is an olenid, but *Hedinia* (i. e. *Hedinaspis*) differs from the Olenidae in many features, as for instance in the pleurae which have a transverse instead of an oblique furrow and have distinct marginal ridges, and in the shape of the glabellar furrows, especially the queer S1. The latter reminds one, curiously enough, rather much of S1 in the Ceratopygidae, also well represented in the T'ien-Shan fauna (*Lopnorites*, *Diceratopyge*). The resemblance between the glabellae of *Hedinaspis* and *Lopnorites* was

noticed already by Hupé (1953, p. 204, footnote 1). The cranidium and free cheeks of *Hedinaspis* might belong to a ceratopygid, but the thorax differs in the great number of segments and different type of pleurae, and the pygidium is small and without long spines. Troedsson (1937, p. 59) stated that there is an indication of another boundary between the thorax and the pygidium in some young specimens, which may have had relatively larger pygidia. A glabellar node is well developed in *Hedinaspis*, but is not known in the Olenidae, whereas it occurs in the Ceratopygidae and many other families. It is uncertain whether the resemblance between *Hedinaspis* and the Ceratopygidae indicates any closer relationships, but I believe that *Hedinaspis* in no case should be assigned to the Olenidae.

Highgatella Shaw 1955 (type species: *Terranovella gelasinata* Shaw 1951). See under *Parabolinoidea*.

Holubaspis Přibyl 1950 (= *Holubia* Klouček 1931; type species: *H. bohémica*). In 1926 Ružička described two supposed olenids as *Olenus* (*Cyclognathus*?) sp. I and *Olenus* sp. II from the Tremadocian of Bohemia. Only incomplete cranidia have been found, but none of them look very olenid-like. Especially the thickened border is suspicious, and I do not believe that they belong to the Olenidae. Later Klouček (1931) assigned one (or both?) of them to the genus *Holubia* in a paper not available to me. *Holubaspis* (= *Holubia*) was listed as an olenid genus by Přibyl in 1953, but should in my opinion be excluded from the Olenidae.

Isidrella Rusconi 1955a, assigned to the Olenidae by Rusconi, 1955b, apparently is no olenid (cf. p. 25).

Loganellus Devine 1863 was included in the Olenidae by Clark (1924, p. 20). However, it is probably related to the Richardsonellidae (cf. p. 29).

Namiolenoides, erected as a subgenus of *Parabolina* by Rusconi in 1952 (cf. p. 24).

Orkekeia Rusconi 1955a, tentatively assigned to the Olenidae by Rusconi 1955b, apparently is no olenid (cf. p. 25).

Panarchaeogonus Öpik 1937 (type species: *P. parvus*) from the Ordovician of Esthonia was tentatively assigned to the Olenidae by Öpik (1937). It is certainly not an olenid, and may possibly belong to the Dimeropygidae as suggested by Jaanusson (1956).

Papyriaspis Whitehouse 1939 (type species: *P. lanceola*). Whitehouse (1939, p. 215) erected a subfamily Papyriaspinae (recte: Papyriaspidae), which he included in the Olenidae, and which he believed included forms ancestral to *Olenus*. Besides the two new Australian genera *Papyriaspis* (Middle Cambrian) and *Rhodonaspis* (Upper Cambrian), he also assigned the Korean genus *Pianaspis* (early Middle Cambrian) and the Central Asiatic genus *Hedinia* (i. e. *Hedinaspis*) to the Papyriaspidae. I have already removed *Hedinaspis* from the Olenidae, and I do not believe that the other genera assigned to the Papyriaspidae are olenids either. I even doubt that they are closely related to each other at all. *Papyriaspis* itself clearly differs

from the olenids in the type of glabella, glabellar furrows, and thoracic segments. *Rhodonaspis* bears more resemblance to an olenid, but differs i. a. in the type of palpebral lobes and thoracic segments. *Pianaspis* is the most olenid-like of these genera, but it is apparently closest to genera like *Elrathia* Resser 1937 and should not be assigned to the Olenidae.

Parabolinoides Frederickson 1949 (type species: *P. contractus*). Wilson (1954, p. 265) suggested that part of the *Conaspis* fauna in North America was olenid derived (*Parabolinoides* and *Bernia* of Frederickson, 1949) and that Shaw's "*Terranovella*" (i. e. *Terranovella gelasinata* Shaw 1951, type species of *Highgatella* Shaw 1955) was another olenid derivative. However, they all seem to be closer to non-olenid groups. They should possibly be included in the family Elviniidae (s. l.) which may be related to, but not derived from the Olenidae (cf. text-fig. 3).

Pianaspis Saito & Sakakura 1936 (type species: *P. kodairai*). See under *Papyriaspis*.

Proaulacopleura Kobayashi 1936 (type species: *P. buttsi*) was originally described by Butts (1926) as *Olenus* cf. *truncatus*. *Proaulacopleura* (early Upper Cambrian) was regarded as an ancestor of *Aulacopleura* by Kobayashi (1936a), and Hupé (1953, p. 207) included *Proaulacopleura* in the subfamily Aulacopleurinae Angelin 1854, which he assigned to the Olenidae. However, in a revision of *Aulacopleura*, Pribyl (1947, p. 543) pointed out the difference between this genus and *Proaulacopleura*, and concluded that "there appears to be no close relation between these genera", with which I quite agree. As discussed elsewhere (p. 27), *Proaulacopleura* appears to be a non-olenid related to *Olenus*.

Sao Barrande 1846 has often been referred to the Olenidae, e.g. by Pribyl (1953). Its type species, *Sao hirsuta* comes from the Middle Cambrian of Bohemia. It differs profoundly from the Olenidae i. a. in the glabella and pleurae, and can safely be excluded from the Olenidae. For its accommodation, Hupé (1953, p. 193) erected the family Saoidae, which was regarded as a subfamily, Saoinae, of the Solenopleuridae by Poulsen (1954, p. 445).

Zacompsus Raymond 1924 (type species: *Z. clarki*) was originally erected as an olenid genus. However, it has little in common with the olenids, and has for a long time been excluded from the Olenidae, although its relationships are uncertain.

Species excluded from or with doubt retained in the Olenidae.

Several species which previously were assigned to olenid genera have later proved not to be olenids, predominantly species from outside the Acado-Baltic province. Some species which more recently have been assigned to the Olenidae, but which have no or doubtful affinities with the family, are mentioned below.

Boeckia? descensus Clark 1924 is based on an incomplete cranidium, but its eyes strongly suggest that it is no olenid.

MIDDLE CAMBRIAN (Upper part)	UPPER CAMBRIAN (Olenid Series)	TREMADOCIAN
	Elviniidae	
Andrarinidae	Olenidae	
Anomocaridae		Richardson- ellidae
	Ceratopygidae	
	Asaphidae	

Fig. 3. Possible relationships between the Olenidae and some other families.

Besides *Olenus* sp. I and *Olenus* sp. II described by Ružička (1926) and later assigned to *Holubaspis* (apparently a non-olenid genus, cf. p. 21), *Olenus* sp. III was described by him in a later paper (1931). Only an incomplete cranidium is known, but it does not appear very olenid-like. Like the two other "*Olenus*" species it is from the Tremadocian of Bohemia and does at least not belong to the genus *Olenus*. Prantl & Ružička (1941, p. 22) have described another fragmentary cranidium from the Tremadocian of Bohemia and suggested it to be an olenid. Too little is known of this form to be able to decide whether it is an olenid or not.

Kobayashi (1936a, p. 91) discussed some species originally assigned to *Olenus*: *Olenus?* *indicus* Waagen 1891, *Olenus haimantensis* Reed 1910, *Olenus* sp. Lorentz 1906, *Olenus* cf. *truncatus* Butts 1926, and *Olenus* sp. Resser 1933. He proved that the three first species did not belong to the Olenidae, whereas Butts' *Olenus* cf. *truncatus* was redescribed as *Proaulacopleura buttsi* (cf. p. 30) and Resser's *Olenus* sp. as *Parabolinella? evansi*.

Parabolinella? evansi Kobayashi 1936 was originally described from a black limestone north of Mt. Jubilee, British Columbia. It has later been described from the Marathon uplift in Texas by Wilson (1954). If the material from Texas is correctly assigned to this species, it may be removed from the olenids, although it may be related to them. Thus the wide anterior border is a non-olenid character, and the strongly diverging facial sutures in front of the eyes is a feature not known in *early* olenids. The species may be close to genera like *Proaulacopleura* and perhaps especially *Aphelaspis*, with which the specimens from Texas are associated. For the time being, the

species may tentatively be assigned to *Aphelaspis*, although it should probably be assigned to a new genus.

Parabolinella occidentalis Wilson 1951 apparently is related to the associated genera *Taenicephalus* and *Conaspis*, and is at least not an olenid. It resembles *Parabolinoides* perhaps even more, and may provisionally be referred to as *Parabolinoides? occidentalis*. Wilson (1954, p. 282) suggested that it might be related to *Parabolinella evansi*.

In various papers Rusconi has erected a number of Cambrian species from Argentina, which he assigned (some tentatively) to olenid genera, as well as two species of *Triarthropsis*, a genus which he in some cases attributes to the Triarthridae, in others to the Olenidae. He has further erected *Namiolenoides* as a subgenus of *Parabolina*, and *Mendoparabolina* as a new olenid genus.

Unfortunately, most of these forms are rather poorly known. Some are based solely on the pygidium.

Several of the species are stated to be Middle Cambrian, these being:

Olenus multicostatus Rusconi 1948 (p. 187)

Olenus? tellecheai (Rusconi 1945) (p. 1, fig. 1) (transferred from *Calymene* by Rusconi in 1948, p. 187)

Olenus? triangulatus Rusconi 1946 (p. 2, figs. 2—3)

Parabolina? (Namiolenoides) asperoensis Rusconi 1952 (p. 110, figured as *Olenoides asperoensis* in pl. II, fig. 6)

Protopeltura? asperoensis Rusconi 1952 (p. 102, pl. V., figs. 2—3)

Parabolinella? pentacantha Rusconi 1955a (p. 1, no fig.) (1955b, p. 15, pl. II, fig. 2)

Isidrella bispinata Rusconi 1955a (p. 1, no fig.) (1955b, p. 15, pl. II, fig. 1)

Orkekeia ornata Rusconi 1955a (p. 1, no fig.) (1955b, p. 17, pl. II, fig. 4)

Triarthropsis australis (Rusconi 1951) (also recorded from the Upper Cambrian (cf. below).

It seems rather unlikely that olenids should occur in the Middle Cambrian, and especially genera like *Parabolina*, *Protopeltura*, and *Parabolinella*. I have unfortunately not seen the original description (and figures) of *Olenus? triangulatus*.

Parabolina? (Namiolenoides) asperoensis and *Protopeltura? asperoensis* are based on pygidia only. Both differ from olenid pygidia in having rather strong pleural ribs, and I believe that they can safely be excluded from the Olenidae. Most probably they belong to some zecanthoidaceans. Since *Parabolina? (Namiolenoides) asperoensis* is the type species (and only known species) of *Namiolenoides*, this subgenus may be excluded from the Olenidae.

The figure of *Olenus? tellecheai* (a complete dorsal shield) shows that this species has very little in common with the Olenidae, and may be excluded

from the family. No figures and only a very brief and insignificant diagnosis are given of *Olenus? multicostatus*, which is compared with *O.? tellecheai*.

Only the pygidium is known of *Parabolinella? pentacantha*, too. It does not seem to belong to an olenid.

Isidrella bispinata (type species, and only known species), which was assigned to the Olenidae, is likewise based on a pygidium. It resembles that of "*Parabolinella*" *pentacantha*.

Orkekeia ornata (type species, and only known species) was tentatively assigned to the Olenidae by Rusconi. It is based on a pygidium, definitely of a non-olenid type.

Some other species described by Rusconi are stated to come from Upper Cambrian beds, viz.:

Olenus? obliquocnsis Rusconi 1954a (p. 43, pl. III, fig. 9)

Mendoparabolina pirquiensis Rusconi 1951 (p. 3, fig. 4)

Mendoparabolina brevicauda Rusconi 1955a (p. 2) (1955b, p. 30, pl. II, fig. 15)

Peltura? jarillana Rusconi 1953a (p. 2, fig. 5)

Triarthropsis australis (Rusconi 1951) (p. 3, fig. 3) (transferred from *Parabolina?* by Rusconi in 1953b, p. 3)

Triarthropsis pampanus Rusconi 1953b (p. 3, fig. 6) (Also figured by Rusconi in 1954a, pl. III, figs. 1—3).

Olenus? obliquocnsis is not an *Olenus* species, as is shown by the markedly diverging pre-ocular sutures and the rather wide border. The latter feature furthermore excludes it from the Olenidae.

Mendoparabolina pirquiensis (type species). Both cranidia and pygidia are known, but neither are very olenid-like. The species may be related to *Triarthropsis australis*. *Mendoparabolina brevicauda* is based on a pygidium. Its affinities are best regarded as uncertain.

Peltura? jarillana is based on a pygidium. The pygidium might belong to a pelturine, but it could equally well belong to some non-olenid genus. Some cranidia attributed to the species have not been figured, but are stated to have a granulate glabella and a relatively long (sag.) preglabellar field (cf. Rusconi, 1954a, p. 15). Granulation is very rare among the olenids, and no *Peltura* species have a well-developed preglabellar field.

Both cranidia and pygidia are known of *Triarthropsis australis*, but it seems unlikely that this species is an olenid (or a *Triarthropsis* species). The species is recorded both from the Upper Cambrian (horizonte *Peladense*, cf. Rusconi, 1954b, p. 103) and the Middle Cambrian (horizonte *Isidrense*, cf. Rusconi, 1954b, p. 89).

The figures of *Triarthropsis pampanus* presented by Rusconi in 1954a (pl. III, figs. 1—3) show that the cranidium at first sight resembles that of some late olenids like *Bienvillia*. However, the palpebro-ocular ridge reminds one more of e. g. *Irvingella*. As *T. pampanus* is accompanied by an *Irving-*

ella-Elvinia fauna, it is quite possible that it belongs to this group of trilobites, with which it also shares the rather narrow (tr.) frontal area.

None of the Middle and Upper Cambrian forms assigned to the Olenidae by Rusconi can with certainty be included in the Olenidae. Several may safely be excluded from the family. The others are insufficiently known, but should perhaps be given the benefit of doubt.

Position of the Olenidae within the class Trilobitae

In my "Remarks on the classification of trilobites" (1951) I included the Olenidae in the superfamily Conocoryphacea Swinnerton 1915, thus abandoning a superfamily Olenidea Swinnerton 1915.¹ The superfamily Conocoryphacea was taken in rather a wide sense, but I suggested (1951, p. 210) that it would perhaps be split up again when its different trends had been worked out. A "splitting up" has later been carried out by Hupé (1953), who divided the superfamily Conocoryphacea into 6 superfamilies, including the superfamily Olenoidae. The grouping of families proposed by Hupé seems to be rather provisional in these cases, and I still believe that much work is needed to find out the relationships between the great number of families earlier assigned to the Conocoryphacea. Hupé (1953) included 12 families in the Olenoidae. They do not all seem related, and only a few of them may possibly be more closely related to the Olenidae. As discussed below, the Olenidae may be related to the Andrarinidae, Elviniidae, Anomocaridae, Asaphidae, Ceratopygidae, Richardsonellidae, and Remopleurididae. However, this is put forward only as a working hypothesis, and if a superfamily Olenacea is recognized, I would at present restrict it to the family Olenidae.

Remarks on some possibly related trilobite families

Text-fig. 3 (p. 23).

Andrarinidae.

When Raymond (1937, p. 1106) erected the genus *Andrarina*, he assigned it to a new family Andrarinidae, and this family name may of course be used for *Andrarina* and allies, even if the present concept of *Andrarina* is different from that of Raymond (cf. Westergård, 1948, p. 13, on the type species of *Andrarina*: *Liostracus costatus* Angelin 1854). In 1948 Westergård assigned *Andrarina* and the apparently closely related genus *Nericia* Westergård 1948 to the subfamily Richardsonellinae, which he, with doubt,

¹ According to the "Copenhagen Decisions on Zoological Nomenclature" (London, 1953), superfamilies belong to the Family Group of taxonomic units. Consequently the author of the superfamily Conocoryphacea is Angelin 1878 (who erected the family Conocoryphidae), and of the superfamily Olenacea it is Burmeister 1843 (who erected the family Olenidae).

included in the family Dikelocephalidae Miller 1890. The reference of *Andrarina* to the Richardsonellinae was based upon the resemblance between *Andrarina* and *Loganellus* Devine 1863 from the North American *Hungaia* zone. However, there is a considerable span of time between these genera, and they do not appear to be so closely related as suggested by Westergård, one difference being that the free cheeks of *Loganellus* are united ventrally, as later observed by Rasetti (1945, p. 470). In 1953 Westergård tentatively included *Grönwallia* Kobayashi 1935 in the Andrarinidae. It seems rather probable that the three Scandinavian genera *Andrarina*, *Nericia*, and *Grönwallia* are related, and should all be included in the Andrarinidae. Wilson (1954, p. 250) observed that the North American genus *Aphelaspis* Resser 1935 closely resembles *Grönwallia*, and I believe that it may belong to the Andrarinidae, as well as the related genera *Dytremacephalus* and *Labiostra* (both Palmer, 1954) and probably also *Proaulacopleura* Koboayshi 1936, which resembles *Aphelaspis*, as pointed out by Howell & Lochman (1939, p. 119). A species described by Kobayashi (1936b) as *Parabolinella? evansi* apparently also belongs to this group (see especially figure of cranidium in Wilson, 1954, pl. 25, fig. 17). As discussed elsewhere (p. 23), it should not be regarded as an olenid, and may provisionally be referred to as *Aphelaspis? evansi*. It is probable that it eventually should be assigned to a new genus. The Australian genus *Eugonocare* Whitehouse 1939 may be another member of the Andrarinidae.

Andrarina and *Nericia* occur in the uppermost zone of the Middle Cambrian in Scandinavia (zone of *Lejopyge laevigata*), whereas *Grönwallia* comes from the underlying Andrarum Limestone. *Aphelaspis* (also *Aphelaspis? evansi*) and *Proaulacopleura* occur in the North American *Aphelaspis* zone, and *Eugonocare* in the Australian *Eugonocare* stage, regarded as basal Upper Cambrian.

Andrarina and *Proaulacopleura* appear to be rather close to the Olenidae, which may have developed from the Andrarinidae (cf. p. 30).

Elviniidae.

Kobayashi (1935c, p. 282) erected a subfamily Elviniinae (which was assigned to the family Crepicephalidae Kobayashi 1935), and to this he assigned *Elvinia* Walcott 1924, *Maladioides* Kobayashi 1934, *Moosia* Walcott 1924 (subjective synonym of *Elvinia*), *Taenicephalus* Ulrich & Resser 1924, and *Conaspis* Hall 1863. The subfamily Elviniinae was raised to family rank by Henningsmoen (1951, p. 208), Hupé (1953, p. 206), and Lochman (1953, p. 893). Hupé also recognized a subfamily Elviniinae, which more or less corresponded to Kobayashi's concept of it. Lochman expressed a different view, and included in Elviniidae, besides *Elvinia* and *Maladioides*, only *Drumaspis* Resser 1942 and *Chariocephalus* Hall 1863. Furthermore she

pointed out the relationships to genera like *Irvingella* Ulrich & Resser 1924, which was assigned to the family Komaspidae Kobayashi 1935.

Taenicephalus from the *Conaspis* zone of North America is rather similar to *Elvinia*. Very probably they are closely related, even if *Taenicephalus* did not necessarily develop from *Elvinia*. I therefore believe that *Taenicephalus* should be included in the same family as *Elvinia*. However, if one recognizes a subfamily Elviniinae corresponding with Lochman's concept of the Elviniidae, *Taenicephalus* and allies should rather be assigned to a new subfamily of the Elviniidae. Several North American genera from the *Conaspis* zone appear to be related to *Taenicephalus*, such as *Bernia* Frederickson 1949, *Parabolinoides* Frederickson 1949, *Bemaspis* Frederickson 1949, *Maustonia* Raasch 1939, *Meeria* Frederickson 1949, *Orygmaspis* Resser 1937, *Wilbernia* Walcott 1924, and apparently also *Idahoia* Walcott 1924. Some of them are rather olenid-like, as e. g. *Parabolinoides*, which, however, has rather a wide anterior border.

Anomocaridae, Ceratopygidae, Asaphidae, and Richardsonellidae
(= *Kainellidae*).

The family Anomocaridae Poulsen 1927 from the late Middle Cambrian resembles the Andrarinidae. Compare for instance *Anomocare* as figured by Westergård (1950, pl. 3) with *Grönwallia*, as figured by Westergård (1953, pl. 7, figs. 13—20). Their cranidia agree in many features, as in the long glabella, type of glabellar furrows, and type of frontal area. Furthermore both genera have developed forms with long occipital spine. The hypostoma of *Anomocare* (e. g. Westergård, 1950, pl. 3, fig. 19) is very similar to those of *Andrarina* and *Nericia* (e. g. Westergård, 1948, pl. 4, figs. 4 and 9). Furthermore the pygidium of *Grönwallia* resembles that of *Anomocare*. The anomocarids differ from the andrarinids in having longer eyes, fewer thoracic segments (10), and a larger pygidium. Nevertheless, these two families may be rather closely related.

Proceratopyge, a late Middle Cambrian and early Upper Cambrian genus of the family Ceratopygidae Raymond 1927, has some features in common with the Anomocaridae, such as long glabella and rather similar glabellar furrows. Early ceratopygids have a number of features in common with early members of the family Asaphidae Burmeister 1843, quite probably indicating relationships (Henningsmoen, 1951, p. 196).

It may thus be possible that the Andrarinidae, Anomocaridae, Ceratopygidae, and Asaphidae are all related. It is interesting to note that they all have facial sutures which tend to meet in front, or in fact do meet, and that the facial sutures often tend to diverge in front of the eyes. Furthermore, the pygidium is often more or less asaphid-like, and macropleural spines are developed by some andrarinids (*Grönwallia*), some early asaphids (*Prome-*

galaspides), as well as in the pygidium of most ceratopygids. A pre-occipital node is commonly developed in all four families.

Loganellus Devine 1863, *Levisella* Ulrich 1930, and *Lauzonella* Rasetti 1944 from the *Hungaia magnifica* zone in Quebec seem to be closely related. No name has been given to this group, which I shall refer to as the *Loganellus* group. It resembles the Andrarinidae, and the type species of *Andrarina* was once assigned to *Loganellus* (by Strand, 1929), but there is a considerable span of time between the Andrarinidae and the *Loganellus* group, and the origin of the *Loganellus* group is as yet uncertain. In several features it reminds one of the early asaphids and ceratopygids, and it may possibly be related to these. Although *Loganellus* has rather an asaphid-like pygidium, it was considered as being related to *Richardsonella* by Rasetti (1944, p. 247), with whom I agree. The *Loganellus* group may also be related to *Hungaia*, which differs in having a richardsonellid-like pygidium. However, the cranidium of *Hungaia* may have developed from a type like that of *Lauzonella*. Raymond (1924) erected a subfamily Hungaiinae, which he placed in the family Dikelocephalidae Miller 1890, together with i. a. the subfamily Richardsonellinae Raymond 1924. The Hungaiinae and Richardsonellinae appear to be related, but I doubt that they should be included in the Dikelocephalidae. Kobayashi (1953) discussed the family Kainellidae Ulrich & Resser 1930, which he divided into the subfamilies Kainellinae Kobayashi 1953, Richardsonellinae Raymond 1924, Apatocephalinae Kobayashi 1953, and Macropyginae Kobayashi 1953. *Macropyge* was suggested to be related to the asaphids by Ross (1951, p. 123), and since this appears to be rather probable, the Macropyginae should be removed from the Kainellidae. A subfamily Kainellinae should be credited to Ulrich & Resser 1930, even if they erected the group as a family. Since the Richardsonellinae was erected earlier than the Kainellidae, the name of the family should be Richardsonellidae Raymond 1924, with the subfamilies Richardsonellinae Raymond 1924, Kainellinae Ulrich & Resser 1930, Apatokephalinae Kobayashi 1953, and probably also Hungaiinae Raymond 1924. The *Loganellus* group may provisionally be assigned to this family. Undoubtedly the subfamily Apatokephalinae gave rise to the family Remopleurididae Corda 1847. It is interesting to observe the likeness between *Loganellus* and *Parabolina*. It is even more stressed now that it is known that *Parabolina*, too, had united free cheeks. One main difference is the relatively larger pygidium of *Loganellus*.

Origin of the Olenidae

The origin of the Olenidae has often been discussed. Whitehouse (1939, p. 216) summarized the viewpoints of earlier writers, and himself suggested that the olenids arose from the Ptychopariidae (possibly from *Lyriaspis*), as Papyriaspinæ (recte: Papyriaspidinae), which he regarded as a primitive subfamily of the Olenidae. However, Whitehouse's subfamily Papyrias-

pidinae appears to be a rather heterogenous group, and I do not believe that any of its genera should be assigned to the Olenidae (cf. p. 21). The glabella of the Papyriaspidinae has quite a different kind of glabellar furrows, and the thoracic segments are of a type never encountered in the Olenidae, from which I have excluded *Hedinia* (i. e. *Hedinaspis*).

There are other Middle Cambrian genera which remind one much more of olenids. As early as in 1922 Westergård suggested *Andrarina* [*Liostracus*] *costata* (Angelin) as a possible ancestor of the olenids, although he in 1948 (p. 14) believed that the lower number of thoracic segments (12) and the larger pygidium in *Andrarina costata* indicate that it is more advanced than *Olenus* (13 or more segments) and thus could not be ancestral to the Olenidae, but that there nevertheless was a possibility of *Andrarina costata* having arisen from the same stock as the Olenidae. I do not think that the number of thoracic segments and the size of the pygidium exclude the possibility of the olenids having arisen from *Andrarina*. There are evolutionary lines within the olenids where the number of thoracic segments are increased, and lines where the size of the pygidium is reduced (cf. p. 84). If one or two more segments had become free thoracic segments in *Andrarina costata*, and the pygidium correspondingly smaller, the post-cephalic part would be quite *Olenus*-like. It is interesting that a pygidium of *Andrarina costata* figured by Strand (1929, pl. II, fig. 11) has the triangular shape often developed in *Olenus*, and that *Nericia*, probably a member of the Andrarinidae, has a comparatively small pygidium, which, furthermore, is dentate.

Since the number of thoracic segments and the size of the pygidium of *Andrarina* are not considered as an obstacle for the assumption that the Olenidae arose from *Andrarina*, it is of interest to stress the great resemblance between *Andrarina* and *Olenus*. Their cranidia are rather similar, except for the anterior branches of the facial sutures diverging in front of the eyes in *Andrarina*, and, as pointed out by Strand (1929), apparently not meeting in front axially, as in *Olenus*. The free cheeks are of the same type, with the same type of slender spine. The thoracic segments are similar. Apart from the relative size, the pygidium of *Andrarina* resembles that of *Olenus*, too. *Olenus truncatus*, for instance, has the same flattened border as *Andrarina*.

Altogether, *Andrarina* resembles *Olenus* so much that they are probably related. The age of *Andrarina costata* (late Middle Cambrian) fits in well for an ancestor of the olenids. However, I do not believe that the olenids necessarily developed from *Andrarina*, although I believe that they probably developed from the group to which *Andrarina* belongs.

Proaulacopleura Kobayashi 1936, with the one known species *P. buttsi* Kobayashi 1935, is a North American genus which also is rather like *Olenus*, but seems to be contemporaneous with it. It has 13 thoracic segments and a rather small pygidium. In these respects it is closer to *Olenus* than is

Andrarina. However, it agrees with *Andrarina* in having divergent preocular facial sutures. Its free cheeks have a rather broad-based spine, and is thus less olenid-like than *Andrarina*. *Proaulacopleura* appears to be close to another North American genus, *Aphelaspis*, which appears to be contemporaneous, and which likewise may have 13 segments and a rather small pygidium (as *A. hamblensis* Resser 1938). Both *Proaulacopleura* and *Aphelaspis* may belong to the Andrarinidae. If this is the case, this family could produce forms with a small pygidium. *Proaulacopleura* and *Aphelaspis* may have developed from earlier Andrarinidae more or less along the same line as *Olenus*.

Geographic, stratigraphic, and lithologic occurrence of olenids

Occurrence of olenids in Norway

The greater part of the olenids in Norway occur in the Upper Cambrian Olenid Series and a few in the Tremadocian Ceratopyge Series. A single olenid species (*Triarthrus* sp.) has been found in later beds, namely in the lower Middle Ordovician Ogygiocaris Series.

The Olenid Series in Norway.

Occurrence and Lithology.

The Olenid Series is known in the Oslo region and in the belt of Caledonian overthrusts in southern Norway. The Oslo region was divided into 11 Cambro-Silurian districts by Størmer in 1953. The Olenid Series is exposed in all these except the Holmestrand district (cf. text-fig 4). The northernmost district, Ringsaker, which is one of the districts bordering Lake Mjøsa, has usually been included in the Oslo region. However, the allochthonous Eocambro-Silurian rocks of Ringsaker geologically form a part of the belt of Caledonian overthrusts, and the northern border of the Oslo region should perhaps be drawn south of the Ringsaker district (cf. Størmer, 1953, p. 52). Fossils proving the existence of the Olenid Series have been found in the belt of Caledonian overthrusts east of Ringsaker in the Rena—Trysil area, northwest of Ringsaker in the Gausdal area, and west of Ringsaker in the Snertingsdal—Vardal—Valdres area. So far, no Upper Cambrian fossils have been found further west in Norway, but the existence of Dictyonema Shales on the Hardangervidda plateau (Størmer, 1940b, p. 164) and Middle Cambrian shales in Rogaland (Henningmoen, 1952) indicate that they eventually may be found. No Cambrian fossils are known from the Trondheim region, but Upper Cambrian strata may be included in the Brek Series (cf. Vogt, 1945, p. 519). No Upper Cambrian fossils have been found in northern Norway.

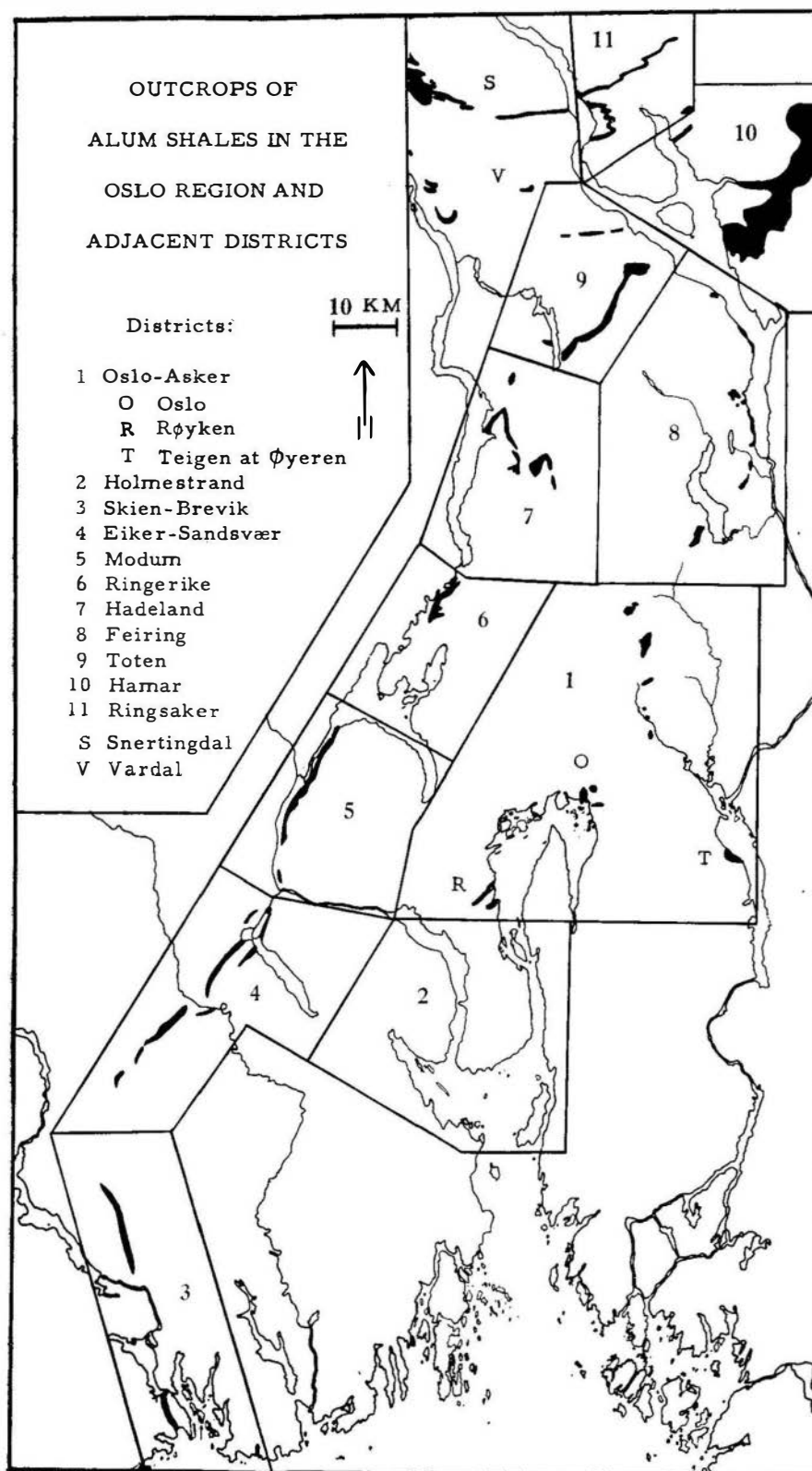
The Olenid Shales in Norway are developed as black bituminous shales (alum shales) with concretions of black bituminous limestone (stinkstone). The concretions may be more frequent in some horizons than in others, and may occasionally form a layer. No conglomerates are known, except an intraformational conglomerate in the *Parabolina spinulosa* zone (2b) at Løyten (Hamar district).

The alum shales are easily affected by tectonical disturbances, and even in the southern parts of the Oslo region, where the Caledonian folding is very slight in the overlying beds, the alum shales are rather disturbed, although this may be partly due to Permian faulting. It is thus impossible to give any exact data on the thickness of the Olenid Shales. This is especially the case in the northern areas. Brøgger (1882, p. 3) suggested that the "Olenusetage" (i.e. the Olenid Shales + the Dictyonema Shales) is about 45–50 m thick, and that there were no great local variations within the Oslo region. This would mean that the Olenid Shales are about 40–45 m thick. Diamond drill borings through the Olenid Shales in the Eiker—Sandsvær district suggest the thickness of the Olenid Shales there to be between 40 and 57 m. Roughly, the lower 35 m contain very few stinkstone lenses and seem to belong to the *Olenus* and *Parabolina* zones, whereas the *Leptoplastus* and *Peltura* zones and the lower part of the *Acerocare* zone is rather rich in lenses. The upper part of the *Acerocare* zone seems to be missing in the cores. Most probably the Olenid Shales further north are at least as thick as in the Eiker—Sandsvær district. In the extreme south of the Oslo region the Olenid Shales are only about 12 m thick. The whole of the *Acerocare* zone is missing there, and so are probably other parts of the series. However, few fossils have been found, as the alum shale has been disturbed and somewhat metamorphosed by Permian sills.

By far the greater number of fossils in the Olenid Shales in Norway are trilobites, predominantly olenids. The olenids often occur in incredible numbers, but only rarely as complete shields (cf. text-fig. 5). The stinkstone concretions are usually fossiliferous, whereas the intervening shale may be practically devoid of them. The fossiliferous horizon in a stinkstone lens, may, however, continue in the surrounding shale. The remains in the shales are always compressed and often distorted by tectonical disturbances, whereas the fossils in the stinkstones are well preserved.

Fig. 4. The map shows the outcrops of Middle Cambrian, Upper Cambrian, and Tremadocian alum shales. Upper Cambrian alum shales occur in all areas with alum shales. Tremadocian alum shales occur in all districts except the southernmost (Skien-Brevik district). The map is based on a map of the Oslo region by W. C. Brøgger and J. Schetelig (Norges geol. unders., 1923), with some adjustments of the extensions of the northern outcrops, kindly suggested to me by S. Skjeseth of the Geological Survey of Norway.

Boundaries of districts after Størmer (1953).



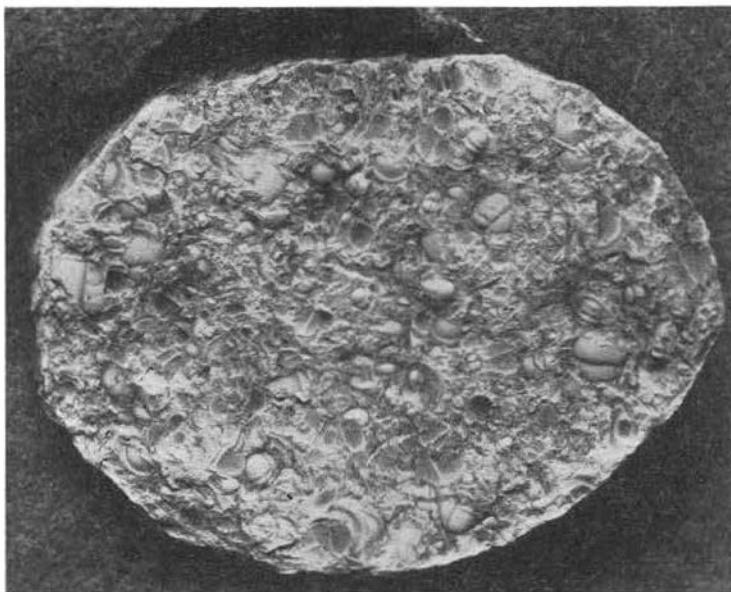


Fig. 5. Bedding surface of a small stinkstone concretion crowded with fragments of *Peltura scarabaeoides scarabaeoides* and *Sphaerophthalmus humilis*. About natural size. Surface whitened; photograph not retouched. P. M. O. no. 29532. Slemmestad in Røyken, Oslo-Asker district, Norway.

Biostratigraphy of the Olenid Series in Norway.

Chart 2

The "Olenusetage" ("Étage" 2) was divided into 5 "Niveaus" by Brøgger in 1882: 2a ("Olenus-Niveau"), 2b ("Parabolina spinulosa-Niveau"), 2c ("Eurycare-Niveau"), 2d ("Peltura-Niveau"), and 2e ("Dictyonema zone"). It has later become the practice to exclude the *Dictyonema* zone from the Upper Cambrian Olenid Series, and include it in the Lower Ordovician Ceratopyge Series, thus restricting the Olenid Series to 2a-2d. Brøgger was aware that the Olenid Series could be further subdivided, and this was done by Westergård in 1922 for the corresponding succession in Sweden. Strand (1929) divided the Upper Cambrian beds of the Mjøsa districts in Norway in accordance with Westergård's scheme, and elaborated Brøgger's system of symbols. Thus 2a was divided into 2a α (zone of *Agnostus pisiiformis*) and 2a β (zone of *Olenus*). 2b was called the zone of *Parabolina spinulosa*, 2c the zone of *Leptoplastus* and *Eurycare*, and 2d the zone of *Peltura*, *Sphaerophthalmus*, and *Ctenopyge*. The latter was divided into four subzones: 2d α , 2d β , 2d γ , and 2d δ . He furthermore recognized a zone of *Parabolina heres*, which he gave the symbol 2e. This symbol had previously been given to the *Dictyonema* zone (by Brøgger in 1882), and Størmer (1934a, p. 332) changed the symbol of the beds with *Parabolina*

heres into 2d ϵ , retaining 2e for the *Dictyonema* zone. This was done as it has become the practice not to transfer a symbol introduced by Brøgger or later writers from one unit to another since this would lead to confusion, not least regarding the extensive use of symbols on museum labels. In 1944(a) Westergård presented a more detailed division of the Olenid Shales in Sweden. He slightly revised it in 1947, recognizing 6 zones and 23 subzones. The present investigation has shown that the subzonal division may be carried even further, and 29 subzones are recognized in the Norwegian succession. Three subzones established in Sweden have not been found in Norway, so that the total number of subzones of the Olenid Shales in Scandinavia now amounts to 32. No doubt even more subzones may eventually be recognized.

It appears practical also to recognize more zones than hitherto. Some of the earlier zones are thus regarded as zone complexes. They may be called "megazones" or "superzones", but these terms are not commonly used. Another possible term is "stage", but Hedberg (1954, p. 223) has recommended to restrict this term to time-stratigraphic units. I therefore propose simply to use the plural form "zones" (e. g. *Peltura* zones) for these zone groups.

The symbols in use for the Cambro-Silurian succession in the Oslo region have been given to stratigraphic units, some of which are litho-stratigraphic, others bio-stratigraphic or chrono-stratigraphic. I have proposed to retain the symbols for chrono-stratigraphic units only (Henningsmoen, 1955). However, in the case of the Olenid Shales, the chrono-stratigraphic units (2a α , 2a β , etc.) are all based on bio-stratigraphic units and the symbols may also be used for the zones (e. g. 2a α for the zone with *Agnostus pisiformis*). I have preferred not to introduce a rigid system of numbers or letters for the subzones, since the position of some subzones are uncertain, and more subzones may eventually be recognized. Instead I suggest that the symbol of a subzone be formed by adding the abbreviated specific name of the subzonal index fossil to the symbol of the zone, e. g. "2d β *tum.*" for the subzone of *Ctenopyge tumida*.

Some of the zones and subzones may be regarded as teil-zones, since the index fossil occurs throughout the whole of the unit, but not below or above it. Apparently some of the teil-zones come very close to being biozones, that is where the index fossil appears to have developed from an earlier species in the underlying beds and to be ancestral to a later species in the overlying beds.

The Norwegian faunules studied for the greater part occur in samples (mainly chips of stinkstone lenses) which have not been collected stratigraphically, i. e. their relative or absolute position in the section is not stated. However, the faunule in a sample usually suggests from which subzone it comes; its horizon is easily determined in a ready-made scheme. The samples only rarely contain more than one subzone. In some cases the faunule of a

sample (or rather a number of samples) justified the recognition of a new subzone, of which the adjoining subzones were not known. Difficulties arose when the new subzone should be placed in the scheme. In plotting these subzones, their faunules were sometimes rather suggestive, especially when they were of a type between those of already established subzones. Westergård's scheme for the Olenid Shales in Sweden (1922, 1947) and especially his data from borings in Sweden (1941, 1944a, 1944b) have often been of the greatest help. I would like to emphasize that the succession of the olenid species in the Olenid Series in Scandinavia never differs from place to place, whenever this can be controlled, with the exception, of course, that parts of the succession may be lacking, and that the fossils sometimes may be secondarily deposited. Data from Brøgger (1882) have been useful in plotting subzones in some cases, and Høltedahl has collected some material stratigraphically at the beach at Slemmestad in Røyken, near Oslo, although unfortunately not detailed enough. This classical locality no longer is accessible, owing to the filling up of the beach with debris from Slemmestad Cement Factory. Borings through alum shales in Norway have also been of some help, but the core diameters are rather small (from 21 to 37 mm), and only a restricted number of fossiliferous lenses have been pierced.

The *Olenus* zones (2a).

The zone of *Agnostus pisiformis* (2aα) is not divided into subzones. The find of *Olenus alpha* n. sp. in this zone shows that it is a true member of the Olenid Shales (cf. p. 58).

The zone of *Olenus* and *Agnostus obesus* (2aβ). The corresponding zone in Sweden was divided by Westergård (1922) into 6 subzones, named after (from below): *Olenus gibbus* & *O. transversus*, *O. truncatus*, *O. wahlenbergi*, *O. attenuatus*, *O. dentatus*, and *O. scanicus* & *Polyphyma angelini*. The two upper subzones have not been found in Norway. Kaufmann (1933) showed that *O. transversus* is characteristic of its own subzone in Scania (Sweden), and that the ranges of *O. attenuatus* and *O. dentatus* overlap (cf. text-fig. 15, p. 99).

The *Parabolina spinulosa* zone (2b).

The corresponding zone in Sweden was divided into two subzones by Westergård in 1922, a lower one with *Parabolina brevispina* and *Protopeltura aciculata*, and an upper one with *Parabolina spinulosa* and *Protopeltura aciculata pusilla*. These subzones are also recognized in Norway. *Parabolina brevispina* and *Protopeltura aciculata* have not been found associated in Norwegian material. According to Westergård's data (1944a) from borings in Scania, the latter species occurs only in the upper part of the subzone, and ranges higher up than *Parabolina brevispina*.

The *Leptoplastus* zone (2c).

Westergård (1944a, 1947) listed 5 subzones from the corresponding zone in Sweden. They are as follows (from below): the subzones of *Leptoplastus paucisegmentatus*, *L. raphidophorus*, *L. ovatus* & *Eurycare latum*, *Eurycare angustatum* (here *L. angustatus*), and *L. stenotus*. Only the subzone of *L. paucisegmentatus* has not been recognized in Norway. The Norwegian material suggests on the other hand that more subzones may be separated between the subzones of *L. raphidophorus* and *L. angustatus*. Until more data are available on the stratigraphic range of the many *Leptoplastus* and *Eurycare* species, I establish only one new subzone, that of *L. crassicorne*. This species occurs in Sweden between layers with *L. raphidophorus* and layers with *L. ovatus* (cf. Westergård, 1944a). *L. ovatus* is either associated with *E. explanatum* and *L. crassicorne* var. or with *E. latum* ± *E. brevicauda*. *E. latum* probably extends into the subzone of *L. angustatus*, since these two species have been found associated in several samples of stinkstone, whereas other samples yield *L. ovatus* and *E. latum* or *L. angustatus* alone. It does not seem as if *E. latum* is secondarily deposited with *L. angustatus*.

The subzones of the *Leptoplastus* zone will thus be as shown below (with the possible distribution of the nonindex fossils):

Subzone of:

L. stenotus

<i>L. angustatus</i>	{	Alone (upper part?)
		{	<i>Eurycare latum</i> (lower part?)
<i>L. ovatus</i>	{	<i>E. latum</i> , <i>E. brevicauda</i> (upper part?)
		{	<i>E. explanatum</i> , <i>L. crassicorne</i> var. (lower part?)
<i>L. crassicorne</i>	{	<i>L. norvegicus</i>
<i>L. raphidophorus</i>			
<i>L. paucisegmentatus</i>			(not known in Norway).

The *Peltura* zones (2dα-δ).

Three *Peltura* zones are recognized, the two lower agreeing with Strand's subzones 2dα and 2dβ, the upper zone with his two subzones 2dγ-δ.

Most of the subzones recognized here are founded on *Ctenopyge* species. If they instead had been based on pelturines, the subzones would not correspond to the *Ctenopyge* subzones; there would, in fact, have been fewer subzones. I preferred to found the subzones on *Ctenopyge* species partly because I believe it is practical to base them on as short-ranged fossils as possible, and partly because the *Ctenopyge* species usually are easier to determine. Furthermore, specimens of *Ctenopyge* are usually present in all

but the smallest samples of fossiliferous rock from these strata, whereas this is not the case for the pelturines.

The zone of *Protopeltura praecursor* (2d α). In material collected by Høltedahl in 1908 at the no longer accessible beach section at Slemmestad in Røyken, *Protopeltura broeggeri* and *Protopeltura holtedahli* n. sp. occur in stinkstone lenses from the junction between the *Leptoplastus* zone and the zone of *Protopeltura praecursor*. The two species do not occur together in one lens, and are not associated with any other species. *P. broeggeri* has also been met with in a boring core from Stablum in Eiker, where it occurred between layers with *Leptoplastus angustatus* (2c) and layers with *L. neglectus* (2d α). The morphology of *P. holtedahli* n. sp. suggests that this species, too, occurs below *P. praecursor*. It is possible that *P. broeggeri* and *P. holtedahli* n. sp. (or one of them) may come from the uppermost part of the *Leptoplastus* zone, but this is not likely since they have never been found in the rather large collection of lenses from the subzones of *L. angustatus* and *L. stenotus* in Scandinavia. It is more probable that they occur in layers between the subzones of *Leptoplastus stenotus* (2c) and *L. neglectus* (2d α). *P. broeggeri* and *P. holtedahli* n. sp. are regarded here as index fossils of two provisional subzones. It is not known which is the younger. Since at least *P. holtedahli* n. sp. is closely related to *P. praecursor*, the new subzones are tentatively included in the zone of *Protopeltura praecursor*.

Westergård (1944a) has recorded the succession of the index fossils of the following three subzones, *Leptoplastus* ("Ctenopyge") *neglectus*, *Ctenopyge postcurrens*, and *Ct. flagellifera*. *Protopeltura praecursor* is regularly found in all three subzones, and I have not been able to see any differences between the specimens from the different subzones.

The zone of *Peltura minor* (2d β). In this zone I include four subzones, with the following index fossils (from below): *Ctenopyge similis* n. sp., *Ct. spectabilis*, *Ct. tumida*, and *Ct. affinis*. It has been demonstrated by Westergård (1944a) that *Ct. affinis* occurs above *Ct. tumida* in Scania. *Ct. spectabilis* was reported by Westergård (1922) to occur together with *Ct. angusta* and *Ct. tumida*. Actually the latter form is *Ct. tumidoides* n. sp. and the subzone of *Ct. spectabilis* lies immediately below the subzone of *Ct. tumida*. The fauna of the subzone of *Ct. similis* n. sp. (also containing *Ct. modesta* n. sp.) occurs in Norwegian stinkstone lenses, the exact stratigraphic horizon of which are not known. The subzone may fairly safely be regarded as directly underlying that of *Ct. spectabilis* (also containing *Ct. angusta*), since *Ct. modesta* n. sp. morphologically appears to be intermediate between *Ct. flagellifera* and *Ct. angusta*. Furthermore, *Ct. modesta* n. sp. is known to occur below *Ct. spectabilis* and above *Ct. flagellifera* in Sweden.

The zonal index species, *Peltura minor*, occurs in the subzones of *Ct. affinis* and *Ct. tumida*.

The zone of *Peltura scarabaeoides* (2dγ-δ). *Peltura scarabaeoides scarabaeoides* and *Sphaerophthalmus humilis* are the most common fossils in the two lower subzones (established here), the subzone of *Ctenopyge bisulcata* and the subzone of *Ct. linnarssoni*, which together form the lower part (2dγ) of the zone. *Ct. bisulcata* has been shown to occur below *Ct. linnarssoni* in Scania (Westergård, 1922). It is possible that more subzones may be distinguished when the ranges of the different *Ctenopyge* species become better known. *Ct. pecten*, which occurs in the subzone of *Ct. linnarssoni* in Norway, is in Sweden also known from the subzone of *Ct. bisulcata*. According to Westergård (1944a, p. 42), *Ct. fletcheri* (= *laticornis*) continues a little higher up than *Ct. pecten*. No *Ctenopyge* or *Sphaerophthalmus* species are known to extend into the upper part (2dδ) of the zone of *Peltura scarabaeoides*, which is here regarded as comprising the subzone of *Parabolina lobata* and the subzone of *Peltura paradoxa*. *Peltura paradoxa* is associated with a species which probably is *Parabolina megalops*. As *Peltura paradoxa* seems to occur together with *Parabolina megalops* in Sweden, the subzone of *Peltura paradoxa* apparently corresponds to the subzone of *Parabolina megalops* in Sweden, which overlies the subzone of *Parabolina lobata* (= *P. longicornis*) (cf. Westergård, 1944a). According to Westergård (1944a), *Parabolina lobata praecursor* occurs at a slightly lower level than *P. lobata lobata*, and the subzone of *Parabolina lobata* may consequently be divided into two zonules. *Peltura scarabaeoides westergårdi* n. sp. is known only from the subzone of *Parabolina lobata*.

The *Acerocare* zone (2de).

This is divided into 4 subzones, based on pelturines, as they are easier to distinguish and more frequent than the *Parabolina* species. The two lower subzones are those of *Peltura transiens* and *Peltura costata*. *Peltura transiens* occurs at a slightly lower level than *Peltura costata* (cf. Brøgger, 1882, p. 109). *Parabolina heres* occurs in both subzones, which may more or less correspond to Westergård's subzone of *Parabolina heres* and subzone of *Cyclognathus* (i. e. *Acerocarina*). The subzone of *Westergårdia* has been shown by Westergård (1944a) to occur above these. It may possibly be divided into two subzones or zonules, as *Westergårdia scanica* occurs at a slightly lower level than *W. illaenopsis* in Scania (Westergård, 1944a, p. 44). The subzone of *Acerocare ecorne* was first shown to occur above that of *Westergårdia* by Westergård in 1944(a), and this succession has been confirmed in sections at Nærnes in Røyken, near Oslo (cf. text-fig. 6).

The Ceratopyge Series in Norway.

O C C U R R E N C E.

The Ceratopyge Series is known in the Oslo region and in the belt of Caledonian overthrusts in southern Norway (including Ringsaker). It occurs in all the districts of the Oslo region except in the Holmestrand district (where only younger strata are exposed) and in the Skien-Brevik district (where the younger *Orthoceras* Limestone rests directly on the *Peltura* zones). In the Eiker-Sandsv  r district the series occurs in the northern part (Eiker), but is missing in the southern part (Sandsv  r). The series is known in the belt of Caledonian overthrusts both east and west of Ringsaker. The most westerly locality where fossils of this series have been found, is the Dictyonema Shales at Holberget on the plateau Hardangervidda (cf. St  rmer, 1940b, p. 164). Dictyonema Shales have also been found in the south-eastern part of the Trondheim region, at Holt  len north of R  ros (cf. St  rmer, 1940b, p. 162). The Sm  la Limestone, on the island of Sm  la, north-west of the Trondheim region, corresponds in age to the Ceratopyge Series, but contains fossils of another province (the North American-Arctic province), and thus no olenids. The Ceratopyge Series or contemporary strata are not known from northern Norway.

L i t h o l o g y a n d s t r a t i g r a p h y.

The Ceratopyge Series consists of the Dictyonema Shales and the overlying Ceratopyge Beds. The complete succession is somewhat more than 20 m thick in the Oslo region.

The Dictyonema Shales are developed mainly as alum shales with stinkstone concretions, like the underlying Olenid Shales, in which they originally were included by Br  gger (1882). The Dictyonema Shales are regarded as comprising one zone, the zone of *Dictyonema flabelliforme* (Br  gger's "Niveau" 2e). St  rmer (1940b) divided it into 4 subzones (2e  -  ), based on subspecies of the index fossil. His scheme was slightly modified by Bulman in 1954.

The Ceratopyge Beds were divided by Br  gger in 1882 into 3 "Niveaus"; Shale and Limestone with *Symphysurus incipiens* (3a  ), Ceratopyge Shale (3a  ), and Ceratopyge Limestone (3a  ). The shales are blackish grey or grey. The Symphysurus Limestone is black, and the Ceratopyge Limestone consists of different types of limestone (black, bluish, and glauconitic) with discontinuity surfaces and thin shale partings. Br  gger's "Niveaus" are partly based on the lithology. One may provisionally recognize two faunizones, the zone of *Symphysurus incipiens* (3a  ) and the zone of *Ceratopyge forficula* (3a  -  ). The latter contains the so-called *Ceratopyge*- or *Euloma-Niobe*-fauna. The graptolites in the Ceratopyge Shale have been studied by Monsen (1925), who recognized two graptolite subzones.

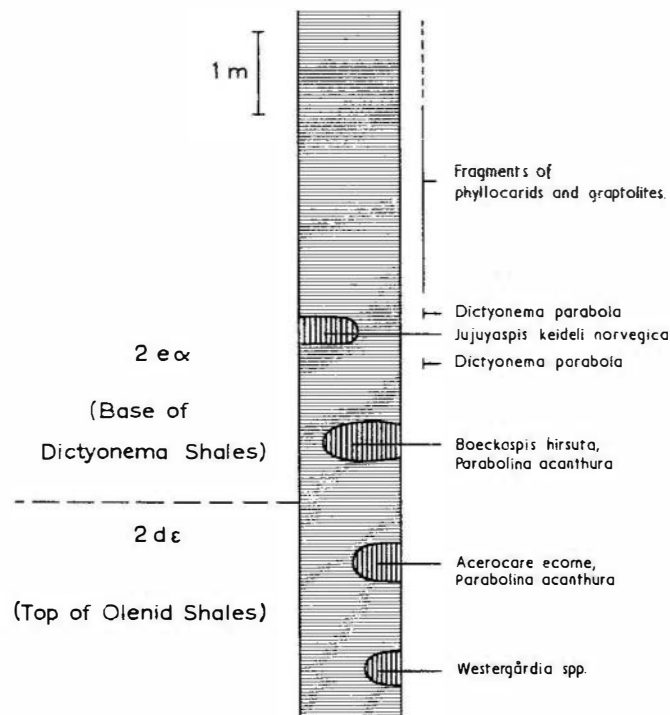


Fig. 6. Section through the boundary between the Upper Cambrian Olenid Series and the Tremadocian Ceratopyge Series at Nærnes.

Stratigraphic distribution of olenids in the Ceratopyge Series.

The zone of *Dictyonema flabelliforme* (2e).

A continuous section through the Upper Cambrian Acerocare Shales and the base of the Lower Ordovician Dictyonema Shales (text-fig. 6) has been discovered in a road cut (A on text-fig. 7) south-east of the chapel at Nærnes in Røyken, near Oslo. 1 m above stinkstone lenses with *Acerocare ecome* and *Parabolina acanthura* there is another horizon with stinkstone lenses, here containing *Boeckaspis hirsuta* and *Parabolina acanthura*. No fossils have been found in the intervening alum shale, but *Dictyonema flabelliforme parabola* occurs in the shale 0.40 m above the *Boeckaspis* lenses (cf. Bulman, 1954, p. 27). 0.50 m above this graptolite horizon there is a stinkstone lens containing *Jujuyaspis keideli norvegica* n. subsp. Above this the shale again contains *Dictyonema flabelliforme parabola*. At the beach at Nærnes (B on text-fig. 7), there is another section through the same beds. The section is somewhat disturbed and can only be studied at very low water, but is of interest because it contains two layers of stinkstone lenses yielding *Boeckaspis hirsuta*, with *Dictyonema flabelliforme parabola* in the intervening shale. For this reason I regard the beds with *Boeckaspis hirsuta* as belonging to the base of the Dictyonema Shales. The shale above the upper

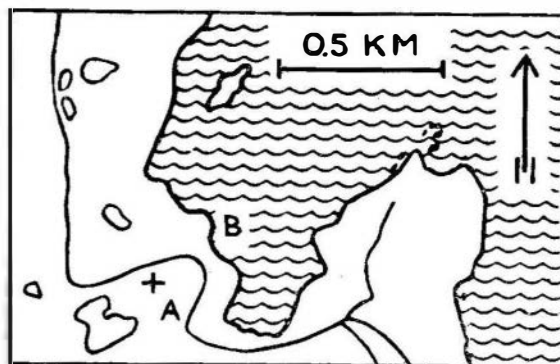


Fig. 7. Map of Nærsnes in Røyken, Oslo-Asker district. + = Nærsnes chapel, A and B the two fossil localities mentioned in the text.

lenses with *Boeckaspis hirsuta* contains *Dictyonema flabelliforme parabola*, as well as a stinkstone lens with *Jujuyaspis keideli norvegica* n. subsp.

The stratigraphic position of *Boeckaspis hirsuta* was earlier not known.¹ Like the overlying *Jujuyaspis keideli norvegica* n. subsp. it may be regarded as belonging to the subzone of *Dictyonema flabelliforme sociale*¹ (2e α).

In other localities in the Oslo region, *Boeckaspis mobergi* and *Bienwillia? wimani* occur in the subzone of *Dictyonema flabelliforme flabelliforme* (2e β) (cf. Størmer, 1922a, and Strand, 1929). A single lens from the same subzone at Steinsvika in Ringsaker contains *Jujuyaspis angusta* n. sp. and probably also *Bienwillia? wimani*.

Three or four olenid horizons are thus known from the *Dictyonema* Shales in Norway. The two lower horizons, the horizon with *Boeckaspis hirsuta* and the horizon with *Jujuyaspis keideli norvegica* n. subsp. appear in this order, but it is not known whether *Jujuyaspis angusta* n. sp. occurs below, in, or above the horizon with *Boeckaspis mobergi*.

The zone of *Symphysurus incipiens* (3a α).

Peltocare norvegicum and *Bienwillia tetragonalis broeggeri* n. subsp. are rather common in the *Symphysurus* Limestone (cf. Størmer, 1920).

The zone of *Ceratopyge forficula* (2a β - γ).

The *Ceratopyge* Shale, and especially its limestone lenses contain *Parabolinella limitis*. *Triarthrus angelini angelini* occurs in the uppermost part of this formation.

Triarthrus angelini angelini furthermore occurs in the *Ceratopyge* Limestone, especially in the black limestone nodules at the base, but also higher

¹ Material collected by T. Strand and H. Neumann at Nærsnes in 1945, labelled as *Boeckia hirsuta*, proved to include *Westergårdia* species only.

up. Other olenids are very rare in the Ceratopyge Limestone. So far, two specimens of *Parabolinella rugosa* and one specimen of *Parabolinella lata* n. sp. have been found.

Olenids occurring in Norway and their regional distribution.

Chart 1 shows the known regional distribution of the Upper Cambrian and Tremadocian olenids in Norway. Several of them were previously not recorded from Norway, including a number of new species and subspecies.

Some species which were recorded previously, have been re-determined, and the generic name has been changed for many species. The following list may be useful when consulting earlier papers on olenids in Norway.

Name used by:

Brøgger 1882

Name used by:	Revised name:
<i>Olenus truncatus?</i>	<i>Olenus gibbosus</i>
<i>Olenus aculeatus</i>	<i>Olenus attenuatus</i>
<i>Protopeltura acanthura</i>	<i>Protopeltura praecursor</i>
<i>Peltura bidentata</i>	<i>Protopeltura bidentata</i>
<i>Peltura planicauda</i>	<i>Protopeltura planicauda</i>
<i>Cyclognathus transiens</i>	<i>Peltura transiens</i>
<i>Cyclognathus costatus</i>	<i>Peltura costata</i>
<i>Cyclognathus costatus</i> var. minor	<i>Peltura minor</i>
<i>Cyclognathus micropygus</i>	<i>Peltocare norvegicum</i>
<i>Sphaerophthalmus alatus</i>	<i>Sph. alatus</i> and <i>Sph. humilis</i>
<i>Ctenopyge? lobata</i>	<i>Parabolina lobata</i>
<i>Boeckia hirsuta</i>	<i>Boeckaspis hirsuta</i>
<i>Parabolinella limitis</i>	<i>P. limitis</i> and <i>Bienvillia tetragonalis brøggeri</i> n. subsp.

Holtedahl 1910

<i>Leptoplastus ovatus</i>	<i>Leptoplastus raphidophorus</i>
<i>L. ovatus</i> var. <i>explanata</i> {	<i>Eurycare explanatum</i>
{ cranidium	
{ free cheeks	<i>Leptoplastus ovatus</i>
<i>Leptoplastus longispinus</i>	<i>Leptoplastus norvegicus</i>
<i>Eurycare angustatum</i> {	<i>Leptoplastus norvegicus</i>
var. <i>norvegicum</i> {	
{ axial shield	<i>Leptoplastus crassicorne</i>
{ free cheeks	
<i>Leptoplastus brøggeri</i> {	<i>Protopeltura brøggeri</i>
{ thorax, pygidium	
{ cranidium, free cheeks	<i>Leptoplastus neglectus</i>
<i>Peltura praecursor</i> {	<i>Protopeltura praecursor</i>
{ cephalon, pygidium	
{ thorax	<i>Protopeltura holtedahli</i> n. sp.

Strand 1929

<i>Leptoplastus minor</i>	<i>Leptoplastus raphidophorus</i>
<i>Leptoplastus minor explanatus</i>	<i>Eurycare explanatum</i>
<i>Sphaerophthalmus major</i>	<i>Sphaerophthalmus alatus</i>
<i>Sphaerophthalmus alatus</i>	<i>Sphaerophthalmus humilis</i>
<i>Boeckia illænopsis</i>	<i>Westergårdia lata</i>
<i>Parabolinella wimani</i>	<i>Bienvillia? wimani</i>
<i>Boeckia mobergi</i>	<i>Boeckaspis mobergi</i>

Chart 1 may give the impression that some species have a rather restricted geographic distribution, or that parts of the sequence often are missing locally. However, an insufficient amount of fossils have been collected or reported from most districts, and a closer survey most probably would widen the regional distribution of the species considerably. It is consequently not advisable to discuss the regional distribution of the fossils on the basis of this list. Attention should be drawn to the fact that there is no reason to suspect any local faunas in the Olenid Series in Norway. Holtedahl (1910, p. 11) believed that the fauna in the northern (Mjøsa) districts of the Oslo region differed somewhat from that in the Oslo district, referring especially to the *Leptoplastus* zone, as he found *Leptoplastus ovatus* and *Eurycare explanatum* in the Mjøsa districts only. However, these species are now known to occur in southern districts of the Oslo region as well.

Hansen (1945) has suggested that the stinkstone lenses are more common the nearer the shore the sediment was deposited. As the fossils of the Olenid Series usually are found in these lenses in Norway, and rarely in the surrounding shale, the absence of fossils of a certain subzone at a locality may just as well be due to this subzone having been deposited in deeper water (at least without the formation of lenses), as to not having been deposited at all. A list of fossils alone thus hardly gives any definite clues as to whether and at what time there have been transgressions and regressions in a certain locality.

In this connection it may be pointed out that the absence of records of fossils from certain zones in some districts is due to true gaps in the sequence. This is for instance the case in the Skien-Brevik district, where the thickness of the Olenid Series is considerably less than further north, and where at least the *Acerocare* zone and the whole of the Ceratopyge Series is missing. Except for the most southern districts of the Oslo region, the Cambro-Silurian strata in Norway have been folded or overthrust, and apparent gaps in the sequence may be due to tectonic disturbances.

Only one olenid is so far known from post-Tremadocian beds in Norway, a *Triarthrus* from dark shales of the Ogygiocaris Series in the Hamar and Ringsaker districts.

Occurrence of Upper Cambrian and Tremadocian Olenids in the Acado-Baltic Province

The Olenid Series.

Charts 1 and 3.

The marine faunal province characterized by olenids in the Upper Cambrian epoch usually is referred to as the Acado-Baltic (or North Atlantic) province.

The Olenid Series is known in Scandinavia (Sweden, Denmark, Norway), Poland, France(?), Great Britain (England, Wales), and eastern Canada (Newfoundland, Nova Scotia, New Brunswick).

Lithology and content of olenids.

Scandinavia.

The Olenid Series in Sweden, Denmark, and Norway is very monotonous, consisting almost exclusively of black bituminous shales (alum shales) with concretions or occasional layers of dark bituminous limestone (stinkstone) and a few intraformational conglomerates. Only in one northern area (Norrland in Sweden) beds of quartzite are intercalated with Upper Cambrian alum shales. Where it has been possible to measure the thickness of the series, viz. outside (south and west of) the belt with heavy Caledonian overthrusts, it does not exceed 50 m and is considerably thinner in many areas, owing to the thinning out or absence of some zones. The succession in Norway is discussed above, that in Sweden by Westergård in 1922, with supplementary data in 1940, 1941, and 1944. The succession in Denmark (Bornholm) was last described by Hansen in 1945.

The Upper Cambrian olenids known to occur in Denmark, Norway, and Sweden are listed in chart 1. Norway and Sweden have the most complete successions of the Olenid Series, but, as will be seen from chart 3, there are a few subzones which have been recognized only in Norway or only in Sweden. Accordingly, some olenid species have been found only in one of the countries. These differences are due to gaps in the sequence (or the corresponding beds have not been found) and therefore do not indicate any faunal dissimilarities. However, a few species which occur in one of the countries, have not been found in the others, even when contemporary beds are present. This is the case mainly with rare species, and there is a possibility of them later being found in the other areas, when more material has been collected. In any case, when corresponding beds are present, they have most species in common so that there does not seem to have been local variations of the faunas of any importance.

It may be noted that the exact horizon of the Swedish species *Acerocare tullbergi* is not known and that it may possibly represent an unestablished

subzone. As discussed above, the subzones of *Protopeltura broeggeri* and *Protopeltura holtedahli* in Norway are provisional, as the exact horizons of their index fossils are not known.

Poland.

The Olenid Series is known in the Święty Krzyż (Ste. Croix) area in southern Poland. The sequence has not been described in detail. According to Samsonowicz (1934, p. 69) it is 550 m thick and consists of alternating layers of variously coloured sandstones and shales with some layers of quartzite, and, rarely, greywackes. Apparently no black shales occur.

Two different Upper Cambrian faunas, containing olenids, have been reported (Czarnocki, 1927a, pp. 11—12; 1927b, pp. 198—199). The fossils have not been described, which is the more unfortunate as the collections were destroyed during World War II.

The olenids listed from the lower faunas are: *Beltella Samsonowiczi* (nomen nudum), *Parabolina acuminata* (nomen nudum), *Eurycare* n. sp., *Ctenopyge angusta*, *Parabolina* sp., *Protopeltura* sp., and *Peltura* sp. (cf. *cornigera* Westergård). The presence of *Ctenopyge* and *Protopeltura* suggests that the fauna belongs to the zone of *Protopeltura praecursor* or the lower part of the zones of *Peltura minor*. It is not very likely that *P. cornigera* (i. e. *P. transiens*) should occur in this fauna, since it is a rather late species. It seems possible that *Peltura* cf. *cornigera* is a *Protopeltura* species. However, the fauna cannot be compared with those of the Scandinavian subzones before new material has been studied.

From the upper fauna Czarnocki listed the olenids *Sphaerophthalmus alatus* (i. e. *Sph. humilis*), *Peltura scarabaeoides*, *Parabolina longicornis* (i. e. *P. lobata*), and *Parabolina mobergi*. The three first definitely suggest the zone of *Peltura scarabaeoides*. Apparently both the lower part (with *Sphaerophthalmus humilis*) and the upper part (with *Parabolina lobata*) are present. *Parabolina mobergi* occurs somewhat lower in Scandinavia, but as the *Parabolina* species often are rather alike, one should perhaps not lay too much stress on its assumed occurrence.

France.

In the Montagne Noire (Hérault) in southern France there is an about 500 ft. thick succession which is believed to be Upper Cambrian, partly because it occurs between Middle Cambrian and Lower Tremadocian beds, and partly because it has yielded some *Peltura*-like cranidia (Thoral, 1935, p. 65, pl. 5, figs. 5—7). The beds consist of psammitic shales with some small calcareous lenses and an occasional layer of calcareous shale (Thoral, 1946, pp. 12, 25).

Great Britain.

Only a few, partly incomplete sections through the Upper Cambrian beds are known in England. A section near Bentleyford Farm in Shropshire (Stubblefield, 1930) contains 63 ft. of grey micaceous shales with grey calcareous nodules (Grey Orusia Shales), belonging to the zone of *Parabolina* and *Orusia*. The shales rest on Middle Cambrian grits and are succeeded by a one-inch band of fine-grained sandstone. Above this comes 13 ft. of black shales (alum shales) with stinkstone concretions showing cone-in-cone structure. The olenids found belong to the lower part of the *Peltura* zones. The overlying beds belong to the Tremadocian Shington Shales. The White-leaved-Oak Shales of Malvern Hills are divided into a lower series of uncertain age, suggested by Groom (1902, p. 132) to belong to the uppermost part of the Middle Cambrian, and an upper series of some 550 ft. of black, coal-black or very dark grey shales with fossils of the *Leptoplastus* and *Peltura* zones. No fossils have been obtained from the uppermost layers, which are overlain by the Tremadocian Grey Bronsil Shales. In Central England (the Nuneaton district) the Olenid Series is represented by (from below) the Outwoods Shales, Moor Wood Flags, and Monk Parks Shales, together approximately 1,700 ft. thick. They consist mainly of thin-bedded dark grey shales with layers of intensely black carbonaceous shales (apparently alum shales), but thick-bedded crumbly mudstones, flagstones and greenish shales occur at intervals (Edmunds & Oakley, 1947, p. 13). The fossils towards the base belong to the *Olenus* zones, those near the top to the *Peltura* zones.

In Wales the Olenid Series is represented by the thick Lingula Flags. They are most completely developed in North Wales, where they may be divided into (from below) the Maentwrog Beds (about 2,200 ft.), the Ffestiniog Beds (about 1,500 ft.), and the Dolgelley Beds (about 500 ft.). According to Smith & George (1948, p. 23) "The two lower groups are broadly similar, consisting of rhythmically alternating layers of dark shale and compact fine-grained light-grey micaceous sandstone. The individual beds are usually not more than a few inches thick, and in bulk vertical section the groups display ribbon banding. The harder bands (called "ringers") are often ripple-marked and current-bedded and contain an abundance of worm-casts — — — The Dolgelley Beds, on the other hand, consist of an uninterrupted succession of shales and slates, the upper part of which is intensely black (the "Black Band") — —." The Maentwrog Beds belong to the *Olenus* zones, the Ffestiniog Beds may be more or less transitional between the *Olenus* zones and the *Parabolina* zone, whereas the olenids in the Dolgelley Beds belong to the *Parabolina spinulosa* zone and *Peltura* zones. No olenids from the *Leptoplastus* zone have been recorded with certainty, and the *Acerocare* zone appears to be missing. In South Wales only the Lower Lingula Flags (equivalent to the Maentwrog Beds in North Wales) are exposed. They consist of about 2,000 ft. of olive and dark-coloured micaceous and

flaggy shales, and sandy mudstones interbedded with bands of siliceous sandstone (Pringle & George, 1948, p. 20).

The Upper Cambrian olenids known to occur in England and Wales are listed in chart 1. Modern descriptions have been given by Lake (1908, 1913, 1919, 1946) and Cobbold (1934, Shropshire olenids).

The Upper Cambrian fauna described by Cobbold (1934, p. 391) from loose blocks found in the course of Dryton Brook in the Rushton area, Shropshire, was suggested by him "to represent a junction between Westergård's Zone 4 (with *Leptoplastus* and *Eurycare*) and his sub-zone 5a (with *Ctenopyge flagellifera* and *Protopeltura præcursor*)". The olenids reported by Cobbold to occur in these blocks were: *Leptoplastus raphidophorus*, *Eurycare angustatum*, *Ctenopyge flagellifera*, *Ct. flagellifera angusta*, *Ct. drytonensis*, and *Sphaerophthalmus? parabola*. Another Upper Cambrian faunule reported by Stubblefield (1930) from the brook section east-south-east of Bentleyford Farm, Shropshire, was likewise considered to contain a mixture of forms from the *Leptoplastus* zone and the zone of *Protopeltura præcursor* in Scandinavia, viz. *Ctenopyge flagellifera*, *Ct. flagellifera angusta*, and *Eurycare angustatum*.

As such a mixture of forms occurring at different levels in Scandinavia would be of considerable bearing, not the least on the use of olenids for correlation, I was anxious to see the material. Thanks to the kindness of Dr. C. J. Stubblefield, Geological Survey and Museum, London, it was arranged that I could borrow material both from Cobbold's and his collections of Shropshire olenids, for which I am very grateful.

The material from the neighbourhood of Bentleyford Farm included two types of cranidia. The smaller type agrees well with *Ctenopyge modesta* n.sp., a species which is rather close to *Ct. angusta*. The material furthermore included free cheeks and hypostomae similar to those of *Ct. modesta* n. sp. The larger type of cranidia and some fragments of free cheeks are not very well preserved, but seem to belong to the *Ct. spectabilis* group. Since some associated hypostomae are exactly similar to the hypostoma of *Ct. similis* n.sp. (of the *Ct. spectabilis* group), I believe that the two leptoplastines in this material are *Ct. modesta* n. sp. and *Ct. similis* n. sp. These two species furthermore occur associated in Scandinavia, in the subzone of *Ctenopyge modesta*. The material also included a single pelturine pygidium. The pygidium has no spines, and recalls that of some earlier species of *Protopeltura*.

The material from Dryton Brook consisted of samples of the blocks A, C, D, and E. Block C contained cranidia and free cheeks which apparently belong to *Leptoplastus raphidophorus*, as far as can be determined from the fragmentary material. The two free cheeks figured by Cobbold (1934, p. 45, fig. 18) came from block C (G. S. M. no. 51772), but in the text Cobbold (1934, p. 351) stated that the species is well represented in block D and that two very indifferent free cheeks were recognized from block A. It appears rather reasonable to assume that "block D" in this case is an error for

"block C". This assumption is supported by the fact that Cobbold has determined no specimens as *Leptoplastus raphidophorus* in the samples (G. M. S. nos. 51767—69) from block D, which I have examined. I have not been able to find any free cheeks assignable to *Leptoplastus raphidophorus* in the 14 samples from block A which I have seen. Of the 8 samples stated to come from block C, 7 contained *Leptoplastus raphidophorus* and no other olenids. One piece (G. S. M. no. Pe. 2607) instead contained *Ctenopyge flagellifera*. Most probably this sample came from another block and has by mistake been labelled as coming from block C. This is supported by the fact that there were no specimens of *Lingulella* cf. *concinna* in this sample, whereas this brachio-pod occurs in all the 7 samples with *Leptoplastus raphidophorus*, but never in samples from the other blocks. There is, of course, a possibility of the sample coming from another fossiliferous horizon in block C than the one which yielded the other samples, but this is not very likely. Most probably *Leptoplastus raphidophorus* is the only olenid in block C. It is at least certain that I have been unable to find this species together with any other olenids in any single sample.

The samples from blocks A, D, and E all contain *Ctenopyge drytonensis*, indicating that these blocks came from the same horizon. As discussed elsewhere (p. 189), I believe that the material assigned to *Eurycare angustatum*, *Ctenopyge flagellifera*, and *Ct. flag. angusta* by Cobbold (1934) and most probably also the material described by him as *Sphaerophthalmus? parabola* belongs to the associated *Ct. drytonensis*. I therefore believe that the blocks A, D, and E contain only one olenid, *Ct. drytonensis*, or, at the most, also a very closely related form, *Ct. parabola*.

The re-examination of the Shropshire olenids has shown that there is no mixture of species which occur at different levels in Scandinavia. I must admit that this is what I had hoped, but I am, nevertheless, fully convinced that this really is the case.

Of the Dryton Brook material (Cobbold's material) the block C comes from the subzone of *Leptoplastus raphidophorus*, whereas the blocks A, D, and E represent the younger subzone of *Ctenopyge flagellifera* (containing i. a. *Ct. drytonensis* in Scandinavia). The abovementioned material from near Bentleyford Farm represents the overlying subzone of *Ctenopyge modesta*.

The generic reference of some Upper Cambrian British olenids has been changed here, i. e. *Beltella bucephala* (to *Olenus?*), *Parabolinella williamsoni* (to *Parabolinites* n. gen.?), and *Olenus longispinus* (to *Parabolinites* n. gen.?). The species which was assigned to *Sphaerophthalmus alatus* by Lake (1913), is here assigned to *Sph. humilis*.

The vertical distribution of the Upper Cambrian olenids in Great Britain is not known in detail. It is usually only known whether they occur in the Lower, Middle, or Upper Lingula Flags. There is so far nothing to suggest that there are any differences between the vertical distribution of the olenids in Great Britain and Scandinavia, but this has yet to be proved in detail.

A better knowledge of the vertical distribution of the British olenids would also be of great interest, as several species described from Great Britain have so far not been recognized in Scandinavia. This may to some extent be due to the bad preservation of the specimens on which some species have been founded. Since the true *Olenus* species occur only in the Lower Lingula Flags, and *Parabolina spinulosa* does not occur below the Upper Lingula Flags, it is possible that the passage beds between the zones of *Olenus* and of *Parabolina* and *Orusia* are better represented in Great Britain than in Scandinavia, where these beds are rather poor in fossils and not very well known. It is thus possible that subzones, as yet unknown, at the junction between these zones may be found in and around the Middle Lingula Flags.

Canada.

The Olenid Series in Canada apparently mostly resembles that of England. In Nova Scotia it is represented by the MacNeil formation, estimated to be about 1,000 ft. thick or less (Hutchinson, 1952, p. 33) and consisting of "very pure, soft, dark grey to black clay shale, with a few concretions and irregular beds of black, crystalline limestone. The shales are somewhat micaceous, but are apparently free of silty material. The limestone concretions commonly show cone-in-cone structure" (Hutchinson, 1952, p. 45). The fossils show that the *Parabolina spinulosa* zone, *Leptoplastus* zone, and *Peltura* zones are present. In New Brunswick the Olenid Series is represented by (from below) the Agnostus Cove formation, the Black Shale Brook formation, and the Narrows formation (Hayes & Howell, 1937). The Agnostus Cove formation consists of about 200 ft. of thin-bedded black and grey shales and greenish-grey ripple-marked sandstones with lenses of grey limestone. It belongs to the zone of *Agnostus pisiformis*. The Black Shale Brook formation consists of thin-bedded black shale. 25 ft. are exposed, but many more feet are believed to be concealed beneath the surface. It belongs to the *Olenus* zone. The Narrows formation consists of dark grey and black shales, with limestone concretions and thin sandstone beds. Several hundred feet are exposed. Its fossils belong to the *Parabolina* and *Peltura* zones.

The Upper Cambrian olenids reported from eastern Canada (New Brunswick, Nova Scotia, and Newfoundland) are listed in chart 1.

Just as in Great Britain, the vertical distribution of the olenids is not known in detail. Neither has it been stated which olenids occur associated. On a plastocast from Nova Scotia (P. M. O. no. A 26916) *Peltura scabaeoides*, *Sphaerophthalmus humilis*, *Ctenopyge fletcheri*, *Parabolina dawsoni* and *Lotagnostus trisectus* occur together on the same surface. From the list of fossils it appears that the Upper Cambrian subzones which are indicated in chart 3 are present.

The Upper Cambrian olenids in eastern Canada have been described by Matthew (1892, 1894, 1903) and later by Hutchinson (1952), who erected

the genus *Sphaerophthalmoides* with Matthew's *Leptoplastus latus* as type species. This genus is here considered to be a synonym of *Westergårdia*, and it is even probable that *W. lata* is a senior synonym of the Scandinavian species *W. illaenopsis*. It is possible that the other species assigned to *Sphaerophthalmoides* by Hutchinson (1952, p. 91), *Sph. ornatus*, likewise is a synonym of *W. lata*. *P. heres lata* appears to be a senior synonym of *P. heres hexacantha*, described from Sweden. It is possible that *P. heres grandis* is a synonym of *P. heres lata*, too. The specimens described by Matthew (1892) as *Ctenopyge flagellifer* var. and *Ct. spectabilis* var. (called *Ct. acadia* by Matthew in 1894) probably all belong to *Ct. flagellifera*. As pointed out by Westergård (1922, p. 114) the cranidium assigned by Matthew (1903) to *Sphaerophthalmus pecten* apparently belongs to the group of *Ctenopyge linnarssoni*. As verified by Hutchinson (1952), *Sphaerophthalmus alatus* var. *Canadensis* Matthew is identical with *Sph. alatus* auct. (i.e. *Sph. humilis*). *Sphaerophthalmus fletcheri* is here transferred to *Ctenopyge*, and *Protopeltura acanthura* var. *tetracanthura* to *Parabolina*.

Conclusions on the distribution of Upper Cambrian olenids in the Acado-Baltic province.

It has been possible to give a fairly detailed biostratigraphic division of the Olenid Series in Scandinavia. Faunal lists from corresponding strata outside Scandinavia have sometimes suggested the association of species which occur in widely separated subzones in Scandinavia. Whenever it has been possible to re-examine these faunas, it has turned out that this is not the case, and that either fossils from different horizons have been mixed together, or some of the fossils have not been correctly determined. There is thus so far no evidence that the olenid species do not occur in the same order of appearance within the whole of the Acado-Baltic province. On the contrary, whenever it can be controlled, they seem to do so. This does not mean that the vertical range of some species may not be found to be greater than known at present, e. g. that a species known to occur in a certain subzone may later be found to extend into the overlying subzone. Probably even such adjustments will be few and small.

Previous lists of olenids from areas outside Scandinavia have often suggested that the olenid faunas in these areas were somewhat different from those in Scandinavia. However, these differences are more apparent than real. Many species from other areas have since proved to be identical with Scandinavian species, although they were given different names. Furthermore, a few species first described from outside Scandinavia, have later been recognized in Scandinavia. Since the Upper Cambrian succession has been more intensively studied in Scandinavia than in the other countries, it is not surprising that many species are known only from this area. No doubt more species will subsequently be found also in the other areas when

they are more thoroughly investigated. Even in Scandinavia new species are still being found. In chart 1 some species seem to be endemic to some extra-Scandinavian area. In several cases this may be due to the type material being too badly preserved or too inadequately described to be recognized elsewhere. It is quite possible that some of these species really are synonyms of others. It should also be remembered that not all parts of the Scandinavian sequence are just as well known. It is furthermore possible that there are smaller gaps in the Scandinavian sequence, for instance at the junction between the *Olenus* zone and the zone of *Parabolina spinulosa*, or at the junction between the zone of *Leptoplastus* and the zone of *Protopeltura precursor*, and that the missing parts may be found in some other areas.

In general one may say that the similarity between the olenid faunas in the different areas is the more stressed, the better they have been studied. I believe it is impossible to distinguish any olenid subprovinces in the Acado-Baltic province in Upper Cambrian times.

Chart 3 shows the regional distribution of the zones and subzones of the Olenid Series in the Acado-Baltic province, as far as it could be compiled from the available data. The zonal symbols I—VI, introduced by Wilson (1954) and corresponding to Westergård's symbols 1—6 for the Swedish succession, are retained as international symbols. I have split the zone V into three zones, for which I suggest the symbols Va, Vb, and Vc.

The Tremadocian Series in the Acado-Baltic province.

Occurrence, lithology, and faunas.

The Acado-Baltic province was characterized by olenids, *Dictyonema flabelliforme*, and the so-called *Euloma-Niobe* (or *Ceratopyge*) fauna (cf. Brøgger, 1898) in the Tremadocian epoch.

The Tremadocian Series is known from Scandinavia (Denmark, Norway, Sweden), Esthonia, Russia (Leningrad area), Belgium, Great Britain (England, Wales), eastern North America, and South America (Argentina, Bolivia, Colombia). Tremadocian faunas related to the typical *Euloma-Niobe* fauna are further known from Bohemia, Germany, and France.

The Tremadocian Series is rather condensed in Scandinavia; in the Oslo region, for instance, it is only about 25 m thick. Parts of the succession are often missing locally. The *Dictyonema* Shales constitute the lower part of the Tremadocian Series, and consist chiefly of alum shales with occasional stinkstone lenses. In the overlying *Ceratopyge* Beds the alum shales are replaced gradually by dark grey or grey shales and beds of light-coloured limestones, sometimes glauconitic, but concretions of dark stinkstones still occur at certain levels. The fossil faunas change, too. Olenids still dominate among the trilobites in the *Dictyonema* Shales, although other groups occur as well, but the graptolites form a conspicuous new faunal element. A number of new trilobite families appear in the *Ceratopyge* Beds and the olenids no

longer dominate, except in certain horizons. Graptolites are common in the shales, and brachiopods, gastropods, cephalopods and other invertebrates form part of the faunas.

Also in other parts of the Acado-Baltic provinces there is a similar change in the facies and faunas in Tremadocian times.

A thin band of *Dictyonema* Shales occurs at the top of the *Obolus* Sandstone in Esthonia and in the Leningrad area (Ingermanland) (cf. Schmidt, 1896) and is succeeded by the Upper Tremadocian Glauconite Sand. *Dictyonema* Shales furthermore occur in Belgium (cf. Lecomte, 1949). No olenids have been described from these countries.

Upper Tremadocian shales at Hof in Bavaria (Germany) contain a fauna which is related to the *Euloma-Niobe* fauna in Scandinavia (cf. Barande, 1868; Brøgger, 1898; and Sdzuy, 1955), and this is also the case with the Upper Tremadocian succession in Languedoc (France) (cf. Brøgger, 1898). Somewhat less related Upper Tremadocian faunas have been described from Bohemia (cf. Želízko, 1921).

In England and Wales the Tremadocian Series is developed as a thick succession of grey and blue-grey mudstones and shales, with an occasional band of black shale in the lower part (cf. Fearnside, 1910; Edmunds & Oakley, 1947). The blue-grey Shineton Shales of Shropshire have an estimated thickness of about 3,000 ft. (Pocock & Whitehead, 1948). Both *Dictyonema* and *Euloma-Niobe* faunas are present in Great Britain.

In North America the Tremadocian Series occurs in the same areas as the Olenid Series (Newfoundland, New Brunswick, Nova Scotia) and resembles mostly that in Great Britain (cf. Hayes & Howell, 1937; Hutchinson, 1952; Rasetti, 1954). Tremadocian graptolite faunas are furthermore known from the Matane Shales of Quebec and the Schaghticoke Shale of New York (cf. Bulman, 1950). A Tremadocian trilobite fauna has been described from the Gaspé peninsula of Quebec (Rasetti, 1954).

In South America a very thick succession (partly black shales) of Lower and Upper Tremadocian beds with respectively a *Dictyonema* and a *Ceratopyge* fauna occurs in Argentina (cf. Harrington, 1938). A Lower Tremadocian *Dictyonema* fauna is known in Bolivia (Harrington & Leanza, 1943b), and a Lower Tremadocian shelly fauna is reported from eastern Colombia (Harrington & Kay, 1951).

Distribution of Tremadocian olenids in the Acado-Baltic province.

Charts 1 and 4.

Chart 4 shows the regional distribution of the Tremadocian olenids in the Acado-Baltic province. The olenids are grouped into Lower Tremadocian (*Dictyonema* zone) and Upper Tremadocian species. Only in Norway has it been possible to establish any detailed biostratigraphic division of the Tremadocian based on olenids.

Parabolinella rugosa, described from Norway, is doubtfully recorded from Wales. Apart from this, no Tremadocian olenids are known to be common to Scandinavia and Great Britain, but it is possible that better material of the British species *Peltocare olenoides* may show that it is conspecific with *P. norvegicum*. The Tremadocian olenids in Canada are on the whole poorly known, but *Parabolinella quadrata* may be considered a synonym of the British species *P. triarthra*, and the South American species *Parabolina andina* (i. e. *P. argentina*) has been reported from Newfoundland. A number of species are so far only known from South America, but *Bienwillia tetragonalis tetragonalis* and *Jujuyaspis keideli keideli* appear to be rather close to the two Norwegian forms *Bienwillia tetragonalis broeggeri* n. subsp. and *Jujuyaspis keideli norvegica* n. subsp. Furthermore, *Peltocare glaber* may be a synonym of *P. norvegicum*.

There is a marked difference between the olenid faunas in the various areas of the Acado-Baltic province in Tremadocian times, as contrasted with the uniformity in the Upper Cambrian times. This may to some extent be due to the olenid-bearing levels not being exactly contemporaneous in the different areas, but nevertheless one is left with the impression that there were rather distinct local variations in the olenid faunas.

It does not seem possible to establish any standard scheme of olenid zones and subzones in the Tremadocian for the whole of the Acado-Baltic province. This is the more regrettable as such a scheme would have been of great help in correlating the Tremadocian beds with contemporaneous ones in the North American province, which occasionally yield olenids.

Some olenid genera seem to occur both in the Lower and Upper Tremadocian. Others appear to have a more restricted vertical distribution and may be more useful for correlation. *Jujuyaspis* (South America, Norway) and *Boeckaspis* (Norway, Sweden) have so far only been found in the Lower Tremadocian. *Parabolinella* occurs in Lower Tremadocian beds (Argentina), but is better represented in the Upper Tremadocian (Norway, England, Canada, South America). *Triarthrus*, again, is known only from the Upper Tremadocian, and so is apparently *Peltocare* n. gen.

The generic reference of several Tremadocian species has been altered in this paper. Scandinavian species: *Parabolinella wimani* (to *Bienwillia*?), *Peltura norvegica* (to *Peltocare*). British species: *Triarthrus shinetonensis* (to *Bienwillia*), *Leptoplastus salteri* (to *Leptoplastides*), *Beltella vexata* (to *Angelina*?), *Peltura olenoides* (to *Peltocare*), *Peltura punctata* (to *Triarthrus*). North American species: *Bienwillia terranova* (to *Leobienwillia*), *Beltella latifrons* (to *Angelina*?). South American species: *Parabolinella tetragonalis tetragonalis* (to *Bienwillia*), *Parabolinopsis mariana* (to *Leptoplastides*), and *Cyclognathus glaber* (to *Peltocare*).

It may be recalled that *Parabolina andina* is regarded as a junior synonym of *P. argentinensis*, and that *Protopeltura granulosa* and *Andesaspis argentinensis* both are regarded as synonyms of *Leptoplastides* ("Parabolino-opsis") *marianus*, and *Parabolinella quadrata* a synonym of *P. triarthra*.

Tremadocian olenids with great
meridional range.

Richardson (1948) claimed that the South American olenid *Parabolina andina* (i. e. *P. argentina*) occurred in the Tremadocian Apsey formation of Newfoundland. This was suggested to him by Dr. H. J. Harrington, Argentina, who had received photographs of the Newfoundland specimens. Richardson based his claims on comparison of actual specimens from Argentina and Newfoundland. Newell (1949) questioned the identification, as no statistical method seems to have been used.

However, in 1950 Shaw cited another example of a wide-ranged olenid, viz. *Parabolinella triarthroides*. This species was originally described from Argentina, but Shaw claimed to have identified it by support of statistical analysis in northwestern Vermont. The Vermont material has later been described and illustrated by Shaw (1951).

Both Richardson and Shaw have discussed the possibility of homoeomorphy, and Shaw maintained that the chances are very small that this should apply both to *Parabolina andina* and *Parabolinella triarthroides*. However, I would like to point out that the differences between related olenids often are rather small, and this especially applies to *Parabolina* species and also to *Parabolinella* species. Furthermore it is sometimes difficult to determine a species when only some parts of the shield are known. In the case of the Vermont material assigned to *Parabolinella triarthroides*, only the cranidia have been compared with the Argentinian specimens, and as discussed below (p. 140) there may be slight differences between the cranidia from Vermont and Argentina. I do not deny the possibility of it being correct to assign the North American specimens to *Parabolinella triarthroides*, but it can hardly be said to be proved beyond doubt. In any case, the Vermont form is closely related to it. In this connection it is of interest that the Norwegian olenids *Parabolinella tetragonalis broeggeri* n. subsp. and *Jujuyaspis keideli norvegica* n. subsp. are very close to respectively *Parabolinella tetragonalis tetragonalis* and *Jujuyaspis keideli keideli* of South America. Keeping in mind the short vertical distribution (i. e. the fast rate of development) of most differentiated pelturines, the resemblance between the Argentinian and Norwegian forms of *Jujuyaspis* is striking. Furthermore, the South American species *Peltocare glaber* is very close to, if not identical with *Peltocare norvegicum* in Scandinavia.

It thus appears that some species of olenids had a great meridional range, across the equator, although they have been divided into geographical races or subspecies. As advocated by Shaw (1950) this probably implies a rather even climate at that time. A migration of the poles was mentioned by him as an alternative explanation.

Distribution of Upper Cambrian and Tremadocian olenids outside the Acado-Baltic province

Cf. chart 1.

Upper Cambrian and Tremadocian olenids have from time to time been recorded from various areas outside the Acado-Baltic province. However, later revisions have shown that many of them are not olenids.

At present, Upper Cambrian and Tremadocian olenids outside the Acado-Baltic province are known with certainty only from North America, Siberia, South Korea, and Central Asia. The Tremadocian olenids in South America are regarded as belonging to an extension of the Acado-Baltic province. There is also a possibility of *Olenus* occurring in Australia (cf. p. 97).

Several occurrences are known in the North American province, mainly near the border of the Acado-Baltic province, but also further away. Two obvious Upper Cambrian olenids, *Olenus* sp. and *Olenus? wilsoni* n. sp. occur in a mixed fauna of Acado-Baltic and North American forms in the Woods Hollow boulders in the Marathon uplift, Texas. Furthermore, a number of Tremadocian, or at least late Upper Cambrian forms have been reported, these being *Bienwillia corax* and *Parabolina? incerta* in the *Hungaia magnifica* zone in Quebec, *Bienwillia micula* in the lowest zone of the Gorge formation in Vermont, *Plicatolina kindlei* and *Parabolinella triarthroides?* in the basal beds of the Highgate formation (Tremadocian) in Vermont, *Angelina? latifrons* and *Leptoplastides marianus?* in the basal Marathon formation (Tremadocian) and *Parabolinella triarthroides?* from Woods Hollow boulders (Tremadocian) in the Marathon uplift, Texas. *P. triarthroides* is stated to occur in the Goodwin limestone (Pogonip group) in the Monitor and Antelope Rangēs, Central Nevada (Wilson, 1954, p. 263). *Parabolinella punctolineata* from near the Alaskan-Yukon border apparently is another Tremadocian species. Several Tremadocian species have been described by Kobayashi (1955) from British Columbia (cf. postscript).

The age of the olenid *Westergårdites pelturaeformis* from eastern T'ien-Shan, Central Asia, is not known with certainty, but its resemblance to late Oleninae like *Bienwillia*, *Triarthrus*, and *Plicatolina* suggests that it may be a Tremadocian species.

Remarks on the distribution of post-Tremadocian olenids

Olenids are rather scarce in post-Tremadocian beds. Besides the Arenigian species *Peltocare* ("Cyclognathus") *rotundifrons* and *Parabolinella?* *posthuma* in eastern Canada, and *Saltaspis* and two *Parabolinella?* spp. in Sweden, the only species described belong to *Triarthrus* and its off-shoot *Porterfieldia*. The latest known olenids (*Triarthrus*) occur in the Upper Caradocian zone of *Pleurograptus linearis* or in beds of corresponding age. Post-Tremadocian species of *Triarthrus* occur in Scandinavia, Great Britain, eastern North America, and South America (cf. pp. 151—152). The only known species of *Porterfieldia*, *P. caesigenus*, occurs in eastern North America. It is worth noting that *Triarthrus* usually is found in dark shales (or dark limestone concretions), as the famous pyritized specimens of *T. eatoni* (originally assigned to *T. beekii*) in the Utica Shale near Rome, New York.

Conclusions on the occurrence of the olenids

The olenids are known from the base of the Upper Cambrian to the top of the Middle Ordovician, being most common in the Upper Cambrian.

They are especially characteristic of the Acado-Baltic province (in Tremadocian times including South America), but may occasionally be found outside it, particularly in Tremadocian and later beds.

The Upper Cambrian olenids occur mainly in the black shale facies or in the thick series of pelitic and psammitic sediments, often also containing black shales. The Tremadocian olenids occur in various types of sediments, but in greater numbers especially in black shales or in series containing beds of black shales. The later olenids likewise are commonest in the black shale facies.

Correlation of the Upper Cambrian and Tremadocian series in the Acado-Baltic province with the succession of the North American province

Chart 5.

The Cambrian system has its type area along the axis of the Welsh geosyncline (Twenhofel et al., 1954, p. 251), and thus in the Acado-Baltic province. The lower boundary of the Upper Cambrian in the Acado-Baltic province has always been drawn between the zones of *Lejopyge laevigata* and *Agnostus pisiformis*, thus coinciding with the lower boundary of the Olenid Series. The zone of *Lejopyge laevigata* merges into that of *Agnostus pisiformis*, and Westergård (1922, p. 186) and Wallerius (1930, p. 61) have suggested that the zone of *Agnostus pisiformis* might perhaps be transferred

to the Middle Cambrian. However, this change of the Middle/Upper Cambrian boundary has not been adopted. The find of an *Olenus* species (*O. alpha* n. sp.) in the *Agnostus pisiformis* beds supports the traditional inclusion of the zone of *Agnostus pisiformis* in the Olenid Series. As to the upper boundary of the Upper Cambrian in the Acado-Baltic province, there has been some controversy as to whether the Tremadocian Series should be included in the Cambrian or Ordovician System. While British geologists drew the base of the Ordovician System at the top of the Tremadocian, most geologists on the European continent and in America have drawn it at the base of the Tremadocian, and this practice is also followed here. Recently there has been a growing sentiment among leading specialists in Great Britain to shift the boundary there in accordance with the common usage in other parts of the world (Twenhofel e. a., 1954, p. 252).

At present, neither the lower nor the upper boundary of the Upper Cambrian as drawn in the North American province seem to agree with those of the Upper Cambrian in the Acado-Baltic province. It would seem natural that the boundaries of the Lower, Middle, and Upper Cambrian were as nearly isochronous as possible in all provinces, and that they were based on sections in the Acado-Baltic province (type province of the Cambrian System). The difficulties lie, of course, in the correlations between the different provinces. Many attempts have been made at correlating the Upper Cambrian faunas of the Acado-Baltic and the North American provinces, but the correlations are still uncertain. In the correlation chart of Cambrian formations of North America (Howell e. a., 1944) and also by Howell in 1947, the Olenid Series was correlated with a part of the Dresbachian and the lower part of the Franconian, whereas beds corresponding in age to the rest of the Franconian and the whole of the Trempealeauian apparently were considered to be missing in the Acado-Baltic sections. There is certainly no break of that extent between the Olenid Series and the Tremadocian Series; probably there is no break at all, as suggested by a new section (p. 41) through their junction. As early as in 1939 Howell & Lochman suggested that the Trempealeau faunas of North America possibly were contemporaneous with at least a part (probably the lower part) of the Tremadocian faunas of the Acado-Baltic province. In 1954 Wilson apparently recognized no major break between the Olenid Series and the Tremadoc Series. The *Peltura* zones (V) were suggested to reach as far up as the *Ptychaspis-Prosaugia* zones (s.l.), and the overlying *Saukia* zones were indirectly correlated with the Lower Tremadocian. From his correlation table it appears that he regarded the *Acerocare* zones (VI) as constituting the Lower Tremadocian. However, the *Acerocare* zones have always been regarded as belonging to the Upper Cambrian Olenid Series.

The correlations between the two provinces depend upon occasional occurrences of Acado-Baltic elements in the North American province, and

vice versa. Unfortunately, such occurrences are rather rare. The find of olenids in the Upper Cambrian of the Marathon uplift, Texas (Wilson, 1954) is important and encouraging.

The lowermost zone of the Olenid Series, the zone of *Agnostus pisiiformis* (I), has been correlated with different North American zones, from as low as the *Cedaria* zone (Howell e. a., 1944) and up to the *Elvinia* zone (Howell & Lochman, 1939). Wilson (1954, p. 250) pointed out that there is faunal evidence of the zone of *Solenopleura brachymetopa* possibly being correlated with the *Cedaria* zone. The overlying zone of *Lejopyge laevigata* might then perhaps correspond to the *Crepicephalus* zone. This would explain the fact that no olenids have ever been found in the *Cedaria* and *Crepicephalus* zone (cf. Wilson, 1954, p. 262). The zone of *Agnostus pisiiformis* might then be slightly younger than the *Crepicephalus* zone.

The *Olenus* zone (II) may correspond to at least a part of the *Aphelaspis* zone. This is indicated by the presence of *Agnostus* (*Homagnostus*) *obesus* and *Olenus* cf. *truncatus* (apparently a true *Olenus* species) in an *Aphelaspis* fauna (containing i. a. *Aphelaspis* and *Pterocephalina*) from Cambrian boulders in the Middle Ordovician Woods Hollow Shale of the Marathon uplift in Texas (Wilson, 1954), provided that the fossils within the boulders are not secondarily deposited. The boulders furthermore contain two other species which may indicate that the *Aphelaspis* zone extended as far up as somewhere near the boundary between the *Olenus* zone (II) and the *Parabolina* zone (III), i. e. *Pseudagnostus cyclopyge* (occurring in the lower half of the *Parabolina* zone in Sweden) and an olenid, which Wilson assigned to *Parabolinella incerta* Rasetti. The olenid is discussed below as *Olenus? wilsoni* n. sp.. Apparently it has not been described from the Acado-Baltic province, but may be close to late *Olenus* species and early *Parabolina* species. *Glyptagnostus angelini* Resser 1938 apparently occurs mixed with fossils of the *Blountia* zone in Alabama (cf. Resser, 1938, p. 33). The *Blountia* zone was regarded as a distinct zone between the *Aphelaspis* zone and the *Elvinia* zone by Resser, 1938. *Glyptagnostus angelini* is considered to be a synonym of *G. reticulatus* (Angelin, 1851) by Westergård (1947, p. 5). This species which occurs in the lower part of the *Olenus* zone in Scandinavia, seems to have a world-wide distribution. Its importance for intercontinental correlation has been pointed out by Kobayashi (1949).

The American genus *Irvingella* has been found in Upper Cambrian beds in England and Sweden. Its exact stratigraphic position is unfortunately unknown in both countries, but according to Westergård (1949, p. 606) the Swedish material seems to occur in one of the older Upper Cambrian zones and not higher up than in the subzone of *Parabolina brevispina* (lower part of the *Parabolina spinulosa* zone). *Irvingella* occurs in the *Elvinia* zone and especially in the *Irvingella major* zone in North America, and it is therefore probable that these zones are no younger than the *Parabolina spinulosa* zone.

The *Leptoplastus* zone (IV) cannot at present be correlated directly with any North American zones. It may possibly be more or less contemporaneous with the *Conaspis* zone.

As to the correlation of the *Peltura* zones (V), Howell & Lochman (1939, p. 117) mentioned the discovery in the *Ptychaspis-Prosaukia* faunas (s. s.) of Wyoming of a species "belonging to the same genus as '*Agnostus rudis holmi*'", which is known from the zone of *Peltura scarabaeoides* (Vc) in Sweden. *Agnostus rudis* and *A. rudis holmi* were assigned to *Geragnostus* by Kobayashi (1939), but were included in *Agnostus* (*Homagnostus*) by Westergård in 1947. Wilson (1954, p. 254) reported both *Agnostus* (*Homagnostus*) *rudis* and *A. (H.) rudis holmi*, as well as an undescribed olenid form the lowest beds in the Dagger Flat formation in the Marathon uplift. Unfortunately they were not found accompanied by any North American genera. The olenid was suggested by Wilson to be a *Leptoplastus* or *Ctenopyge* species. Since the agnostids suggest the upper *Peltura* zones, it seems most likely that it is a *Ctenopyge* species.

Two dikelocephalids, "*Dikelocephalus*" *discoidalis* Salter and "*D.*" *celticus* Salter are known from the Upper Lingula Flags (*Peltura* zones) in Wales. They were included in *Briscoia* by Kobayashi (1935a, p. 52; 1936c, p. 169). Dikelocephalids are typical of the North American province. Their occurrence in the *Peltura* beds in Wales suggest that these beds may be as young as the upper subzones of the *Prosaukia-Ptychaspis* zone (s. l.).

The *Acerocare* zone (VI) cannot be directly correlated with any North American zones at present.

The correlation between the Acado-Baltic and North American provinces are somewhat hampered because the age of the *Hungaia magnifica* fauna (Gorge fauna) has not yet been settled. It was earlier suspected to be of late Trempealeauian age (Rasetti, 1944, p. 231; Shaw, 1951, p. 99), but has later been suggested to be of Franconian age (Wilson, 1954, p. 263; Shaw, 1955, p. 187). The occurrence of *Bienwillia* in this zone suggests that it may be correlated with the Tremadocian, since *Bienwillia* is not known from earlier beds in the Acado-Baltic province. The occurrence of primitive richardsonellids (*Richardsonella* and allies) in the *Hungaia magnifica* zone, suggests that the zone is earlier than the Upper Tremadocian, which contains more advanced richardsonellids. If the *Hungaia magnifica* zone belongs to the Franconian, it is possible that the boundary between the Franconian and the Trempealeauian may correspond to a horizon within or near the Lower Tremadocian.

The *Saukia* zones may perhaps be correlated with at least a part of the Lower Tremadocian, since the overlying Gasconade formation (Lowermost Canadian) apparently is no lower than Middle Tremadocian (Wilson, 1954, p. 263). (Cf. postscript, p. 273).

It is possible that a closer study of the agnostids will be an aid to the correlation between the Upper Cambrian of the two provinces.

The Acado-Baltic province in the Upper Cambrian and Tremadocian epochs

The main development of the olenids took place within the Upper Cambrian and Tremadocian epochs in the Acado-Baltic province. The sea in which the Olenid Series was deposited, is here referred to as the Olenid Sea, and that of the Tremadocian Series as the Tremadoc Sea. It is necessary to obtain an impression of the conditions in these seas to be able to discuss the environments of the olenids. Since black muds (black shales) were rather commonly deposited in both seas, their formation will be briefly discussed.

Remarks on the formation of alum shales

The formation of black muds (black shales) has often been discussed. It is agreed that they were deposited under stagnant conditions, and this is no doubt the case with the black bituminous shales called alum shales and the accompanying black bituminous limestones (stinkstones) (cf. Hansen, 1945, p. 34).

It has long been assumed that the condensed succession of Upper Cambrian alum shales in Scandinavia was deposited in shallow waters (Westergård, 1922, p. 104, foot-note 1). Evidences of shallowness are i. a. the many minor breaks and intraformational conglomerates, especially in Sweden. Other evidences have been discussed by Wetzell (1949). Hansen (1945) suggested that some of the stinkstone beds with cone-in-cone structure were formed in the littoral zone. He further assumed that the black calcareous mud (stinkstone) and the black terrigenous mud (alum shale) formed coordinate belts on the sea floor, with the former belt lying nearer the shore (l. c., p. 39). This agrees with the facts that the conglomerates occur in connection with stinkstone beds, and that the frequency of stinkstone beds and concretions is smaller in areas with the most complete successions (e. g. the Oslo region and Scania), i. e. in areas less influenced by regressions and transgressions, where deposition presumably took place in somewhat deeper waters. The 40 m thick succession in Scania has a stinkstone content of only 7—10 % as contrasted to 16—42 % in the only 14 to 5 m thick succession in central Sweden (Kaufmann, 1933a, p. 10). That the stagnant conditions on the sea floor extended right up to the shoreline in Scandinavia is suggested also by the absence of any other facies near breaks due to regression and transgression.

According to Weeks (1953, p. 173) the formation of limestone concretions in black shales in a generally unfavourable (stagnant) area may be due to a localized environment made adequately alkaline around a piece of organic matter. He further states (l. c., p. 171) that "There are probably few stagnant bottom environments where there is not some limited decomposition

of organic matter, even if anaerobic. Bacteriologists and biochemists tell us that where there is anaerobic decomposition there is a localized concentration of ammonia and amines. This would markedly increase the pH; it would be sufficient, no doubt, to precipitate the bicarbonate in solution as carbonate."

Landergren (1954) has shown that the isotope exchange between carbon dioxide and carbonate tended to attain equilibrium in the alum shale milieu, showing that very stable and tranquil water conditions prevailed during the deposition. Very quiet waters are suggested also by the usually perfect preservation of even the finest spines of the olenids.

Strøm (1939, pp. 367—368) came to the interesting conclusion that, from a hydrographical point of view, there can hardly be any doubt that even the oceans and great seas might become insufficiently ventilated at great depths under certain conditions, and that foul waters most probably would occur below 50 metres if the full effects of general stagnation were considered. This might explain the rather wide geographical distribution of Upper Cambrian alum shales (Scandinavia-Canada). However, it does not explain why the alum shales, at least partly, appear to be shallow-water deposits.

Twenhofel (1915) drew attention to fine-grained black deposits heavily charged with hydrogen sulphide in marine swamps on the east shore of the Baltic, and suggested that some black shales were such shallow-water deposits of epi-continental seas that invaded and retreated from lowlands, so that there was a wide shallow-water belt covered with aquatic plants. Another feature of these deposits is that they are not generally flanked by littoral or shore deposits. This fits in very well for the epicontinental alum shales in Scandinavia, and it is possible that they were deposited under similar conditions. However, it has not been proved that plants grew on the bottom where alum shale was deposited, but the chances of finding any proof of this are also very small. Although it is not usual, the olenids may sometimes be pyritized, which is interesting in this connection because H. & G. Termier (1951) suggested that the majority of pyritic faunas were formed in submarine meadows. It is reasonable to assume that at least a part, probably the greater part, of the organic matter in the alum shales is derived from plants, either benthonic and/or pelagic. Svanberg (1848) has shown that there are small quantities of iodine in the alum shale, indicating that at least some of the organic matter is derived from algae. I may add that I have often found fossils in Middle and Upper Cambrian alum shales of a type described by Walcott (1919) as *Morania*, and suggested by him to be floating algae.

The Olenid Sea

The Scandinavian part of the Olenid Sea covered the western part of the Fenno-Scandian shield. Its eastern shore line ran partly through present Sweden, where several transgressions and regressions are recognized (Westergård, 1922, p. 108). The sea was rather shallow and the bottom

waters were stagnant apparently right up to the shore line. There are strong evidences of islands, and the oscillating shore line was irregular. Sedimentation was slow and the bordering land (to the east) apparently was low, although uneven on a small scale. To the northwest this epicontinental sea opened into the Caledonian geosyncline, and to the south it may have been connected, at least at times, with the Polish basin. The conditions towards the southwest are not known.

The Upper Cambrian deposits in the so-called Sandomiridian geosyncline in Poland are regarded as littoral and flysch-like, and are supposed to have been formed in shallow waters near the coast (Samsonowicz, 1934). Sedimentation was rapid, and there were ventilated conditions in this part of the sea. The rather coarse sediments become finer and eventually pelitic towards the west and north-west, indicating a deepening of the sea in this direction, thus suggesting a connection with the Scandinavian part of the Olenid Sea. Towards the close of the Late Cambrian epoch, the Sandomiridian geosyncline ceased to subside, and its deposits soon after became folded into the Sandomiridian mountain chain, which ran east-west.

The Upper Cambrian sediments in the Montagne Noire in Hérault (Southern France) are interpreted by Thorat (1946, pp. 13—14) as having been deposited under neritic conditions in a sea which deepened towards the west and north-west and which may have been bordered by a land area not far away towards the north and northeast. Since no Upper Cambrian deposits are known from north-eastern Africa (cf. Choubert, 1952, p. 109) and no certain Upper Cambrian sediments are known from Spain, it is probable that the Upper Cambrian sea in southern France formed a bay-like extension of the Olenid Sea, and was connected with it towards the northwest. As in Poland, the Upper Cambrian sediments in southern France appear to have been deposited in a local and rather rapidly subsiding trough.

It has been suggested that the fine-grained character of the Upper Cambrian beds in England and their uniformity indicate a deepening of the sea in this part after the Middle Cambrian beds had been laid down, and a gradual depression of the area keeping pace with the deposition of fine mud (Pocock & Whitehead, 1948, p. 34). The black muds which gave rise to the black shales were no doubt deposited under stagnant conditions. However, it is quite possible that they were laid down in shallow waters, as in Scandinavia — at least the beds with stinkstone concretions.

During the Middle and Late Cambrian, North Wales occupied a position more or less intermediate between the main shoreline on the south and east and the deeper troughs of the central parts of the geosyncline to the northwest (Smith & George, 1948, p. 17). The Maentwrog and Ffestiniog Beds are no doubt shallow water deposits. The great thickness indicates a considerable depression of the sea floor keeping pace with the deposition. The Black Band at the top of the Dolgelley Shales has been suggested to be evidence of subbathyal conditions of sedimentation (Smith & George, 1948, p. 23). However, it may have been laid down in rather shallow and quiet waters in the

same way as the alum shales in Scandinavia. This is also suggested by the absence of the *Accrocare* zone in Wales, which indicates that the Black Band was deposited prior to an uplift. There is, of course, a possibility of higher beds having been deposited and later eroded before the Tremadocian beds were laid down, but even so, the Black Band was deposited not long in advance of an uplift. Apparently sedimentation was rapid and took place under ventilated conditions during the most of the Late Cambrian epoch in Wales, but slowed down in the *Peltura* epoch, when stagnant conditions prevailed on the sea floor.

The MacNeil formation of Cape Breton Island (Nova Scotia) was apparently deposited under more or less stagnant conditions. Its black shales (alum shales) and stinkstone lenses may have been formed in the same manner as those in Scandinavia.

According to Hayes & Howell (1937, p. 16) there appears to have been almost continuous sedimentation in shallow waters throughout Cambrian times in the Saint John area (New Brunswick). The black shales of the Narrows formation are supposed to have been laid down in fairly quiet waters, either far from shore or near a low-lying land (l. c., p. 81).

Apparently the conditions in eastern Canada were much as in England; the sea floor seems to have subsided moderately rapidly, and stagnant sediments are rather characteristic.

Hutchinson (1952, p. 60) suggested that the eastern part of Cape Breton Island (Nova Scotia) during Cambrian times lay near the western margin of a geosyncline basin, which subsided intermittently, and that there was a landmass not far to the west, with deeper parts of the geosyncline to the east. It seems that the sea spread somewhat farther west in early *Peltura* times, but there is some evidence to indicate that the sea withdrew from Cape Breton Island at the close of the Cambrian period.

The Olenid Sea thus reached from eastern Canada in the west to Scandinavia in the east. North and north-west of it the central Caledonian geosyncline apparently separated the Acado-Baltic fauna from an Arctic faunal sub-province of the North American province. East of the Olenid Sea there was a continent which apparently separated it fairly well from marine faunal provinces further to the east. Little is known of the southern limit of the Olenid Sea, except within the present Europe (Poland, southern France), but no Upper Cambrian olenids are known from Africa or South America. West of the Acado-Baltic province there was another marine faunal province, the North American province, possibly separated from the Olenid Sea by landmasses (island arcs?). There was at least some seaward connection between the Olenid Sea and the North American province, as is shown by the occasional presence of North American genera in the Acado-Baltic province (e. g. *Irvingella*) and olenids in the North American province (e. g. *Olenus* in Texas), as well as the occurrence of agnostid genera common to both provinces (e. g. *Homagnostus*, *Glyptagnostus*).

The Acado-Baltic marine faunal province in the Late Cambrian epoch was characterized by the dominance of Olenidae and the scarcity or absence of many groups of invertebrates, as far as can be judged from the fossils. Thus no benthonic sessile forms are known from the Olenid Sea, with the exception of a few brachiopods.

Conditions in the Olenid Sea often tended to be stagnant, at least near the bottom. In shallow areas with slow sedimentation, the bottom seems to have been stagnant right up to the shore line (e.g. Scandinavia). In other areas (e.g. Poland, Wales) the sedimentation was much faster, at least at times, and argillaceous and psammitic sediments were deposited under ventilated conditions. Remains of olenids are common in sediments of both environments. Besides the trilobites, the brachiopods form the only invertebrate group worth mentioning. Inarticulate brachiopods are rather regularly met with in the ventilated deposits, but they hardly seem to have been recorded from the alum shales. Articulate brachiopods are known from both environments, but they are rather rare, with the exception of *Orusia lenticularis*, which lived in enormous numbers in the *Parabolina spinulosa* period. As to the non-olenid trilobites, they are on the whole very rare, with the exception of agnostids, which apparently were rather common at certain times, especially in the early part of the epoch. The early Upper Cambrian agnostids may perhaps be regarded as remnants of the earlier *Paradoxides* faunas. The other trilobites may be regarded as accidental intruders. At the end of the epoch, occasional asaphids appear as forerunners of the Tremadocian *Euloma-Niobe* fauna (cf. text-fig. 8, p. 67).

It is interesting to note that the Upper Cambrian strata in Europe apparently were deposited in more or less shallow waters along the southern and eastern border of the Caledonian geosyncline complex, partly in the miogeosyncline, partly on the bordering epicontinental platform or in local troughs at the border of the continent. As pointed out by Wilson (1954, p. 264), the olenids in North America occur in the parts of the geosynclinal belts furthest removed from the foreland. The olenids in Europe thus occur in different belts in relation to continent and geosynclines than in North America. Both in Europe and North America the olenids often occur in sequences with dark sediments, suggesting stagnant conditions. It is probable that the olenid faunas were facies controlled, at least to some degree. This has been suggested for early Paleozoic faunal provinces in general by Wilson (1954, p. 265).

This need not imply that there were no land barriers between the North American and the Acado-Baltic provinces. Quite possibly such barriers existed. Thus Hutchinson (1952, p. 60) favours the theory that the Atlantic

(i. e. Acado-Baltic) and Pacific faunal realms were separated regionally during Cambrian times by a land barrier, which prevented mingling of the marine faunas of the two separate realms. However, the land barriers in that case probably were island arcs, since there was some seaward connection between the two provinces (cf. above).

The Tremadoc Sea

There appears to have been a rather general retreat of the sea in the Acado-Baltic province near the boundary between the Late Cambrian and Tremadocian epochs, just as there had been several, at least local, regressions (followed by transgressions) in the Late Cambrian epoch. The Tremadoc Sea, which succeeded the Olenid Sea, is again transgressive, and even covered areas apparently never covered by the Olenid Sea.

The sediments deposited in the early Tremadoc Sea were to a great extent deposited under stagnant conditions, as in the Olenid Sea. However, in Late Tremadocian times the conditions were much more variegated, as is shown by the sediments which also include limestones deposited under ventilated conditions.

As in the Late Cambrian epoch the Acado-Baltic province reached the Caledonian geosyncline complex to the north and north-west. North of it there was another marine fauna, forming the Arctic subprovince of the North American province. In northern Europe the shoreline of the Tremadoc Sea was at times somewhat further east than that of the Olenid Sea. Further south in Europe the Acado-Baltic province apparently graded into another province, in a sea covering parts of central Europe. This sea probably had connection with the Uralian geosyncline, which again was connected with more eastern seas (cf. H. & G. Termier, 1952, Carte V). The Tremadoc Sea even covered parts of South America (the Andine Sea), possibly in a geosyncline forming an extension of a geosynclinal belt trending along the Appalachian and Ouachita orogenic belts to Colombia through the course of the present Antilles (Harrington & Kay, 1951, p. 657). In eastern North America the Acado-Baltic province was in contact with the North American province to the west.

Because of the expansion of the Tremadoc Sea, the olenids became more widely spread in Tremadocian than in Late Cambrian times. At the same time the olenids also spread to areas outside the Acado-Baltic province. On the other hand, the Acado-Baltic province was invaded by a number of other trilobite families and other invertebrates. According to Shaw (1951, p. 101) the mixture of forms from the east and west in the uppermost Gorge formation¹ of Vermont strongly suggests that the barrier that arose in early Cambrian time and separated the Appalachian and Caledonian geosynclines during most of the Early and Middle Cambrian, had broken down when these

¹ Actually Highgate formation (Tremadocian). cf. Shaw, 1955, p. 187.

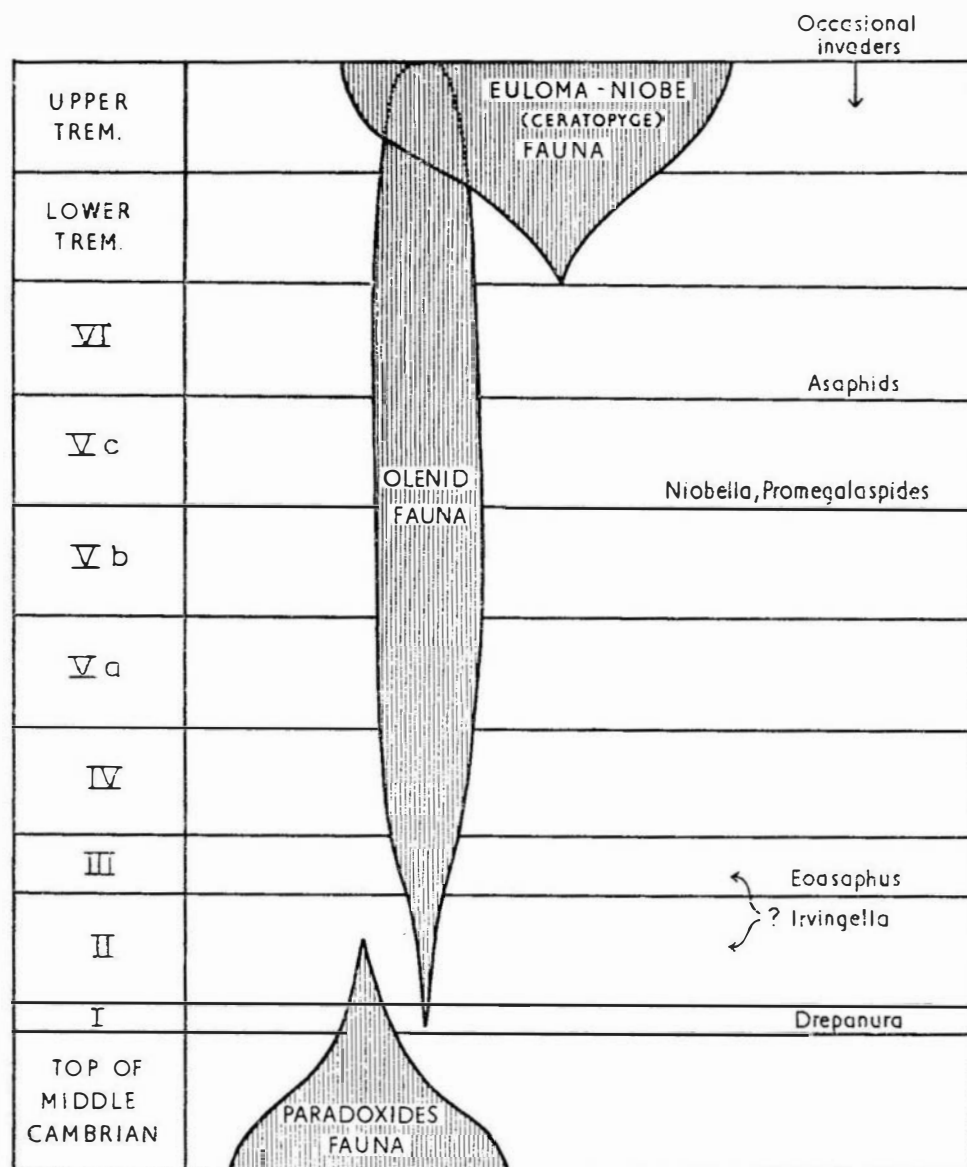


Fig. 8. Upper Cambrian and Tremadocian faunas in Scandinavia.

beds were deposited. The expansion of the Tremadoc Sea apparently led to a better seaward connection between the Acado-Baltic and other provinces. Furthermore, the hydrographical conditions in the Tremadoc Sea altered, perhaps by the appearance of new currents. More and more ventilated sediments were deposited in the Acado-Baltic province, including limestones. The increasingly ventilated conditions in the Acado-Baltic province was followed by the close of the dominance of olenids. Already at the end of the Tremadocian epoch the olenids constitute only a minority of the trilobite fauna, seemingly clinging to such areas where stagnant conditions still prevailed.

The Acado-Baltic faunal province is not so well defined in the Tremadocian as in the Late Cambrian epoch, and it shares a number of invertebrate families and even genera and species with other provinces. In the early Tremadocian Sea (the "Dictyonema Sea") the graptolite *Dictyonema flabelliforme* was very common. However, *Dictyonema* also occurred in far away areas which do not belong to the Acado-Baltic province, as in Korea, Australia, and in the Cordilleran geosyncline in North America. The so-called *Euloma-Niobe* (or *Ceratopyge*) fauna is rather characteristic of the Acado-Baltic province, especially in Late Tremadocian times (cf. text-fig. 8).

One may distinguish between two elements in the Tremadocian faunas in the Acado-Baltic province, that is the olenid element and an element of invading forms including a number of trilobite families (e.g. Asaphidae, Raphiophoridae, Ceratopygidae, Harpididae, Trinucleidae, Cheiruridae, Pliomeridae) which are not, or only sporadically, represented in Upper Cambrian beds of the Acado-Baltic province. The graptolites are new to the Acado-Baltic province, as are also many other invertebrate groups, such as cephalopods, ostracods, and phyllocarids. Groups which rarely were represented in the Upper Cambrian (e.g. brachiopods, gastropods) are common in the Acado-Baltic province, but from where did all the new forms come?

A few strange elements known in the Upper Cambrian of the Acado-Baltic province, such as *Irvingella* and Dikellocephalidae, are characteristic in contemporaneous deposits in the North American province. It thus seems probable that they invaded the Acado-Baltic province from the west. Graptolites are apparently known from earlier beds in the North American than in the Acado-Baltic province, and may likewise have entered the Acado-Baltic province from the west, after having adopted a pelagic habitat, enabling them to spread more easily. The Richardsonellidae (Kainellidae), Asaphidae, Dikellocephalidae, Cheiruridae, and Pliomeridae were represented by many genera in the North American province in Late Cambrian and/or Early Ordovician times, and it seems probable that these families, too, invaded the Acado-Baltic province from the west. The Ceratopygidae are represented in the Acado-Baltic province in late Middle Cambrian and early Late Cambrian times (*Olenus* age). After that, they are not known to have occurred in the Acado-Baltic province until Tremadocian times. True Ceratopygidae are apparently not known from the North American province. They are known in Central Asia (eastern T'ien Shan, cf. Troedsson, 1937) in beds which may be of Upper Cambrian or Tremadocian age, and are accompanied by an obvious olenid, *Westergårdites pelturaeformis*, as well as by asaphids. The olenid shows that there were faunal connections between this area and the Acado-Baltic province, and it is possible that while olenids entered the area from the west, Ceratopygidae may have migrated eastwards. However, as the beds in eastern T'ien Shan may be contemporaneous with the Tremadocian beds in the Acado-Baltic province (cf. p. 154), it is possible that the Ceratopygidae, too, invaded the area from the west.

It appears that at least the greater part of the new faunal element in the Tremadocian epoch in the Acado-Baltic province invaded it from the west, i.e. from the North American province. This is very probable also because we know that a mingling of North American and Acado-Baltic faunas actually took place in early Ordovician times in North America (cf. Shaw, 1951, p. 101). Kobayashi has already in various papers (e.g. 1944a) claimed that North American faunas invaded the Acado-Baltic (Atlantic) province, and that the Acado-Baltic faunas invaded Asia, i. e. that there were marked migrations towards the east in those times, and that this in part may have been controlled by the direction of the currents.

As discussed above, one may distinguish between an "old" (olenid) and a "new" faunal element in the Tremadocian of the Acado-Baltic province. However, one may also divide the Tremadocian fauna in two according to whether the forms occur mainly in sediments deposited under stagnant or ventilated conditions. As might be expected, the olenids are most common in dark bituminous shales and limestones, whereas the "new" fauna dominates in the sediments apparently deposited under ventilated conditions. There is at least one important exception, that is the graptolites which are very common in black shales. This is not surprising, as the graptolites probably were pelagic and thus not dependent on the type of sea floor or the water below them. However, they probably could not live in stagnant waters, and the many immature specimens found in the black shales indicate that they often met a disastrous death, either because they had sunk too deep, or in other ways had drifted into the "poisonous" water. Graptolites may naturally also be found in sediments deposited under ventilated conditions, but they are not so characteristic in these, partly because these beds contain so many other fossils, but probably also because the fragile graptolites were more exposed to destruction on sea floors with ventilated conditions than in the quiet waters of stagnant areas where there furthermore may have been fewer scavengers and other animals which could destroy them. Inarticulate brachiopods and phyllocarids frequently are found in black shales, and may have been more or less pelagic, too. The richardsonellids (e.g. *Apatokephalus*) which apparently had as thin tests as the olenids are also regularly met with in dark shales, and may likewise have been more or less pelagic.

One may distinguish between three ecologic groups of animals in the Tremadocian of the Acado-Baltic province: 1) animals more or less independent of the conditions of the sea floor and the bottom waters, such as more or less pelagic animals (e.g. graptolites), 2) animals which required ventilated waters and sea floor, as most of the new trilobites, gastropods, and brachiopods, and 3) animals which at least could stand stagnant conditions for a restricted period (e.g. olenids, cf. p. 80).

In accordance with the various ecologic habitats, the new fauna invaded the different areas of the Acado-Baltic province at different times. Thus

most of the new trilobite groups did not invade the Scandinavian area until Late Tremadocian times, since stagnant conditions prevailed in Early Tremadocian times, whereas they are known in the more ventilated sediments deposited in Early Tremadocian times in England. The graptolites, however, entered Scandinavia while dark sediments were still being deposited.

The apparent local variations of the olenid faunas in Tremadocian times may perhaps have been caused by the olenids being restricted to the at least at times more or less isolated areas with stagnant sea floor.

Mode of life of the olenids

The mode of life of the olenids has to be deduced from the morphology of their test (usually the hard shields only), the sediments in which they occur, and from eventual tracks and other evidence of the processes of life. Just as with other trilobites, their source of food is uncertain (see also Richter, 1920a).

Ecdysis

Ecdysis in trilobites in general.

Trilobites, like other arthropods, moulted during growth. Whether trilobite exuviae could become fossilized was discussed by Richter (1937, p. 422), as some earlier writers had denied it. He concluded that it seemed even more likely that the cast shield became fossilized than the shield of a dead trilobite. This is supported by an experiment carried out and described by Størmer (1934b, p. 57). He "once kept in a large aquarium, several specimens of *Limulus* together with a number of shrimps and crabs and various other common marine animals. The *Limulus* specimens died and the bodies were immediately attacked by the crustaceans. The ventral, softer parts were removed and the more solid dorsal test was partly torn to pieces along the margin. The shed *Limulus*-skins in the same aquarium were left untouched." It thus seems that a discarded shield has more chances of being preserved than the shield of a dead animal, which usually would be attacked by scavengers. The trilobites moulted frequently, and consequently more exuviae were embedded than shields of dead animals. No doubt the majority of trilobite remains are cast exuviae. It is usually only the harder parts (as dorsal shield and hypostoma) which are preserved.

During the ecdysis the trilobite had to creep out of its old exoskeleton, which formed a continuous cover. In trilobites with a more or less marginal suture, the animal apparently crept out through the opened suture (e. g. Olenellidae, cf. Swinnerton, 1919 and *Harpes*, cf. Richter, 1920b), as does the recent *Limulus* (see illustration of moulting specimen in Størmer, 1934b, fig. 25 on p. 57). The ecdysis in some Phacopidae with small eyes and fused

facial sutures has been worked out by Richter (1937). Their cephalon is sometimes found displaced in front of the shield, where it lies up-side-down and facing backwards. According to Richter, this "Salter'sche Einbettung" shows that the trilobite during ecdysis lifted up the whole cephalon and tipped it forwards, creeping out through the opening thus formed. The hypostoma may be found more or less in situ in front of the postcephalic shield, indicating that the ventral parts of the exoskeleton were not displaced.

Less is known about the ecdysis in trilobites with functional facial sutures (as Olenidae). It is generally assumed that the cephalic sutures facilitated ecdysis, although doubts have been put forward as to whether they existed only for this purpose (cf. Stubblefield, 1936, p. 410). No doubt the facial sutures facilitated the liberation of the eyes (cf. Richter, 1937, p. 418). The gap produced by the opened facial sutures would probably in many cases enable the trilobite to creep out of its old exoskeleton, thus also being wide enough for the body to be dragged out of the postcephalic exoskeleton. It is quite possible that this is the reason why the facial sutures cut the posterior margin of the cephalon so far out in so many trilobites, as hinted by Henriksen (1926, p. 24).

*A find of shields of *Acerocare ecorne* in moulting position.*

At least 250 more or less "entire" shields of *Acerocare ecorne* were found on a bedding surface in a concretion of bituminous limestone in the alum shales at Nærsnes, Røyken in Norway (pl. 31).

The shields may represent: 1) either dead animals which died on this surface, or 2) had been deposited there, or 3) they may represent moults (exuviae) which were shed on the spot, or 4) had been transported there from somewhere else. There are certain indications that they represent moults which were shed at the place of entombment. It would be of considerable interest if this could be proved to be the case, and for this reason I shall describe the find in more detail.

The shields are all of young holaspids, from 4 to 8 mm long. In places they almost cover the bedding surface, partly overlapping each other. Some lie with the dorsal side up, others with the ventral side up. The original orientation of the bedding surface is not known with certainty, but if the assumed orientation is correct, the shields with the dorsal side up slightly outnumber the others. The shields are oriented in all directions in the plane of the bedding surface. They do not seem to have been flattened, at least not to any extent of importance. None of the shields are preserved intact, inasmuch as some parts of the shield (at least the free cheeks) are more or less displaced in relation to the rest of the shield.

The specimens may be grouped according to the arrangement of the different parts of the shield.

In many specimens the axial shield (cranidium + thoracic shield + pygidium) is entire, whereas the free cheeks are slightly to considerably displaced (pl. 31; pl. 30, fig. 6). In many other specimens the axial shield may be broken along one or more joints, thus also between the cranidium and the thoracic shield or between the thoracic shield and the pygidium, but the different parts of the axial shield are often only slightly displaced.

A rather characteristic preservation of this find is shown by the many specimens where the cranidium is missing, while the free cheeks lie only slightly displaced in front of the postcephalic shield (pl. 31; pl. 30, fig. 5). I have in vain tried to excavate a cranidium in the counterpiece of three such specimens. Apparently it was well removed from the rest of the shield. In a few cases, an isolated cranidium lies next to one of these specimens, but it is hardly possible to tell whether it belonged to the same individual. Other specimens agree with these, except for the free cheeks being considerably displaced. The postcephalic shield may be broken along one or more joints, but the parts are often only slightly displaced.

In a few cases, the free cheeks, cranidium, parts of the thoracic shield, and pygidium of apparently one individual lie more or less irregularly associated. Isolated parts of the dorsal shield also occur.

It is a striking feature that the two free cheeks often lie symmetrically to each other even when considerably displaced from the rest of the shield. Very often the hypostoma lies only slightly displaced between the free cheeks. The free cheeks of *Acerocare* may have been united in front as in at least some olenids (cf. p. 91), but the narrow connection may easily have broken. Its hypostoma was not fused with the free cheeks. It appears as if the free cheeks and hypostoma had been connected by some softer substance, probably the ventral membrane.

If the specimens of this find are interpreted as representing dead animals, one might suggest that the different parts of the shield, after the softer parts of the animal had decayed, could have been disordered by movements of the water, by animals, or by gas bubbles. However, it is difficult to explain why only the cranidium was removed in so many specimens, and not for instance the free cheeks. As to movement of the water, there are no other indications of this; on the contrary, the rather haphazard orientation of the shields suggests quiet waters.

The find may be discussed on the presumption that it represents moults shed in situ, and that the facial sutures opened during ecdysis. The cranidium would then be connected with the rest of the exoskeleton only by the joint between it and the thoracic shield. The free cheeks would be connected with the rest of the shield solely by the ventral membrane (thus not with the cranidium).

No doubt the opening formed would be large enough for the animal to creep out through it, especially if the cranidium was bent up with the joint as hinge-line. One can imagine how easily the joint between the cranidium

and the thoracic shield could be broken during the animal's struggle to get loose from its old exoskeleton, thus explaining why the cranidium is missing in many specimens. It may have been flung away by the movements of the animal, or it may have been carried off by the trilobite crawling away from its old exoskeleton. A similar assumed moulting position has been recognized in a specimen of *Telephus* (cf. Glaessner, 1948, p. 531).

The occurrence of the hypostoma close to the free cheeks, even when they are found at some distance from the thoracic shield, was suggested above to be due to them being kept together by the ventral membrane. The membrane apparently split easily between the cephalon and thorax, since the free cheeks often are displaced in relation to the thoracic shield. It seems likely that this could happen when the animal struggled to get free, whether there was a kind of "suture" across the ventral membrane or not. The unit thus split off would consist of the free cheeks, the cephalic ventral membrane, and the hypostoma. It is possible that this unit, which may be called the acranidial cephalic unit, normally was split off. It would easily be further displaced by the animal crawling out of the rest of the exoskeleton, which was dragged along for some distance. This could explain the frequent occurrence of the acranidial cephalic unit (now found only as the free cheeks and hypostoma) below the thoracic shield. The cranidium could probably easily get entangled in the isolated acranidial cephalic unit. This would explain the cases where one of the free cheeks partly lies below the cranidium, while the other partly covers the postocular cheek or where both free cheeks mainly lie above the cranidium. Even so, the free cheeks appear to have been united by the ventral membrane, forming a pocket, into which the cranidium got stuck. In accordance with this, the anterior parts of the free cheeks lie just anterior to the anterior margin of the cranidium, when both free cheeks lie above the cranidium. In these cases the animal had to creep out ventral to the acranidial cephalic unit. In several specimens one or more joints in the thoracic shield have been broken. This could very well have happened when the animal wriggled itself out. The associations of different parts of the shield, considerably damaged, but apparently belonging to one individual, may indicate that the ecdysis had gone less smoothly than usual. There is, of course, also the possibility of it representing an exuvia which had been disordered by an animal crawling over it.

About half the specimens are lying up-side-down. This could have been explained, even if the animals had died in situ, if we, like Pompeckj (1892, p. 93) and Richter (1920a, p. 34), assume that all trilobites could roll up, but that most Cambrian trilobites (including the Olenidae) had no special device preventing the shields from straightening out again after death. Assuming that the specimens in question had rolled up when they died and straightened out again afterwards, it could easily happen that some shields would then settle with the ventral side down, others with the dorsal side down (cf. Richter, 1937, p. 421). However, it also seems likely that exuviae

might be lying up-side-down because of the animal's struggle during the ecdysis.

If the specimens represent exuviae, they no doubt were shed where they were embedded, since it is quite improbable that all parts of a shield of a single individual could have been deposited so near to each other in so many cases if they had been shed somewhere else.

It seems as if the different arrangements of the shield parts in this find may all be explained as representing exuviae shed where they were embedded, and that some of them hardly can be explained in any other way.

Mode of locomotion

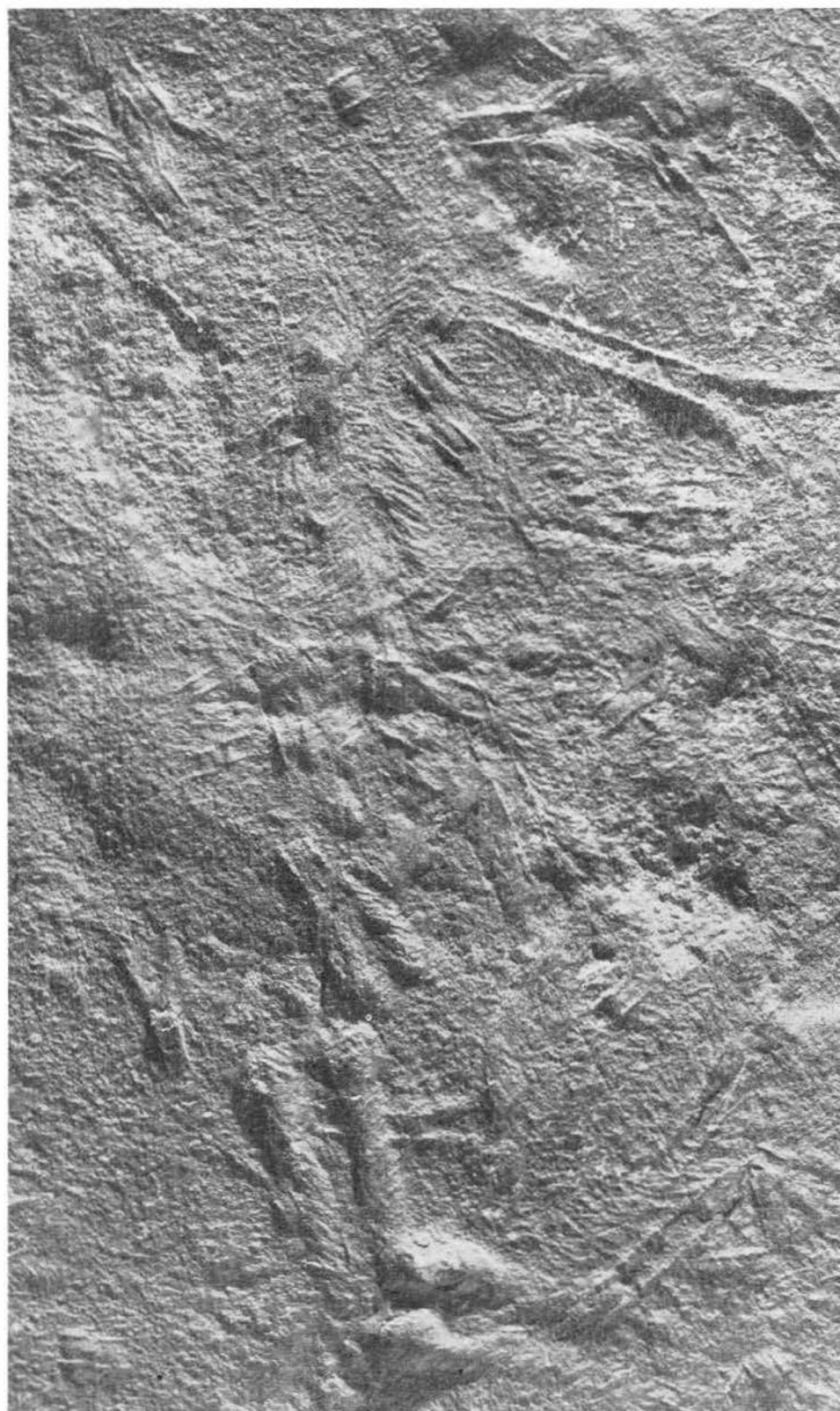
Tracks of olenids?

Text-fig. 9.

To my knowledge only one find of tracks attributed to olenids has been described, that is by Holm in 1887. The find consists of slabs of calcaceous sandstone with tracks on one surface, from Östergötland in Sweden. The thin sandstone beds occur near the border between beds with *Peltura scarabaeoides* and beds with *Dictyonema flabelliforme*, the intervening zones apparently being missing. Holm suggested that the tracks might have been made by *Peltura scarabaeoides*, but Westergård (1922, pp. 43, 44) included these sandstone beds in the Dictyonema Shales, as *Dictyonema flabelliforme* was found below some of them. As pointed out by Westergård, the tracks could then not have been made by *Peltura scarabaeoides*. However, even if the tracks are from the Dictyonema Shales, it is possible that they were made by olenids, since they are the most abundant trilobites in these beds.

The tracks partly show impressions of appendages, and partly two parallel furrows probably made by some spine-like, hard processes. According to Holm, the parallel furrows might have been made by the posterior pair of marginal spines in the pygidium of *Peltura scarabaeoides*. No furrows had in that case been left by the other spines of the pygidium of this species, but Holm suggested that this might be due to them lying further forwards, and thus not necessarily touching the bottom surface when the posterior pair did so. No trilobites have been found in the *Dictyonema* beds in Östergötland, but several olenids are known from these beds e. g. in Norway. If the two parallel furrows were made by pygidial spines, *Boeckaspis hirsuta* or *B. mobergi* could very well have produced such tracks. These species furthermore only have one pair of pygidial spines, and it is thus even easier to believe that they could have produced the tracks than *Peltura scarabaeoides*. The parallel furrows are almost 5 mm apart in the tracks made by the larger

Fig. 9. Olenid tracks? Detail of the slab figured by Holm in 1887. About $\times 1.2$. Surface whitened; photograph not retouched.



animals. In the few collected pygidia of *Boeckaspis mobergi* and *B. hirsuta* the spines are no more than 2 mm apart. However, some large cranidia of *B. hirsuta* suggest that the corresponding pygidia had the spines at least 4 mm apart. The only non-olenid trilobite known from the Dictyonema Shales in Scandinavia, the ceratopygid *Hysterolenus törnquisti*, also has one pair of pygidial spines. It is a large species with the spines up to more than 30 mm apart. If the tracks were made by this species, it must have been by larval forms. As it is a rare species, there is a greater chance of the tracks having been made by olenids.

As cautioned by Holm, the tracks might possibly have been made by some unknown animal, not necessarily a trilobite. As the parallel furrows apparently were made by some stiff projections, the animal probably had a shield or at least spines, and as trilobites furthermore occurred in great numbers at that time, it is rather probable that the tracks were made by trilobites.

The slab surfaces only show the casts of tracks. The tracks themselves were apparently left in the black mud, and were preserved by the (probably rapid) sedimentation of calcareous sand on top of them. They are all rather short, and Holm is no doubt right in assuming that they were made by animals which swam above the bottom and occasionally darted down to it and up again.

Locomotion in trilobites in general.

The habits of locomotion of the trilobites have been thoroughly discussed by Richter (1919, 1920a, 1926), who concluded that the trilobites were adapted to benthonic life. They could crawl (walk) on the bottom of the sea, occasionally also out of the water on tidal plains, but they could also swim. They could roll up, which they probably did when they were frightened. If this happened while they were above the bottom, they would probably sink more swiftly in this position than they could swim down. It is also possible that they rolled up between tides, if they were trapped on the tidal plains.

When crawling, they no doubt used their walking legs. As discussed by Richter (1920a), it is rather unlikely that forms with terminal spines used the spines for locomotion (pushing), or that forms with genal spines used the spines as a sort of sledge, as suggested by Staff & Reck (1911).

Earlier it was often believed that forms like *Harpes* and *Trinucleus* were adapted to burrowing. Richter (1920a) showed that these forms would be among the least suited for a burrowing mode of life. Neither could the forms with a rather flat dorsal shield be adapted to burrowing. The only forms which might be able to burrow, were the trilobites with a rather smooth (spineless) shield and a rather narrow and vaulted dorsal shield (like *Peltura*). There is, however, no evidence of them burrowing, and the shape of the body also indicates that they were good swimmers. Richter

(1920a, p. 29) concluded that in case the trilobites did burrow, it would not be in the same way as a mole, but a scooping through the surface of the bottom.

That the trilobites really did swim, is indirectly indicated by the many ways in which they counter-balanced the heavy head-shield in forms with large head-shield, e. g. by developing a large pygidium or long genal spines, which will move their point of balance further back and prevent them from tipping over. This would hardly have been so common if the animals only crawled on the bottom. Some forms apparently developed a floating apparatus. If the tracks discussed above are correctly interpreted as having been made by trilobites, they, too, show that the trilobites could swim.

As to how the trilobite swam, the use of the pygidium as a swimming organ was suggested by Spencer (1903), Dollo (1910), and Staff & Reck (1911). The pygidium was believed to have been used either as the tail of a whale, or as the tail of a lobster. In the latter case a sudden flap of the pygidium should result in a backward darting motion. Richter (1919) has shown that both the methods would hardly be possible, at least this would be very unlikely, and that it is most reasonable to assume that they swam forwards with their legs. Another question is whether they swam with the dorsal or the ventral side up. Like many recent crustaceans there is a possibility of them doing both, but some may have preferred the dorsal side up, others the ventral side. *Aeglina*, with eyes curving round on the ventral side, was suggested by Dollo (1910) to have swum with the ventral side up, just below the surface of the water (cf. Richter, 1920a, p. 41). It is also possible that some trilobites could more or less have floated on the surface with the ventral side up, using the shield as a kind of boat, as the recent *Limulus* may do (see photographs in "Life", European edition, 1953, January 11, p. 29). Størmer (1930, p. 107) suggested that *Reedolithus* swam with the ventral side up and that its carinate glabella served as a keel. Richter (1919, p. 224) believed that trilobites with spines oriented upwards-backwards only swam with their ventral side down.

As a whole, the trilobites seem to be well adapted to benthonic life, but they could probably all swim. According to Richter (1919, p. 226) there is no reason to believe that any of them had lost their ability to swim, and neither is there any indication that they could not all crawl on the sea floor (cf. Richter, 1926, pp. 305—307). Thus the trilobites do not have a cylindrical body as do animals which practically exclusively move by swimming (e. g. fishes).

The swimming ability may, however, have varied. The size of the pygidium gives no clue as to whether a trilobite was a good swimmer or not (Richter, 1919, p. 227), and neither does the position of the eyes alone, although a marginal position of the eyes suggests that it could have been a good swimmer. There is no reason to believe that trilobites with more centrally placed eyes could not swim (Richter, 1919, p. 227).

Some trilobites had rather smooth, narrow, and vaulted dorsal shields. As discussed by Richter (1919, p. 229) this type (the so-called *Phacops-Calymene* type) had more room for muscles, thus probably having stronger muscles, and being more rapid and vigorous in their movements, no doubt when swimming, but no less when crawling. The absence of a floating and steering apparatus (spines) further suggests that they could swiftly change their direction of movement.

Other trilobites are flatter and usually wider. They are well fitted for benthonic life, but may have been able to swim with less effort than the *Phacops-Calymene* type, since the shape of the body hindered sinking. On the other hand, they could hardly swim so fast. This morphological type may be called the *Olenus* type.

A third type of trilobites, which may be regarded as a variety of the *Olenus* type, has long, horizontal spines, thus hindering sinking even better than the *Olenus* type. They have long been regarded as adapted to floating, whereas crawling (benthonic life) would have been rather awkward to at least some of them. To keep floating, they had to swim, but they could do so with a minimum of effort. Their spines prevented them from being rapid swimmers. This type, which may be called the *Acidaspis* type (Staff & Reck, 1911: "Acidaspis-Deiphon Types"), may have been planktonic.

Locomotion in olenids as deduced from their types of shield.

Returning to the olenids, we may likewise distinguish between three types of dorsal shields.

The *Peltura* type corresponds to the *Phacops-Calymene* type in trilobites in general. *Triarthrus*, *Sphaerophthalmus*, *Peltura*, and most *Protopeltura* species belong here. The extremes of this type, *Peltura* and *Triarthrus*, usually have no long spines. As mentioned above, trilobites with this type of dorsal shield were probably vigorous animals, and may have been good swimmers. The eyes of *Peltura* are situated fairly near the anterior margin. In *Triarthrus* they are further back, but near the lateral margin of the head, since the narrow free cheeks slope downwards rather steeply. The marginal position of the eyes in this type may also indicate that these forms were good swimmers.

The *Olenus* type is represented by *Olenus* itself, and many other olenids, e. g. *Parabolina*, *Parabolinella*, *Eurycare*, *Accerocare*, many *Leptoplastus*, and some *Ctenopyge* species. Many of the most typical forms have rather many thoracic segments. The olenids with an *Olenus* type of dorsal shield could probably swim well, although presumably not so fast or vigorously as those of the *Peltura* type.

The *Ctenopyge* type corresponds to the *Acidaspis* type. To this type belong many *Ctenopyge* species, especially of the subgenus *Ctenopyge* (as *Ct. pecten*, cf. pl. 5), *Leptoplastus abnormis*, *Boeckaspis* and *Jujuyaspis*.

The flattened horizontal spines can hardly be interpreted as anything else than floating equipment acting as a frictional hindrance to sinking.

Many species belong to types intermediate between the *Peltura* and *Olenus* type, or between the *Olenus* and *Ctenopyge* type, but none seem to be intermediate between the *Peltura* and *Ctenopyge* type. Accordingly, *Boeckaspis* and *Jujuyaspis* apparently did not develop directly from *Peltura*, but through forms more or less of the *Olenus* type like *Westergrardia* and *Acero-carina*. This, too, indicates that the way of living of the *Ctenopyge* type was closer to that of the *Olenus* type than to that of the *Peltura* type.

Apparently the *Ctenopyge* type was more or less pelagic. This does not exclude the possibility of members of this type also having crawled on the bottom at times. The *Olenus* and *Peltura* types may have been more active swimmers, the *Peltura* type being the more vigorous and faster.

The position of the eyes, both the distance from the glabella and the distance from the anterior margin, differs more within the Olenidae than within any other trilobite family. The significance of this is difficult to explain. The position of the eyes tends to be rather marginal within the *Peltura* type, which may have a connection with better swimming possibilities. Within the *Olenus* type and *Ctenopyge* type both forms with more or less marginal eyes and more centrally placed eyes (with regard to the lateral margin) occur. The species with the relatively widest pleural regions usually have the eyes furthest away from the margins.

Larval olenids seem in general to be well equipped with spines, thus also larval stages of species with adults with the *Peltura* type of shield, perhaps indicating that the larvae led a more planktonic life.

The olenids had thin tests, which would be an advantage to swimmers and almost a necessity to planktonic forms.

Ecology

To obtain an impression of the mode of life of the olenids, one must take their environment into consideration. As discussed above, the olenids are found as fossils mainly in two types of sediments, one type being represented by pelitic and psammitic sediments which were deposited comparatively fast under ventilated conditions not far from the shore, the other type being alum shales with stinkstone beds and lenses, apparently deposited relatively slowly in quiet waters and under stagnant conditions, and, at least in some areas, on a rather shallow sea floor.

There is no reason to doubt that the olenids lived in the environment where the first type of sediments were deposited. However, the olenids are perhaps more often found in sediments of the black shale facies. Black muds were deposited over vast areas in the seas in which the olenids lived. The bottom waters were probably depleted of oxygen and contained hydrogen

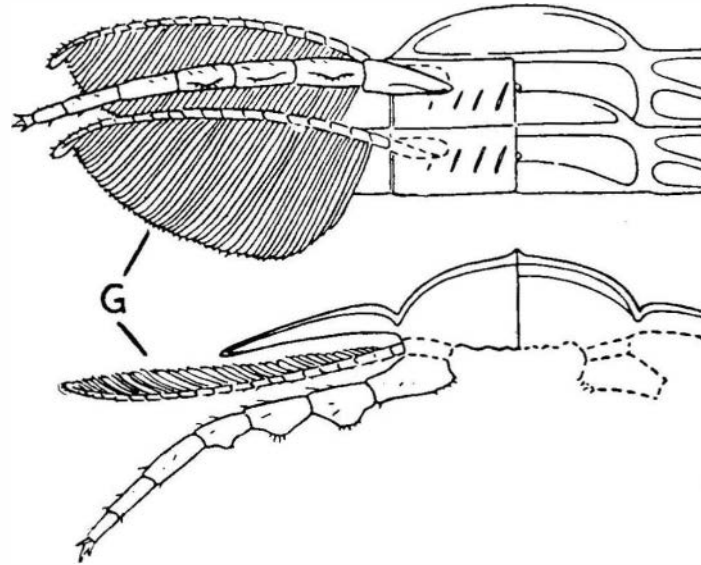


Fig. 10. Reconstruction of the appendages in thoracic segments of *Triarthrus eatoni* (Hall). Above: ventral view; below: anterior view. G = gill-branches.
After Størmer, 1939, text-fig. 23 (p. 208).

sulphide. The surface waters were of course ventilated, because of the contact with the air. It is difficult to tell at which depth the foul waters began; it may have been as little as 50 metres below the surface in deeper parts of the sea, and close to the surface in shallow areas (cf. p. 62).

If the olenids lived in the areas where black muds were deposited on the sea floor, they may have lived in the ventilated surface waters or in the stagnant deeper waters, on or above the foul bottom. Quite possibly they shifted from one biotope to the other.

The possible olenid tracks and especially the specimens of *Accerocare* which appear to be moults shed on the bottom, suggest that the olenids actually could sojourn in the foul bottom waters. Since there probably was no oxygen in this part, or at least very little, they could not have lived there constantly. Observations on invertebrates in waters with low or no oxygen content show that the ability to live in such waters for a restricted period of time is very different for the various groups and species (von Brandt, 1946). Among the crustaceans the copepods seem to stand a reduced oxygen content very well, whereas this is not true of the decapods. During the winter, the copepod *Calanus finmarchicus* is more abundant in the nutritious but stagnant bottom waters of the Oslofjord with only 0.2 to 0.0 ml oxygen per litre, than in the oxygen-rich waters above (Beyer & Føyn, 1951, p. 300).

Possibly the olenids, like *Calanus finmarchicus*, could stand a low oxygen content for a restricted time, and perhaps better than trilobites in general. According to Størmer (1939, p. 220), the gill branch of the trilobite limb

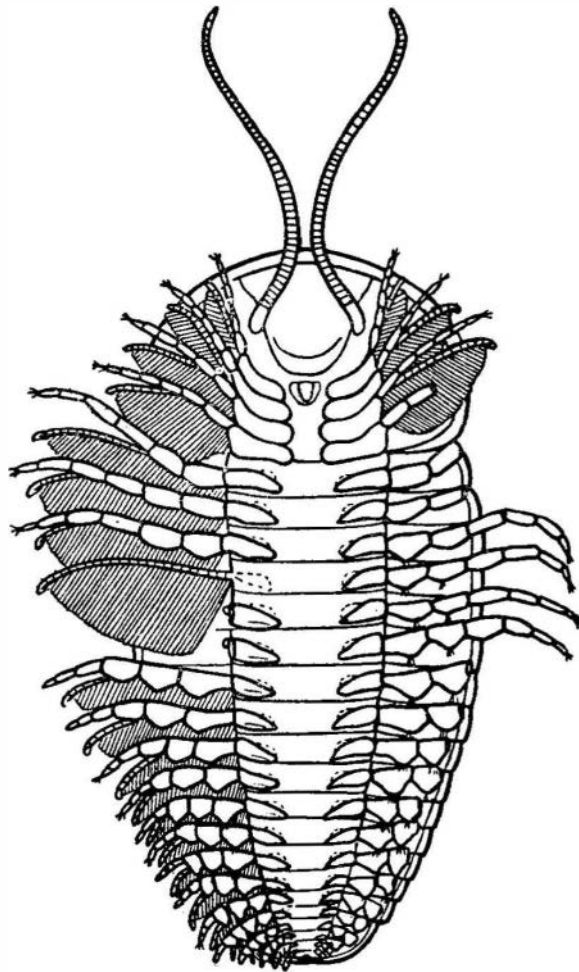


Fig. 11. Ventral view of *Triarthrus catoni* (Hall). Parts of the appendages omitted.
After Størmer, 1944, text-fig. 5:24 (p. 28).

is usually considerably shorter than the walking leg, in the few species where the limb is known, and restricted to the space below the pleuron. *Triarthrus* (the only olenid whose limbs are known) forms an exception in having long gill-appendages extending beyond the lateral borders of the thorax, and being almost as long as the walking legs (text-figs. 10, 11). It is possible that the large gills would enable *Triarthrus* to live in waters with a smaller content of oxygen than usual. It is well known that many planktonic animals migrate towards the surface in the evenings. The olenids may similarly have migrated between the foul bottom, rich in nutrients, and the upper ventilated waters. It would no doubt have been a great advantage to the olenids to have access to the rich food supply at the bottom, and it is perhaps not too daring to imagine that this was the case, especially for the more benthonic types.

It is difficult to judge whether the olenids preferred to have access to stagnant waters, or whether competition and persecution of other animals,

less tolerant to stagnant waters, forced them to take refuge in such areas.

The olenids are often found in enormous numbers in certain beds of the alum shales, while few or no fossils are found in the intervening beds. It is possible that the conditions at times were unfavourable for the olenids; the waters may for instance have been too poisonous. It appears as if the olenids in many areas lived near the border of what was possible for higher invertebrate animals. The very large numbers of specimens but small number of species which characterize the olenid faunas, are typical features for faunas in environments generally unfavourable for animal life.

It is correct to mention the possibility of the olenids not having lived in the areas where black muds were deposited, but that they could have drifted into them, as the graptolites. Some of the olenids may have been planktonic, like the graptolites, but most olenids seem to have been better adapted to a benthonic free-swimming life. This, the very long distances they should have drifted, and the indications of the olenids being capable of sojourning on the foul bottom, are reasons why I believe it probable that they lived in these areas.

The dominance of the Olenidae in the Upper Cambrian Olenid Sea may be due to their adaptation to stagnant waters. In this connection it is interesting that Tremadocian and later olenids often are found in dark shales and limestones.

Phylogeny and evolution of the olenids

Brief account of the phylogeny

As the relationships of the genera and species are discussed under each genus only a brief account of the phylogeny is given here (see also chart 6).

The main phylogenetic lineages of the olenids are on the whole rather easily detected. This is especially true of the Upper Cambrian olenids in Scandinavia (pls. 3—8), which occur in great numbers in a succession where a detailed biostratigraphic division has been possible, and which were developed under rather similar conditions during the whole of the epoch.

The earliest known olenid is *Olenus alpha* n. sp. from the zone of *Agnostus pisiformis* (I) at the base of the Upper Cambrian. The olenids are represented solely by *Olenus* species in the following zone of *Olenus* (II), too. The typical *Olenus* has a well-developed preglabellar field, medium-sized eyes set well off from the glabella, sinuous postocular facial sutures, and free cheeks with genal spine. Some of the latest *Olenus* species, like *O. scanicus*, have smaller eyes and straighter postocular sutures, thus trending toward the earliest *Parabolina* and *Protopeltura* species (*Parabolina brevispina* and *Protopeltura aciculata*), appearing in the *Parabolina* zone (III). Both these species have small eyes rather close to the glabella, hardly

any preglabellar field, and convex postocular sutures (*Peltura* type of cranium). They seem to have had a common origin and no doubt descended from *Olenus* of the *scanicus* type. *Parabolina* ranges through the whole of the Upper Cambrian into the Tremadocian. The genus apparently gave rise to *Parabolinites* n. gen. *Bienwillia* (Trem.) developed either from *Parabolinites* or perhaps rather directly from *Parabolina* through forms like *Bienwillia? zwimani*. *Triarthrus* (Trem.-Middle Ordov.) undoubtedly developed from *Bienwillia*, and *Parabolinella* (Trem.) is also very close to *Bienwillia*. The relationships of *Leobienwillia* (Trem.), *Angelina* (Trem.), *Plicatolina* (Trem.), and *Westergårdites* (Trem.?) are less certain, but they apparently all belong to the late Oleninae.

Returning to *Protopeltura*, this genus lasted on into the zone of *Peltura minor* (Vb), where it lost its genal spines and developed into *Peltura*, which ranges into the *Acerocare* zone (VI). The rigid plan of construction was broken in several off-shoots. Though they all bear the pelturine stamp in the pelturoid free cheeks, in the convex postocular sutures, as well as in other details, they deviate considerably from *Peltura*. Thus the position of the eyes may vary quite a lot, and also the width of the fixed cheeks. These "advanced" pelturines are placed in a number of genera. *Nericiaspis* (Vc), *Acerocarina* (VI), and *Pelturina* n. gen. (VI) seem to have developed directly from *Peltura*, as may also be the case with *Acerocare* (VI), if it did not develop through *Acerocarina*. *Saltaspis* (Trem.) apparently developed from *Acerocare*, and *Peltocare* n. gen. (Trem.) may also be related to this group. *Westergårdia* (VI) most probably developed from *Acerocarina*, and seems to have given rise to *Jujuyaspis* (Trem.) and the closely related *Boeckaspis* (Trem.).

The origin of *Leptoplastides* (Trem.) and the very closely related *Beltella* (Trem.) is uncertain, but they appear to be closest to the Pelturinae. *Paenebeltella* (Trem.) is probably a related genus.

The Leptoplastinae form a group of closely related genera. The earliest member of this group, *Leptoplastus*, appears at the base of the zone of *Leptoplastus* (IV) and lasts into the zone of *Protopeltura praecursor* (Va). It is uncertain whether it developed directly from *Olenus* or branched off from the *Protopeltura-Parabolina* group. There is an even transition from *Leptoplastus* to *Eurycare* (IV), and likewise from *Leptoplastus* to *Ctenopyge* (*Eoctenopyge*) (Va-b), which gave rise to *Ctenopyge* (*Mesoctenopyge*) (Vb) and *Sphaerophthalmus* (Vb-c). *Ctenopyge* (*Ctenopyge*) (Vb-c) developed from *Ctenopyge* (*Eoctenopyge*) or *Ctenopyge* (*Mesoctenopyge*), most probably from the former.

On the whole, the generic divergence of the olenids forms a spindle pattern rather than a burst pattern, as defined by Cooper & Williams (1952). This supports Cooper's view (Cooper & Williams, 1952, p. 331) that better known groups will show a spindle pattern, while most bursts are the product of insufficient palaeontological research.

Items of general interest to trilobite phylogeny and classification

1. An increase in the number of thoracic segments may take place in a phylogenetic lineage [e. g. *Leptoplastus* (10—12 segments) → *Eurycare* (14—17); *Parabolina* (12) → *Parabolinella* (16—21)], just as well as a reduction [e. g. *Olenus* (13—15) → *Parabolina* (12); *Olenus* (13—15) → *Peltura* (12) → *Accrocarina* (10) → *Westergårdia* (9)].

2. A decrease in the length of the pygidium in relation to the length of the cranidium (or in relation to the over-all length) may take place in a phylogenetic lineage [e. g. early *Leptoplastus* species (length of pygidium: length of cranidium c. 0.45) → *Ctenopyge flagellifera* (c. 0.3); *Peltura* (c. 0.4) → *Accrocarina micropyga* (c. 0.27)]. The opposite is better known from other trilobite families, but seems to have occurred in the Olenidae as well. Thus *Sphaerophthalmus* apparently had a relatively larger pygidium than most species of *Ctenopyge*, but the lack of entire dorsal shields prevents numerical comparison. In spite of the variations of the relative size of the pygidium, the olenids are micropygous (i.e. the pygidia are markedly smaller than the cephalon), with the exception of *Ctenopyge pecten*, which is provided with an aberrant pygidium as long as the cranidium, and may be regarded as a macropygous off-shoot.

Statements 1 and 2 are of some interest as it generally has been believed that the number of thoracic segments could not increase in a phylogenetic series and that the pygidium could not become relatively smaller, i. e. that many thoracic segments and small pygidium were regarded as primitive features. Thus Westergård, who in 1922 regarded *Andrarina* [*Liostracus*] *costata* as a probable forerunner of *Olenus*, later (1944) was inclined to believe that this opinion could not be upheld, because Strand (1929) meanwhile had shown that *Andrarina costata* has 12 thoracic segments, whereas *Olenus* has 13 or more, and also because of the slightly larger pygidium of *Andrarina costata*.

It should be remembered, as emphasized by Størmer (1942, p. 129), that "all the postcephalic segments — — — migrate forward through a coalesced protopygidium or transitory pygidium (as shown by Stubblefield in *Shumardia*), and only secondarily become free thoracic segments". It is not surprising that the number of segments which become free may vary both ways in a phylogenetic lineage.

3. Features that for a long time remain stable in a lineage, may later be subject to great variations. While for instance the eyes in later *Protopeltura* species and in *Peltura* have an anterior position close to the glabella, the eyes in later pelturine genera may be close to or remote from the glabella, and have an anterior, intermediate, or posterior position, thus also duplicating the position of the eyes in early *Protopeltura* species and in *Olenus*, from which the pelturines developed.

4. Some features that may seemingly be lost in a phylogenetic lineage, at least in the adults, may reappear later in the lineage, as e. g. axial spines (disappearing in *Peltura*, reappearing in *Boeckaspis*), spines of the free cheeks (absent in early *Peltura* and *Triarthrus* species, reappearing in some later *Peltura* and *Triarthrus* species), and glabellar furrows (obsolete in later *Peltura* species, reappearing in e. g. *Acerocare*).

5. The size of the trilobite may increase and decrease in the same phylogenetic lineage [e. g. *Peltura* (medium-sized) → *Acerocarina* (small) → *Westergårdia* (small) → *Boeckaspis* (medium-sized)]. The same applies to restricted areas of the shield. Thus the postocular cheeks are wide in *Olenus*, rather narrow in *Protopeltura* and especially in *Peltura*, and very wide again in *Acerocare*. In the same way the width of the pleural regions in relation to the width of the axis may alternately decrease and increase [e. g. *Protopeltura* (moderately wide) → *Peltura* (narrow) → *Acerocare* (wide)]. A decrease and an increase in the number of thoracic segments may take place in the same phylogenetic lineage [e. g. *Olenus* (13—15 segments) → *Parabolina* (12) → *Parabolinella* (16—21)].

Statements 3 to 5 agree with the conception that evolution is known to be reversible (cf. Romer in Jepsen et al., 1949, p. 110). This, of course, should not be confused with Dollo's statement that structures once lost are not regained, which, as discussed by Romer (l. c., p. 113) seems to be essentially a statement of fact. However, as further mentioned by Romer, phenotypic disappearance of a structure may result from a single masking mutation (or even an environmental change in developmental conditions), and it may readily reappear a few generations later after the removal of the "block" to its expression.

The reappearance of a genal spine in some later *Triarthrus* species could perhaps be explained as due to the removal of a masking mutation, but it is possible that genal spines are present in early larval stages of *Triarthrus* species without genal spines in the adult. If so, the development of a spine in the adult of later *Triarthrus* species may be regarded as a kind of arrested development ("partial neoteny" or merostasis), since lack of genal spines is an advanced characteristic in the olenids. Unfortunately I have not been able to find any larval stages of early *Triarthrus* species. The same could be advocated for the reappearance of spines in the free cheeks of some late *Peltura* species (*P. paradoxa*, *P. transiens*).

As to the axial spines, they usually seem to be present in larval stages, or are represented by axial nodes.

All the features mentioned in statement 4 are, of course, features of the shield. Thus the organs connected with the glabellar furrows are probably always present, even in species with a smooth glabella (cf. statement 6), and this explains why glabellar furrows may again be developed in descendants of forms with a smooth glabella.

6. In some olenid genera the position of the eyes varies greatly from species to species (e. g. *Westergårdia*), whereas the position is rather constant in other genera (e. g. *Peltura*). Other features that may vary considerably in closely related species are i. a.: width of fixed cheeks and pleural areas (e. g. *Ctenopyge*), sagittal length of prelabellar field (e. g. *Parabolina*), length of spines (e. g. *Parabolina*), position of spine in the free cheeks (e. g. *Ctenopyge*), distinctness and thus also the number of glabellar furrows (e. g. *Peltura*, *Ctenopyge*). The same features may be rather constant in other genera.

Thus features distinguishing a certain genus may be of taxonomic value at the specific level only in other, even closely related genera. This is a well-known fact to taxonomists of different groups of animals, but students of trilobites have sometimes neglected it and have carried out an unnecessary splitting of genera in some families. As stressed by Mayr (1947, p. 22), it is important that all classifications be based on the greatest possible number of different features.

7. Some olenid species fit well in a genus except that they have "gone crazy" in a single feature. *Leptoplastus abnormis*, for instance, is a typical *Leptoplastus* species, except for having unusually long and wide pleural spines.

I agree with Mayr (1947, p. 287) that such species should be regarded "as a whole" and be included in the same genus as the related species.

8. The in general opisthoparian family Olenidae gave rise to proparian off-shoots. Thus the leptoplastine *Ctenopyge tumida* may be regarded as proparian, since its postocular facial sutures cut the margin well in front of the genal angle, although behind the spines of the free cheeks. Furthermore the pelturines *Saltaspis* and *Nericiaspis* are typical proparian genera. According to Tjernvik (1955, p. 211, text-fig. 2), they developed independently from opisthoparian ancestors, among which is *Peltura*. As demonstrated by Poulsen (1923, p. 58), early meraspid stages of *Peltura* have a proparian suture. It is difficult to judge whether the proparian suture in the adult *Saltaspis* and *Nericiaspis* is an example of arrested development, or whether the proparian suture in early meraspid stages of *Peltura* is an example of a new morphologic character which appears phylogenetically first in an early ontogenetic stage, and which may be developed also in the adult of geologically younger forms (cf. Størmer, 1942, pp. 152—157; 1944, p. 42).

Rates of evolution in olenids

As discussed by Simpson (in Jepsen e. a., 1949, p. 205), "rate of evolution" has many possible meanings. I shall give here a few examples of what he terms "rates of taxonomic diversification" (l. c., p. 208).

The rate seems to be slower for the pelturines than for the leptoplastines during the time corresponding to zones IV—Vc. Only 3 genera (and no

subgenera) of pelturines are known from this time span, as compared to 6 genera and subgenera of leptoplastines. The difference in rates probably was even greater than 6 to 3, since there were more different trends within the leptoplastine genera and subgenera than within the pelturine genera. This is furthermore shown by two other examples. *Protopeltura praecursor* occurs as the only pelturine in three succeeding subzones (of zone Va), containing four species of leptoplastines (difference of rates 1 to 4). *Peltura scarabaeoides* and *Nericiaspis robusta* occur as the only known pelturines in two subzones (of zone Vc) containing at least 8 leptoplastine species (difference of rates 2 to 8).

It is more difficult to compare the rate of taxonomic diversity at different time spans within a single lineage, since the absolute time is not known at present. However, it seems reasonable to assume that zone VI represents a shorter time interval than zones III—Vc, or at least not a longer interval. Nevertheless, there are only 3 pelturine genera known from zones III—Vc, as compared to 6 in zone VI.

From the above it appears that the rate of evolution was different among the various olenid trends within the same time interval and varied from time to time within one trend.

Evolution of olenids in relation to way of living and environment

As discussed above (p. 78), one can distinguish between three main morphologic types of shields in the olenids, probably indicating different ways of living, viz. the *Peltura* type (suggesting vigorous and active swimming), the *Olenus* type (suggesting less vigorous swimming), and the *Ctenopyge* type (suggesting a more passive planktonic life). If so, a phylogenetic lineage leading from one type to another indicates adaptation to a different way of living.

The *Olenus* type appeared first, and from this both the other types evolved. Already the later *Olenus* species tend towards the *Peltura* type, which is found in the earliest known pelturine (*Protopeltura aciculata*) as well as in the earliest known *Parabolina* species (*P. brevispina*). Already the next *Parabolina* species to appear, *P. spinulosa*, has returned to the *Olenus* type. The leptoplastines mainly developed forms of the *Olenus* and *Ctenopyge* types. *Sphaerophthalmus* may be regarded as developing a *Peltura* type of shield. The rather sudden disappearance of the Leptoplastinae is difficult to explain, but may in part be due to competition from the Oleninae and Pelturinae, which developed further, side by side. For a long time the Oleninae produced forms of the *Olenus* type only, and the Pelturinae of the *Peltura* type. However, at the close of the Late Cambrian epoch and in the Tremadocian epoch there seems to have been a struggle for the complete

hegemony between the two subfamilies. Thus the Pelturinae also developed a number of forms with an *Olenus* type of shield (e. g. *Acerocare tullbergi*) and of the *Ctenopyge* type (*Boeckaspis*, *Jujuyaspis*), while the Oleninae developed forms of the *Peltura* type (e. g. *Triarthrus*) and the *Ctenopyge* type (e. g. *Parabolina lobata*). During the Tremadocian epoch the olenids soon became a minority among the trilobites in the Acado-Baltic province, and neither the Oleninae nor the Pelturinae conquered the hegemony (cf. below). The Oleninae won in the family struggle, since *Triarthrus* outlived any other olenid genera.

From the above it is seen that all three subfamilies were capable of producing the three types of shields. The shield could shift to and fro between the *Olenus* and *Peltura* type in a single lineage, indicating alternating adaptation to one or the other way of living, as demonstrated i. a. in the phylogenetic lineage *Olenus* (*Olenus* type) → *Parabolina brevispina* (*Peltura* type) → later *Parabolina* species (mainly *Olenus* type) → *Triarthrus* (*Peltura* type). Some off-shoots from the *Olenus* type developed into the *Ctenopyge* type. The great resemblance between e. g. *Triarthrus* and *Peltura* may be due to adaptation to a similar way of living.

Besides the adaptations mentioned above, one may mention the development of small forms (*Sphaerophthalmus*, *Westergårdia*) and large forms (*Parabolinella*, *Angelina*). The position of the eyes is subject to great variation in the Olenidae, but the significance of this is difficult to explain (cf. p. 79). However, it is interesting that the same position of the eyes occurs in different trends. Thus the extremely distal position of the eyes in *Eurycare latum* may be compared with that of *Ctenopyge pecten*. This may be another example of adaptation to a similar mode of life.

The olenids constitute a suitable object for the study of evolution, since they occur in great numbers in successive horizons. Kaufmann (1933a, 1933b, 1935) was able to distinguish several successive evolutionary series in *Olenus* in southern Scandinavia (cf. p. 98), and in each of them there was an evolution from a rather transverse to a narrow pygidium (cf. text-fig. 15). Kaufmann explained this by assuming that there was a repeated invasion of forms with transverse pygidia to this area, where the species developed into forms with narrow pygidia and finally became extinct. He accordingly postulated a "Konservativstamm" of *Olenus* developing elsewhere. It is possible that extremely stagnant conditions may have caused the narrowing of the shields and the apparently repeated extinction of evolutionary trends in southern Scandinavia. Unfortunately, no data are available on evolutionary trends in *Olenus* in other areas.

Remembering that the olenids formed practically the only thriving group of trilobites in the Acado-Baltic province during almost the whole of the Late Cambrian epoch, it is not surprising that they developed a number of species and apparently were adapted to somewhat different ways of living. Nevertheless, in spite of considerable variation in proportions of the parts

of the shield, the general plan of structure is rather conservative. One may wonder why the olenids did not develop a greater variety of forms. It may be ascribed to several reasons. Firstly, the conditions were rather uniform in the Acado-Baltic province during the Late Cambrian epoch. Another thing is that the apparent scarcity of other animals may indicate that the olenids were not preyed upon, and thus did not need to develop any intricate equipment of defence. Thus the olenids did not develop strong tests, on the contrary they had thin tests with deep furrows. Furthermore the olenids did not have any serious competition from other trilobites during most of the Late Cambrian epoch. Apparently the olenids were protected by the uniform, often stagnant conditions.

The rather rapid decline of the olenids at the close of the Tremadocian epoch probably was caused by the decrease and splitting up of areas with stagnant conditions and the invasion of the Acado-Baltic province by other trilobites and invertebrates, some no doubt competing with the olenids, and some (e. g. cephalopods) perhaps preying on them. In this connection it is interesting to note that some of the largest known olenids (e. g. *Angelina* and *Parabolinella*) developed in the Tremadocian epoch, perhaps as a result of competition with large trilobites of other families (e. g. asaphids). Furthermore, it may perhaps be significant that whereas most olenids had a smooth test, some later genera like *Acerocarina*, *Westergårdia*, and *Boeckaspis* were equipped with small tubercles (probably spine bases), possibly for defence.

Although the olenids spread to new areas during the Tremadocian epoch, they apparently were unable to cope with the new conditions. Few olenids lived in the Arenigian epoch, and only *Triarthrus* and its off-shoot *Porterfieldia* are known from post-Arenigian deposits. However, *Triarthrus* managed to carry on with remarkably small morphological changes in the shield from the Tremadocian till around the close of Middle Ordovician times, rather an unusually long period for an Ordovician trilobite genus. Apparently it was adapted to and clinging to such areas where stagnant conditions still prevailed. Its extinction brought an end to the history of the Olenidae.

Remarks on ontogeny and certain morphologic features

Ontogeny

Ontogenetic series have been described in detail in *Olenus gibbosus* by Strand (1927) and Størmer (1942, p. 82), in *Olenus transversus* by Kaufmann (1933a, p. 15), and in *Leptoplastides salteri* by Raw (1925). The larval development of *Triarthrus eatoni* (referred to as *T. becki*) was described by Walcott (1879, 1918). Poulsen (1923, p. 58) described several larval stages of *Peltura scarabacoides*, including early meraspid stages with a

distinct proparian facial suture. Furthermore a number of authors have described single larval shields of olenids, as e. g. Westergård (1922). Spines are common in early larval shields, even if the adult has few or none. Apparently the early larvae were planktonic forms (cf. Størmer, 1944, p. 38).

Larval shields and especially parts of larval shields are not uncommon in Norwegian material of olenids. I have made no observations of importance beyond what is already known on the larval development of olenids, but then I have not especially searched for ontogenetic series.

I would like to stress that there is often a marked difference in proportions even between later stages of a species. This is easily seen in species with wide fixed cheeks, where large cranidia have relatively wider fixed cheeks than smaller cranidia, as e. g. in *Acerocare ecorne*, *Eurycare latum*, and *Leptoplastus norvegicus* (cf. p. 172). Thus in a small cranidium of *Acerocare ecorne* (pl. 21, fig. 1) the proportion between the width of the occipital ring and the width of the postocular cheek is 1.45, whereas it is 1.3 in an adult cranidium (pl. 21, fig. 2).

Whittington (1954, p. 193) declared that he knew of no example in trilobites of ontogeny recapitulating phylogeny, i. e. he knew of no ontogenetic stage that resembles a geologically older adult. One might perhaps cite as examples the above-mentioned olenid species with wide fixed cheeks, where the relative width of the fixed cheeks increases during the ontogeny, so that at some larval stage the proportions may be as in adults of a geologically older species.

Kaufmann (1933a, p. 51) pointed out that larval pygidia of *Olenus* resemble the adult pygidia of the geologically younger *Parabolina*. It is possible that the adult *Parabolina* was adapted to a life which resembled more that of the larval than of the adult *Olenus*.

On certain morphologic features

Cephalic sutures.

Text-figs. 12—13.

The facial sutures are quite well known in the Olenidac. Whenever it can be controlled, they seem to meet in front axially. The postocular branches of the facial sutures usually are olenoid or pelturoid, in some cases transverse (the terms are illustrated in text-fig. 2). Most adult olenids are opisthoparian, i. e. the free cheeks include the genal angles. A few off-shoots have proparian facial sutures, i. e. the postocular branches of the facial sutures cut the lateral margin of the cephalon in front of the genal angles (e. g. *Ctenopyge tumida*, *Saliaspis*). The preocular parts of the facial sutures are convergent, sub-parallel, or diverging, whereas the anterior parts are always strongly converging.



Fig. 12. United free cheeks. Above: *Parabolina spinulosa* (Wahlenberg), P. M. O. no. 30777, Fure in Modum, Norway. Below: *Olenus attenuatus* (Boeck), P. M. O. no. 28948, Krekling in Eiker, Norway. The genal fields are damaged in both specimens. Not retouched. $\times 3.5$.

The existence or non-existence of ventral cephalic sutures (connective sutures or median suture, hypostomal suture) apparently has never been ascertained in the Olenidae. This is no doubt partly due to the fact that most olenids have extremely narrow doublures, and that complete and undisturbed shields are very rare.

Among some material of *Parabolina spinulosa* preserved in shale from Fure in Modum, Norway, there are several isolated pairs of free cheeks which are united and show no traces of a median suture or a pair of connective sutures across the doublure (text-fig. 12). In a specimen of *Parabolina lobata* (pl. 9, fig. 11) the facial sutures are united in front inside the anterior margin. There are no traces of other sutures crossing the border in front of the facial sutures (text-fig. 13). At least in these two species the free cheeks are fused into a single piece. Some shale material of *Olenus attenuatus* from Krekling in Eiker, Norway, likewise includes united pairs of free cheeks (text-fig. 12), but the preservation is not good enough to ascertain that the doublure is not crossed by a suture (or a pair of sutures). The mere fact that the pair of free cheeks occur isolated but united in the correct position to each other, renders it most unlikely that there were any sutures crossing the doublure. The same applies to similarly preserved united pairs of free cheeks of *Parabolina frequens*, described and figured by Sdzuy (1955, p. 16, pl. 3, fig. 64), who suggests an at least beginning fusion of the median suture.



Fig. 13



Fig. 14

Fig. 13. Cephalon of *Parabolina lobata* (Brøgger). Outline drawing based on the specimen figured in pl. 9, fig. 11. $\times 1.7$.

Fig. 14. Muscle marks on the cephalic axis of *Acerocare ecorne* Angelin. Drawing based on the specimen figured in pl. 30, fig. 4. $\times 5.1$.

Single free cheeks are very common in material of olenids, and one may wonder whether there was not at least a median suture in other species. However, it is quite possible that they all had united free cheeks, but that the very narrow connection was easily broken. Thus, in the large Scandinavian collections of *Parabolina spinulosa* preserved in stinkstone, I have never seen any united pairs of free cheeks. Neither have I seen any in Scanian material of *Olenus* preserved in a somewhat calcareous alum shale. Apparently extremely tranquil conditions at the sea floor were necessary for the preservation of united pairs of free cheeks. It seems as if it would be recommendable to search for specimens preserved in pure alum shale, instead of collecting from stinkstone lenses, as is generally done because the stinkstone specimens are not compressed.

As to the presence of a hypostomal suture, I know of no olenid specimens showing the hypostoma close to the doublure of the cephalon. On the contrary, in many specimens where the hypostoma is preserved, it seems to be situated too far posteriorly to have been separated from the doublure by a suture only (cf. e. g. cranidium of *Parabolinella triarthra* showing outline of hypostoma, figured by Lake, 1913, pl. VII, fig. 8). Of course the hypostomae may have been somewhat displaced, but there is also a possibility of the hypostoma not having been directly connected with the doublure of the cephalic shield, but only through the ventral membrane. This is also suggested by the isolated assemblages consisting of the two free cheeks and the hypostoma of *Acerocare ecorne*, described above (p. 72).

Cranidial muscle marks.

Text-fig. 14; pl. 30, fig. 4.

Two counterpieces of cranidia of *Acerocare ecorne* in loose blocks from Blockhusudden in Uppland, Sweden, show symmetrically arranged spots which no doubt represent muscle marks. The counterpieces are preserved in a light brownish limestone and have a thin white coating, except for the

marks in question. There are 5 pairs of muscle marks, which I shall refer to as M0, M1, M2, M3, and M4, counted from the rear. Broadly speaking, their position agrees with that of the occipital furrow (S0) and the glabellar furrows (S1—S4). However, M0 is not connected across the glabella as is the occipital furrow. The anterior part (in front of S0) is somewhat longer (tr.) than the posterior part (behind S0). M1 and M2 are of the same order of size, but are not transversely divided into two parts. M3 is rather small and appears more oblique than S3. M4 is long (tr.) and narrow. While the muscle marks may easily be compared with the occipital and glabellar furrows, it is difficult to say to which muscles they belong. If the head of *Acerocare ecorne* had four pairs of biramous appendages and a pair of uniramous antennae as seems to be the case in trilobites where the cephalic appendages are known (including the olenid *Triarthrus*, cf. text-fig. 11), M0—M3 may belong to muscles of the four pairs of biramous appendages. M4 might then belong to muscles of the antennae, but its shape renders this less likely. It is possible that M4 does not belong to muscles of appendages, but e.g. to muscles of the hypostoma. The small size and the position of M3 may suggest that it rather belonged to the muscles of the antennae, but it would then be difficult to interpret M0—M2 as representing four pairs of appendages.

In material of *Olenus gibbosus*, recently collected at Trolmen quarry, Kinnekulle, Västergötland, Sweden, I have observed corresponding muscle marks, which, however, are narrower than in *Acerocare ecorne*.

Some other morphologic features.

Anterior pits are often discernible in the dorsal furrow at the anterior corners of the glabella, immediately in front of the eye ridges. They are often best seen in internal moulds, since the anterior bosses on the inner side of the cranidium are more pronounced than the corresponding pits on the external surface.

In a paper on the visual organs in trilobites, Lindström (1901) described the lateral eyes in several olenids. The leptoplastines *Eurycare*, *Ctenopyge*, and *Sphaerophthalmus* were found to have hemisphaeric eye globes, and the pelturines *Peltura* and *Acerocare* to have semiglobose visual fields. However, he found no ocular globes with facets in the two olenine genera mentioned, *Olenus* and *Parabolina*, and he was inclined to believe that they probably were blind (l. c., p. 22). I have observed visual fields similar to those in *Peltura* also in *Protopeltura* (see fig. of free cheek of *Protopeltura holtedahli* n. sp., pl. 23, fig. 18). Like Lindström, I have not observed any visual fields in *Olenus* and *Parabolina* (or other olenines). Nevertheless, it seems less probable that their lateral eyes were reduced, since the facial sutures usually are considerably modified in other trilobite families where the lateral eyes are lost.

As is well known, g e n a l c a e c a (cf. Raymond, 1920b, p. 82) often are very distinct in the olenids, probably because the olenids have so thin tests. They are now usually explained as being impressions in the test of the intestinal diverticulae (cf. Hupé, 1953, p. 84). They are seen as vein-like ridges on the outer surface of the cephalon. When the ridges cross the border furrow, this appears pitted, each pit representing a part of the furrow between two crossing ridges.

A p o s t o r a l p l a t e ("metastoma") is described by Beecher (1894) and Raymond (1920b, p. 42) in specimens assigned to *Triarthrus becki*, but now regarded as belonging to *T. eatoni*. The postoral plate is seen behind the hypostoma in the reconstruction of *T. eatoni* reproduced here (text-fig. 11). I have found no postoral plates in the present material, but the chances of finding any are small, since the material mainly consists of detached parts of the shield. Neither have I found any a n a l p l a t e s like that described in the same species by Raymond (1920b, p. 44).

A new type of an olenid p y g i d i u m is described below in *Ctenopyge erecta*.

Systematic descriptions

Type data and diagnosis are as a rule given for each taxonomic unit, and the occurrence is stated for genera, species, and subspecies. Detailed morphologic descriptions are added for species based on Norwegian material. For terminology, see p. 12. The relationships of the species are discussed under each genus. The species are treated in alphabetical order within the genus, except doubtful species, which are treated after the others. I have tried to compile critical and as complete synonymy lists of the species as possible, but I have not included references to papers where the species is only briefly mentioned and no new information or illustrations are given (e. g. text books). I have not always provided photographs of a species occurring in Norway, when it occurs in Sweden and has been adequately illustrated by Westergård (1922).

Family Olenidae Burmeister 1843.

T y p e g e n u s : — *Olenus* Dalman 1827.

D i a g n o s i s : — Trilobites with more or less flattened or transversely convex dorsal shields, between 0.5 and 11 cm long in adult specimens.

Cephalon sub-semicircular, wider than long. Facial sutures opisthoparian, rarely proparian; meeting in front axially; preocular parts of facial sutures straight or convex, convergent, subparallel, or divergent; postocular parts oblique backwards or transverse, and sinuous, straight or convex. Axial furrow distinct. Occipital ring well defined, with or without axial node or spine; occipital furrow distinct, simple or composite. Glabella tapering for-

wards, or with subparallel or slightly convex sides, or widening slightly forwards. 0—4 pairs of glabellar furrows; not connected across glabella, except $S1 \pm S2$ in some species; $S1$ simple, geniculate or digeniculate or bifurcate; $S2$ simple or geniculate; $S3$ simple and usually short; $S4$ simple and usually short. Anterior pits often discernible at anterior corners of glabella. Preglabellar field short or absent. Border furrow usually distinct. Border narrow to very narrow, straight, convex or concave, more or less vaulted, and with short to long cranial part. Palpebral lobes medium-sized to small, close to to far from glabella, with anterior to posterior position. Eye ridges usually present, oblique backwards, transverse or slightly oblique forwards, and straight or slightly convex. Interocular cheeks and postocular cheeks narrow to very wide. Intergenal points or spines present or not. Free cheeks without spine or with spine confluent with, or diverging outwards from lateral margin; inner spine angle obtuse to acute; spine long to short, round or flattened, straight or curved.

Thorax with 9—19 segments (where number is known). Pleural regions narrow to wide. Axis well defined, tapering backwards or spindle-shaped. Axial rings with or without axial node or spine. Pleurae simple, with oblique pleural furrows, and with truncate ends, or, usually, with pleural spines. Pleural spines long or short, round or flattened. Pleural and/or axial macrospines developed in some species.

Pygidium small, with exception of aberrant pygidium of *Ctenopyge pecten*; entire or with marginal spines; sub-semicircular to sub-triangular or sub-trapezoidal in outline. Axis well defined. Axial rings well defined or fused, with or without axial node or spine. 2—8 axial rings (including end lobe)

Doublure narrow to extremely narrow.

Hypostoma with simple central body and entire posterior margin or with two posterior denticles.

Surface of test smooth, or, less commonly, granulate or pitted. Cephalon often with genal caeca, especially on preglabellar field and free cheeks. Terrace lines may be developed on doublures, borders, and pygidium.

Remarks: — I agree with Rasetti (1951, p. 202) that "it is impossible to formulate a set of diagnostic features that will give an objective description of the olenid shield and enable one to decide whether a certain trilobite belongs to the Olenidae or not". However, the following combination of features seems to be rather characteristic of the Olenidae, and hardly of any other trilobite: Facial sutures meeting in front, narrow border and doublure, simple and well-defined glabella, pleurae with oblique pleural furrows, small pygidium.

Subfamily Oleninae Burmeister 1843.

Pl. 1.

Type genus: — *Olenus* Dalman 1827.

Diagnosis: — Olenids with free cheeks with straight spine confluent with course of lateral margin or deviating only very slightly outwards. Exceptions: Some species of *Parabolina* with free cheeks with slightly curved spine. Some species of *Triarthrus* with free cheeks without spine.

Remarks: — Olenidae was erected as a group of the family Trilobitae by Burmeister (1843, p. 77). Beecher (1897, p. 192) was the first to recognize a subfamily Oleninae. Triarthridae Ulrich (1931, p. 214) is regarded here as a synonym of the subfamily Oleninae (cf. p. 17).

Genus *Olenus* Dalman 1827.

Remarks on the name: — The name *Olenus* was actually proposed by Dalman (1827, p. 124; reprint, p. 12) as a new name for *Paradoxides* Brongniart 1822. Dalman (1827, pp. 254, 256; reprint, pp. 69, 71) divided *Olenus* into two divisions, Cornigeri and Mutici. Cornigeri included *O. Tessini* (= *Paradoxides paradoxissimus*), *O. spinulosus* (= *Parabolina spinulosa*), and *O. bucephalus* (= *Paradoxides paradoxissimus*). Mutici embraced two subdivisions (Dalman, 1827, pp. 282, 283; reprint, pp. 97, 98), one including *Olenus gibbosus*, and the other including *O. scarabaeoides* (= *Peltura scarabaeoides*). No type species had been designated either for *Paradoxides* by Brongniart or for *Olenus* by Dalman. Burmeister (1843) and Goldfuss (1843) were the first to regard *Paradoxides* and *Olenus* as two separate genera. Both applied the name *Paradoxides* to a group corresponding to Dalman's division Cornigeri and *Olenus* to a group corresponding to Dalman's division Mutici, except that Goldfuss transferred "*Olenus*" *scarabaeoides* to a new genus, *Anthes*. Miller (1889) designated *Paradoxides tessini* (= *paradoxissimus*) as type for *Paradoxides* and Salter (1864, VIII, p. 3) designated *Olenus gibbosus* as type for *Olenus*.

Since *Olenus* was proposed as a new name for *Paradoxides*, it is not a valid name. However, as *Olenus* is such a well-known genus, and the name has been in use for such a long time, it would be unfortunate to change the name. Dr. Chr. Poulsen has therefore proposed to ICZN to legalize the name *Olenus* (Bull. zool. Nomencl., vol. 12, pt. 1, pp. 3—13, London 1956).

Type species: — *Entomostracites gibbosus* Wahlenberg 1821, designated by Salter (1864, VIII, p. 3).

Diagnosis: — Oleninae with: facial sutures subparallel in front of eyes; medium-sized to small palpebral lobes, with centres opposite S2; 3 pairs of glabellar furrows; distinct preglabellar field; free cheeks with spine which continues course of lateral margin, or diverges very slightly outwards

from it; 13 (12?) to 15 (16?) thoracic segments; pleurae with pleural spines; pygidium with or without marginal spines.

Included species: — *Olenus* is the earliest established olenid genus, and many species which were assigned to *Olenus* in earlier days, have later been transferred to other genera, both olenid and non-olenid. It hardly seems necessary to mention all these species here. A few of them are mentioned above (p. 23). The following species are included in *Olenus*:

O. aculeatus Angelin 1854 (= *O. attenuatus*)

O. alpha n. sp.

O. asiaticus Kobayashi 1944

O. attenuatus (Boeck 1838)

O. cataractes Salter 1864

O. dentatus Westergård 1922

O. gibbosus (Wahlenberg 1821)

O. micrurus Salter 1849

O. mundus Lake 1908

O. rotundatus Westergård 1922

O. scanicus Westergård 1922

O. transversus Westergård 1922

O. truncatus (Brünnich 1781)

O. wahlenbergi Westergård 1922

and possibly also *O.?* *bucephalus* (Belt 1868) and

O.? *wilsoni* n. sp.

Some of the British species of *Olenus* may possibly turn out to be conspecific with Scandinavian species, when they become better known. The species referred to as *O. longispinus* (Belt 1868) by Lake (1908) is possibly a *Parabolinites* species (cf. p. 131). *Olenus?* sp. described by Westergård (1922) is probably a *Parabolina* species, as suggested by Westergård (1947, p. 24), and is described below (p. 128) as *Parabolina?* *quadrisulcata* n. sp. *Olenus argentinus* Kayser 1867, referred to by Kobayashi (1937c) and Harrington (1938) as "*Olenus*" *argentinus* is without doubt a *Parabolina* species. An *Olenus?* sp. recorded by Whitehouse (1939, p. 222, pl. XXIII, fig. 14) from Australia is badly preserved, and it is difficult to say whether it is an olenid or not. A specimen consisting of the posterior part of the thorax and the pygidium, from the black slate at Salitre, Bolivia, was described as *Olenus?* sp. by Kobayashi (1937c, p. 475, pl. IV, fig. 14). It should rather be referred to as Olenid sp., as it may equally well belong to some other genus, such as e. g. *Parabolina*, and because it seems improbable that *Olenus* should occur at such a high horizon (Tremadocian). A dorsal shield without cephalon from the Lower Tremadocian of South America was likewise described as *Olenus?* sp., by Harrington (1938, p. 192, pl. VII, fig. 12). In this case, too, it appears better to refer to it as Olenid sp. It somewhat resembles *Plicatolina kindlei* Shaw 1951, and may possibly belong to this genus.

Some doubtful species assigned to *Olenus* by Rusconi are discussed above (p. 24).

Occurrence: — Norway (*Olenus* zone), Sweden (*Olenus* zone), Denmark (*Olenus* zone), England (Outwoods Shales), Wales (Lower Lingula Flags, Middle Lingula Flags?), E. Canada (*Olenus* zone), Texas (Woods Hollow boulders), Korea (*Glyptagnostus* zone), ?Australia (*Eugonocare* stage).

Phylogeny: — The earliest known *Olenus* species (and olenid) is *Olenus alpha* n.sp. from the zone of *Agnostus pisiformis* in Norway. Its thorax is not known, but it is no doubt a true *Olenus*, closely related to the other members. It differs from the later species in having relatively narrower postocular cheeks. Its free cheeks have an obtuse inner spine angle, as those of other early species of *Olenus*, and its pygidium is entire. *O. alpha* n.sp. may very well belong to the ancestral stock of the later *Olenus* species.

The phylogeny of the *Olenus* species in southern Scandinavia has been discussed by Kaufmann (1933a, 1933b, 1935), who carried out a detailed statistic investigation of the species and also found intraspecific evolutions in this area. In an obituary to him, Teichert (1946) wrote that "Rudolf Kaufmann will be best remembered by his fundamental research on the evolution of *Olenus* in the Upper Cambrian of Sweden and the island of Bornholm. These beds are characterized by numerous species of that genus, each distinctive of its own biozone. With immense care Kaufmann collected a large material of cranidia and pygidia from carefully selected beds, usually not more than 3 cm apart and, with the help of a specially constructed device, measured the proportions of a number of comparatively easily recognizable features. He found that each species possesses a number of features that are constant and others that are variable. The latter command considerable interest, because it was shown that these variable features undergo certain directional modifications during the geological history of each species and that, surprisingly, the trend of these modifications is more or less identical in successive species, that is it is usually the same set of features which are modified in the same way. Kaufmann called this process "Artabwandlung", an admirably short and precise term for which the writer [Teichert] is elsewhere proposing the unavoidably more cumbersome term "intraspecific directional modification". Intraspecific modification anticipates (in the earlier species) and repeats (in the later species) the phylogenetic evolution of the genus."

Kaufmann (1933a) showed (cf. text-fig. 15, p. 99) that the species *Olenus gibbosus* (with 5 succeeding modifications), *O. transversus* (only one modification), *O. truncatus* (6 succeeding modifications), *O. wahlenbergi* (one modification), *O. attenuatus* (3 succeeding modifications) and *O. dentatus* (5 successive modifications) succeed each other in that order in Scania, except that the ranges of the two uppermost species (*O. attenuatus* and *O. dentatus*) slightly overlap. *O. transversus* may have given rise to

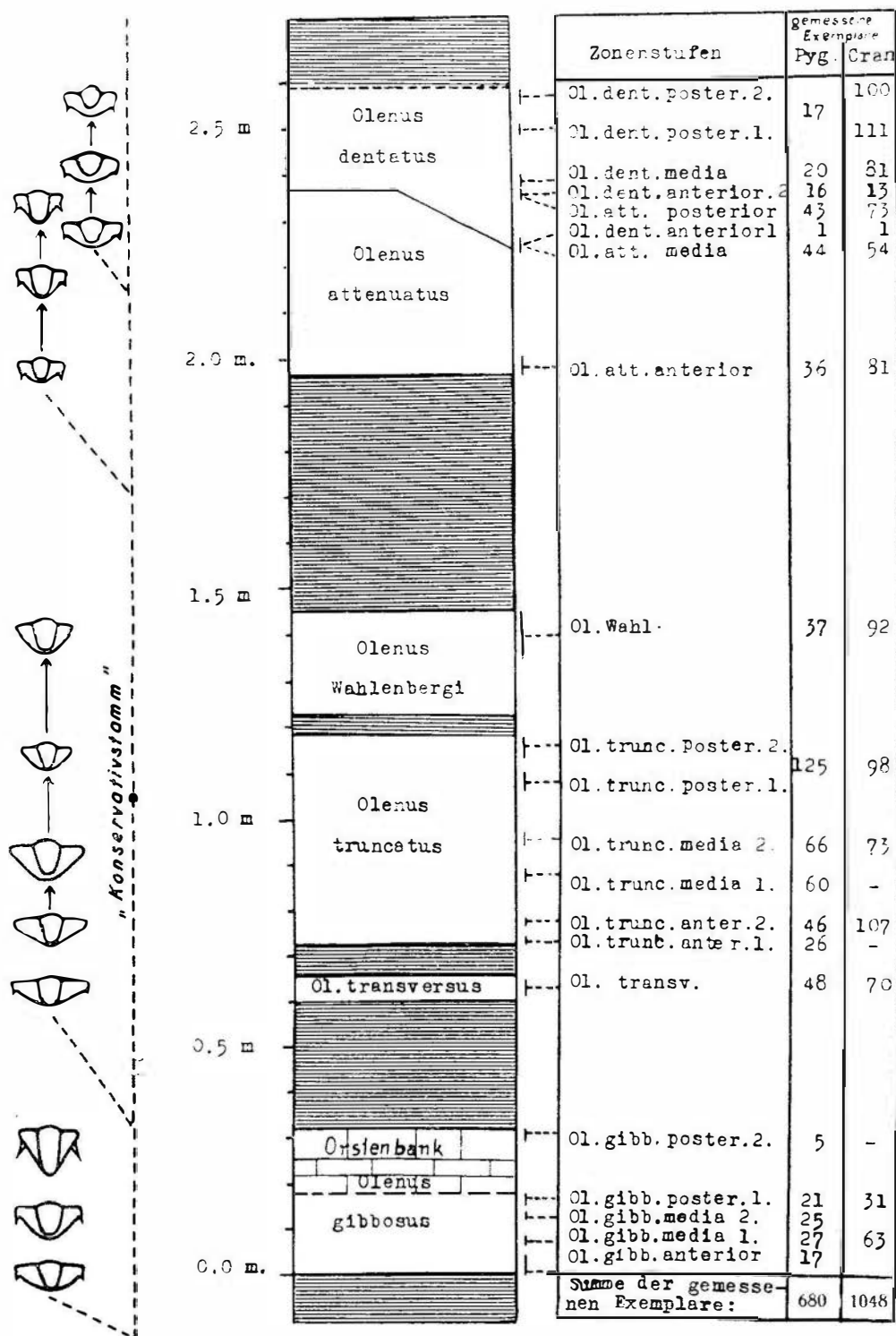


Fig. 15. Distribution of species of *Olenus* in the *Olenus* zone in Andrarum in Scania, Sweden. After Kaufmann, 1933a, p. 9, except that the photographs of the pygidia are substituted with outline drawings.

O. truncatus, which differs in having no pygidial spines. *O. wahlenbergi*, likewise without pygidial spines, apparently developed from *O. truncatus*. The pygidium developed from a transverse to a rather narrow pygidium within this series, thus corresponding to the evolution of the pygidium within the other species.

Kaufmann further showed that if one compares the above-mentioned species, there are certain features which undergo an evolution from the earlier to the later species. Thus the flip of the free cheek becomes more and more acute, the width of the glabella increases in relation to the length of the cranidium, and the sagittal length of the preglabellar field decreases. Altogether, the Scandinavian species of *Olenus* seem to form a group of closely related forms. The main differences between them are seen in plate 3.

If we compare the two latest known Scandinavian species (*O. rotundatus* and *O. scanicus*) with earlier species, it is interesting to observe that their palpebral lobes are smaller, especially in *O. scanicus*, which furthermore has the palpebral lobes closer to the glabella. These features anticipate the succeeding genera *Parabolina* and *Protopeltura*.

Three species which have so far only been recorded from Great Britain, namely *O. cataractes*, *O. micrurus*, and *O. mundus*, are less well known, and their stratigraphic position in relation to the Scandinavian species is not known. They all seem to be closely related, and *O. mundus* may possibly represent young specimens of *O. cataractes*, as pointed out by Lake (1908, p. 58). Their pygidia remind one especially of those of the later Scandinavian species, with which they may be closely related. It is even possible that a better knowledge of the British forms will show that some of them are conspecific with Scandinavian species. *O. ? bucephalus* (s. s.) from the Middle Lingula Flags in Wales is rather poorly known. It has small palpebral lobes, thus resembling *O. scanicus*, but it is possible that it is closer to early *Parabolina* species. Much the same can be said about *O. ? wilsoni* from the Woods Hollow boulders in Texas. *O. asiaticus* apparently is closest to *O. gibbosus*.

Olenus alpha n. sp.

Pl. 3; pl. 9, figs. 1—6.

N a m e: — The name *alpha* is given as this species is the earliest known *Olenus* species, and because it occurs in stage 2aa.

H o l o t y p e: — A cranidium (P. M. O. no. 66756) from the zone of *Agnostus pisiiformis* at Mælum, Ringsaker, Norway.

D i a g n o s i s: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine continuous with course of lateral margin; inner spine angle slightly obtuse; postocular cheeks somewhat narrower than glabella;

pygidium spineless. — It differs from the type species in having comparatively longer and wider glabella, shorter pygidium without spines and with wider pleural regions.

Description: — This is based on 8 cranidia and parts of cranidia, 7 more or less complete free cheeks, and one almost complete pygidium, all preserved in limestone.

Size of cranidium from 4.2 (length) \times 7.5 (width) to 7.8 \times 11.2 mm. Cranidium moderately convex (tr. & sag.). Cranidial furrows distinct. Cephalic axis tapered, truncate. Occipital ring without node, except in the smaller specimen. Curving furrow separates central lobe of occipital ring. S0—S3 present. S0 composite, continuous, S1—S3 discontinuous. S1 longest, bigeniculate, oblique backwards. S2 convex, less oblique. S3 short, almost transverse, less distinct. Length of preglabellar field somewhat less than one-fourth of that of cephalic axis. Border narrow, slightly convex in dorsal view, well arched in frontal view. Preocular margins almost parallel, but with rounded anterior corners. Eye ridges slightly oblique backwards. Palpebral lobes medium-sized, length about one-third of that of cephalic axis. Centres of palpebral lobes opposite S2. Width of interocular cheek about half that of glabella at eye-line. Postocular cheeks somewhat narrower than occipital ring (tr.). Postocular margins divergent, almost straight, only slightly sinuous.

Free cheeks elongate. Lateral border narrow and confluent with straight genal spine. Posterior border narrow and short, forming slightly obtuse angle with spine. Marginal furrows well impressed. Intramarginal area with genal caeca radiating from eye sinus. Doublure unknown.

Hypostoma and thorax unknown.

Pygidium transverse, about one-third as long as wide (2.7 \times 8.8 mm). Axis prominent, occupying about one-fourth of total width, with two rings and end-lobe of 2 or 3 fused rings, almost reaching posterior border. Pleural regions rather flat, with two pairs of shallow interpleural grooves. Facets small. No spines.

Test. Outer surface of cranidium appears smooth, but seems to be somewhat uneven in a very small scale.

Affinities: — *Olenus alpha* n. sp. resembles *O. dentatus* Westergård in having a comparatively large glabella, but otherwise the new species resembles more earlier forms like *O. gibbosus*. The cranidium of *O. alpha* looks "coarser" than those of the other *Olenus* species, and seems to point backwards to the non-olenid ancestral stock.

Occurrence: — Norway: Ringsaker (Mælum) — Zone of *Agnostus pisiformis* (2a α), associated with *Agnostus pisiformis* and *Proceratopyge nathorsti*.

Olenus asiaticus Kobayashi 1944.

- 1944b *Olenus asiaticus* Kobayashi, new species. — Kobayashi, p. 229, figs. 1a—b. (Descr. and figs. of cranidium.)
 1949 *Olenus asiaticus* Kobayashi — Kobayashi, p. 1. (Mentioned.)

Type data: — Holotype is the cranidium figured by Kobayashi (1944b), from the *Glyptagnostus* zone (black slate in the Upper Machari formation) in South Korea.

Diagnosis: — Differs from *Olenus gibbosus* in having longer prelabellar field and slightly larger palpebral lobes located more posteriorly. (Only the cranidium is known.)

Occurrence: — South Korea (*Glyptagnostus* zone).

Olenus attenuatus (Boeck 1838).

Pl. 3; text-fig. 16.

- 1838 *Trilobites attenuatus* — Boeck, p. 143. (Indifferent, short descr.)
 1854 *Olenus attenuatus* Boeck — Angelin, p. 43, pl. XXV, fig. 2. (Diagn. and rough fig. of dorsal shield.)
 1854 *Olenus aculeatus* n. sp. — Angelin, p. 43, pl. XXV, fig. 4. (Diagn. and rough fig. of dorsal shield.)
 1882 *Olenus aculeatus*, Ang. — Brögger, p. 99, pl. XII, figs. 6, 6a. (Remarks. Figs. of pygidium, restored thoracic segment, and restored cephalon.)
 1882 *Olenus attenuatus*, Boeck? — Brögger, p. 98, pl. XII, figs. 4, 4a—b. (Figs. of free cheek and pygidium.) (Fig. 4c is of *O. wahlenbergi*.)
 1907 *Olenus attenuatus*, Boeck? — Høltedahl, p. 14. (Recorded.)
 1910 *Olenus truncatus* (Brünnich) — Høltedahl, p. 5, pl. II, fig. 12. (Fig. of hypostoma of *O. attenuatus* or of the associated *O. wahlenbergi*.)
 1922 *Olenus attenuatus* (Boeck) — Westergård, p. 128, pl. IV, figs. 15—19; pl. V, figs. 1—9. (Descr. Figs. of dorsal shield, free cheeks, thoracic segment, pygidia, hypostoma, and 3 axial shields; one probably Angelin's original for *O. aculeatus*, another probably his original for *O. attenuatus*.)
 1923 *Olenus attenuatus* Boeck — Poulsen, p. 27, pl. I, fig. 7. (Descr. Fig. of fragment of cranidium and thoracic segments.)
 1933a *Olenus attenuatus* (Boeck) — Kaufmann, fig. 12. (Statistical investigation. Figs. of 3 pygidia.)
 1933b *Olenus attenuatus* (Boeck) — Kaufmann, p. 60, fig. 3. (Statistical investigation. Figs. of 2 pygidia.)
 1935 *Olenus attenuatus* — Kaufmann, fig. 6. (Figs. of 3 pygidia, copied from Kaufmann, 1933a.)
 1940a *Olenus attenuatus* (Boeck) — Størmer, p. 144. (A copy of Boeck's descr. Remarks.)
 1947 *Olenus attenuatus* (Boeck) — Westergård, p. 22. (Listed.)

Type data: — As pointed out by Størmer (1940a, p. 144) it has not been possible to trace any specimens of this form in the old collection of the Paleontological Museum in Oslo. Boeck (1838) based his species on material from Andrarum, Scania, Sweden. I select as neotype an axial shield

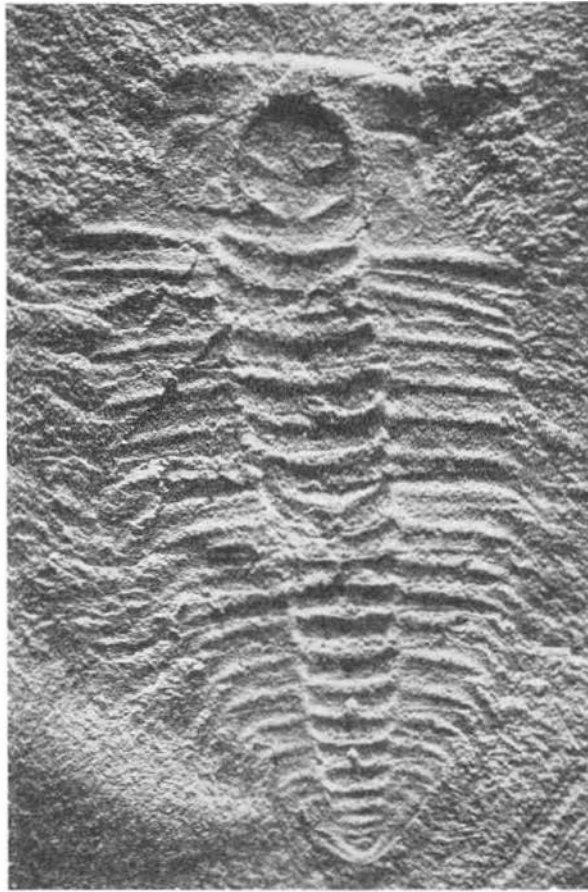


Fig. 16. Axial shield of *Olenus attenuatus* (Boeck), preserved in shale. Whitened with ammonium chloride. Not retouched. $\times 6.3$. P. M. O. no. 30843.
Toten in Østerdalen, Norway.

from this locality, figured by Westergård (1922, pl. V, fig. 2); probably Angelin's original.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine continuous with lateral margin; inner spine angle right-angled to slightly obtuse; 15 (or 16?) thoracic segments; axial spines; pygidium with 1 pair of marginal spines and 4—7 axial rings.

Remarks: — *O. attenuatus* seems to have had united free cheeks (cf. p. 91). The axial spines distinguish *O. attenuatus* from all other known *Olenus* species. According to Kaufmann (1933a) there are three successive intraspecific modifications of this species in Scania, namely, from below, "anterior", "media", and "posterior", the latter having the narrowest pygidium. Angelin's figured specimen of his *O. aculeatus* appears to belong to the early modification, and may be recognized as a subspecies of *O. attenuatus*. Angelin's figured specimen of *O. attenuatus* probably belongs to the modification "media" or "posterior".

Norwegian material: — This consists of detached parts of the dorsal shield, showing, however, the occipital spine and axial spines of thoracic segments and pygidia.

Occurrence: — Norway: Sandsvær (Krogsrud, Sandbakk core), Eiker (Krekling, Stablum core, Teigen core), Øyeren (Teigen), Østerdalen (Toten) — *Olenus* zone (2aβ), subzone of *Olenus attenuatus*; alone or associated with *Agnostus obesus*, and subzone of *Olenus wahlenbergi*; associated with *Agnostus obesus* and *Olenus wahlenbergi*. — Sweden (subzone of *Olenus attenuatus*), Denmark (Bornholm, subzone of *Olenus attenuatus*).

Olenus cataractes Salter 1864.

- 1864 *Olenus cataractes* — Salter, pl. VIII, figs. 14, 14a—b, p. 1. (Descr. Figs. of restored dorsal shields, pygidium, and pleurae.)
 1866 *Olenus cataractes*, n. sp. — Salter, p. 300, pl. 5, figs. 23, 23a—b. (Descr. Figs. of dorsal shield.)
 1873 *Olenus cataractes*, Salter — Salter, p. 7. (Remarks.)
 1908 *Olenus cataractes*, Salter — Lake, p. 56, pl. V, figs. 13—17; pl. VI, fig. 1. (Descr. Figs. of more or less complete axial and dorsal shields.)

Type data: — According to Lake (1908, p. 58), the specimen on which Salter (1864) based his description and restoration probably is an incomplete dorsal shield, preserved at the Museum of Practical Geology (no. 8946). The specimen was refigured by Lake (1908, pl. V, fig. 13).

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; 14 (or 15?) thoracic segments; no axial spines; pygidium with one pair of marginal spines and 4 axial rings.

Occurrence: — Wales (Lower Lingula Flags), England (Outwoods Shales, Lingula Flags Series).

Olenus dentatus Westergård 1922.

Pl. 3.

- 1922 *Olenus dentatus* n. sp. — Westergård, p. 130, pl. V, figs. 10—15. (Descr. Figs. of cranidia, free cheek, thoracic segments, and pygidia.)
 1933a *Olenus dentatus* Wdg. — Kaufmann, figs. 12, 18. (Statistical investigation, Figs. of 3 pygidia and free cheek.)
 1933b *Olenus dentatus* Westergård — Kaufmann, pp. 58—59. (Mentioned, recorded.)
 1935 *Olenus dentatus* — Kaufmann, fig. 6. (Figs. of 3 pygidia, copied from Kaufmann, 1933.)
 1947 *Olenus dentatus* Wgård. — Westergård, p. 22. (Distribution in Sweden.)

Type data: — As lectotype I select a cranidium figured by Westergård (1922, pl. V, fig. 10), from Andrarum in Scania, Sweden.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine continuous with course of lateral margin; inner spine angle slightly acute; narrow interocular cheeks; no axial spines; pygidium

with 1 pair of marginal spines; rounded anterior corners, and 3—4 axial rings.

Occurrence: — Sweden (*Olenus* zone, subzone of *Olenus dentatus*), Denmark (Bornholm, same horizon).

Olenus gibbosus (Wahlenberg 1821).

Pl. 1, fig. 1; pl. 3; pl. 9, fig. 7.

- 1821 *Entomostracites gibbosus* [partim] — Wahlenberg, p. 39, pl. I, fig. 4 [partim]. (Diagn., inadequate fig. of restored axial shield. According to Westergård, 1922, only the pygidium belongs to *O. gibbosus*.)
- 1822 *Paradoxides gibbosus* [Wahlenberg] — Brongniart, p. 35, pl. III, fig. 6 [partim]. (Remarks. Diagn. and fig. copied from Wahlenberg.)
- 1827 *Olenus gibbosus* [Wahlenberg] — Dahman, p. 256 (71) (1828; p. 56). (Descr.)
- 1827 *Trilobites gibbosus* [Wahlenberg] [partim] — Boeck, p. 24, figs. 2—9 [partim]. (Descr. of cranidium from Ringerike, Norway, and dorsal shield, cephalon, cranidium, free cheeks, and pygidium from Andrarum, Scania, Sweden. The Swedish specimens are stated to be kept in the collections of the Berlin University, and it has not been possible to trace the Norwegian specimen in the collections of the Paleontological Museum, Oslo. Judging from Boeck's figures, at least two different species seem to be present in his material.)
- 1837 *Olenus gibbosus* [Wahlenberg] — Hisinger, p. 19, pl. IV, fig. 3 [partim]. (Diagn. Fig. copied from Wahlenberg, 1821.)
- 1840 *Paradoxide gibbeux* [Wahlenberg] — Milne Edwards, p. 344. (Descr.)
- 1843 *Olenus gibbosus* [Wahlenberg] — Burmeister, p. 81, pl. 3, fig. 9. (Diagn., fig. of restored dorsal shield.)
- 1843 *Olenus gibbosus* Wahlenb. — Goldfuss, p. 545. (Listed.)
- 1847 *Olenus gibbosus* — Hawle & Corda, p. 84, pl. 5, fig. 47. (Mentioned. Inadequate fig. of restored dorsal shield.)
- 1847 *Odontopyge spinulosa* — Hawle & Corda, pp. 167—168, 175. (The description suits *Olenus gibbosus*.)
- 1854 *Olenus gibbosus*, Wahl. — Angelin, p. 44, pl. XXV, fig. 5. (Diagn., rough fig. of restored dorsal shield.)
- 1867 *Olenus gibbosus*, Wahl. — Belt, p. 295, pl. XII, figs. 5a—b. (Rough figs. of two dorsal shields.)
- 1882 *Olenus truncatus*, Brönn. ? — Brögger, p. 98, pl. XII, figs. 5, 5a—c. (Figs. of incomplete cranidium and 3 pygidia.)
- 1882 *Olenus gibbosus*, Wahl. — Brögger, p. 373. (Recorded.)
- 1884 *Olenus gibbosus*, Wahlenb. — Brögger, p. 257. (Recorded.)
- 1901 *Olenus truncatus* Brönn. (?) — Münster, p. 24. (Recorded.)
- 1908 *Olenus gibbosus* (Wahlenberg) — Lake, p. 54, pl. V, figs. 8—10. (Descr. Figs. of nearly complete dorsal shield and two cephalae with attached thoracic segments.)
- 1910 *Olenus truncatus* Brönn. — Høltedahl, p. 21, pl. II, fig. 11. (Fig. of larval cranidium.)
- 1922 *Olenus gibbosus* (Wahlenberg) — Westergård, p. 124, pl. III, figs. 1—10. (Descr. Figs. of axial shield, cranidia, free cheeks, and pygidia. The species is based on the pygidium figured and described by Wahlenberg, 1821. The pre-pygidial part of Wahlenberg's fig. is assigned to *O. wahlenbergi*.)
- 1923 *Olenus gibbosus* Wahlenberg — Poulsen, p. 26, pl. 1, fig. 4, 5? (Descr. Figs. of pygidium, free cheek, and conspecific? cephalon.)

- 1927 *Olenus gibbosus* (Wahlenb.) — Strand, p. 320, pl. II, figs. 1—14d. (Detailed descr. and figs. of larval stages. Figs. of adult cranium, free cheek, pygidium, and hypostoma.)
- 1929 *Olenus gibbosus* (Wahlenb.) — Strand, p. 356. (Recorded.)
- 1933a *Olenus gibbosus* (Wahlenberg) — Kaufmann, p. 12, figs. 5, 12. (Statistical investigation. 5 intraspecific forms are recognized. Figs. of 5 pygidia.)
- 1933b *Olenus gibbosus* (Wahlenberg) — Kaufmann, pp. 58, 59. (Mentioned.)
- 1934a *Olenus gibbosus* — Størmer, p. 333. (Listed.)
- 1935 *Olenus gibbosus* (Wahlenberg) — Kaufmann, p. 22, fig. 6. (Statistical investigation. Figs. of 5 pygidia, copied from Kaufmann, 1933a.)
- 1942 *Olenus gibbosus* (Wahlenberg) — Størmer, p. 81, figs. 9 a—e, 10a—e. (Descr. and figs. of 5 larval stages.)
- 1944b *Olenus gibbosus* (Wahlenberg) — Kobayashi, p. 230, text-fig. 2. (Mentioned. Fig. of restored dorsal shield.)
- 1947 *Olenus gibbosus* (Wahl.) — Westergård, p. 22. (Distribution in Sweden.)
- Non 1838 *Trilobites gibbosus* var. — Boeck, p. 143 (= *Parabolina spinulosa*).

Type data: — Wahlenberg's figure (1821, pl. I, fig. 4) is based on the pygidium of one species and the prepygidial part of another. Westergård (1922) preferred to maintain the name *gibbosus* for the species represented by the pygidium, and give the name *O. wahlenbergi* to the other species. A neotype should be chosen from material from Andrarum, Sweden, preferably from material collected by Wahlenberg.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine continuous with course of lateral margin; obtuse inner spine angle; 15 thoracic segments; no axial spines; subtriangular pygidium with 1—2 pairs of marginal spines and 5—8 axial rings.

Remarks: Material from Trolmen quarry, Kinnekulle, Västergötland, Sweden, with unusually well-preserved test shows that the inner surface of the test is very finely tuberculate.

Norwegian material — Some pygidia from Ringsaker seem to belong to Kaufmann's intraspecific modification "anterior", the earliest modification of this species. Other material agrees exactly with Kaufmann's "posterior 2", his uppermost modification. Intermediate modifications appear to be present, but owing to the state of preservation it is often difficult to determine the modification. Free cheeks with a more expanded flip than usual in *O. gibbosus* are often found in the Ringsaker material.

Occurrence: — Norway: Skien-Brevik (Ombordsnes), Eiker-Sandsvær (Sandbakk core), Ringerike (Viul), Ringsaker (Evjevika, Ringstrand, Vinjalandet), Fluberg (Bratland), Snertingdal, Vardal, Østerdalen (Nødseter near Osensjøen, boulder at Eidskog) — *Olenus* zone (2a β), subzone of *Olenus gibbosus*; alone or associated with *Agnostus obesus* \pm *Glyptagnostus reticulatus reticulatus*. — Sweden (same horizon), Denmark (Bornholm, same horizon), Wales (Lower Lingula Flags).

Olenus micrurus Salter 1849.

- 1849 *Olenus micrurus* — Salter, pl. IX, figs. 1—2, (3?), p. 1. (Descr. Figs. of dorsal shield and an imperfect axial shield, which may not belong to this species.)
 1866 *Olenus micrurus*, Salter — Salter, p. 300, pl. 2, figs. 5, (6?). (Remarks. Figs. of dorsal shield, and an imperfect axial shield, which may not belong to this species.)
 1873 *Olenus micrurus*, Salter — Salter, p. 11. (Remarks.)
 1908 *Olenus micrurus*, Salter — Lake, p. 55, pl. V, figs. 11—12. (Descr. Figs. of 2 incomplete dorsal shields, Salter's originals.)

Type data: — As lectotype I select an incomplete dorsal shield figured by Salter (1849, pl. IX) and refigured by Lake (1908, pl. V, fig. 12). Lower Lingula Flags, Trawsfynydd.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine continuous with lateral margin; 14 thoracic segments; axial tubercles; pygidium with 3—4 axial rings.

Occurrence: — Wales (Lower Lingula Flags).

Olenus mundus Lake 1908.

- 1908 *Olenus mundus*, sp. nov. — Lake, p. 58, pl. VI, figs. 2—5. (Descr. Figs. of 2 dorsal shields and two larval dorsal shields.)

Type data: — As lectotype I select a dorsal shield figured by Lake (1908, pl. VI, fig. 2), from the Lower Lingula Flags at Trefgarn Bridge, Haverfordwest, Wales.

Remarks: — As suggested by Lake, this form may represent young specimens of *O. cataractes*.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; 14 thoracic segments; no axial spines; pygidium with 1 pair of marginal spines and 2 axial rings.

Occurrence: — Wales (Lower Lingula Flags).

Olenus rotundatus Westergård 1922.

Pl. 3.

- 1922 *Olenus rotundatus* n. sp. — Westergård, p. 131, pl. VI, figs. 1—5. (Descr. Figs. of cranidia, free cheek, and pygidia.)
 1947 *Olenus rotundatus* Wgård. — Westergård, p. 22. (Distribution in Sweden.)

Type data: — As lectotype I select a cranidium figured by Westergård (1922, pl. VI, fig. 1). *Olenus* zone, Mossebo, Västergötland, Sweden.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine deviating slightly from course of lateral margin; slightly obtuse inner spine angle; no axial spines; pygidium with 1 pair of marginal spines, rounded anterior corners, and 5—6 axial rings.

Occurrence: — Sweden (*Olenus* zone, subzone of *Polyphyma angelini* and *Olenus scanicus*).

Olenus scanicus Westergård 1922.

Pl. 3.

- 1922 *Olenus scanicus* n. sp. — Westergård, p. 131, pl. VI, figs. 6—8. (Descr. Figs. of cranium, free cheek, and pygidium.)
1947 *Olenus scanicus* Wgård. — Westergård, p. 22. (Distribution in Sweden.)

Type data: — As lectotype I select the cranium figured by Westergård (1922, pl. VI, fig. 6), from Andrarum in Scania, Sweden.

Diagnosis: — An *Olenus* species with: small palpebral lobes; cheek spine continuous with lateral margin; inner spine angle right-angled; no axial spines; pygidium with 3 pairs of marginal spines and 3—4 axial rings.

Occurrence: — Sweden (*Olenus* zone, subzone of *Polyphyma angelini* and *Olenus scanicus*).

Olenus transversus Westergård 1922.¹

Pl. 3.

- 1922 *Olenus transversus* Linnarsson in museo — Westergård, p. 125, pl. III, figs. 11—17 (pl. V, figs. 16—17?). (Descr. Figs. of almost complete axial shield, crania, free cheeks, and pygidia.)
1933a *Olenus transversus* Linnarsson in museo Wdg. — Kaufmann, figs. 3 (St. 4b—St. 7b), 6, 12, 17. (Statistical investigation. Figs. of larval and adult pygidia.)
1935 *Olenus transversus* — Kaufmann, fig. 6. (Fig. of pygidium, copied from Kaufmann, 1933a.)
1947 *Olenus transversus* (Linnr.) Wgård. — Westergård, p. 22. (Distribution in Sweden.)

Lectotype (here selected): — An almost complete axial shield figured by Westergård (1922, pl. II, fig. 11). Collected by G. C. v. Schmalensee in 1878 in shale at Andrarum, Scania, Sweden.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine continuous with lateral margin; obtuse inner spine angle; 13 thoracic segments; no axial spines; spineless pygidium with 4—5 axial rings.

Norwegian material: — A few pygidia and a cranium apparently belonging to this species have been found.

Occurrence: — Norway: Ringsaker (Evjevika), Østerdalen (Boulder at Eidskog) — *Olenus* zone (2aβ), associated with *Olenus gibbosus* "posterior 2". — Sweden (In Scania Kaufmann, 1933a, found *O. transversus* in a separate horizon, well above that of *O. gibbosus* "posterior 2").

¹ Linnarsson used this name on museum labels, but Westergård must be considered the author, as he described the species.

Olenus truncatus (Brünnich 1781).

Pl. 3.

- 1781 *Trilobus truncatus* — Brünnich, p. 391. (Inexpressive diagn., remarks.)
- ?1843 *Olenus gibbosus* [Wahlenb.] — Burmeister, p. 81, pl. III, fig. 9. (Indifferent diagn. and descr. Inadequate fig. of restored dorsal shield.)
- 1854 *Olenus truncatus* Brünn. — Angelin, p. 43, pl. XXV, fig. 1. (Points out the differences between this species and *O. gibbosus*, believed to be synonyms by earlier writers. Rough fig. of dorsal shield.)
- ?1890 *Olenus truncatus* Brünnich — Pompecki, p. 88, pl. IV, figs. 25—26. (De cr. Figs. of cephalon, thoracic segment, and pygidium.)
- 1908 *Olenus truncatus* (Brünnich) — Lake, p. 52, pl. V, figs. 1—7. (Descr. Discussion of species. Figs. of 4 more or less complete dorsal shields, and parts of others.)
- 1915 *Olenus truncatus* Brünn. — Høltedahl, p. 14. (Recorded.)
- 1922 *Olenus truncatus* (Brünnich) — Westergård, p. 126, pl. III, figs. 18—19; pl. IV, figs. 1—4. (Descr. Figs. of dorsal shield, axial shield, cranidium, free cheeks, and hypostoma.)
- 1923 *Olenus truncatus* Brünnich — Poulsen, p. 25, pl. I, fig. 6, text-fig. 6. (Descr. Figs. of free cheek and hypostoma, copied from Westergård, 1922, and of dorsal shield.)
- 1929 *Olenus truncatus* (Brünnich) [partim] — Strand, p. 357. (Recorded. A great part of Strand's material belongs to *O. gibbosus*.)
- 1933a *Olenus truncatus* (Brünnich) — Kaufmann, fig. 12. Statistical investigation. Figs. of 3 pygidia.)
- 1933b *Olenus truncatus* (Brünnich) — Kaufmann, p. 60, fig. 2. (Statistical investigation. Figs. of 2 pygidia.)
- 1934a *Olenus truncatus* — Størmer, p. 333. (Listed.)
- 1935 *Olenus truncatus* (Brünnich) — Kaufmann, p. 25, fig. 6. (Statistical investigation. Figs. of 3 pygidia, copied from Kaufmann, 1933a.)
- 1947 *Olenus truncatus* (Brünn.) — Westergård, p. 22. (Distribution in Sweden.)
- 1953 *Olenus truncatus* Brünnich — Hupé, p. 208, fig. 125; 1. (Fig. of restored dorsal shield.)
- 1953 *Olenus truncatus* — Høltedahl, p. 183, fig. 69, 18—19. (Figs. of cranidium and pygidium.)
- Non 1882 *Olenus truncatus* Brünn.? — Brögger (= *O. gibbosus*); non 1901 *Olenus truncatus* Brünn.? — Münster (= *O. gibbosus*); non 1910 *Olenus truncatus* Ang. — Høltedahl, p. 23, pl. II, fig. 11 (= *O. gibbosus*); non 1910, *Olenus truncatus* Ang. — Høltedahl, p. 23, pl. II, fig. 12 (= *O. attenuatus* or *O. wahlenbergi*); non 1926 *Olenus* cf. *O. truncatus* — Butts (= *Proaulacopleura buttsi* Kobayashi 1936).

Type data: — A neotype should be chosen, preferably from Andrarum in Scania, Sweden, which is the locality mentioned by Brünnich.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine continuous with course of lateral margin; right-angled inner spine angle; 13 thoracic segments; no axial spines; spineless pygidium with 5—6 axial rings.

Norwegian material: — Kaufmann's modification "posterior" seems to be the most common. A form from Ringerike appears to be inter-

mediate between *O. truncatus* "posterior 2" and *O. wahlenbergi*. This is not so surprising, as Kaufmann believed that *O. wahlenbergi* developed from *O. truncatus*. I have preferred to regard the intermediate form as belonging to *O. truncatus*, as the apertures of the eyes are not as large as in *O. wahlenbergi*, and the cheek spine does not deviate from the lateral rim.

Occurrence: — Norway: Ringerike (Hval, Viul), Ringsaker (Evjevika), Valdres (Tonsåsen) — *Olenus* zone (2a β), subzone of *Olenus truncatus*; alone, or associated with *Agnostus obsesus*. — Sweden (same horizon), Denmark (Bornholm, same horizon), Great Britain (Wales, Lower Lingula Flags), ?Texas (Marathon uplift).

Olenus wahlenbergi Westergård 1922.

Pl. 3.

- 1821 *Entomostracites gibbosus* [partim] — Wahlenberg, p. 39, pl. I, fig. 4 [partim]. (According to Westergård, 1922, the prepygidial part of the reconstruction of the dorsal shield belongs to *O. wahlenbergi*, whereas the pygidium belongs to *O. gibbosus*.)
- 1882 *Olenus attenuatus*, Boeck [partim] — Brögger, p. 98, pl. XII, fig. 4c (non figs. 4, 4a—b = *O. attenuatus*). (Fig. of pygidium.)
- ?1910 *Olenus truncatus*, Brünn. — Høltedahl, p. 5, pl. II, fig. 12. (Fig. of hypostoma of *O. wahlenbergi* or the associated *O. attenuatus*.)
- 1922 *Olenus Wahlenbergi* n. sp. — Westergård, p. 128, pl. IV, figs. 5—14. (Descr. Figs. of 2 axial shields, cranium, free cheeks, and pygidium.)
- 1923 *Olenus Wahlenbergi* Westergård — Poulsen, p. 28, text-fig. 7. (Descr. Figs. of cranium and free cheek copied after Westergård 1922.)
- 1933a *Olenus Wahlenbergi* Westergård — Kaufmann, fig. 12. (Statistical investigation. Fig. of pygidium.)
- 1933b *Olenus wahlenbergi* Westergård — Kaufmann, p. 59. (Mentioned.)
- 1935 *Olenus wahlenbergi* — Kaufmann, fig. 6. (Fig. of pygidium, copied after Kaufmann, 1933a.)
- 1947 *Olenus wahlenbergi* Wgård. — Westergård, p. 22. (Distribution in Sweden.)

Lectotype (here selected): — An axial shield figured by Westergård (1922, pl. IV, fig. 5), from Andrarum, Scania, Sweden.

Diagnosis: — An *Olenus* species with: medium-sized palpebral lobes; cheek spine deviating just very faintly from course of lateral margin; inner spine angle right-angled to slightly obtuse; 15 (or 16?) thoracic segments; spineless pygidium with 5—6 axial rings.

Remarks: — The free cheek of this species is rather characteristic, with large eye aperture, well expanded flip, and the cheek spine deviating slightly from the course of the lateral rim.

Norwegian material: — Detached parts of dorsal shields. The material from Teigen, Øyeren, described by Brögger, 1882, as *O. truncatus*, belongs to two associated species; *O. wahlenbergi* and *O. attenuatus*. The teil-zones of these two species are well separated in Scania (Kaufmann, 1933a). Both species from Teigen seem to agree well with the Swedish material, but the Teigen material is too small to allow a detailed comparison.

Occurrence: — Norway: Øyeren (Teigen), Ringsaker (Båshus) — *Olenus* zone (2aβ), subzone of *Olenus wahlenbergi*; associated with *Agnostus obesus* ± *Olenus attenuatus*. — Sweden (same subzone, but not associated with *O. attenuatus*), Denmark (Bornholm, as in Sweden).

Olenus? bucephalus (Belt 1868).

- 1868 *Conocoryphe? bucephala*, spec. nov. — Belt, p. 10, pl. II, figs. 1—6. (Descr. Somewhat schematic figs. of almost complete dorsal shield, cranidia, and pleuron.)
 ?1873 *Conocoryphe Williamsons*, n. sp. — Salter, p. 12. (Remarks.)
 1900a *Conocoryphe bucephala* (Belt) — Reed, p. 252. (Provisionally assigned to *Olenus*.)
 1919 *Beltella bucephala* (Belt) — Lake, p. 106, pl. XII, figs. 13—15, 11?, 12? (Descr. Figs. of incomplete dorsal shield and cranidia, and axial shield and dorsal shield of *Conocoryphe williamsoni* Salter.)
 1919 *Beltella verisimilis* (Salter) [partim] — Lake, pl. XIII, figs. 4—5 only. (Figs. of cranidia with some attached segments.)
 1922 *Beltella bucephala* (Belt) — Westergård, p. 141. (Compared with *Protopeltura? solitaria*.)
 1954 *Beltella bucephala* (Belt) — Wilson, p. 276. (Remarks.)
 Non 1827 *Olenus bucephalus* [(Wahlenberg 1821)] — Dalman (= *Paradoxides paradoxissimus*.)

Type data: — As lectotype I select the almost complete dorsal shield figured by Belt (1868, pl. II, fig. 1) from the Upper Ffestiniog Beds, Wales.

Remarks: — The generic reference of this species is uncertain. As figured by Belt (1868), its genal spines are confluent with the lateral margin of the fixed cheeks, and it therefore does not seem to belong to *Beltella*. Lake (1919) included in this species also *Conocoryphe williamsoni* Salter 1873, which, however, comes from a higher level (Upper Lingula Flags) and may not be conspecific. Two compressed specimens which were assigned to *Beltella verisimilis* by Lake may belong to the present species. They come from the same horizon and the differences appear to be due to the different compression. I assign the species tentatively to *Olenus*, but it may possibly belong to a group intermediate between *Olenus* on the one side and *Protopeltura* and *Parabolina* on the other. The rather similar *Protopeltura? solitaria* is of about the same age. *O.? bucephalus* and *P.? solitaria* may be related to species like *Olenus micrurus* and *O. cataractes*.

Occurrence: — Wales (Upper part of Middle Lingula Flags, ?Upper Lingula Flags).

Olenus? wilsoni n. sp.

Text-fig. 17.

- 1954 *Parabolinella incerta* (Rasetti) — Wilson, p. 280, pl. 26, figs. 18—22. (Descr. Figs. of cranidia and free cheeks.)

Name: — Given in honour of J. L. Wilson, who first described it.

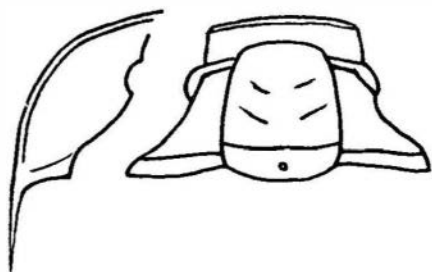


Fig. 17. *Olenus? wilsoni* n. sp. Outline drawing of free cheek and cranidium, based on photographs published by Wilson (1954, pl. 26). $\times 4$.

Holotype: — A cranidium figured by Wilson (1954, pl. 26, fig. 21), from a Woods Hollow boulder (type 5), Marathon uplift, Texas. University of Texas, Bureau of Economic Geology, no. CW-216.

Diagnosis: — An *Olenus?* species with comparatively short preglabellar field; small palpebral lobes; inner spine angle obtuse.

Description: — An adequate description is given by Wilson. The genal angle of the free cheek is best seen in the free cheek figured by him in figure 22 of plate 26.

Remarks: — This species was assigned to *Parabolinella incerta* (Rasetti) by Wilson (1954). It differs from this in having a more parabolic outline of the glabella, a shorter preglabellar field, and apparently also in having the eyes further forwards. *Olenus? wilsoni* n. sp. occurs in the Upper Dresbachian (*Aphelaspis* zone?), whereas *Parabolinella? incerta* occurs in the *Hungaia* zone, which most probably is of Trempealeauian age, although it has been suggested that it is of Middle Franconian age (Wilson, 1954). Even if the *Hungaia* zone is of Middle Franconian age, it would be most unusual that an olenid had such a long vertical range.

The taxonomic position of *Olenus? wilsoni* n. sp. is questionable, also because its pygidium is not known. It resembles both *Olenus* and *Parabolina*. Its cranidium is rather *Parabolina*-like, but the course of the facial sutures behind the eyes is more sinuous and convex, thus reminding one more of *Olenus*. Its free cheeks with slightly obtuse angle between the spine and the posterior margin, is only equalled in some *Olenus* species, whereas this angle in *Parabolina* is acute or at the most right-angled. The posterior marginal furrow in the free cheek of *Olenus? wilsoni* runs obliquely forwards. This is another feature which is known in *Olenus*, but not in *Parabolina*. The comparatively large size of the glabella in *Olenus? wilsoni* n. sp. reminds one of *Parabolina*. However, also the late *Olenus* species *O. dentatus* has a rather dominating glabella. On the whole, *O.? wilsoni* n. sp. appears to be intermediate between *Olenus* and *Parabolina*, but perhaps closest to the late *Olenus* species, like *O. dentatus* and *O. scanicus*. In the main features of the cranidium it resembles mostly *O. dentatus*, but its small eyes and free cheeks resemble more those of *O. scanicus*.

Occurrence: — Texas (*Aphelaspis* zone?).

Genus *Parabolina* Salter 1849.

Synonyms: — Corda (1847, p. 167) erected a genus *Odontopyge*, and cited as the only species *Od. spinulosa*. On page 167 he referred to it as *Odontopyge spinulosa*, nob., but this does not mean that he regarded it as

a new species, as he added "nob." to all species which he transferred to a new genus. Furthermore, it appears from the text that he meant the Swedish species "*Olenus*" *spinulosus*. It is obvious that his description of the species is not based on material of *Parabolina spinulosa*, but of *Olenus gibbosus*. Fortunately, *Odontopyge* Corda 1847 is a homonym of *Odontopyge* Brandt 1841, and thus not valid.

Type species: — *Entomostracites spinulosus* Wahlenberg 1821, by monotypy.

Diagnosis: — Oleninae with: facial sutures subparallel or converging in front of eyes; small or medium-sized palpebral lobes with anterior or intermediate position; 3 (—4?) pairs of glabellar furrows; preglabellar field absent or present; free cheeks with spine continuous with lateral margin, or diverging very slightly from it outwards; 12 thoracic segments (where known); pleurae with pleural spines (sometimes macrospines); transversely subelliptical to sub-semicircular pygidium, with or without marginal spines.

Remarks: — *Parabolina* resembles *Olenus* rather much. *Olenus* shows, however, less variation, and usually a *Parabolina* species shows one or more features which are rare or unknown in *Olenus* such as: small, anteriorly situated palpebral lobes, very short or no preglabellar field, S1 united across the glabella, longer pygidial spines, and presence of macropleurae.

Namiolenoides was erected as a subgenus of *Parabolina* by Rusconi (1953). However, its type species is probably no olenid, and the subgenus is here removed from the Olenidae (cf. p. 24).

Included species: —

- Parabolina acanthura* (Angelin 1854)
- P. andina* (Hoek 1912) (= *P. argentina*)
- P. argentina* (Kayser 1867)
- P. brevispina* Westergård 1922
- P. dawsoni* Matthew 1901
- P. expectans* (Barrande 1868) (= *P. frequens*)
- P. frequens* (Barrande 1868)
- P. guembeli* (Barrande 1868) (= *P. frequens*)
- P. heres heres* Brögger 1882
- P. heres grandis* Matthew 1892 (= ? *P. heres lata*)
- P. heres hexacantha* Westergård 1943 (= ? *P. heres lata*)
- P. heres lata* Matthew 1892
- P. jemtlandica* Westergård 1922
- P. kinnekullensis* n. sp.
- P. lapponica* Westergård 1947
- P. lobata lobata* (Brögger 1882) (earlier: *Ctenopyge*?)
- P. lobata praecurrens* Westergård 1944
- P. longicornis* Westergård 1922 (= *P. lobata*)
- P. longicornis praecurrens* Westergård 1944 (= *P. lobata praecurrens*)

P. megalops Moberg & Möller 1898
P. mobergi Westergård 1922
P. serrata (Salter 1864) (= *P. spinulosa*)
P. sexdentata (Brøgger 1884) (= *P. spinulosa*)
P. spinulosa (Wahlenberg 1821)
P. tetracanthura (Matthew 1892) (earlier: *Protopeltura*)
 and possibly also:
P.? *quadrisulcata* n. sp.

The two incomplete cranidia described as *Conocephalites contiguus* by Matthew (1892, p. 58, pl. XIII, figs. 14a—b) may possibly be immature cranidia of some olenid, perhaps a *Parabolina* species.

Parabolina? *incerta* Rasetti 1945 has been removed to *Parabolinella?*

Parabolina? *australis* Rusconi 1951 and *Parabolina?* (*Namiolenoides*) *asperoensis* Rusconi 1952 are probably not olenids (cf. pp. 24, 25). *P.?* *australis* was transferred to *Triarthropsis* by Rusconi (1953b).

Occurrence: — Norway (*Parabolina* zone to Lower Tremadocian), Sweden (*Parabolina* zone to *Acerocare* zone), Denmark (*Parabolina* zone to *Acerocare* zone), Poland (*Peltura* zones), Germany (Lower? Tremadocian), England (Orusia Shales), Wales (Upper Lingula Flags), E. Canada (*Parabolina* zone, *Peltura* zones), S. America (Tremadocian).

Phylogeny: — The earliest known *Parabolina* species, *Parabolina brevispina* from the lower half of the *Parabolina spinulosa* zone, resembles *Olenus scanicus*, which has a similar pygidium, and smaller and more anteriorly situated palpebral lobes than are usual in *Olenus*. *Parabolina brevispina* furthermore resembles *Protopeltura*, especially in the cranidium, whereas it differs from it in having the cheek spines continuing the course of the lateral margin, and in having a typical *Parabolina* pygidium with distinct pleural furrows entering the base of the marginal spines. There can be no doubt that *Parabolina brevispina* and *Protopeltura* are closely related, and that this group developed from *Olenus*. In spite of its pelturoid cranidium, *Parabolina brevispina* is very close to, and apparently a forerunner of *P. spinulosa*, the type species, which occurs in the upper half of the *Parabolina spinulosa* zone. *P. spinulosa* differs in having wider pleural regions and fixed cheeks, and in having longer spines. The only specimen known of *Parabolina?* *quadrisulcata* n. sp., a cranidium, comes from the same horizon as *P. spinulosa*. The cranidium is remarkable in having 4 distinct pairs of glabellar furrows, and in having the palpebral lobes rather far from the glabella; in this respect recalling *Olenus*, although the palpebral lobes are small and have a rather anterior position. *P. tetracanthura* from the *Parabolina* zone in New Brunswick may be rather close to *P. spinulosa*. *P. spinulosa* occurs also at the very base of the *Leptoplastus* zone (subzone of *Leptoplastus paucisegmentatus*), but no other *Parabolina* species are known from this zone. The first species known to occur after *P. spinulosa*, is *P. mobergi*

from the upper half of the zone of *Peltura minor*. It has the typical *Parabolina* pygidium and free cheeks, but the borders of the free cheeks are unusually wide. Its cranidium differs from those of earlier species in having diverging preocular margins. The next species to appear are *P. lapponica* and *P. dawsoni* in the zone of *Peltura scarabaeoides*. *P. lapponica* is incompletely known. *P. dawsoni* (from New Brunswick, associated with i. a. *Ctenopyge pecten*) is a typical *Parabolina* species, but has only one pair of marginal spines in the pygidium. Several *Parabolina* forms occur in the subzone of *Parabolina lobata* in the upper part of the zone of *Peltura scarabaeoides*, namely *P. lobata praecurrens*, *P. lobata lobata*, and *P. kinnekullensis* n. sp.. Whereas *P. lobata praecurrens* has no preglabellar field like the earlier species except *P. lapponica* and *P. dawsoni*, the others have a short preglabellar field. *P. lobata* differs from earlier species in having some pleural macrospines and more broad-based marginal spines in the pygidium. Furthermore it has wider pleural regions and fixed cheeks. *P. kinnekullensis* n. sp. is interesting because it has an almost entire pygidium, with only very small marginal spines. Above these species come *P. megalops* in the subzone of *Peltura paradoxa*, and *P. heres heres*, *P. heres lata* (= *P. heres hexacantha*), and *P. acanthura*, which succeed each other in that order in the *Acerocare* zone. *P. acanthura* is also known from the base of the Dictyonema Shales. These late species are surprisingly like *P. spinulosa*, except that they have a distinct preglabellar field. Furthermore, all but *P. acanthura* have the palpebral lobes more distant from the glabella, and *P. acanthura* and *P. megalops* have an acute (instead of right-angled) inner spine angle. The stratigraphic position of *P. jemtlandica* is not quite certain; apparently it comes from the zone of *Acerocare*. Its pygidium is a typical *Parabolina* pygidium, but the free cheeks have a rather wide border, thus recalling *P. mobergi*. *P. argentina* from the Lower Tremadocian in South America, somewhat resembles *P. lobata*, i. a. in having pleural macrospines, but differs in having an entire pygidium. *P. frequens* from the Lower? Tremadocian in Germany seems to be closest to *P. argentina*, but has a spinose pygidium.

Regarding the phylogeny of *Parabolina* as a whole, there is a change from the pelturoid cranidium of *P. brevispina* to the typical *Parabolina* cranidium of *P. spinulosa*, but later evolutionary changes are surprisingly small, except that the later species usually have a preglabellar field, as had *Olenus*, the ancestral genus of *Parabolina*. Furthermore, some of the later *Parabolina* species have an acute instead of a right-angled inner spine angle, thus recalling the evolutionary development of the free cheeks of *Olenus*. New features in later *Parabolina* species are the development of pleural and axial macrospines, S1 united across the glabella, and entire pygidium (in *P. argentina*). As discussed elsewhere (p. 130), *Parabolina* may have given rise to other genera with entire pygidia.

Parabolina acanthura (Angelin 1854).

Pl. 7; pl. 10, figs. 1—6.

- 1854 *Olenus? acanthurus* n. sp. — Angelin, p. 44, pl. XXV, fig. 7. (Inexpressive diagn. Inadequate fig. of restored dorsal shield.)
- 1898 *Parabolina acanthura* Ang. sp. — Moberg & Möller, p. 259, pl. 12, figs. 1—7; pl. 14, figs. 15—16. (Descr. Figs. of hypostoma and all parts of dorsal shield, also almost complete dorsal shield.)
- 1922 *Parabolina acanthura* (Angelin) — Westergård, p. 137, pl. VII, figs. 9—16. (Figs. copied from Moberg & Möller, 1898.)
- 1923 *Parabolina acanthura* Angelin — Poulsen, p. 31, text-figs. 10—11. (Figs. of hypostoma, free cheek, pleurae, and copies of some of Moberg & Möller's figs.)
- 1947 *Parabolina acanthura* (Angelin) — Westergård, p. 24. (Distribution in Sweden.)
- Non 1882 *Protopeltura acanthura*, Ang. — Brögger (= *Protopeltura praeursor*).

Type data: — As lectotype should be chosen a specimen from Angelin's locality (Sandby, Scania, Sweden), from Angelin's material.

Diagnosis: — A *Parabolina* species with: moderately wide pleural regions and fixed cheeks; short preglabellar field; small palpebral lobes far forwards and close to glabella; free cheeks with acute inner spine angle; 12 thoracic segments; moderately long pleural spines; pygidium with 3—4 axial rings and 3—4 pairs of short marginal spines.

Norwegian material: — Only a few detached parts of the dorsal shield have been found, including free cheeks with the characteristic acute angle between the spine and the posterior margin. One free cheek was found in the Stablum core (Eiker) about 40 cm above layers with *Parabolina heres* and about 160 cm below layers with *Dictyonema flabelliforme*.

Occurrence: — Norway: Røyken (Nærsnes), Eiker (Stablum core). — *Accrocare* zone (2d_e), subzone of *Acerocare ecorne*. Alone, or associated with *Accrocare ecorne* and *Pelturina punctifera* n. sp. Also occurs at base of the Lower Tremadocian, associated with *Boeckaspis hirsuta*. — Sweden (*Acerocare* zone, subzone of *Accrocare ecorne*.)

Parabolina argentina (Kayser 1876).

- 1876 *Olenus argentinus* n. sp. — Kayser, p. 6, pl. I, figs. 1—3. (Descr. Figs. of cranidia and cephalon.)
- 1882 *Olenus argentinus*, Kayser — Brögger, p. 148. (Doubts its inclusion in *Olenus*.)
- 1897 *Olenus argentinus* — Kayser, p. 306. (Suggests that it may belong to *Crepicephalus*.)
- 1912 *Olenus* cf. *argentinus* Kayser — Hoek, p. 209, pl. VII, fig. 10. (Descr. Figs. of cranidium and free cheek.)
- 1912 *Parabolinella andina* n. sp. — Hoek, p. 214, pl. VII, figs. 7—9. (Descr. Figs. of dorsal shields and pygidium.)
- 1936a *Olenus? argentinus* Kayser — Kobayashi, p. 95. (Discussed.)
- 1937c "*Olenus*" *argentinus* (Kayser) — Kobayashi, p. 474, pl. IV, figs. 6—9, text-fig. 6. (Descr. Figs. of cranidia and free cheeks. A copy of Kayser's figure.)

- 1937c *Parabolina andina* (Hoek) — — Kobayashi, p. 477, pl. IV, figs. 10—13; pl. VIII, fig. 3. (Remarks. Figs. of dorsal and axial shields, pygidium, thoracic segments and hypostoma.)
- 1938 "*Olenus*" *argentinus* Kayser — — Harrington, pp. 138, 267, 269, 251, 256, 258. (Mentioned.)
- 1938 *Parabolina andina* (Hoek) Kobayashi — — Harrington, p. 198, pl. IX, figs. 7, 9, 11. (Remarks. Figs. of parts of dorsal shields.)
- 1943b *Parabolina andina* (Hoek) Kobayashi — — Harrington & Leanza, p. 347, pl. II, figs. 1, 6. (Descr. Figs. of dorsal shield and cranidium.)
- 1948 *Parabolina andina* (Hoek) — — Richardson, p. 369. (Reports it from Newfoundland.)
- 1949 *Parabolina andina* (Hoek) — — Newell, p. 221. (Questions the identity of the Newfoundland material.)
- 1950 *Parabolina andina* (Hoek) — — Shaw, p. 110. (Mentioned.)

Type data: — As lectotype should be selected a specimen from Tilcuya, Argentina, from Kayser's material.

Diagnosis: — A *Parabolina* species with: moderately wide pleural regions and fixed cheeks; S1 and S2 united across the glabella; short preglabellar field; free cheeks with spine that deviates slightly from the course of the lateral margin and with obtuse inner spine angle; 12 thorax segments, some of the posterior segments with pleural macrospines (longest in the 8th segment); axial macrospine in the 12th segment; entire pygidium.

Remarks: — Professor Horacio J. Harrington has kindly informed me (letter May 13., 1950) that *Parabolinella andina* Hoek is identical with *Olenus argentinus* Kayser.

Parabolina argentina resembles *Bienwillia*, but differs from it in having S1 and S2 united across the glabella, and differs at least from *Bienwillia shinetonensis* in having long pleural spines in some of the posterior thoracic segments, those of the 8th segment being longest. In the latter feature it agrees well with a rather late Scandinavian *Parabolina* species, *P. lobata* (= *P. longicornis*), which also has S1 united across the glabella, whereas S2 is not quite united. *P. argentina* differs from *P. lobata* in having an entire pygidium, but for the time being it may be included in *Parabolina*, although it is possible that it should be regarded as an off-shoot from *Parabolina*.

Occurrence: — Argentina (Lower Tremadocian, Province of Jujuy and Salta), Bolivia (Lower Tremadocian, Salitre), E. Canada (Apsey formation, Newfoundland).

Parabolina brevispina Westergård 1922.

Pl. 3.

- 1922 *Parabolina brevispina* n. sp. — — Westergård, p. 133, pl. VI, figs. 9—13. (Descr. Figs. of dorsal shield, cranidium, free cheek, pygidium, and hypostoma.)
- 1947 *Parabolina brevispina* Wgârd. — — Westergård, p. 22. (Distribution in Sweden.)

Lectotype (here selected): — A dorsal shield from Andrarum, Scania, Sweden, figured by Westergård, 1922 (pl. VI, fig. 9).

Diagnosis: — A *Parabolina* species with: narrow pleural regions and narrow fixed cheeks; pelturoid cranidium without preglabellar field and small palpebral lobes close to glabella and far forwards; free cheeks with acute inner spine angle; 12 thoracic segments; short pleural spines; pygidium with 3—4 pairs of short marginal spines and 3 axial rings.

Norwegian material: — This is scanty, but agrees very well with the Swedish. The largest cranidium is almost 5 mm long.

Occurrence: — Norway: Oslo (Gamlebyen) — *Parabolina spinulosa* zone (2b), subzone of *Parabolina brevispina*; alone. — Sweden (same horizon).

Parabolina dawsoni Matthew 1901.

- 1901 *Parabolina Dawsoni*, n. sp. — Matthew, p. 282, pl. V, figs. 6a—f. (Descr. Figs. of all parts of dorsal shield and hypostoma.)
 1903 *Parabolina Dawsoni*. — Matthew, p. 223, pl. XVII, figs. 6a—f. (Descr. Figs. copied from Matthew, 1901.)
 1952 *Parabolina dawsoni* Matthew — Hutchinson, p. 80, pl. III, figs. 11—13. (Descr. Figs. of cranidium and pygidia.)

Type data: — As lectotype should be chosen one of the specimens figured by Matthew from the *Peltura* zone at Esconie shore, East Bay, Nova Scotia, Canada.

Remarks: — The rather characteristic pygidium with only one pair of short spines points towards the entire pygidium of *Parabolinella*. In other features, *P. dawsoni* resembles species like *P. heres*. Hutchinson (1952, p. 82) showed that *P. dawsoni* has wider postocular cheeks than is seen in Matthew's figure of the cranidium. Nevertheless, I do not think that *P. longicornis* (= *P. lobata*) should be considered conspecific, as this species has a different pygidium with three pairs of spines, and occurs at a slightly higher horizon.

Occurrence: — E. Canada (Narrows formation. *Peltura* zone. Associated with *Peltura scarabaeoides* *scarabaeoides*, *Ctenopyge pecten*, *Sphaerophthalmus humilis*, and *Lotagnostus trisectus*).

Parabolina frequens (Barrande 1868).

- 1868 *Olen. Guembeli*. Barr. — Barrande, p. 78, fig. 14. (Descr. and fig. of fragmentary axial shield without pygidium.)
 1868 *Olen. frequens*. Barr. — Barrande, p. 79, figs. 15—17, 19. (Descr. and fig. of pygidium.)
 1868 *Olen. expectans*. Barr. — Barrande, p. 81, fig. 18. (Descr. and fig. of pygidium.)
 1868 *Olenus* — Barrande, p. 80, figs. 20—21. (Figs. of free cheeks suggested to belong to *Olenus*.)
 1879 *Olenus Guimbeli* Barrande, *Olenus frequens* Barrande, *Olenus expectans* Barrande — Gümbel, pp. 443, 439. Text-fig. 5.
 1896 *Olenus frequens* Barr. — Pompeckj, p. 96. (Mentioned.)
 1896 *Parabolinella? Guimbeli*, Barr. (emend. Brögger) — Brögger, pp. 211—213. (Remarks. Includes *Olenus frequens* and *O. expectans*.)
 1925 *Acantholenus frequens* Barrande sp. — Wurm, p. 50, pl. 1, fig. 6. (Listed.)

1925 *Olenus? expectans* Barrande — Wurm, p. 50. (Listed.)

1955 *Parabolina frequens* (Barrande) — Sdzuy, p. 15, text-fig. 10, pl. 3, figs. 58—70. (Descr., figs. of cranidia, hypostoma, free cheeks, parts of thorax, and pygidia.)

Type data: — A neotype was selected by Sdzuy (1955). It is a cranidium (Forschungs-Institut Senckenberg, no. X 1802a) from Leimitz near Hof, Germany.

Diagnosis: — A *Parabolina* species closely resembling *P. argentina*, but differing in having marginal spines in the pygidium (3, rarely 2 or 4 pairs).

Occurrence: — Germany (Lower? Tremadocian).

Parabolina heres heres Brögger 1882.

Pl. 8.

1882 *Parabolina heres*, n. sp. — Brögger, p. 101, pl. I, figs. 13a—d. (Descr. Figs. of cranidium, free cheek, thoracic segment, and pygidium.)

1898 *Parabolina heres* Brögger — Moberg & Möller, p. 267, pl. 12, figs. 8—15; pl. 14, figs. 13, 14? (Descr. Figs. of all parts of dorsal shield and conspecific? hypostoma.)

1922 *Parabolina heres* Brögger [partim] — Westergård, p. 137, pl. VII, figs. 24—29, 33—34. (Copies of Moberg & Möller's figs. Figs. 30—32 are of *P. heres lata*.)

1929 *Parabolina heres* Br. — Strand, p. 357. (Recorded.)

1934a *Parabolina heres* — Stormer, p. 332. (Listed.)

1947 *Parabolina heres* Brögger — Westergård, p. 24. (Distribution in Sweden.)

See also under *P. heres lata* for forms that have been assigned to *P. heres*.

Type data: — It has not been possible to retrace the cranidium and free cheek figured by Brögger, and as lectotype I select the pygidium (P. M. O. no. 19948) figured by Brögger (1882, pl. 1, fig. 13d). It was collected at Vestfossen in Eiker, Norway, by Brögger in 1879, and is associated with *Peltura costata* and other parts of *Parabolina heres*.

Diagnosis: — A *Parabolina* species with: moderately wide pleural regions and fixed cheeks; distinct preglabellar field; small palpebral lobes opposite S3 and not very close to glabella; free cheeks with right-angled inner spine angle; 12 thoracic segments; short pleural spines; pygidium with 4—5 axial rings and 4—5 pairs of moderately long, slender marginal spines.

Remarks: — The type material of *P. heres* is not too well preserved. I have found no occipital spine in the rather few cranidia, but the occipital ring has a keel-like node. The lectotype is the only pygidium in this material. The axis has 3 rings and an end lobe of 2 fused rings. There are 4 pairs of marginal spines in the pygidium. The largest cranidium is about 5 mm long, but the missing specimen figured by Brögger was 10 mm long. Material from other Norwegian localities is also rather poor.

Occurrence: — Norway: Eiker (Vestfossen, Teigen core), Røyken (Slemmestad), Ringsaker (Evjevika) — *Acerocare* zone (2d ϵ), subzones of *Peltura transiens* and *Peltura costata*. Associated with *Peltura transiens*, or *Peltura costata*, or *Acerocarina microphyga*. — Sweden (same horizon).

Parabolina heres lata Matthew 1892.

Pl. 8.

- 1892 *Parabolina heres* Brögger var. *lata* n. var. — Matthew, p. 51, pl. XIII, figs. 6a—c, 6d?, 6e—f. (Descr. Sketches of axial shield, cranidia, free cheek, pygidium and conspecific? hypostoma.)
- ?1892 *Parabolina heres* Brögger var. *grandis*, n. var. — Matthew, p. 52, pl. XIII, fig. 7. (Descr. and fig. of pygidium.)
- 1898 *Parabolina heres* Brögger var. — Moberg & Möller, p. 274, pl. 14, figs. 10—12. (Descr. Figs. of dorsal shield and pygidia.)
- 1898 *Parabolina heres* Brögger var. — Moberg, p. 315, pl. 16, figs. 7—8. (Figs. of pygidia.)
- 1909 *Parabolina heres* Brögger var. — Westergård, p. 48, pl. I, figs. 5—8. (Figs. of cranidia, free cheek, and pygidium.)
- 1922 *Parabolina heres* Brögger [partim] — Westergård, p. 137, pl. VII, figs. 30—32. (Figs. copied from Westergård, 1909.)
- 1943 *Parabolina heres hexacantha* var. n. — Westergård, p. 56, text fig. 37. (Figs of cranidium, free cheek, and pygidium, copied after Westergård, 1909.)
- 1947 *Parabolina heres hexacantha* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Type data: — As lectotype I select a pygidium figured by Matthew (1892, pl. XIII, fig. 6b) from Division 3b, Navy Island, St. John Harbour, New Brunswick, Canada.

Diagnosis: — Differs from *Parabolina heres heres* in being narrower, having narrower free cheeks, and in having a pygidium with 3 (4?) axial rings and only 3 pairs of marginal spines.

Remarks: — *P. heres lata* was stated by Matthew to differ from *P. heres* i. a. in having a rather narrow free cheek, thus reminding one more of *P. spinulosa* than of *P. heres*, and a pygidium with only 3 pairs of spines. *P. heres hexacantha* Westergård 1943 differs from *P. heres* in the same features. I have examined some specimens of *P. heres lata* collected by G. F. Matthew. They are not well preserved, but it is seen that they occur together with *Westergårdia*. *P. heres lata* and *P. heres hexacantha* thus come from the same subzone, and it seems highly probable that they are conspecific. The pygidium described by Matthew as *P. heres grandis* may belong to the associated *P. heres lata*, but the specimen figured by Matthew as the probable hypostoma of *P. heres lata* does not seem to belong here.

Norwegian material: — Poorly preserved, but showing the narrow free cheek and the pygidium with three pairs of spines.

Occurrence: — Norway: Røyken (Slemmestad), Brummunddalen. — *Acerocare* zone (2d ϵ), subzone of *Westergårdia*. Associated with *Westergårdia* spp. \pm *Pelturina punctifera* n. sp. — Sweden (same horizon), E. Canada (Narrows formation, same horizon).

Parabolina jemtlandica Westergård 1922.

1922 *Parabolina jemtlandica* n. sp. — Westergård, p. 138, pl. VII, figs. 35—38.
(Descr. Figs. of cranidium, free cheek, pygidium, and hypostoma.)

1947 *Parabolina jemtlandica* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Lectotype (here selected): — The pygidium figured by Westergård (1922, p. VII, fig. 37) from Klövsjö in Jämtland, Sweden.

Diagnosis: — A *Parabolina* species with: moderately wide fixed cheeks; distinct preglabellar field; small palpebral lobes far forwards and relatively distant from glabella; free cheeks with acute inner spine angle; pygidium with 3 axial rings and 4 pairs of marginal spines. Thorax unknown.

Occurrence: — Sweden (*Acerocare* zone?)

Parabolina kinnekullensis n. sp.

Pl. 9, fig. 12.

Name: — From Kinnekulle, Västergötland, Sweden.

Holotype: — An almost complete dorsal shield (RM. no. Ar. 38115) from Trolmen, Kinnekulle, Västergötland, Sweden.

Diagnosis: — A *Parabolina* species with: moderately wide pleural regions and fixed cheeks; S1 digeniculate, faintly connected across glabella; short preglabellar field; small palpebral lobes far forwards and not very close to glabella; preocular facial sutures slightly diverging (?); 12 thoracic segments; short pleural spines; pygidium with 4 axial rings and 3 pairs of short broad-based marginal spines.

Description: — This is based on the holotype, which is the only known specimen. It is 57 mm long.

Cranidium with fixed cheeks slightly narrower than glabella. Glabella slightly tapered, rounded in front. S1 digeniculate, faintly connected across glabella. S2 digeniculate, less oblique backwards than S1. S3 curved, fainter and shorter than S2 and S3. Palpebral lobes small, opposite L3, distance from glabella about 1/3 width of glabella at eye line. Anterior border relatively wide. Short preglabellar field. Facial sutures slightly diverging(?) in front of eyes.

Only one damaged free cheek is present. Unfortunately it does not show the inner spine angle.

Thorax with 12 segments. Fulcrum halfway between axial line and pleural ends. Short, slender pleural spines. Pleural region slightly wider than axis.

Pygidium with axis of 4(?) rings and 3 pairs of broad-based very short spines. Faint posterior border furrow.

Affinities: — *P. kinnekullensis* n. sp. resembles *P. lobata lobata*, but differs i. a. in having no pleural macrospines, in having narrower fixed cheeks and pleural regions, in not having S1 so distinctly connected across

the glabella, and in having shorter marginal spines in the pygidium. It also appears to be a larger species.

Occurrence: — Sweden: Vestergötland (Kinnekulle) — Zone of *Peltura scarabaeoides*, subzone of *Parabolina lobata*. Associated with *Peltura scarabaeoides westergårdi* n. subsp.

Parabolina lapponica Westergård 1947.

Pl. 6.

1947 *Parabolina lapponica* sp. n. — Westergård, p. 14, pl. 3, fig. 8. (Descr. Fig. of cranidium.)

Holotype: — The cranidium figured by Westergård (1947, pl. 3, fig. 8) from a boulder at Storberget, Lake Vojmsjön, Southern Lapland, Sweden.

Remarks: — Only a cranidium is known. It somewhat resembles that of *P. kinnekullensis* n. sp., but has relatively narrower glabella.

Occurrence: — Sweden (*Peltura* zone, subzone of *Peltura scarabaeoides*).

Parabolina lobata lobata (Brögger 1882).

Pl. 8; pl. 9, figs. 9–11.

1882 *Ctenopyge*(?) *lobata*, n. sp. — Brögger, p. 121, pl. XII, fig. 11. (Descr. and fig. of cranidium.)

1898 *Parabolina megalops* n. sp. [partim] — Moberg & Möller, p. 275, pl. 13, figs. 1, 4, 7, 10. (Figs. of free cheek, pygidia, and dorsal shield.)

1922 *Parabolina longicornis* n. sp. — Westergård, p. 136, pl. VII, figs. 1–8. (Descr. Figs. of dorsal shield, cranidia, free cheeks, pygidia, and hypostoma.)

1922 *Parabolina megalops* Moberg & Möller [partim] — Westergård, p. 137, pl. VII, figs. 18–20, 23. (Figs. copied from Moberg & Möller, 1898.)

1927a *Parabolina longicornis* Westergård — Czarnocki, p. 12. (Recorded.)

1927b *Parabolina longicornis* Westergård — Czarnocki, p. 199. (Recorded.)

1934a *Parabolina* cf. *longicornis* — Størmer, p. 332. (Listed.)

1944a *Parabolina longicornis* Westergård — Westergård, p. 39, pl. 1, figs. 4–8. (Remarks. Figs. of cranidium, free cheek, and thoracic segment with long axial spine.)

1947 *Parabolina longicornis* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

1951 *Parabolina longicornis* Westergård — Hutchinson, p. 82. (Suggests that it may be a synonym of *P. dawseni*.)

Lectotype (here selected): — A cranidium (P. M. O. no. 19937) figured by Brögger (1882, pl. XII, fig. 11). It is from Vestfossen, Eiker, Norway, and is associated with other parts of the same species and *Peltura scarabaeoides westergårdi* n. subsp.

Diagnosis: — A *Parabolina* species with: wide pleural regions and fixed cheeks; S1 united across glabella; short preglabellar field; relatively large palpebral lobes situated opposite L2; occipital ring with axial node and

axial spine; free cheeks with slightly acute inner spine angle; 12 thoracic segments with long pleural spines, 8th segment with pleural macrospine; pygidium with 4 axial rings and 3 pairs of short, broad-based spines. The diagnostic features of free cheeks, thorax, and pygidium is based on Swedish material (of *P. longicornis*).

Remarks: — Comparison of the type material of *Ctenopyge? lobata* Brögger 1882 and *Parabolina longicornis* Westergård 1922 has convinced me that they represent the same species. Unfortunately, Brögger's material is rather incomplete, consisting of young more or less damaged cranidia and fragments of free cheeks. The lectotype of *P. lobata lobata* is the best preserved cranidium. It has rather straight eye ridges and the eyes relatively far from the glabella. In the other specimens the eye ridges are more oblique and the eyes closer to the glabella, but there are transitional forms as well, and the variations are probably not of greater taxonomic importance. The same variations are seen in Swedish material of *P. longicornis*, which is also associated with *Peltura scarabaeoides westergårdi* n. subsp. The occipital ring of *P. lobata lobata* has both an axial node and, behind it, an axial spine.

As pointed out by Westergård (1944a, p. 40), some of the specimens figured by Moberg & Möller (1898) and refigured by Westergård (1922) as *P. megalops*, belong to *P. longicornis* (i. e. *P. lobata*).

Hutchinson (1952, p. 82) suggested that *P. longicornis* might be a synonym of *P. dawsoni*. This is rather unlikely, since *P. dawsoni* differs i. a. in having a pygidium with only one pair of spines, and moreover occurs at a lower horizon.

A rather complete specimen (pl. 9, fig. 11) from Sweden has relatively narrower fixed cheeks and pleural regions and very short preglabellar field, and may possibly be close to *P. lobata praecurrens*. The specimen apparently had united free cheeks (cf. p. 91).

Occurrence: — Norway: Eiker (Vestfossen, Kårtveit), Hamar district (Stange) — Zone of *Peltura scarabaeoides* (2dδ), subzone of *Parabolina lobata*. Associated with *Peltura scarabaeoides westergårdi* n. subsp. ± *Agnostus rudis holmi*. — Sweden (same horizon), Poland? (Upper Cambrian).

Parabolina lobata praecurrens Westergård 1944.

1944a *Parabolina longicornis praecurrens* var. n. — Westergård, p. 39, pl. 1, figs. 9—11. (Figs. of cranidia.)

1947 *Parabolina longicornis praecurrence* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Holotype: — By original designation the cranidium figured by Westergård (1944a, pl. 1, fig. 9) from Gislövhammar, Scania, Sweden.

Diagnosis: — Differs from *Parabolina lobata lobata* in having no preglabellar field and narrower fixed cheeks. Thorax and pygidium unknown.

Norwegian material: — A few incomplete cranidia.

Occurrence: — Norway: Oslo (Gamlebyen, Rosenkrantz gate 8), Røyken (Slemmestad) — Zone of *Peltura scarabaeoides* (2d8), subzone of *Parabolina lobata*. Associated with *Peltura scarabaeoides westergårdi* n.subsp. — Sweden (same horizon, just below *Parabolina lobata lobata*).

Parabolina megalops Moberg & Möller 1898.

Pl. 7.

- 1898 *Parabolina megalops* n.sp. [partim] — Moberg & Möller, p. 275, pl. XIII, figs. 2, 6, 8 only. (Descr. Figs. of cranidium and pygidia. According to Westergård, 1942, the figs. 1, 4, 7, 10 are of *P. longicornis* = *P. lobata*, whereas fig. 9 is of *Peltura scarabaeoides*.)
- 1922 *Parabolina megalops* Moberg & Möller [partim] — Westergård, p. 137, pl. VII, figs. 17—21 only. (Copies of Moberg & Möller's figs.)
- ?1929 *Parabolina* sp. — Strand, p. 357. (Mentions cranidia and pygidia suggested to belong to *P. heres* or *P. longicornis*.)
- 1942 *Parabolina megalops* Moberg & Möller — Westergård, p. 14. (Remarks on the species.)
- 1944a *Parabolina megalops* Moberg & Möller — Westergård, p. 39, pl. 1, figs. 12—19. (Remarks. Figs. of cranidia, including lectotype, free cheek, and pygidia, partly with attached thoracic segments.)
- 1947 *Parabolina megalops* Mob. & Möll. — Westergård, p. 24. (Distribution in Sweden.)

Lectotype: — By subsequent designation (Westergård, 1944a) a cranidium figured by Moberg & Möller (1898, pl. XIII, fig. 2). The figure was reproduced by Westergård in 1922 (pl. VII, fig. 17), and a new figure of the specimen given by Westergård in 1944a (pl. 1, fig. 12). It is from Åkarpsmölla, Scania, Sweden.

Diagnosis: — A *Parabolina* species with: moderately wide pleural regions and fixed cheeks; preglabellar field; subparallel facial sutures in front of small palpebral lobes far forwards and moderately close to glabella; well-developed occipital spine; free cheeks with slightly acute inner spine angle; long pleural spines (at least in posterior part of thorax); pygidium with 6(—7?) axial rings and 5(—6?) short and slender marginal spines.

Remarks: — Westergård (1944a, p. 40) pointed out that Moberg & Möller based their description of *P. megalops* on three species. The species to which Westergård restricted the name is very close to *P. heres*. After having examined the type material of *P. megalops*, Westergård concluded that this poorly preserved material indicates that *P. megalops* may be distinct from *P. heres*. As possible differences Westergård noted that *P. megalops* has a slender and fairly long occipital spine; that there are indications of a long axial spine on one of the two last thoracic segments, and that the pygidium has six (to seven?) segments and five (to six?) pairs of short marginal spines. *P. heres heres* seems to have no occipital spine, and its pygidium has only five segments and four pairs of spines.

Norwegian material: — In a lens from Modum I have found not too well preserved specimens that may belong to *P. megalops*. A fairly young cranidium (only 2 mm long, excluding spine) has a distinct occipital spine. Larger cranidia (up to 6 mm long) have no spine, but show signs of having had it broken off. A detached thoracic segment shows a long axial spine. These features agree with *P. megalops*. The pygidium has, however, only 5 rings in the axis and thus seems to be intermediate between *P. megalops* with 6 rings and *P. heres* with 3 rings and an end lobe of 2 fused rings. The Modum material does not allow a determination of the number of marginal spines. The free cheek is of the type common to *P. megalops* and *P. heres*. It is of special interest that the Modum form is associated with *Peltura paradoxa*, as this seems to be the case also with some of the Swedish material of *P. megalops*.

Some specimens associated with *Peltura scarabacoides westergårdi* n. subsp. from Evjevika, Ringsaker, may probably also belong to *P. megalops*. They were mentioned by Strand (1929, p. 356) as *Parabolina* sp.

Occurrence: — Norway: Modum (Furetangen), Ringsaker (Evjevika)? — *Acerocare* zone (2dε), subzone of *Peltura paradoxa*. Alone, or associated with *Peltura paradoxa*. — Sweden (apparently same horizon).

Parabolina mobergi Westergård 1922.

Pl. 6.

- 1922 *Parabolina mobergi* n. sp. — Westergård, p. 135, pl. VI, figs. 21–24. (Descr. Figs. of cranidium, free cheek, and pygidia.)
 ?1927a *Parabolina Mobergi* Westergård — Czarnocki, p. 12. (Recorded.)
 ?1927b *Parabolina Mobergi* Westergård — Czarnocki, p. 199. (Recorded.)
 1947 *Parabolina mobergi* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Lectotype (here selected): — A cranidium from Kloksåsen, Jämtland, Sweden, figured by Westergård (1922, pl. VI, fig. 21).

Diagnosis: — A *Parabolina* species with: moderately wide fixed cheeks; short prelabellar field; relatively small palpebral lobes far forwards and moderately close to glabella; free cheeks with right-angled inner spine angle; long occipital spine; pygidium with moderately wide pleural regions, 4 (5?) axial rings, and 3 pairs of short marginal spines. Thorax unknown.

Norwegian material. — This is scanty and not well preserved, but it seems to conform with the Swedish.

Occurrence: — Norway: Oslo (Nedre Slottsgate, Tøyen), Hadeland. — Zone of *Peltura minor* (2dβ), subzone of *Ctenopyge similis*. Associated with *Ctenopyge similis* n. sp., *Ct. modesta* n. sp., and *Protopeltura bidentata*. — Sweden (same horizon), Poland? (Upper Cambrian).

Parabolina spinulosa (Wahlenberg 1821).

Pl. 1, fig. 2; pl. 3; text-fig. 12.

- 1759 *Entomolithus paradoxus* [partim] — Linnæus, p. 21, fig. 1. (Descr. and figs. of imperfectly preserved dorsal shield, possibly belonging to *P. spinulosa*. Linnæus described a pair of antennae in this specimen. According to Beecher 1896, the supposed antennae are really portions of the anterior border.)
- 1781 *Entomolithus paradoxus* — Brünnich, p. 392. (Examined Linnæus' specimen and denies that it had antennae.)
- 1821 *Entomotrachites spinulosus* — Wahlenberg, p. 38, pl. I, fig. 3. (Descr. Rough, partly inadequate fig. of dorsal shield.)
- 1822 *Paradoxides spinulosus* — Brongniart, p. 32, pl. IV, figs. 2—3. (Descr. Fig. of dorsal shield and copy of Wahlenberg's fig.)
- 1827 *Olenus spinulosus* — Dalman, p. 256, pl. VI, fig. 4. (Short descr. Inadequate fig. of dorsal shield.)
- 1837 *Olenus spinulosus* — Hisinger, p. 19, pl. IV, fig. 2. (Diagn. A copy of Dalman's fig.)
- 1838 *Olenus gibbosus* var. — Boeck, p. 143. (Boeck's material shows that it is *P. spinulosa*.)
- 1840 *Paradoxides spinulosus* — Milne Edwards, p. 342. (Descr.)
- 1843 *Paradoxides spinulosus* — Burmeister, p. 80. (Hardly this species, as far as can be judged from the descr. and the associated fauna.)
- 1854 *Parabolina spinulosa* Wahl. — Angelin, p. 46, pl. XXV, fig. 9; pl. XXVII, fig. 3. (Rough, inadequate fig. of dorsal shield and fig. of hypostoma.)
- 1857 *Olenus spinulosus* Wahl. — Kjerulf, p. 284, reprint p. 92. (Recorded.)
- 1864 *Olenus (Parabolina) spinulosa*, Wahl. — Salter, pl. VIII, fig. 16, p. 10. (A copy of Wahlenberg's fig.)
- 1864 *Olenus (Parabolina) serratus*. — Salter, pl. VIII, fig. 5, p. 4. (Descr. Figs. of cranidium and pygidium.)
- 1865 *Parabolina spinulosa* Wahl. — Kjerulf, p. 2. (Recorded.)
- 1866 *Olenus (Parabolina) serratus*, n. sp. — Salter, p. 301, pl. V, figs. 6—7. (Descr. Figs. of cranidium and pygidium.)
- 1873 *Olenus (Parabolina) spinulosus*, Wahl. — Salter, p. 11. (Remarks. States that *O. serratus* is the same species.)
- 1875 *Parabolina spinulosa* Wahl. — Brögger, p. 575. (Recorded.)
- 1882 *Parabolina spinulosa*, Wahlenb. — Brögger, p. 100, pl. I, figs. 12a—e. (Descr. Figs. of all parts of dorsal shield and hypostoma.)
- 1884 *Parabolina spinulosa*, Wahlenb. — Brögger, p. 257. (Recorded.)
- 1884 *Parabolina sexdentata* — Brögger, p. 258. (Short descr.)
- 1892 *Parabolina spinulosa*, Wahl. — Matthew, p. 51, pl. XIII, figs. 5a—d. (Figs. of cranidium, free cheek, and pygidia.)
- 1896 *Parabolina spinulosa* Wahlenberg — Beecher, p. 303 (Suggests that what Linnæus described as antennae is a portion of the rim.)
- 1896a *Parabolina spinulosa*, Wahlenb. — Törnquist, p. 142. (Calls attention to the so-called antennae, described by Linnæus.)
- 1896b *Parabolina spinulosa*, Wahlb. — Törnquist, p. 567. (Opposes Beecher's view that the so-called antennae are a portion of the border.)
- 1898 *Parabolina spinulosa*, Wahlenb. — Bjørlykke, p. 12, text fig. 2. (Copies of Angelin's and Brögger's figs.)
- 1901 *Parabolina spinulosa* Wahlb. — Münster, p. 26. (Recorded.)
- 1901 *Parabolina spinulosa* Wahlenb. — Lindström, p. 33, pl. V, figs. 31—32. (Figs. of free cheek.)
- 1902 *Parabolina spinulosa* — Schiøtz, p. 8. (Recorded.)

- 1904 *Parabolina spinulosa* Wahlenb. — — Persson, p. 513, pl. IX, fig. 24. (Fig. of larval pygidium.)
- 1908 *Parabolina spinulosa* (Wahlenberg) — — Lake, p. 62, pl. VI, figs. 8—11. (Descr. Figs. of dorsal shields.)
- 1910 *Parabolina spinulosa*, Wahl. — — Høltedahl, p. 5, pl. II, fig. 13. (Fig. of hypostoma.)
- 1920b *Parabolina spinulosa* (Wahlenberg) — — Raymond, p. 17. (Supports the view that the so-called antennae described by Linnæus are portions of the border.)
- 1922 *Parabolina spinulosa* (Wahlenberg) — — Westergård, p. 134, pl. VI, figs. 14—20. (Descr. Figs. of dorsal shields, pygidium, free cheek, hypostoma, and axial shields of young individuals.)
- 1923 *Parabolina spinulosa* Wahlenberg — — Poulsen, p. 29, text fig. 8, p. 57, text fig. 20. (Descr. Figs. of dorsal shield, copied from Westergård, 1922, and of larval pygidium.)
- 1927 *Parabolina spinulosa* (Wahlenberg) — — Cobbold, pp. 556, 557. (Recorded.)
- 1929 *Parabolina spinulosa* (Wahlenb.) — — Strand, p. 357. (Recorded.)
- 1934a *Parabolina spinulosa* — — Störmer, p. 333. (Listed.)
- 1944a *Parabolina spinulosa* (Wahl.) — — Westergård, p. 21. (Reported from the subzone of *Leptoplastus paucisegmentatus*.)
- 1944b *Parabolina spinulosa* (Wahlenberg) — — Kobayashi, p. 231, text-figs. 3a—b. (Figs. of hypostoma and restored dorsal shield.)
- 1946 *Parabolina spinulosa* (Wahlenberg) — — Lake, p. 341. (Remarks.)
- 1947 *Parabolina spinulosa* (Wahlb.) — — Westergård, p. 24. (Distribution in Sweden.)
- 1952 *Parabolina spinulosa* (Wahlenberg) — — Hutchinson, p. 79, pl. III, figs. 7—10. (Descr. Figs. of cranidia and free cheek.)
- 1953 *Parabolina spinulosa* — — Høltedahl, p. 182, fig. 69; 20—21. (Figs. of cranidium, thoracic segment, and pygidium.)
- Non 1847 *Odontopyge spinulosa* — — Corda (= *Olenus gibbosus*).

Type data: — A lectotype should be chosen from Swedish material, from Wahlenberg's material.

Diagnosis: — A *Parabolina* species with: moderately wide pleural regions and fixed cheeks; no or practically no preglabellar field; small palpebral lobes far forwards and close to glabella; free cheeks with about right-angled inner spine angle; 12 thoracic segments; pleural spines progressively longer from anterior segments (short spines) to posterior segments (long spines); pygidium with 5—6 axial rings and 3—5 pairs of marginal spines, all but the inner pair long.

Remarks: — *P. spinulosa* apparently had united free cheeks (cf. p. 91).

Norwegian material: — Cranidia reach a length of 9.8 mm, and pygidia reach a length of 6.3 mm and a width of 14.8 mm. Brögger (1884, p. 258) proposed the name *Parabolina sexdentata* for a form from N. Stulen, near Skien, Norway, which was stated to differ from *P. spinulosa* in being considerably larger, and in having only three pairs of pygidial spines. However, his material shows that it does not reach a greater size than specimens undoubtedly belonging to *P. spinulosa*. Three pairs of pygidial spines are seen in the one pygidium present, but as it is very poorly preserved, it is quite possible that it may have had four pairs. I believe that *P. sexdentata* should be considered a synonym of *P. spinulosa*.

Westergård (1922, p. 135) mentioned a small form of *P. spinulosa* with only three pairs of pygidial spines, and less distinct glabellar furrows. It occurs at a slightly higher level than the typical form at Andrarum in Scania. A small form has also been encountered in the Norwegian material, and here, too, it appears to occur in slightly younger beds, as it is associated with *Protopeltura aciculata pusilla*. The cranidia reach a length of 4.2 mm, but the glabellar furrows are rather distinct, and the pygidia carry 4 pairs of spines, although the posterior ("inner") pair is very small.

Occurrence: — Norway: Skien-Langesund (N. Stulen, Saltboden cores), Eiker-Sandsvær (Krekling, Teigen core, Stablum core), Oslo (Gamlebyen, Nedre Slottsgate, Prinsensgate), Røyken (Slemmestad), Møclum (Fure), Ringerike (S of Hvalsmoen), Hadeland (Boulder at Mæna), Ringsaker (Steinsodden, Evjevika), Østerdalen (Øksna). — *Parabolina spinulosa* zone (2b), subzone of *Parabolina spinulosa*. Alone, or associated with *Orusia lenticularis*, or (the small form) also with *Protopeltura aciculata pusilla*. — Sweden (same horizon and also in the *Leptoplastus* zone, subzone of *Leptoplastus paucisegmentatus*), Denmark (Bornholm, *Parabolina* zone, subzone of *Parabolina spinulosa*), England (Orusia Shales), Wales (Upper Lingula Flags), E. Canada (MacNeil and Narrows formations, *Parabolina* zone).

Parabolina tetracanthura (Matthew 1892).

1892 *Protopeltura acanthura* Angelin var. *tetracanthura*, n. var. — Matthew, p. 53, pl. XIII, figs. 8a—c. (Descr. Figs. of cranidium, free cheek, and pygidium.)

1903 *Protopeltura acanthura*, var. *tetracanthura* — Matthew, p. 225. (Mentioned.)

Lectotype (here selected): — The pygidium figured by Matthew (1892, pl. XIII, fig. 8c), from Division 3a, Germaine Street, St. John, New Brunswick, E. Canada.

Remarks: — This form differs from *P. acanthura* besides in the pygidium (with only 2 pairs of marginal spines), also by not having the characteristic acute angle between the spine and the posterior margin in the free cheek. Moreover, as *P. tetracanthura* occurs in a much lower horizon (Division 3a = *Parabolina spinulosa* zone), I do not think it should be regarded as a subspecies of *P. acanthura*. It may, however, be closely related to *P. spinulosa* with which it shares axial tubercles in the pygidium.

Occurrence: — E. Canada (Narrows formation, *Parabolina* zone).

Parabolina? quadrisulcata n. sp.

Pl. 3; pl. 9, fig. 8.

1922 *Olenus* (?) sp. — Westergård, p. 132, pl. VI, fig. 25. (Descr. and fig. of cranidium.)

1947 *Parabolina?* sp. — Westergård, p. 24. (Listed.)

Name: — The name *quadrisulcata* alludes to the four pairs of glabellar furrows.

H o l o t y p e: — The cranidium (R.M. no. Ar. 149) figured by Westergård (1922), from Funäs, Myssjö, Jämtland, Sweden.

D i a g n o s i s: — An olenid with cranidium with: truncate, tapered glabella with 4 pairs of glabellar furrows; S1 oblique backwards; S2 very slightly oblique backwards; S3 short, transverse, not reaching axial furrow; S4 short, transverse, reaching axial furrow; fixed cheeks about as wide as occipital ring; small, anteriorly situated palpebral lobes about as far from glabella as width of glabella at eye line; eye ridges distinct, slightly oblique forwards; preocular margins converging; preglabellar field present. Other parts unknown.

R e m a r k s: — Although only a cranidium is known of this form, I have preferred to give it a specific name, as it is rather characteristic. It is the earliest known olenid with 4 distinct pairs of glabellar furrows. It furthermore shows some features which resemble *Olenus* (as well-developed preglabellar field, eyes far from glabella) and others which resemble early species of *Parabolina* (small eyes, converging preocular margins). It may possibly represent a separate off-shoot from *Olenus*, more or less along the same lines as *Parabolina*, but it is perhaps more probable that it belongs to *Parabolina*.

What appears to be the posterior part of the right-hand fixed cheek in Westergård's illustration of the cranidium, is really a fragment of a free cheek of *Parabolina spinulosa* (cf. pl. 9, fig. 8).

O c c u r r e n c e: — Sweden: Jämtland (Funäs) — *Parabolina spinulosa* zone, subzone of *Parabolina spinulosa*. Associated with *Parabolina spinulosa*.

Genus *Parabolinites* n. gen.

N a m e: — The name *Parabolinites* alludes to the likeness to *Parabolina* and *Parabolinella*.

T y p e s p e c i e s: — *Parabolinella laticauda* Westergård 1922.

D i a g n o s i s: — Oleninae with: *Parabolina*-like cranidium, but with larger preglabellar field; facial sutures subparallel or diverging in front of palpebral lobes; glabella tapered forwards, rounded in front; free cheeks with spine (when known); pygidium entire.

I n c l u d e d s p e c i e s: —

Parabolinites laticaudus (Westergård 1922) (earlier: *Parabolinella*) and possibly also:

P.? *leptoplastorum* (Westergård 1947) (earlier: *Parabolinella*)

P.? *longispinus* (Belt 1868) (earlier: *Conocoryphe?*, *Olenus*)

P.? *plantii* (Salter 1873) (earlier: *Olenus*) (= *P. williamsonii*)

P.? *williamsonii* (Belt 1868) (earlier: *Conocoryphe?*, *Olenus*, *Parabolinella*)

O c c u r r e n c e: — Sweden (*Leptoplastus* zone?, *Peltura* zone), Wales? (Upper Lingula Flags).

Relationships: — For reasons discussed below (p. 132), *Parabolinella laticauda* has been excluded from *Parabolinella*. It is regarded as type species of a new genus, *Parabolinites*, which probably is close to *Parabolina*, but which differs in having a longer preglabellar field. *Parabolinites* furthermore has an entire pygidium, which is unusual in *Parabolina*. In both these features *Parabolinites* resembles *Parabolinella*, which, however, has a more squarish glabella and usually a more complicated pattern of the glabellar furrows.

Only a single cranidium is known of *Parabolinites? leptoplastorum*. Westergård (1947, p. 15) suggested that it is a young specimen, and that the full-grown *P.? leptoplastorum* may prove to display closer resemblance to the full-grown *P. laticaudus*, considering the differences in *P. laticaudus* due to different stages of growth. Since the pygidium of *P.? leptoplastorum* is unknown, the species is only tentatively assigned to *Parabolinites*.

P.? williamsonii is most probably congeneric with *P. laticaudus*, and differs mainly in having more diverging facial sutures in front of the palpebral lobes and in having digeniculate S1 (best seen in the specimen illustrated by Reed, 1900b, pl. XII, fig. 1 as *Olenus Planti*). S1 thus resembles that of *Parabolinella*, but *P.? williamsonii* does not have the typical squarish *Parabolinella* glabella. The glabella of *P.? longispinus*, on the other hand, is more squarish, but has only simple glabellar furrows, suggesting that it may belong to *Parabolinites*.

Parabolinites apparently developed from *Parabolina*. It is at present difficult to decide whether all the species which have been tentatively assigned to *Parabolinites* really are congeneric with *P. laticaudus*, or whether some or all of them represent separate off-shoots from *Parabolina*, more or less along the same lines as *P. laticaudus*.

Parabolinites laticaudus (Westergård 1922).

Pl. 1, fig. 9; pl. 6.

1922 *Parabolinella laticauda* n. sp. — Westergård, p. 139, pl. VIII, figs. 1—7. (Descr. Figs. of all parts of dorsal shield.)

1947 *Parabolinella laticauda* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Lectotype (here selected): — The cranidium figured by Westergård (1922, pl. VIII, fig. 1) from Andrarum, Scania, Sweden.

Diagnosis: — A *Parabolinites* species with: small palpebral lobes far forwards and close to glabella; slightly convex, subparallel preocular facial sutures; fixed cheeks about as wide as occipital ring; free cheeks with slender spine, acute inner spine angle, and slightly convex posterior margin; thorax with axial nodes and very short pleural spines; pygidium entire and with 3 axial rings.

Occurrence: — Sweden (*Peltura* zone, subzone of *Peltura minor* and *Peltura acutidens*. Associated with *Ctenopyge tumida* and *Sphaerophthalmus alatus*.)

Parabolinites? leptoplastorum (Westergård 1947).

Pl. 4.

- 1947 *Parabolinella leptoplastorum* sp. n. — Westergård, p. 15, pl. 3, fig. 7. (Descr. Fig. of cranidium.)

H o l o t y p e: — The cranidium figured by Westergård, from Röstånga, Scania, Sweden.

D i a g n o s i s: — A *Parabolinites?* species with: moderately-sized palpebral lobes opposite L2; subparallel, almost straight preocular facial sutures; fixed cheeks slightly wider than occipital ring. Free cheeks, thorax, and pygidium unknown.

O c c u r r e n c e: — Sweden (Zone of *Leptoplastus* and *Eurycare*, subzone of *Leptoplastus ozatus*).

Parabolinites? longispinus (Belt 1868).

- 1868 *Conocoryphe? longispina*, spec. nov. — Belt, p. 9, pl. II, figs. 12—14. (Descr. Figs. of cranidium, pygidium, and restored dorsal shield.)
 1900a *C[onocoryphe]? longispina*, Belt — Reed, p. 254. (Suggested to belong to *Olenus*, subgenus *Parabolinella*.)
 1908 *Olenus longispinus* (Belt) — Lake, p. 60, pl. VI, figs. 6—7. (Descr., figs. of 2 dorsal shields.)

T y p e d a t a: — As lectotype I select the dorsal shield collected by Belt from Upper Dolgelley Beds, Dolgelley (B. M. N. H., no. I 7577), and figured by Lake (1908, pl. VI, fig. 7).

D i a g n o s i s: — A *Parabolinites?* species with: moderately wide pleural regions and fixed cheeks; palpebral lobes placed half-way between anterior and posterior border of cranidium; 14 thoracic segments with axial nodes and pointed pleural ends; pygidium entire and with 3—4 axial rings.

O c c u r r e n c e: — Wales (Upper Dolgelley Beds).

Parabolinites? williamsonii (Belt 1868).

- 1868 *Conocoryphe? Williamsonii*, spec. nov. — Belt, p. 9, pl. II, figs. 7—11. (Descr. Figs. of cranidia, thoracic segments, pygidia, and restored dorsal shield.)
 1873 *Olenus Plantii*, Salter, n. sp. — Salter, p. 11. (Remarks.)
 1877 *Olenus Plantii*, Salter — Woodward, p. 47.
 1891 *Olenus Plantii*, Salter — Woods, p. 149.
 1900b *Olenus* (s. g. *Parabolinella*) *Plantii*, Salter — Reed, p. 303, pl. XII, fig. 1. (Descr. Fig. of dorsal shield.)
 1908 *Parabolinella williamsoni* (Belt) — Lake, p. 64, pl. VI, fig. 12; pl. VII, fig. 1. (Descr. Fig. of dorsal shield, same as figured by Reed as *Olenus Plantii*; enlarged fig. of pygidium of this specimen.)
 1913 *Parabolinella williamsoni* (Belt) — Lake, p. 65. (Continuation of description by Lake in 1908.)

Type data: — As lectotype should be selected one of the specimens in Belt's collection.

Diagnosis: — A *Parabolinites* species with: small palpebral lobes far forwards and close to glabella; diverging preocular facial sutures; fixed cheeks about as wide as occipital ring; thorax with short pleural spines and without(?) axial nodes; pygidium entire, with 4 axial rings and postaxial ridge. Free cheeks unknown.

Remarks: — Comparison of type material of Belt's *Conocoryphe? williamsoni* and of *Olenus plantii* led Lake (1913, p. 65) into concluding that the two forms are identical. The specimen figured by Reed and Lake occurs associated with a *Sphaerophthalmus* species, which suggests the zone of *Peltura scarabaeoides*.

A species referred to by Stubblefield (1930, p. 57) as *Parabolinella* aff. *williamsoni* from the Orusia Shales of Shropshire, was stated to differ in its shorter preglabellar field and its narrower palpebral lobes.

Occurrence: — Wales (Upper Lingula Flags).

Genus *Parabolinella* Brögger 1882.

Type species: — *Parabolinella limitis* Brögger 1882, designated by Bassler (1915).

Diagnosis: — Oleninae with: subquadrate to subrectangular cephalic axis, bluntly rounded, truncate, or indented in front; S1 bifurcate; well developed preglabellar field; anterior dorsal furrow often pitted; preocular facial sutures diverging or subparallel; palpebral lobes large to medium-sized, with centres situated from opposite outer ends of S2 to opposite L2; interocular cheeks from about 0.25 to 0.4 as wide as glabella at eye line; postocular cheeks more than half as wide as occipital ring; free cheeks with long spine, which continues course of lateral margin; 16 to 21 (22?) thoracic segments (when number is known); pleural ends pointed or with short spines; pygidium entire.

Included species: — A number of *Parabolina*-like species with well-developed preglabellar field and entire pygidium have been assigned to *Parabolinella*. However, they are not all necessarily congeneric with *Parabolinella limitis* (type species, redescribed below). As defined above, *Parabolinella* is restricted to species with subquadrate to subrectangular cephalic axis, bifurcate S1, and with postocular cheeks wider than half the width of the occipital ring. *Parabolinella tetragonalis* and, tentatively, *P. wimani* have been transferred to *Bienwillia* which has long, unforked glabellar furrows and narrower postocular cheeks. *Parabolinella laticauda* is regarded as type species of a new genus, *Parabolinites*, which differs from *Parabolinella* i. a. in having a parabolic outline of the glabella and in having unforked glabellar furrows. *Parabolinella leptoplastorum* and *P. williamsoni* are tentatively also included in *Parabolinites* n. gen. *Parabolinella evansi* and *P. occidentalis* are

excluded from the Olenidae (cf. p. 23). The following species are retained in *Parabolinella*:

P. argentinensis Kobayashi 1936

P. lata n. sp.

P. limitis Brögger 1882

P. quadrata Matthew 1900 (= ? *P. triarthra*)

P. rugosa Brögger 1882

P. triarthra (Callaway 1877)

P. triarthroides Harrington 1938

and possibly also:

P.? *bisulcata* Kobayashi 1955 (cf. postscript)

P.? *caesa* Lake 1913

P.? *incerta* (Rasetti 1945)

P.? *posthuma* Matthew 1892

P.? *punctolineata* Kobayashi 1936

P.? *simplex* (Salter 1866)

Two *Parabolinella*? spp. are reported from the lower Arenigian in Sweden by Tjernvik (1956).

Occurrence: — Norway (Ceratopyge Series = Tremadocian), Sweden (Ceratopyge Series = Tremadocian; lower Arenigian?), Wales (Upper Lingula Flags?, Tremadocian), Canada (Upper Cambrian?, *Hungaia* zone?, Tremadocian), ?Alaskan-Yukon border (Franconian or Trempealeauian beds), Vermont (Gorge formation), Nevada (Goodwin Limestone and Dunderberg group),¹ Argentina (Tremadocian).

Phylogeny and relationships: — The Tremadocian species *P. argentinensis*, *P. triarthra*, *P. triarthroides*, and *P. quadrata* are all very close to the type species, *P. limitis*, likewise Tremadocian. The rather late Tremadocian species *P. lata* n. sp. may have developed from the above-mentioned group. *P. lata* n. sp. differs from all the other *Parabolinella* species in having the eyes rather remote from the glabella. In spite of having simple glabellar furrows and narrower fixed cheeks, the Tremadocian genus *Bienwillia* appears to be close to *Parabolinella*. Judging from the Scandinavian species alone, the Lower Tremadocian species *Bienwillia*? *wimani* might be regarded as ancestral both to *Bienwillia* and *Parabolinella*. However, if the poorly known species *P.?* *caesa* and *P.?* *simplex* really belong to *Parabolinella*, the genus occurs also in the Upper Cambrian, since they are stated to come from the Upper Lingula Flags. *P.?* *incerta* and *P.?* *punctolineata* from the North American province are likewise rather poorly known, and their age in relation to the species of the Acado-Baltic province is uncertain. As discussed above, some incompletely known species from the Upper Lingula Flags tentatively assigned to *Parabolinites* n. gen. show trends towards *Para-*

¹ cf. Wilson, 1954, p. 263.

bolinella. It is unfortunate that so many *Parabolinella*-like species from the Upper Lingula Flags are so poorly known, because it is difficult to judge whether *Parabolinella* + *Bienwillia* developed from *Parabolinites* n. gen., which has a similar well-developed preglabellar field and entire pygidium, or whether *Parabolinella* + *Bienwillia* developed directly from *Parabolina*, through forms like *Bienwillia? wimani*. In the latter case, *Parabolinites* n. gen. and *Parabolinella* + *Bienwillia* would represent two different off-shoots from *Parabolina*, both with well-developed preglabellar field and an entire pygidium. This would perhaps not be so surprising, since there are *Parabolina* species (later than *Parabolinites* n. gen.) with an entire or almost entire pygidium, and since the length of the preglabellar field varies within *Parabolina*. In favour of the view that *Parabolinella* + *Bienwillia* developed directly from *Parabolina* might be pointed out that some late *Parabolina* species, like *P. acanthura* from the Upper Cambrian/Tremadocian boundary, resemble *Bienwillia? wimani* in certain features, as for instance in having free cheeks with an acute inner spine angle.

Parabolinella argentinensis Kobayashi 1936.

- 1936a *Parabolinella argentinensis*, new species — Kobayashi, p. 88, pl. XV, figs. 1—5. (Descr. Figs. of anterior part of axial and dorsal shields.)
 1937a *Parabolinella argentinensis* Kobayashi — Kobayashi, p. 13. (Listed.)
 1937b *Parabolinella argentinensis* Kobayashi — p. 406. (Listed.)
 1938 *Parabolinella argentinensis* Kobayashi — Harrington, p. 193, pl. VII, figs. 1—2, 7—8. (Remarks. Figs. of a cranium and dorsal shields.)
 1943a *Parabolinella argentinensis* — Harrington & Leanza, pp. 219, 220, 222. (Recorded.)
 1944b *Parabolinella argentinensis* Kobayashi — Kobayashi, p. 231, text-fig. 4. (Fig. of restored dorsal shield.)

Type data: — As lectotype I select the cephalon with 3 attached thoracic segments figured by Kobayashi (1936, pl. XV, fig. 1) from Argentina.

Diagnosis: — A *Parabolinella* species with: sagittal length of preglabellar field about twice that of occipital ring; cephalic axis somewhat longer than wide; interocular cheeks from 1/3 to 1/4 as wide as glabella at eye line. Centres of palpebral lobes opposite outer ends of S2; preocular facial sutures markedly diverging; fixed cheeks about as wide as occipital ring; free cheeks with slightly obtuse inner spine angle; 19 (or 1 or 2 more?) thoracic segments with pointed pleural ends and axial nodes; pygidium with 3 axial rings.

Remarks: — The species was compared with *P. triarthra* by Kobayashi (1936) and Harrington (1938). *P. argentinensis* differs especially in having the facial sutures diverging markedly more in front of the eyes, and in having a stronger pattern of genal caeca across the preglabellar field.

Occurrence: — Argentina (Lower Tremadocian).

Parabolinella lata n. sp.

Pl. 8; pl. 12, fig. 8.

Name: — The species is called *lata* because of its wide interocular and postocular cheeks.

Holotype: — A cranidium (P. M. O. no. 1287a) from Ceratopyge Limestone (3aγ) at S. Bjerkåsholmen near Slemmestad in Røyken, Norway.

Diagnosis: — A *Parabolinella* species with: posterior cheeks slightly wider than occipital ring; width of interocular cheeks 0.4 that of glabella at eye line; preglabellar field bent ventrad. Only cranidium known.

Description: — This is based on the holotype cranidium, which is the only specimen present. It is preserved in limestone, and is 9.2 mm wide and 4.6 mm long.

Cranidium twice as wide as long. Cephalic axis subrectangular, slightly longer than wide, widening slightly forwards and faintly convex in front. Occipital ring with axial node. Occipital furrow distinct. The glabellar furrows are not well preserved, as the frontal lobe is somewhat compressed. S1 sigmoidal and possibly bifurcated. S2 oblique backwards, possibly with faint geniculum. Neither S1 nor S2 reach the dorsal furrow. Axial length of preglabellar field almost one third of that of cephalic axis. Preglabellar field bent rather strongly ventrad, except just in front of glabella where it is convex. Anterior border furrow distinct, pitted. Border narrow. Frontal area slightly arched in front view. Eye ridges slightly oblique forwards, distinct. Palpebral lobes crescentic, relatively small. Eye line slightly in front of S2. Interocular cheeks relatively wide, about 0.4 as wide as glabella at eye line. Postocular cheeks slightly wider than occipital ring.

Facial sutures diverge slightly between eyes and anterior border furrow, and diverge strongly behind eyes, where they are slightly convex.

No other parts of the species are known.

Affinities: — *P. lata* n. sp. is no doubt close to *P. triarthra*, from which it differs mainly in having wider fixed cheeks, and in having the eye ridges running obliquely forwards instead of backwards.

Occurrence: — Norway: Røyken (S. Bjerkåsholmen) — Ceratopyge Limestone (3aγ).

Parabolinella limitis Brögger 1882.

Pl. 1, fig. 8; pl. 8; pl. 12, figs. 1—5.

1882 *Parabolinella limitis*, n. sp. [partim] — Brögger, p. 102, pl. III, figs. 2, 2a—b. (Descr. Figs. of cranidium, free cheek, and pleura. Fig. 4 is of *Bienwillia tetragonalis broeggeri* n. subsp.)

?1903 *Parabolinella*(?) cf. *limitis*, Brögger. — Matthew, p. 226. (Descr. of small cranidium.)

1906 *Parabolinella limitis* Brögger [partim] — Moberg & Segerberg, p. 82. (Mentioned.)

- 1915 *Parabolinella limitis* Brögger — — Bassler, p. 943. (Designated type species of *Parabolinella*.)
1934a *Parabolinella limitis* [partim] — — Stormer, p. 332. (Listed.)
1938 *Parabolinella limitis* [partim] — — Harrington, p. 196. (Remarks.)
1952 *Parabolinella limitis* Brögger — — Harrington & Leanza, p. 192. (Remarks on species.)

Type data: — Lectotype (selected by Harrington & Leanza, 1952) is a cranidium, figured by Brögger (1882, pl. III, fig. 2), from Ceratopyge Shale (3a β), St. Olavs gate, Oslo, Norway.

Diagnosis: — A *Parabolinella* species with: sagittal length of preglabellar field about equal to that of occipital ring; cephalic axis somewhat longer than wide, bluntly rounded in front, preocular facial sutures somewhat diverging; palpebral lobes reaching from opposite S3 to opposite anterior branch of S1, with centres opposite inner end of S2; interocular cheeks about 1/4 as wide as glabella at eye line; postocular cheeks about 3/4 as wide as occipital ring; free cheeks with slightly obtuse inner spine angle; pleural ends with short spines. Number of thoracic segments unknown. Pygidium unknown.

Description: — This is based on detached parts. The lectotype cranidium is 15.5 mm long and 31 mm wide. The largest cranidium is 22 mm long.

Cranidium twice as wide as it is long. Cephalic axis squarish, bluntly rounded and somewhat truncate in front, and with obtuse anterior corners. Occipital ring with axial node. Well developed composite occipital furrow, deepest laterally, but, like glabellar furrows, not quite reaching the axial furrow. S1 forked, oblique backwards, deep. S2 oblique backwards, slightly geniculate, deep. S2 short, transverse, situated midway between axial furrow and axial line, shallower than S1 and S2. S4 almost pit-like, situated close to anterior corners of glabella. Preglabellar field between one-fifth and one-sixth as long as cephalic axis. Anterior border furrow distinct, pitted. Border narrow, gently convex in dorsal and front view. Eye ridges short, slightly oblique, widening gradually into palpebral lobes, which reach from opposite S3 to opposite anterior branches of S1. Interocular cheeks narrow, about one-fourth as wide as glabella at eye line. Postocular cheeks about three-fourths as wide as occipital ring. Preocular facial sutures slightly diverging. Postocular facial sutures diverging, very slightly sinuous, almost straight.

Free cheeks elongate, with long spine. Angle between spine and posterior border slightly obtuse. Border well developed, with very fine terrace lines. Genal field ornamented with genal caeca.

Hypostoma with rather convex middle body. A faint furrow separates anterior lobe from posterior lobe, which carries a pair of maculae. Border up-turned, collar-like, expanded ear-like at posterior corners. Anterior wings bent ventrad.

Thorax known only from fragments of thoracic segments. Pleurae with short spine.

Pygidium unknown.

Remarks: — As pointed out by Harrington & Leanza (1952), Brögger based his description of *P. limitis* on two species. The one species comes from 3a α , the other from 3a β . As the lectotype is of the upper form (from 3a β), the name *P. limitis* is restricted to this species. The other form is described below as *Bienwillia tetragonalis broeggeri* n.subsp.

Affinities: — *P. limitis* is very close to *P. triarthra*, which differs in having shorter eyes, which do not reach further back than opposite the middle of L2, and in having more rounded anterior corners of the glabella.

Occurrence: — Norway: Oslo (Vekkerø, St. Olavs gate), Ringelike (Viul), Hadeland (Gran, Jaren). — Ceratopyge Shale (3a β). — E. Canada? (Nova Scotia, *Asaphellus* zone).

Parabolinella rugosa Brögger 1882.

Pl. 12, fig. 9.

1882 *Parabolina rugosa*, n. sp. — Brögger, p. 104, pl. III, fig. 3. (Descr. and fig. of incomplete cranidium.)

?1896 *Parabolinella*, sp. nov. — Crosfield & Skeat, p. 537, pl. XXVI, figs. 11–12. (Descr. and figs. of incomplete cranidium.)

1906 *Parabolinella rugosa* Brögger — Moberg & Segerberg, p. 82. (Mentioned.)

?1913 *Parabolinella rugosa*, Brögger, var. — Lake, p. 67, pl. VII, fig. 3. (Descr. and new fig. of the cranidium described by Crosfield & Skeat.)

1951 *Parabolinella rugosa* (Brögger) — Shaw, p. 103. (Suggests that it may possibly belong to *Plicatolina*.)

Type data: — Holotype (by monotypy) is the incomplete cranidium described and figured by Brögger (1882), from the lowermost part of the Ceratopyge Limestone (3a γ) at Vestfossen, Eiker, Norway. I have not succeeded in finding the specimen in the collections of the Palaeontological Museum in Oslo, and as no other specimens can be assigned to this species with certainty, it is not possible to select any neotype at present.

Remarks: — As stated by Lake (1913, p. 67), the specimen described and figured by Crosfield & Skeat (1896) as *Parabolinella*, sp. nov., is certainly very closely allied to *P. rugosa*, and such differences as there are, may be due to differences in the mode of preservation. Shaw (1951, p. 103) suggested that *P. rugosa* might possibly belong to *Plicatolina*. However, *P. rugosa* differs from this genus in having a more complicated pattern of the glabellar furrows, and I do not think it should be assigned to *Plicatolina*. H. J. Harrington has suggested (personal communication, 1950) that *P. rugosa* belongs to an undescribed genus present in S. America. He has kindly sent me photographs of two species of this genus, and the likeness between the cranidia is rather striking. The specimen described below as *P. cf. rugosa* resembles even more one of these species.

A single incomplete cranidium from exactly the same horizon as the holotype of *P. rugosa* (namely the small dark limestone lenses just below the typical Ceratopyge Limestone) was collected in 1915 at S. Bjerkåsholmen, Røyken, Norway. The glabella is 5 mm long (as compared to 7 mm of the holotype). More than half of the occipital ring is missing, and it is not possible to say whether it had an axial node or not. Occipital furrow distinct and composite; oblique laterally and slightly convex in middle part. Glabellar furrows not united across glabella. S1 oblique backwards, bifurcated. The two branches unite again near axial furrow, thus delimiting ovate area of glabella. S2 oblique backwards, slightly geniculate, and not quite reaching axial furrow. S3 and S4 almost transverse. S4 is rather close to S3, and almost continues S3 towards axial furrow. Apart from the four pairs of glabellar furrows, there are also two pairs of faint furrows between the occipital furrow and S1. The preglabellar field is badly preserved, but is relatively long (sag.). As in the holotype, no distinct border is developed. Facial sutures slightly diverging in front of eyes. Eye ridges short, oblique backwards. Most of the palpebral lobe is missing, but it seems to be relatively wide and consists of an inner lobe-like part and an outer rim-like ridge. Interocular cheeks rather narrow. The postocular cheek present is imperfect, but is at least half as wide as the occipital ring. The surface of the cranidium is finely granulate.

The specimen seems to agree with *P. rugosa* in most features, except for S2 being curved more markedly backwards in the holotype. It seems, however, rather probable that they are conspecific.

Occurrence: — Norway: Eiker (Vestfossen), ?Røyken (S. Bjerkåsholmen) — Lowermost part of Ceratopyge Limestone (3ay) — ? Wales (Tremadoc Slates).

Parabolinella triarthra (Callaway 1877).

Pl. 12. figs. 6—7.

- 1877 *Olenus triarthrus*, n. sp. — Callaway, p. 666, pl. XXIV, fig. 6. (Descr. Fig. of restored dorsal shield.)
 1902 *Parabolinella quadrata*, n. sp. — Matthew, p. 411, pl. XVIII, fig. 7.
 1903 *Parabolinella?* *quadrata*, — Matthew, p. 225, pl. XVIII, fig. 7. (Descr. Fig. of cranidium.)
 1913 *Parabolinella triarthra* (Callaway) — Lake, p. 68, pl. VII, figs. 4—12. (Descr. Figs. of cranidia and more or less complete axial and dorsal shields.)
 1915 *Parabolinella quadrata* Matthew — Bassler, p. 943. (Listed.)
 1936a *Parabolinella triarthra* (Callaway) — Kobayashi, p. 89. (Mentioned.)
 1938 *Parabolinella triarthra* (Callaway) — Harrington, p. 194. (Mentioned.)
 1952 *Parabolinella triarthra* (Callaway) — Hutchinson, p. 82, pl. III, fig. 14. (Remarks. Fig. of cranidium.)

Type data: — As lectotype should be chosen a specimen from the Shineton Shales, Shineton, Shropshire, England, namely one of the specimens examined by Callaway.

D i a g n o s i s: — A *Parabolinella* species with: cephalic axis about as long as wide, indented in front; width of interocular cheek about 1/4 of width of glabella at eye line; centres of palpebral lobes opposite outer ends of S2; glabella widening slightly forwards; fixed cheeks as wide as, or slightly narrower than occipital ring; up to 21 thoracic segments, the last more or less firmly attached to pygidium; pleural ends with short points, progressively less pointed backwards, two last segments with rounded pleural ends; pygidium small and with 1 axial ring.

R e m a r k s: — All the specimens figured by Lake are flattened and more or less crushed. It is probable that the preglabellar field was rather steep as in *P. lata* n. sp., and that this is the reason why the preglabellar field often is cracked along the axial line. In a specimen (P. M. O. no. A 17390) collected at the type locality by J. Kiær, at least some of the original steepness of the preglabellar field is preserved.

Hutchinson (1952) examined Matthew's type material of *P. quadrata* and regarded it as conspecific with *P. triarthra*.

Kobayashi (1936) mentioned a number of differences between *P. triarthra* and *P. argentinensis*. Some of these differences are perhaps not so significant, and Harrington (1938) maintained that the two species are rather closely related.

O c c u r r e n c e: — England (Shinerton Shales), E. Canada (Nova Scotia, *Asaphellus* zone).

Parabolinella triarthroides Harrington 1938.

- 1938 *Parabolinella triarthroides* sp. nov. — Harrington, p. 194, text fig. 9, pl. VII, figs. 10—11. (Descr. and figs. of cranidia.)
1950 *Parabolinella triarthroides* Harrington — Shaw, p. 110. (Reported from Vermont.)
1951 *Parabolinella triarthroides* Harrington — Shaw, p. 102, pl. 22, figs. 1—10. (Descr. Figs. of cranidia and pygidium.)

T y p e d a t a: — Holotype (by original designation) is a cranidium figured by Harrington (1938, text fig. 9; pl. VII, fig. 10), from Quebrada de Coquena, Jujuy, Argentina.

D i a g n o s i s: — A *Parabolinella* species with: sagittal length of preglabellar field about twice that of occipital ring; cephalic axis almost parallel-sided, bluntly rounded in front, somewhat longer than wide; fixed cheeks about as wide as occipital ring; interocular cheeks about 1/3 as wide as glabella at eye line. Only cranidium known.

R e m a r k s: — The species seems to be very close to *P. triarthra*, but differs in having a bluntly rounded preglabellar furrow, at least not indented as in *P. triarthra*, and in having shorter glabellar furrows. It should be remembered, however, that the specimens of *P. triarthra* are compressed, which may have exaggerated the differences from *P. triarthroides*.

Shaw (1950, 1951) assigned some Vermont specimens to *P. triarthroides*. According to him (1951, p. 103), the North and South American specimens are not separable on either qualitative or quantitative grounds. I do not think this is unlikely, but would like to point out that it has so far only been possible to compare the cranidia, and, judging from the illustrations, that it seems as if the fixed cheeks are as wide as the occipital ring in the Argentine cranidia, whereas they are only three-fourths as wide as the occipital ring in the Vermont cranidia. However, this may possibly be due to a better preserved convexity of the Vermont cranidia. If the difference is real, the Vermont material should perhaps rather be assigned to a separate subspecies.

O c c u r r e n c e: — Argentina (Upper Tremadocian), Vermont (Gorge formation).

Parabolinella? caesa Lake 1913.

1913 *Parabolinella caesa*, sp. nov. — Lake, p. 66, pl. VII, fig. 2. (Descr. and fig. of incomplete axial shield.)

T y p e d a t a: — Holotype (by monotypy) is the incomplete axial shield figured by Lake (1913), from the Upper Lingula Flags at Dolgelley.

R e m a r k s: — The cranidium of this species is unfortunately not well known, but it appears to be of the *Parabolinella* type. Its thorax has 16 segments with pointed pleural ends, and its pygidium has 4 axial rings and an axial ridge.

O c c u r r e n c e: — Wales (Upper Lingula Flags.)

Parabolinella? incerta Rasetti 1945.

1945 *Parabolinella? incerta*, n. sp. — Rasetti, p. 471, pl. 61, fig. 16. (Descr. and fig. of cranidium.)

1951 *Parabolinella incerta* (Rasetti) — Shaw, p. 102. (Remarks.)

Non 1954 *Parabolinella incerta* (Rasetti) — Wilson. (= *Olenus? wilsoni* n. sp.)

T y p e d a t a: — Holotype (by original designation) is the cranidium figured by Rasetti (1945), from the Lévis conglomerate, probably from North Ridge, Lévis, Quebec, Canada.

R e m a r k s: — The taxonomic position of this species is still best regarded as uncertain. It recalls *Parabolinella*, with which it shares a truncate glabella, but S1 does not seem to be bifurcate, and it is possible that it is related to *Parabolinites* n. gen. Some specimens assigned to this species by Wilson (1954) are here referred to as *Olenus? wilsoni* n. sp.

O c c u r r e n c e: — Canada (Quebec, *Hungaria* zone).

Parabolinella? posthuma Matthew 1892.

1892 *Parabolinella posthuma*, n. sp. — Matthew, p. 107, pl. VII, figs. 15a—b. (Descr. Rough sketch of cranidium and free cheek.)

?1892 *Parabolinella?* sp. — Matthew, p. 107. (Remarks.)

1915 *Parabolinella posthuma* Matthew — Bassler, p. 943. (Listed.)

Type data: — As lectotype should be selected one of Matthew's specimens from Div. 3d at the Suspension Bridge, St. John, New Brunswick, Canada.

Remarks: — The affinities of this species are difficult to trace from the short description and rough sketches given by Matthew. Its small palpebral lobes and more or less continuous glabellar furrows suggest *Parabolina*, whereas its preglabellar field appears to be of the *Parabolinella* type.

A *Parabolinella?* sp. was stated by Matthew to differ in having genal caeca across the preglabellar field. As the genal caeca may be more or less developed or preserved within one species, it is possible that this form belongs to *P.?* *posthuma*, with which it occurs.

Occurrence: — E. Canada (New Brunswick, Bretonian, Div. 3d).

Parabolinella? punctolineata Kobayashi 1936.

1936b *Parabolinella? punctolineata*, n. sp. — Kobayashi, p. 166, pl. 21, figs. 19—20. (Descr. Figs. of cranidium and free cheek.)

1951 *Parabolinella punctolineata* Kobayashi — Shaw, p. 102. (Remarks.)

Type data: — Holotype (by original designation) is a cranidium figured by Kobayashi (1936b, pl. 21, fig. 19) from white limestone at Jones' Ridge, north of Tatonduk River, International Boundary, Canada.

Remarks: — Only a fragmentary cranidium and a fragmentary free cheek have been described. The cranidium resembles *Parabolinella*, but S1 does not seem to bifurcate. Shaw (1951) suggested that *P. punctolineata* and *P. incerta* may be synonymous, and pointed out that they resemble the North American material of *P. triarthroides* described by him.

Occurrence: — Canada (Upper Cambrian?, near Yukon-Alaska boundary).

Parabolinella? simplex (Salter 1866).

1866 *Conocoryphe? simplex*, n. sp. — Salter, p. 306, pl. 5, fig. 17. (Descr. and fig. of cranidium.)

1878 *Ellipsocephalus* sp. — Cat. Cambr. and Silur. Fossils Mus. Pract. Geol., p. 12. (Listed.)

1898 *Conocoryphe simplex*, Salt. — Brögger, p. 200 (1896, separate copies, p. 37). (Assigned to the genus *Cyclognathus*.)

1900a *Conocoryphe? simplex*, Salter — Reed, p. 255. (States that it may be assigned to *Cyclognathus*.)

1919 *Parabolina simplex* (Salter) — Lake, p. 110, pl. XIII, fig. 6.

Type data: — Holotype (by monotypy) is the incomplete cranidium described by Salter, from the Upper Lingula Flags at Penmorfa Church, Portmadoc, Wales.

Remarks: — The species is known only from an incomplete cranidium, and it is difficult to assign it with certainty to any genus at present.

Occurrence: — Wales (Upper Lingula Flags.)

Genus *Bienwillia* Clark 1924.

Type species: — *Dikelocephalus? corax* Billings 1865, by original designation.

Synonym: — *Diatemnus* Raymond 1937 (type: *D. miculus* Raymond 1937).

Diagnosis: — Oleninae which resemble both *Parabolinella* and *Triarthrus*, but differ from the first in having unforked S1 and narrower posterior cheeks, and from *Triarthrus* in having wider posterior cheeks and better developed preglabellar field.

Remarks: — I had intended to establish a new genus for species like *Parabolinella tetragonalis* (transferred to *Triarthrus* by Harrington & Leanza in 1952) and *Triarthrus shinetonensis*, which apparently are closely related to, but differ from both *Parabolinella* and *Triarthrus*. When Rasetti published a new photograph of a cranidium of *Bienwillia corax* in 1954 (pl. 61, fig. 15), I was firstly convinced that *Bienwillia* is a true olenid (which was not so obvious in earlier figures) and also that it most probably is congeneric with the species mentioned above. Unfortunately only the cranidium of *Bienwillia corax* seems to have been described. However, this is strikingly similar to those of *Triarthrus shinetonensis* and *Parabolinella tetragonalis* (especially the new subspecies *broeggeri*), and it would be unexpected if the other parts of the shield of *B. corax* should prove to differ significantly.

As pointed out by Rasetti (1944, p. 240), *Diatemnus miculus* Raymond 1937 (type species) is extremely similar to *Bienwillia*, and *Diatemnus* may be regarded as a subjective synonym of *Bienwillia*. I am not aware of any other species assigned to *Bienwillia* or *Diatemnus* except *Bienwillia terranova* Rasetti 1954, which I have transferred to *Leiobienwillia*.

The position of *Parabolinella wimani* is not quite certain. I have provisionally included it in *Bienwillia*, but its glabella has a more parabolic outline and recalls also *Parabolinites* n. gen. It may possibly be an intermediate form between *Parabolinites* and *Bienwillia*. It is, however, also possible that *Bienwillia* developed from *Parabolina*. *Bienwillia* and *Parabolinella* are apparently rather close, but *Bienwillia* is no doubt closest to *Triarthrus*, of which it is apparently a forerunner.

Included species: — The following species may be assigned to *Bienwillia*:

B. corax (Billings 1865)

B. micula (Raymond 1937) (type species of *Diatemnus* Raymond 1937)

B. shingtonensis (Lake 1913) (transferred from *Triarthrus*)

B. tetragonalis tetragonalis (Harrington 1938) (transferred from *Triarthrus*)

B. tetragonalis broeggeri n.subsp.

and possibly also:

B.? *canadensis* (Kobayashi 1955) (cf. postscript)

B.? *wimani* (Westergård 1917) (transferred from *Parabolinella*)

Occurrence: — Norway (Tremadocian), Sweden (Tremadocian), Great Britain (Upper Tremadocian), Argentina (Lower Tremadocian), Newfoundland (Tremadocian), Quebec (*Hungaia* zone), Vermont (Base of Gorge formation).

Phylogeny and relationships: — As discussed above (p. 134), *Bienwillia* is probably closely related to *Parabolinella*. Either *Parabolinella* developed from *Bienwillia*, or the two genera had a common origin. *Bienwillia* appears to be restricted to the Tremadocian and beds of corresponding age. All its species seem to be closely related, as far as their shields can be compared. *Bienwillia* apparently gave rise to *Triarthrus* which differs in having narrower fixed cheeks, smaller or no preglabellar field, and usually no genal spines.

Bienwillia corax (Billings 1865).

Pl. 1, fig. 6.

- 1865 *Dikelocephalus?* *corax*. (N. sp.) — — Billings, p. 334, fig. 322a. (Descr. and fig. of fragmentary cranium. The pygidium, fig. 322b, tentatively assigned to this species, does not belong to it.)
- 1915 *Apatokephalus corax* (Billings) [partim] — — Bassler, p. 55. (Listed.)
- 1924 *Bienwillia corax* (Billings) — — Clark, p. 20.
- 1944 *Bienwillia corax* (Billings) — — Rasetti, p. 240, pl. 36, figs. 51–52. (Recorded. Fig. of holotype and another cranidium.)
- 1954 *Bienwillia corax* (Billings) — — Rasetti, p. 583, pl. 61, fig. 15. (Mentioned. Fig. of well-preserved cranidium.)

Holotype: — The cranidium figured by Billings (1865), Nat. Mus. Canada no. 876a (by monotypy).

Diagnosis: — A *Bienwillia* species with: fixed cheeks half as wide as occipital ring; small palpebral lobes close to glabella and with centres opposite L3; S1 and S2 subparallel, long, faintly united across glabella; S3 shorter and fainter; preglabellar field about as long as occipital ring; glabella bluntly rounded in front. Only cranidium known.

Occurrence: — Canada (Quebec, Lévis conglomerate, boulders of the *Hungaia* zone).

Bienwillia micula (Raymond 1937).

- 1937 *Diatemnus miculus* sp. nov. — Raymond, p. 1092, pl. 1, fig. 19. (Descr. and fig. of cranidium.)
1944 *Diatemnus miculus* Raymond — Rasetti, p. 240. (Transferred to *Bienwillia*.)

Holotype: — By original designation the cranidium figured by Raymond (1937). No. 14709 in the Yale Univ. Museum.

Diagnosis: — Differs from *Bienwillia corax* in having a more quadrate shape of the cephalic axis.

Occurrence: — Vermont (Lowest zone of the Gorge formation at Highgate Falls).

Bienwillia shingletonensis (Lake 1913).

Pl. 1, fig. 7.

- 1908 *Triarthrus shingletonensis* sp. nov. — Raw, p. 512. (Listed.)
1913 *Triarthrus shingletonensis*, Raw — Lake, p. 70, pl. VII, figs. 13–16. (Descr. Figs. of more or less complete dorsal shields.)
1952 *Triarthrus shingletonensis* Raw — Harrington & Leanza, p. 192. (Mentioned.)

Type data: — As lectotype I select the dorsal shield without pygidium figured by Lake (1913, pl. VII, fig. 13), from the Shingleton Shales, Shingleton, Shropshire, England.

Diagnosis: — A *Bienwillia* species with: fixed cheeks about three-fourths as wide as occipital ring; centres of eyes opposite L2; glabella bluntly rounded in front; free cheeks with long spine; 14 thoracic segments, the axial rings of the last two fixed to the pygidium, thoracic axis with axial nodes, 14th segment with long axial spine; pygidium entire with 3 axial rings.

Remarks: — Since *B. shingletonensis* was first described and figured by Lake (1913), he must be regarded as the author.

Occurrence: — England (Shingleton Shales).

Bienwillia tetragonalis tetragonalis (Harrington 1938).

- 1938 *Parabolinella tetragonalis* sp. nov. — Harrington, p. 196, pl. VII, figs. 3–4. (Descr. Figs. of cranidia.)
1952 *Triarthrus tetragonalis* (Harrington) — Harrington & Leanza, p. 192. (Remarks.)

Type data: — As lectotype I select a cranidium figured by Harrington (1938, pl. VII, fig. 3), from the Quebrada de Rupasca, Argentina.

Diagnosis: — A *Bienwillia* species with: fixed cheeks about half as wide as occipital ring; centres of palpebral lobes opposite L2; glabella slightly indented in front; S1 and S2 rather oblique backwards, long, but not united across glabella; S3 very short, almost pit-like and on line with inner ends of S1 and S2. Only cranidium known.

Remarks: — A closely related form is described below as *B. tetragonalis borealis* n. subsp.

Occurrence: — Argentina (Lower Tremadocian).

Bienwillia tetragonalis broeggeri n. subsp.

Pl. 8; pl. 11, figs. 1—7.

- 1882 *Parabolinella limitis*, n. sp. [partim] — Brögger, p. 102, pl. III, fig. 4 only. (Fig. of cranidium.)
 1920 *Parabolinella limitis*, Brögger — Størmer, p. 9, pl. I, figs. 7—8. (Descr. Figs. of cranidium, free cheeks, and pygidium.)
 1952 Un *Triarthrus* — Harrington & Leanza, p. 192. (Remarks.)

Name: — This subspecies is named in honour of the late Professor W. C. Brögger, who first drew attention to it.

Holotype: — A cranidium (P. M. O. no. 488) from 3aα at Vekkerø, Oslo, Norway, collected by L. Størmer in 1918.

Diagnosis: — Differs from *Bienwillia tetragonalis tetragonalis* Harrington 1938 in having shorter glabellar furrows.

Description: — This is based on 9 cranidia and a few free cheeks and pygidia. The largest cranidium is 11 mm long.

Cranidium rather convex transversely. Flattened cranidia therefore appear wider, and may be broken (as the cranidium figured by Størmer, 1920). Cephalic axis squarish, but with slightly convex sides and bluntly rounded or truncate in front, where it may be slightly indented in the middle. Occipital ring with small axial node. Occipital furrow with its convex middle part slightly shallower and wider than oblique lateral parts. Three pairs of glabellar furrows. S1 slightly oblique, convex, with faint geniculum. S2 slightly oblique, almost straight. Both S1 and S2 almost effaced adjacent to axial furrow, and not connected across glabella. S3 represented by a pair of pit-like impressions on line with inner ends of S1 and S2. Preglabellar field slightly tumid and slightly less than one-sixth as long as cephalic axis. Anterior border furrow distinct, faintly and irregularly pitted, due to crossing of genal caeca, faintly developed on preglabellar field. Border narrow, convex, and arched up in front view. Eye ridges faint, short, and oblique. Interocular cheeks narrow. Palpebral lobes moderately long, with centres opposite L2, and posterior ends opposite anterior end of S1. Postocular cheeks narrow, about half as wide as occipital ring. Preocular facial sutures slightly diverging. Postocular facial sutures diverging moderately, almost straight.

Free cheeks elongate, with very narrow genal fields. Spine long and strong. Angle between spine and posterior margin slightly acute. Faint genal caeca.

Hypostoma and thorax unknown.

Pygidium about twice as wide as long. Posterior margin evenly curved, without spines. Axis with two rings and an end lobe, which may be divided in two by a transverse furrow. Four pairs of pleural furrows.

Affinities: — This form resembles the Argentine *B. tetragonalis tetragonalis*, of which, however, only the cranidium has been described. As the Argentine specimens are flattened, they should be compared with the flattened cranidia of the present form. It is seen that they agree in most features, but that the glabellar furrows are longer in the Argentine form. Harrington & Leanza (1952) have already pointed out that the Norwegian form resembles *B. tetragonalis tetragonalis*, and also *B. shinctonensis*. The latter is known only from flattened specimens, and its cranidium is not well enough known for a detailed comparison with *B. tetragonalis broeggeri*. It appears, however, that the glabella of *B. shinctonensis* widens more forwards, and it seems to be a smaller species.

Occurrence: — Norway: Oslo (Vekkerø), Østerdalen (Glomstad) — Tremadocian, zone of *Symphysurus incipiens* (3a). Associated with *Peltocare norvegicum* and *Symphysurus incipiens*.

Bienwillia? wimani (Westergård 1917).

Pl. 8; pl. 10, figs. 7—9.

- 1905b *Acerocare?* sp. — Wiman, p. 82, pl. V, fig. 15. (Fig. of pygidium.)
 1905b *Boeckia mobergi*. n. sp. [partim] — Wiman, p. 81, pl. V, fig. 10. (Descr. and fig. of free cheek.)
 1909 *Acerocare* sp. — Westergård, p. 55. (Mentions pygidium reported by Wiman.)
 1917 *Parabolinella Wimani* n. sp. — Westergård, p. 639, pl. 7, figs. 10—17. (Descr. Figs. of cranidia, free cheeks, thoracic segment, and pygidium.)
 1922a *Parabolinella limitis*, Brøgger — Størmer, p. 7, pl. I, fig. 11. (Descr. and fig. of pygidium.)
 1929 *Parabolinella wimani* Wgd. — Strand, p. 360. (Remarks.)

Type data: — As lectotype I select a free cheek figured by Westergård (1917, pl. 7, fig. 13), from the Dictyonema Shale, Tåsjöberget, Ångermanland, Sweden.

Diagnosis: — A *Bienwillia?* species with: fixed cheeks about half as wide as occipital ring; centres of palpebral lobes opposite outer ends of S2; S1 and S2 relatively short, curved backward; S3 short, curved, on line with inner ends of S1 and S2; glabella rounded or bluntly rounded in front; free cheeks with spine which deviates slightly from course of lateral margin, and with acute inner spine angle; number of thoracic segments unknown, at least some segments have short pleural spines and axial node; pygidium entire with 3 axial rings.

Remarks: — *Bienwillia? wimani* differs from unquestionable *Bienwillia* species in having shorter and more curved S1 and S2 and a more parabolic outline of the cephalic axis. It resembles *Parabolinites* n. gen., too, but is probably closer to *Bienwillia*.

The rather convex, almost angulate anterior margin of a cranidium figured by Westergård (1917, pl. 7, fig. 10) is not typical for the species. The usual outline is seen in the small cranidium figured by him in pl. 7, fig. 12. Specimens of *Parabolinella* and *Bienwillia* species may sometimes show the same angulate anterior margin. It may perhaps be due to the preservation, since the anterior margin is considerably vaulted in uncompressed specimens.

The pygidium figured by Størmer (1922a) as *Parabolinella limitis* belongs to *Bienwillia? wimani*, as already suggested by Strand (1929). I have succeeded in finding determinable cranidia and free cheeks in Størmer's material.

Norwegian material: — This consists of detached parts, which are not too well preserved, but which agree very well with the Swedish material.

Occurrence: — Norway: Hadeland (Jaren), Ringsaker (Steinsodden, Mælum), Hamar district (Øksna). — Dictyonema Shale, subzone of *Dictyonema flabelliforme flabelliforme* (2cβ). Associated with *Bocchaspis mobergi* + *Dictyonema flabelliforme flabelliforme*. — Sweden (Dictyonema Shale).

Genus *Triarthrus* Green 1832.

Type species: — *Triarthrus beckii* Green 1832, by monotypy. (According to Vogdes, 1893, a junior synonym of *Brongniartia carcinodea* Eaton, 1832).

Diagnosis: — Oleninae with: pelturoid cranidium; dominating, subrectangular or subquadrate axis, broadly rounded, truncate, or slightly indented in front; S1 and S2 equally long and distinct; S3 and S4 faint or missing; palpebral lobes close to glabella, opposite L2 or further forwards; preglabellar field very short; postocular cheeks narrow, as wide as or narrower than half the width of occipital ring; free cheeks narrow, pelturoid, with or without spine; thorax with 12—14 segments; narrow pleural areas; entire pygidium.

Remarks: — The genus is famous because of the pyritized specimens showing appendages from the Utica Shale near Rome, New York. The specimens were earlier assigned to *Triarthrus beckii* Green 1832, but Ruedemann (1926) has shown that they belong to *T. eatoni* (Hall 1838). Many Ordovician species have been described, ranging from the Tremadocian to early Upper Ordovician. Only Tremadocian forms are dealt with in detail in this paper.

Tremadocian species and subspecies: —

- T. angelini angelini* Linnarsson 1869
- T. angelini rectifrons* Harrington 1938
- T. pacifica* (Kobayashi 1955) (cf. postscript)

T. punctatus (Crosfield & Skeat 1869) (earlier: *Peltura*)

and possibly also:

T.? *belli* Matthew 1902

T.? *variscorum* Szdzy 1955.

T. shinetonensis (Lake 1913) has been transferred to *Bienwillia*.

Occurrence of Tremadocian forms: — Norway (Upper Tremadocian), Sweden (Upper Tremadocian), Wales (Tremadocian), Argentina (Upper Tremadocian), ?Canada (Tremadocian).

Phylogeny and relationships: — There can hardly be any doubt that *Triarthrus* developed from *Bienwillia*, which differs mainly in having wider fixed cheeks and a well-developed preglabellar field. The Tremadocian members of *Triarthrus* are all probably closely related. The free cheeks are known in all forms except *T.?* *belli* and have no spines. Their cranidia are all rather similar, but differ i. a. in the width of the fixed cheeks in relation to the width of the occipital ring, in the frontal outline of the glabella, in the presence or absence of an axial occipital node, and in the size and position of the palpebral lobes. Thus the palpebral lobes are relatively large and with centres opposite S2 in *T. angelini*, whereas they are small and more anteriorly situated in *T. punctatus*. The last feature may indicate that *T. punctatus* is related to *Westergårdites* (cf. p. 154). Whereas also another olenid genus, *Peltocare* n. gen., occurs in beds of Arenigian age, *Triarthrus* appears to be the only olenid genus in later beds, except for its off-shoot *Porterfieldia*. The later members of *Triarthrus* are surprisingly similar to the Tremadocian forms, perhaps especially in the cranidium, except that the later members tend to have no preglabellar field. There are 14 thoracic segments in those later species where the number is known, as compared to 12 in *T. punctatus* which is the only Tremadocian species where the number is known. It is very interesting to observe that one of the later species, *T. spinosus* from the Trenton Group, has free cheeks with spine, a feature which is not known in the Tremadocian species of *Triarthrus* whose free cheeks are known.

Triarthrus angelini angelini Linnarsson 1869.

Pl. 8; pl. 11, figs. 8—10.

1869 *Triarthrus Angelini* n. sp. — Linnarsson, p. 70, pl. 2, fig. 28. (Diagn. and fig. of cranidium.)

1882 *Triarthrus Angelini*, Linnr. — Brögger, p. 112, pl. III, figs. 1, 1a; pl. XII, figs. 1, 1a. (Descr. Figs. of cranidium, free cheek, thoracic segment, and pygidium.)

1906 *Triarthrus Angelini* Linnr. — Moberg & Möller, p. 83, pl. IV, figs. 29—31. (Remarks. Figs. of cranidia.)

Type data: — The specimen figured by Linnarsson is missing. A neotype should be selected from Swedish material.

Diagnosis: — A *Triarthrus* species with: subquadrate, somewhat rounded cephalic axis with convex, but usually indented front; occipital ring

with axial node; S1 and S2 slightly curved, parallel, not united across glabella; preglabellar field about one-third as long as occipital ring; centres of palpebral lobes opposite S2; fixed cheeks slightly narrower than one-third of the width of occipital ring; free cheeks narrow and without spine; thorax with narrow pleural regions and pleural ends with points; pygidium entire with 3 axial rings. Number of thoracic segments unknown.

Occurrence: — Norway: Eiker (Vestfossen), Røyken (Nærsnes, Slemmestad), Asker (Engervik, Bjerkåsholmen), Oslo (Vekkerø, Bygdøy Sjøbad, Tøyen), Hadeland (Gran), Snertingdal. — Ceratopyge Beds (3a β -3a γ) — Sweden (Ceratopyge Beds). Clark (1924, p. 92) mentions a specimen of *T. cf. angelini* from the *Shumardia* Limestone at Lévis, Quebec, Canada.

Triarthrus angelini rectifrons Harrington 1938.

1938 *Triarthrus angelini* Linnarsson var. *rectifrons* nov. — Harrington, p. 20, pl. VIII, figs. 17, 19—20, 22. (Descr. Figs. of cranidia and pygidia.)

Type data: — As lectotype I select a cranidium figured by Harrington (1938, pl. VIII, fig. 20) from Quebrada de Coquena, Jujuy, Argentina.

Diagnosis: — Differs from *Triarthrus angelini angelini* in having convex preglabellar furrow; smaller or no occipital tubercle, and a pitted marginal furrow.

Occurrence: — Argentina (Upper Tremadocian).

Triarthrus punctatus (Crosfield & Skeat 1896).

1896 *Peltura punctata*, sp. nov. — Crosfield & Skeat, p. 535, pl. XXVI, figs. 1—10. (Descr. Figs. of more or less complete dorsal and axial shields, cephalon, free cheek, and thoracic segments.)

1908a *Peltura punctata* Crosfield and Skeat — Raw, p. 512. (Suggests that it may belong to *Triarthrus*.)

1919 *Peltura punctata* Crosfield and Skeat — Lake, p. 99, pl. XI, fig. 13; pl. XII, figs. 1—3. (Descr. Figs. of more or less complete axial shields, cephalon, and cranidium.)

Type data: — As lectotype I select an axial shield figured by Crosfield & Skeat (1896, pl. XXVI, fig. 3), from Tremadoc Beds, Nant-y-Glasdwr, Wales. A new figure of the specimen was given by Lake (1919, pl. XII, fig. 1).

Diagnosis: — A *Triarthrus* species with: subrectangular cephalic axis, slightly convex in front, and with slightly expanded anterior corners; short preglabellar field; pitted marginal furrow; small palpebral lobes opposite posterior part of frontal lobe; fixed cheeks about half as wide as occipital ring without axial tubercle; free cheeks without spine; 12 thoracic segments; pleural ends with short points; pygidium with 4 axial rings.

Remarks: — The species was originally assigned to *Peltura*, but Raw (1907) considered it to be very closely related to *Triarthrus* (here: *Bienwillia*) *shingletonensis* and was inclined to regard the two as forming a special section of the genus *Triarthrus*. Lake (1919, p. 100) advocated that in the number of thoracic segments and in the small size and very forward position of the eyes, it is a typical *Peltura*. Nevertheless, I believe it is a *Triarthrus* species. Its glabella has a tendency to widen a little at the anterior corners. This is a feature seen also in the closely related genera *Bienwillia* and *Parabolinella*. Its two pairs of glabellar furrows are rather distinct, and of about equal length. This is a typical feature in *Triarthrus*, but not known in *Peltura* or related genera. Its border is rather distinct and reminds one more of the later Oleninae than of the later Pelturinae. Finally its anterior margin is punctate. This feature is not known in the Pelturinae, but is very commonly met with among later Oleninae. I must admit that, apart from these features, *T. punctatus* resembles the pelturines, especially *Peltocare* n. gen., which, however, has wider postocular cheeks.

Occurrence: — Wales (Tremadocian).

Triarthrus? belli Matthew 1902.

- 1902 *Triarthrus Belli*, n. sp. — Matthew, p. 412, pl. XVIII, fig. 8. (Descr. Fig. of restored cranidium.)
1903 *Triarthrus Belli* — Matthew, p. 230, pl. XVIII, fig. 8. (Descr. Fig. of restored cranidium.)
1952 *Triarthrus belli* Matthew — Hutchinson, p. 83, pl. III, fig. 15. (Remarks. Fig. of holotype cranidium.)

Type data: — Holotype (by monotypy) is the incomplete cranidium figured by Hutchinson (1952) from McLeod Brook, Cape Breton Island, Nova Scotia.

Remarks: — The only specimen known is not well enough preserved to decide whether it belongs to *Triarthrus* or *Bienwillia*.

Occurrence: — Canada (Nova Scotia; Tremadocian, *Asaphellus* zone). One incomplete cranidium is reported from the Shumardia Limestone at Lévis, Quebec, by Clark (1924, p. 92).

Triarthrus? variscorum Sdzuy 1955.

- 1955 *Triarthrus variscorum* n. sp. — Sdzuy, p. 18, text-fig. 11, pl. 3, figs. 71–76. (Descr., figs. of cranidia and free cheeks.)

Type data: — Holotype is a cranidium from Leinitz near Hof, figured by Sdzuy (1955, pl. 3, fig. 71).

Remarks: — The cephalic axis is not as dominating as in other species of *Triarthrus*, and the glabellar furrows appear to be shorter. I refer the species to *Triarthrus* only with doubt.

Occurrence: — Germany (Lower? Tremadocian).

Post-Tremadocian forms of *Triarthrus*.

The post-Tremadocian forms of *Triarthrus* are not specially treated in this paper. Their descriptions are scattered in various, partly unexpected papers (e. g. Bulman, 1931: "South American graptolites"), and the list given below is probably not complete. However, it may be of use to future students of the genus *Triarthrus*.

T. arcuatus (Harlan 1835). Subjective synonym of *T. becki*.

T. beckii Green 1832. Trenton Group, eastern North America. (For distribution, see Kay, 1937, pp. 270, 271, 273, 275, 301. List of synonyms is given i. a. by Reed, 1903, p. 28. According to Vogdes, 1893, p. 358, a junior synonym of *T. carcinodea*.)

T. beckii humilis Hadding 1913 (p. 69). Lower Dicellograptus Shale, Sweden.

T. beckii macasteyensis Twenhofel 1914 (p. 35). Trenton, Anticosti.

T. beckii var. — — Reed, 1903 (p. 28). Balclatchie Group (Ilandeilian), Girvan, Scotland. (= *T. reedi* Raymond 1925).

T. billingsi Barrande 1872 (p. 427). Utica. (cf. Raymond, 1925, p. 50.)

T. canadensis Smith 1861 (p. 275). Hudson.

T. carcinodea (Eaton 1832). Utica Shale. Senior synonym of *T. beckii* (cf. Vogdes, 1893, p. 358).

T. eatoni (Hall 1838). Trenton Group, eastern North America. (Distribution in Trenton Group, see Kay, 1937, pp. 282, 284—286, 301.) The pyritized specimens from the Utica Shale near Rome, New York, were originally assigned to *T. beckii* (i. a. by Beecher, 1894 and 1902, and Raymond, 1920b), but were shown to belong to *T. eatoni* by Ruedemann (1926).

T. cf. eatoni (Hall) — — Bulman, 1931 (p. 87). Caradocian(?), Peru.

T. fischeri Billings 1865 (p. 291). Quebec Group, Newfoundland.

T. aff. fischeri Billings — — Bulman, 1931 (p. 88). Llanvirnian, Peru.

T. freji Thorslund 1940 (p. 130). Ogygiocaris Shale, Sweden. This name was given by Thorslund to the species assigned by Asklund (1936, p. 3) to *T. beckii*.

T. glaber Billings 1859 (p. 382). Utica Shale, Canada.

T. huguesensis Foerste 1924 (p. 241). Lowermost part of the Lorraine formation, Canada.

T. jemtlandicus Linnarsson 1875 (p. 493). Ogygiocaris Shale, Sweden. (See also Asklund, 1936, p. 7.)

T. linnarssoni Thorslund 1940 (p. 128). Upper Chasmops Beds (Caradocian), Sweden. Thorslund gave this name to the species assigned to *T. beckii* by Linnarsson (1869, p. 70).

T. pygmaeus Törnquist 1884 (p. 38). Black Tretaspis Shale (zone of *Pleurograptus linearis*), Sweden.

T. reedi Raymond 1925 (p. 52). Llandeilian, Scotland.

T. skutensis Thorslund 1940 (p. 130). Upper Chasmops Beds (Caradocian), Sweden.

T. spinosus Billings 1859 (p. 383). Trenton Group, eastern North America. (Distribution in Trenton group, see Kay, 1937, pp. 285—286, 301.)

T. spinosus rougensis Parks 1928 (p. 44). Trenton Group, eastern North America. (Distribution in Trenton Group, see Kay, 1937, p. 285.)

T. triarthrus (Harland 1835). Subjective synonym of *T. beckii*.

T. sp. — — Tjernvik, 1956 (p. 201). Lowermost Arenigian, Sweden.

T. spp. — — Bulman, 1933 (p. 345). Llanvirnian, Peru.

Genus *Porterfieldia* Cooper 1953.

Type species: — *Triarthrus caecigenus* Raymond 1920, by original designation.

Original diagnosis: — *Triarthrus*-like trilobites without eyes. Cheeks very narrow and short. Facial sutures probably ventral. Glabella strongly convex. Thorax with 11 segments and wide axial lobe, narrow pleura, and a small pygidium.

Relationships: — The only known species of this apparently blind genus no doubt developed from *Triarthrus*, to which it was originally assigned.

Porterfieldia caecigenus (Raymond 1920)

Pl. 1, fig. 12.

1920a *Triarthrus caecigenus*, sp. nov. — — Raymond, p. 280. (Descr.)

1925 *Triarthrus caecigenus* Raymond — — Raymond, p. 52, pl. 2, fig. 16. (Descr. and fig. of axial shield.)

1953 *Porterfieldia caecigenus* (Raymond) — — Cooper, p. 8, pl. 2, figs. 7—20; pl. 19, fig. 4. (Descr. Figs. of axial shields and parts of axial shields.)

Type data: — Holotype is the axial shield figured by Raymond in 1925.

Diagnosis: — As for genus.

Occurrence: — Athens shale of eastern North America.

Genus *Plicatolina* Shaw 1951.

Type species: — *Plicatolina kindlei* Shaw 1951, by original designation.

Diagnosis: — Oleninae with: elongate cephalic axis, indented in front; 4 distinct pairs of glabellar furrows: S1 and S2 long and subparallel,

slightly oblique backwards, S3 long and very slightly oblique backwards, S4 shorter and almost transverse; short preglabellar field; free cheeks with spine which continues course of lateral margin; many (16 or more) thoracic segments with spinose pleural ends. Pygidium apparently with marginal spines.

Included species: —

P. kindlei Shaw 1951

P. pheidolopyge (Harrington 1938)

Shaw (1951) suggested that *Parabolinella rugosa* might possibly belong to this genus. However, it differs from *Plicatolina* in many features, as for instance in the pattern of the glabellar furrows, and I do not think that it is closely related to this genus.

Occurrence: — Vermont (Gorge formation), Argentina (Lower Tremadocian), Bolivia (Lower Tremadocian).

Phylogeny and relationships: — *Plicatolina* resembles genera like *Parabolina* and *Bienwillia*, and no doubt developed from late members of the Oleninae. The long subparallel S1 and S2 in *Plicatolina* suggest that it may be closest to *Bienwillia*. *Plicatolina* may furthermore be related to *Westergårdites*. The two species assigned to *Plicatolina* apparently are very closely related.

Plicatolina kindlei Shaw 1951.

Pl. 1, fig. 11.

1951 *Plicatolina kindlei* Shaw, n. sp. — Shaw, p. 103, pl. 22, figs. 11—17. (Descr. Figs. of larval and adult cranidia and part of thorax.)

Type data: — Holotype (by original designation) is an incomplete dorsal shield figured by Shaw (1951, pl. 22, fig. 16) from above the overthrust at Highgate Falls, Vermont, U. S. A.

Diagnosis: — A *Plicatolina* species with tuberculate surface.

Occurrence: — Vermont (Gorge formation).

Plicatolina pheidolopyge (Harrington 1938).

1938 *Parabolina pheidolopyge* sp. nov. — Harrington, p. 198, pl. VII, fig. 6. (Descr. and fig. of pygidium.)

1943 *Parabolina pheidolopyge* Harrington — Harrington & Leanza, p. 348, pl. II, figs. 9—10. (Descr. and figs. of cranidia.)

1951 *Plicatolina pheidolopyge* (Harrington) — Shaw, p. 103. (Remarks.)

Type data: — Holotype (by monotypy) is the cranidium figured by Harrington (1938), from the Lower Tremadocian at Rio Volcanito, Sierra de Famatina, La Rioja, Argentina.

Diagnosis: — A *Plicatolina* species with smooth surface.

Remarks: — The species was erected upon a pygidium, but Harrington & Leanza later (1943) assigned some cranidia to it. As remarked by Shaw (1951, p. 103), the reference of the species to *Plicatolina* is based

on the cranium. If the cranium and pygidium should prove not to belong to the same species, the cranium should remain in *Plicatolina*.

Occurrence: — Argentina (Lower Tremadocian), Bolivia (Lower Tremadocian).

Genus *Westergårdites* Troedsson 1937.

Type species: — *Westergårdites pelturaeformis* Troedsson 1937, by original designation.

Diagnosis: — Oleninae with: subquadrate cephalic axis; 4 pairs of glabellar furrows: S1 and S2 long and subparallel, oblique backwards, S3 and S4 short, S3 far inside and S4 close to the axial furrow; no preglabellar field; palpebral lobes small, close to glabella and situated very far forwards; fixed cheeks narrow; thorax with 19 segments, narrow pleural regions, and short pleural spines; pygidium not very well known, apparently with 3 pairs of short marginal spines. Free cheeks unknown.

Occurrence: — Central Asia (Western Quruq tagh, Eastern T'ien-shan). Only one species (and specimen) is known.

Relationships: — The genus *Westergårdites* resembles especially Tremadocian genera like *Plicatolina* and *Bienwillia-Triarthrus*. It differs from *Plicatolina* in having a more squarish cephalic axis and no preglabellar field, and from *Bienwillia-Triarthrus* in having the palpebral lobes further forwards, a greater number of thoracic segments, and a distinct S4. On the whole, *Westergårdites* seems to agree best with *Plicatolina*, which may be closely related. Both genera have 4 glabellar furrows forming the same pattern, and their thoracic shields are strikingly similar, except for *Westergårdites* having narrower pleural regions and perhaps more segments. I therefore believe that *Westergårdites* should be assigned to the Oleninae, and that it is not closely related to *Peltura*, as suggested by Troedsson (1937, p. 63). This involves that *Westergårdites* may be of Tremadocian rather than Late Cambrian age.

Westergårdites pelturaeformis Troedsson 1937.

Pl. 1, fig. 4; text-fig. 18.

1937 *Westergårdites pelturaeformis* n. gen. & n. sp. — Troedsson, p. 62, pl. VIII, fig. 1. (Descr. Fig. of axial shield.)

Type data: — Holotype (by original designation) is the axial shield figured by Troedsson (1937).

Diagnosis: — As for genus.

Occurrence: — Central Asia (Upper Cambrian or Tremadocian, cf. above).

Fig. 18. Type specimen of *Westergårdites pelturaeformis* Troedsson. Whitened with ammonium chloride. Not retouched. $\times 34$.

Genus *Angelina* Salter 1859.

Synonym: — *Keidelaspis* Harrington 1937.

Type species: — *Angelina sedgwickii* Salter 1859, designated by Vogdes, 1890.

Diagnosis: — Oleninae with: cephalic axis tapering forwards; faint and rather oblique glabellar furrows; well-developed preglabellar field; pitted anterior border furrow; preocular facial sutures slightly diverging or subparallel; free cheeks with large, broad-based spine, continuing course of lateral margin; rather wide cephalic doublure; thorax with 15 segments (when number is known); pleural ends with short pleural spine; pygidium with marginal spines.

Remarks: — As *Keidelaspis saltensis* (type species) is regarded as a synonym of *Angelina steinmanni* by Harrington (1938), *Keidelaspis* becomes a junior synonym of *Angelina*.

Included species: —

Angelina punctolineata Kobayashi 1937

A. saltensis (Harrington 1937) (= *A. steinmanni*)

A. sedgwickii Salter 1859

A. steinmanni (Kayser 1897)

A. subarmata Salter 1859 (= *A. sedgwickii*)

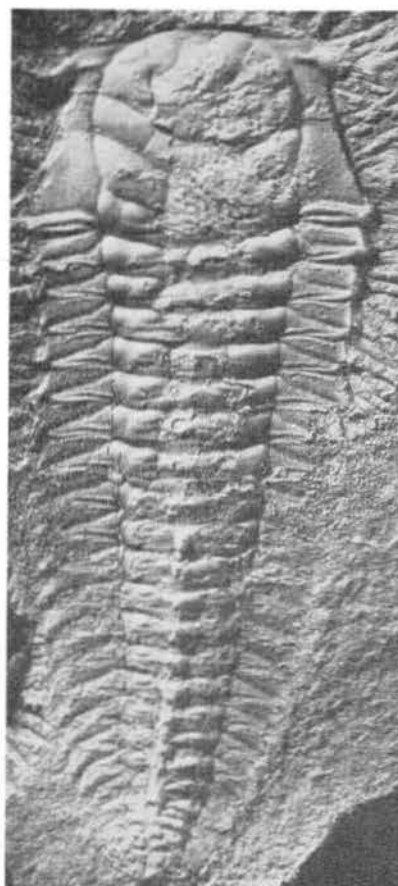
and possibly also:

A.? *latifrons* (Wilson 1954) (earlier: *Beltella*)

A.? *rexta* (Salter 1866) (earlier: *Conocoryphe*, *Beltella*)

A.? sp. — Matthew, 1903, p. 232, pl. XVIII, fig. 9.

Lake (1919, p. 111) mentioned that he has seen a specimen labelled *Angelina salteri* Holm from Yrerstad (i. e. Jerrestad) in Skåne (Scania) in the collections of the Vetenskaps Akademi in Stockholm, but that he has been unable to find any published figure or description. I have examined the material, actually three specimens on two slabs (nos. Ar 1892a-b), now preserved in the Paleozoological Department of the Swedish State Museum of



Natural Science (R. M.). The description of this species was never published. Its thorax and pygidium somewhat resemble *Angelina sedgwickii*, except, as also observed by Lake, that the posterior pleural spines seem to be somewhat larger and the pygidium is entire. Its cranidium is badly preserved, and it is hardly possible to say whether the species really is an olenid. It is perhaps not impossible that it belongs to some Middle Cambrian genus, and for the time being it is best not to include it in *Angelina*.

Occurrence: — Wales (Upper Tremadocian), Argentina (Lower Tremadocian), Argentina (Tremadocian *Kainella* zone), ?Canada (*Asaphellus* zone).

Phylogeny and relationships: — Brögger (1898, p. 198) suggested that *Angelina* is very close to, perhaps congeneric with *Parabolinella*. Lake (1919, p. 112) opposed the view that they could be congeneric, and pointed out some of the differences. He (l. c., p. 111) suggested instead that *Angelina* might be closely related to *Beltella*, but this was contradicted by Harrington & Leanza (1952), who assigned *Angelina* to the Triarthrinae (here = Oleninae) and *Beltella* to the Pelturinae. I agree with Lake that *Angelina* is not congeneric with *Parabolinella*. Its relationships to other genera are rather uncertain. It is possible that *Angelina* is closest to *Parabolina* or perhaps *Parabolinites* n. gen. *Angelina* and *Parabolinites* n. gen. have a rather similar glabella, although the glabellar furrows are fainter and more oblique in *Angelina*. Both genera have a well-developed preglabellar field and slightly diverging or subparallel facial sutures in front of the palpebral lobes. The same applies to *Parabolinella*, which, however, has a differently shaped glabella and a different pattern of glabellar furrows. Professor, Dr. H. J. Harrington has kindly sent me a photograph of an undescribed South American olenid. It resembles both *Parabolinites laticaudus* and *Angelina sedgwickii*. The species is possibly closest to *Angelina*, having rather oblique and faint glabellar furrows and 15 thoracic segments. However, its pygidium is entire, thus resembling that of *Parabolinites laticaudus*.

Angelina punctolineata Kobayashi 1937.

1937a *Angelina punctolineata* Kobayashi — — Kobayashi, p. 13. (Listed.)

1937b *Angelina punctolineata*, new species — — Kobayashi, p. 479, pl. VI, fig. 22. (Descr. and fig. of cranidium.)

1938 *Angelina punctolineata* Kobayashi — — Harrington, p. 201. (Remarks.)

1954 *Angelina punctolineata* Kobayashi — — Wilson, p. 278. (Remarks.)

Type data: — Holotype (by monotypy) is the cranidium figured by Kobayashi (1937b).

Remarks: — Only a single, badly preserved cranidium is known. It resembles *Angelina sedgwickii*, but it appears to have larger eyes and a more truncate glabella.

Occurrence: — Bolivia (Tremadocian *Kainella* zone at Cuesta de Erquis, Tarija).

Angelina sedgwickii Salter 1859.

Pl. 1, fig. 10.

- 1859 *Angelina Sedgwickii*, n. sp. — Salter, p. 53, foss. 9, fig. 2. (Fig. of restored dorsal shield.)
- 1859 *Angelina subarmata*, n. sp. — Salter, p. 53, foss. 9, fig. 3. (Fig. of restored, but laterally compressed dorsal shield.)
- 1864 *Angelina Sedgwickii*, Salter — Salter, pl. VII, figs. 1—5, p. 1. (Descr. Figs. of dorsal shields and hypostoma. Regards *A. subarmata* as a synonym.)
- 1866 *Angelina Sedgwickii*, Salter — Salter, p. 308, pl. 7, figs. 1—5. (Descr. Same figs. as in 1864.)
- 1873 *Angelina Sedgwickii*, Salter — Salter, p. 17. (Remarks, fig. of restored dorsal shield.)
- 1898 *Angelina sedgwickii*, Salter — Brögger, p. 198. (Remarks.)
- 1919 *Angelina sedgwickii*, Salter — Lake, p. 112, pl. XIII, figs. 7—12; pl. XIV; fig. 1. (Descr. Figs. of more or less complete dorsal shields, one showing hypostoma, and of cephalon and cranium.)
- 1954 *Angelina sedgwickii*, Salter — Wilson, p. 278. (Remarks.)

Type data: — As lectotype should be selected one of Salter's original specimens from the Upper Tremadocian of North Wales.

Diagnosis: — An *Angelina* species with preocular facial sutures diverging; length of preglabellar field one-sixth of the length of cephalic axis; palpebral lobes close to glabella; fixed cheeks somewhat narrower than occipital ring.

Occurrence: — Wales (Upper Tremadocian).

Angelina steinmanni (Kayser 1897).

- 1897 *Liostracus Steinmanni* n. sp. — Kayser, p. 277, pl. VII, figs. 2—3. (Descr. Figs. of cranium, free cheek, and restored cephalon.)
- 1937 *Keidelaspis saltensis* gen. & sp. nov. — Harrington, p. 111, pl. VI, figs. 5—7. (Descr. Figs. of cranidia and pygidium.)
- 1937a "*Liostracus*" *steinmanni* Kayser — Kobayashi, p. 13. (Listed.)
- 1938 *Angelina steinmanni* (Kayser) — Harrington, p. 199, pl. VIII, figs. 1—7, 11—12. (Descr. Figs. of cranidia, free cheeks, and pygidium. Claims that *Keidelaspis saltensis* is a synonym.)
- 1954 *Angelina steinmanni* (Kayser) — Wilson, p. 278. (Remarks.)

Type data: — As lectotype I select the cranium figured by Kayser (1897, pl. VII, fig. 2) from the Tremadocian sandstone at Iruyn, Salta, Argentina.

Remarks: — The species is not very well known, but at least differs from *Angelina sedgwickii* in having shorter cephalic axis and longer preglabellar field.

Occurrence: — Argentina (Lower Tremadocian).

Angelina? latifrons (Wilson 1954).

- 1954 *Beltella latifrons* Wilson, n. sp. — Wilson, p. 277, pl. 26, figs. 2, 4–5, 7, 10.
(Descr. Figs. of cranidia, free cheek, and pygidium.)

Type data: — Holotype is the cranidium figured by Wilson (1954, pl. 26, fig. 2), from 4 mi. SW Marathon, Texas, U. S. A.

Remarks: — The species differs from *Beltella* (and *Leptoplastides*) in having a long prelabellar field and a pitted border furrow. These features suggest that the species belongs to the Oleninae, rather than to the Pelturinae (to which *Beltella* has been assigned). Its oblique S1 recalls more that of *Angelina* than of the other late Oleninae, and the species is tentatively assigned to this genus. Some associated cranidia, assigned by Wilson (1954, p. 279) to *Andesaspis argentinensis* (i. e. *Leptoplastides mariana*) apparently do not belong to that species, but may be related to *Angelina? latifrons*.

Occurrence: — Texas (Basal Marathon Formation = Upper Tremadocian).

Angelina? vexata (Salter 1866).

- 1866 *Conocoryphe vexata*, n. sp. — Salter, p. 307, pl. 8, fig. 7. (Descr. Fig. of imperfect cephalon.)
1868 *Conocoryphe? vexata*, Salter — — Belt, p. 10. (Suggested probably to be a synonym of *Leptoplastides depressus*.)
1898 *Conocoryphe(?) vexata*, Salter — — Brögger, p. 203. (Remarks.)
1898 *Parabolinella(?) vexata*, Salt. — — Brögger, p. 205.
1900a *Conocoryphe vexata*, Salter — — Reed, p. 256. (Remarks.)
1919 *Conocoryphe vexata*, Salter — — Lake, p. 105, pl. XII, fig. 10. (Suggested to be a synonym of *Leptoplastides depressus*. New fig. of Salter's type specimen.)
1933 *Beltella vexata* (Salter) — — Stubblefield, p. 367. (Regarded as a distinct species.)

Type data: — Holotype (by monotypy) is the imperfectly preserved cephalon figured by Salter (1866, pl. 8, fig. 7). A new figure of the specimen was given by Lake (1919, pl. XII, fig. 10). It comes from the passage beds between the Lower and Upper Tremadocian, Penmorfa, Wales.

Remarks: — The holotype is the only known unquestionable specimen. It is an incomplete cephalon with two attached incomplete thoracic segments. The specimen does not show the genal corners of the free cheeks, and the anterior part of the cranidium is rather obscure. It is difficult to judge to which genus it belongs. It probably does not belong to *Leptoplastides* [*Beltella*], as the palpebral lobes are situated too far back, and seem to be larger than in that genus. The specimen somewhat resembles late representatives of the Oleninae (cf. Brögger's suggestion that it belongs to *Parabolinella*). Compressed specimens of *Angelina sedgwickii* may have a rather similar appearance, and for the time being it may be assigned, though with considerable doubt, to *Angelina*.

Occurrence: — Wales (Passage beds between Lower and Upper Tremadocian).

Genus *Leiobienwillia* Rasetti 1954.

Type species: — *Leiobienwillia laevigata* Rasetti 1954, by original designation.

Diagnosis: — Olenids with: cephalon without border furrow and with axial furrow, occipital furrow and glabellar furrows present or practically absent on exterior surface (in latter case still visible on internal moulds); subrectangular cephalic axis, bluntly rounded in front; S1 oblique, slightly curved, S2 and S3 and straight; small palpebral lobes closer to anterior than to posterior margin of cephalon; preocular facial sutures converging; postocular facial sutures diverging. Free cheeks incompletely known, thorax and pygidium unknown.

Included species: —

Leiobienwillia laevigata Rasetti 1954.

L. terranova (Rasetti 1954) (earlier: *Bienwillia*)

Occurrence: — Tremadocian in Newfoundland.

Relationships: — Rasetti (1954) erected this genus for the species *Leiobienwillia laevigata*. A related and associated form was described as *Bienwillia terranova*. I have preferred to transfer it to *Leiobienwillia* because it agrees with *L. laevigata* in the unusual feature among the olenids of not having a border furrow, and because it does not have the equally long and straight-lined S1 and S2 of the typical *Bienwillia* species. However, it is not improbable that *L. laevigata* developed from *Bienwillia* or some other late genus of the Oleninae through forms like *L. terranova*.

Leiobienwillia laevigata Rasetti 1954.

Pl. 1, fig. 5.

1954 *Leiobienwillia laevigata* Rasetti, n. sp. — — Rasetti, p. 583, pl. 61, figs. 3—6; text-figure 3. (Descr. and figs. of cranidia.)

Holotype: — A cranidium, Museum of Comparative Zoology at Harvard University, no. 5127.

Diagnosis: — A *Leiobienwillia* species with: glabellar outline and occipital furrow barely visible and no glabellar furrows on exterior surface (all faintly impressed on internal mould); interocular cheeks about one-third as wide as glabella at eye line; postocular cheeks about three-fourths as wide as occipital ring.

Occurrence: — Newfoundland (Tremadocian).

Leiobienwillia terranovica (Rasetti 1954).

1954 *Bienwillia terranovica* Rasetti, n. sp. — Rasetti, p. 582, pl. 61, figs. 7—12. (Descr. and figs. of cranidia and free cheek.)

Holotype: — A cranidium, Museum of Comparative Zoology at Harvard University, no. 5125.

Diagnosis: — A *Leiobienwillia* species with: distinct axial and occipital furrows and faint glabellar furrows; interocular cheeks markedly less than three-fourths as wide as glabella at eye line; postocular cheeks almost three-fourths as wide as occipital ring.

Occurrence: — Newfoundland (Tremadocian).

Genus *Moxomia* Walcott 1924.

Type species: — By original designation, *M. hecuba* Walcott 1924, regarded as a synonym of *Crepicephalus* (*Bathyurus*?) *angulatus* Hall & Whitfield 1877 by Walcott in 1925.

Diagnosis: — Olenids(?) resembling *Bienwillia* and *Parabolinella*, but with narrower postocular cheeks and two pairs of simple, moderately long glabellar furrows. The cranidium is the only part known.

Remarks: — As far as can be judged from the available illustrations of this form, it is quite possibly an olenid, related to genera like *Bienwillia*, *Parabolinella*, and *Triarthrus*. It differs from the latter mainly in having a well developed preglabellar field. This is rather steep as in at least some species of *Parabolinella*. Its border furrow is pitted, as is sometimes the case in later Oleninae. Apparently only one species is described.

Moxomia angulata (Hall & Whitfield 1877).

Text-fig. 19.

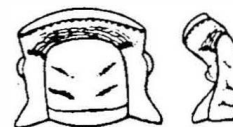
- 1877 *Crepicephalus* (*Bathyurus*?) *angulatus* n. sp. — Hall & Whitfield, p. 220, pl. 2, fig. 28. (Descr., fig. of cranidium.)
1884 *Ptychoparia*? *angulatus* (Hall & Whitfield) — Walcott, p. 269. (Mentioned.)
1916 *Ptychoparia* (*Emmrichella*) *angulatus* (Hall & Whitfield) — Walcott, p. 204. (Mentioned.)
1924 *Moxomia hecuba* new species — Walcott, p. 59, pl. 12, fig. 3. (Figs. of cranidium.)
1925 *Moxomia angulata* (Hall & Whitfield) — Walcott, p. 107, pl. 22, figs. 8—9. (Descr., figs. of cranidium.)

Type data: — A lectotype should be selected from the material studied by Hall and Whitfield.

Diagnosis: — As for genus.

Occurrence: — Ozarkian of Nevada and British Columbia.

Fig. 19. *Moxomia angulata* (Hall & Whitfield). From Walcott (1924, p. 12, fig. 3). $\times 3$.



Subfamily Leptoplastinae Angelin 1854.

Pl. 2, figs. 15—20.

Type genus: — *Leptoplastus* Angelin 1854.

Diagnosis: — Olenids with free cheeks with curved spine deviating from course of lateral margin. Exceptions: Some species of *Leptoplastus* with free cheeks with short and straight spine.

Remarks: — This group was erected as a family Leptoplastidae by Angelin (1854, p. 42) and given subfamily status by Kobayashi (1935c, p. 257).

Genus *Leptoplastus* Angelin 1854.

Type species: — *Leptoplastus stenotus* Angelin 1854, designated by Vogdes in 1890.

Diagnosis: — Leptoplastinae with: tapering or almost parallel-sided cephalic axis with 2—3 pairs of glabellar furrows, moderately-sized palpebral lobes opposite L2 or S2; interocular cheeks from about one-fourth to about three-fourths as wide as glabella at eye line; postocular cheeks from slightly narrower to about 1.5 times as wide as occipital ring; short or no prelabellar field; preocular facial sutures converging, but usually convex, almost angular; postocular facial sutures oblique, slightly sinuous; free cheeks with short to long, slender to coarse spine and acute to obtuse genal angle; thorax with 10 or, usually, 12 segments (when number is known), with short or, rarely, long pleural spines, and with or without long axial spine at 11th segment; sub-semicircular to sub-triangular pygidium with or without marginal spines.

Included species: —

Leptoplastus abnormis Westergård 1944

L. angustatus (Angelin 1854) (earlier: *Eurycare*)

L. bornholmensis (Poulsen 1923) (earlier: *Ctenopyge*)

L. claudicans (Moberg & Möller 1898)

L. crassicorne (Westergård 1944) (earlier: *Eurycare*)

L. intermedius (Westergård 1944) (earlier: *Eurycare*)

L. longispinus Holtedahl 1910 (= *L. norvegicus*)

L. minor Westergård 1922 (= *L. paucisegmentatus*)

L. neglectus (Westergård 1922) (earlier: *Ctenopyge*)

L. norvegicus (Holtedahl 1910) (earlier: *Eurycare*)

L. ostrogothicus Westergård 1940

- L. ovatus* Angelin 1854
L. paucisegmentatus Westergård 1922.
L. raphidophorus Angelin 1854
L. spinosus Matthew 1898
L. stenotus Angelin 1854

L. salteri (Callaway 1877) is included in *Leptoplastides*, *Leptoplastus latus* Matthew 1892 has been transferred to *Westergårdia*, *L. bröggeri* Holte-dahl 1910 to *Protopeltura*, and *L. ovatus* var. *explanatus* Holte-dahl 1910 is referred to as *Eurycare explanatum*. *L. spiniger* and *L. stenotoides* (both Matthew, 1889) were removed from *Leptoplastus* (and the Olenidae) already by Matthew (1894).

Occurrence: — *Leptoplastus* zone in Norway, Sweden, Denmark (Bornholm), England, E. Canada. Base of zone of *Protopeltura praecursor* in Norway, Sweden. *Dictyonema* zone (?) in Sweden.

Phylogeny and relationships: — The *Leptoplastus* species may be arranged in several groups.

Group of *Leptoplastus ovatus*. This includes *L. paucisegmentatus* (and its probable synonym *L. minor*), *L. ovatus*, *L. abnormis*, and probably also the Tremadocian (?) *L. ostrogothicus*. These species have a wider axis than the other *Leptoplastus* species. They have no long axial spine from the 11th segment, and no or very short prelabellar field. Their slender genal spine is short or of medium length, and their genal angle obtuse. Their spinose pygidia are subtriangular, slightly rounded. *L. paucisegmentatus* is the earliest known *Leptoplastus* species. It has only 10 thoracic segments, whereas all other *Leptoplastus* species have 12 (where the number is known). It is considered a forerunner of the no doubt closely related *L. ovatus* by Westergård (1944, p. 40). In *L. abnormis* the pleural spines of the sixth to ninth thoracic segments are greatly prolonged, but otherwise it agrees with *L. ovatus*, to which it appears to be closely related. The Tremadocian (?) *L. ostrogothicus* may possibly have developed from this group, although it does not seem to have marginal spines in the pygidium.

Group of *Leptoplastus raphidophorus*. This includes *L. raphidophorus*, *L. norvegicus* (and its probable synonym *L. longispinus*), *L. bornholmensis*, *L. intermedius*, *L. neglectus*, and *L. spinosus*. A short prelabellar field is always present. The genal spine is moderately long or long, slender or coarse. The genal angle is obtuse to acute. The 11th thoracic segment is provided with a long axial spine (where the thorax is known). The pygidium is subtriangular and spinose. *L. raphidophorus* is the earliest known member of this group. It resembles the slightly earlier *L. paucisegmentatus* in so many features (such as type of cranidium) that it is highly probable that the *ovatus* and *raphidophorus* groups have a common origin. The interocular cheeks of *L. raphidophorus* are about 0.3—0.5 times as wide as the glabella at the eye line, those of *L. norvegicus* are about 0.5—0.7 times as

wide, and those of *L. intermedius* about 0.8 times as wide. As the species seem to appear in this order, they probably represent an evolutionary line where the interocular cheeks become progressively wider. Moreover, this line appears to continue in *Eurycare*, which no doubt developed from the *raphidophorus* group. The rather late *L. neglectus* resembles mostly *L. raphidophorus* inasfar as its interocular cheeks are almost as narrow as those of *L. raphidophorus*. The Canadian *L. spinosus* is not very well known, but appears to belong to this group. It may even turn out to be conspecific with one of the Scandinavian species. *Ctenopyge* apparently developed from the *raphidophorus* group through *L. neglectus*.

Group of *Leptoplastus stenotus*. This embraces the type species, *L. stenotus*, and *L. claudicans*, which may be conspecific. *L. stenotus* has a short preglabellar field, and free cheeks with obtuse genal angle and not very long, slender genal spine. The 11th thoracic segment is provided with a long axial spine. The pygidium is entire, or with one or two pairs of tiny spines. The relationships of *L. stenotus* to the other *Leptoplastus* species are uncertain. Its long axial spine on the 11th segment may indicate that it is nearest to the *raphidophorus* group.

Group of *Leptoplastus angustatus*. This includes *L. angustatus* and *L. crassicorne*, which were previously assigned to *Eurycare*, but are transferred to *Leptoplastus* for reasons discussed below. They have no preglabellar field. Their free cheeks have either acute or obtuse genal angles and rather coarse and long spine. Their thorax is without axial spine. Their pygidium is subtriangular and spinose. *L. angustatus* is probably closely related to the somewhat earlier *L. crassicorne*, which appears slightly later than *L. raphidophorus*. The *angustatus* group may have developed from the *ovatus* or the *raphidophorus* group. It agrees with the *ovatus* group in having no axial spine in the thorax. It seems, however, more probable that it developed from the *raphidophorus* group with which it shares a long genal spine and also a comparatively narrow axis.

Relationships between *Leptoplastus* and *Eurycare*: — From the above it appears that if the *angustatus* group should be included in *Eurycare* as it has been up to now, this would firstly involve that the *raphidophorus* group also should be included in *Eurycare*, since both the *angustatus* group and *Eurycare* (as defined here) seem to have developed from the *raphidophorus* group. This could perhaps be accepted; already Westergård (1922, p. 144) pointed out the resemblance between *L. raphidophorus* and *Eurycare*. However, as *L. stenotus* probably did not develop from the *ovatus* group, it would secondly involve that the *ovatus* group, too, had to be included in *Eurycare* (or assigned to a new genus), which would leave *L. stenotus* as the only certain *Leptoplastus* species. If the *angustatus* group could be proved to have developed, not from the *raphidophorus* group, but from the *ovatus* group, this would likewise involve that

Leptoplastus had to be restricted to *L. stenotus* alone (and possibly also *L. claudicans*), whereas all other species had to be included in *Eurycare*.

I believe that the solution which causes the least confusion is the one adopted here, that is to transfer the *angustatus* group to *Leptoplastus*. It also has the advantage that it becomes easy to distinguish between *Eurycare* (with wide interocular cheeks) and *Leptoplastus*. As defined below, *Eurycare* only includes species with the interocular cheeks as wide as, or wider than the glabella at the eye line.

Leptoplastus abnormis Westergård 1944.

- 1944a *Leptoplastus abnormis* sp. n. — Westergård, p. 41, pl. 1, fig. 23; pl. 2, fig. 1. (Points out the differences from *L. ovatus*. Figs. of axial and dorsal shield.)
 1947 *Leptoplastus abnormis* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

H o l o t y p e: — The axial shield figured by Westergård (1944, pl. 1, fig. 23), from Andrarum in Scania, Sweden.

D i a g n o s i s: — A *Leptoplastus* species with: elongate glabella; interocular cheeks apparently slightly less than half as wide as glabella at eye line; postocular cheeks about three-fourths as wide as occipital ring; no preglabellar field; thorax with 12 segments, 6th to 9th segment with long and flattened pleural spines; no long axial spine; sub-semicircular pygidium with 3 pairs of marginal spines. Free cheeks unknown.

O c c u r r e n c e: — Sweden (*Leptoplastus* zone, subzone of *Leptoplastus ovatus*. Associated with *L. ovatus*.)

Leptoplastus angustatus (Angelin 1854).

Pl. 4; pl. 16, figs. 10–13.

- 1854 *Eurycare angustatum*, n. sp. — Angelin, p. 48, pl. XXVI, fig. 5. (Inexpressive diagn. Rough fig. of dorsal shield.)
 1882 *Eurycare angustatum*, Ang. — Brögger, p. 119, pl. XII, figs. 3, 3a-b. (Figs of cranium, free cheek, and pygidium. As stated by Brögger himself, the figs. are not quite adequate.)
 1904 *Eurycare angustatum* Ang. [partim] — Persson, p. 517, pl. 9, figs. 11–13. (Descr. of axial shield, free cheek, pygidium, and hypostoma. His figs. 9–10 probably are of *Eurycare* species.)
 1922 *Eurycare angustatum* Angelin — Westergård, p. 150, pl. X, figs. 4–9. (Remarks. Figs. of free cheek, cranium, pygidium, and 2 axial shields.)
 1923 *Eurycare angustatum* Angelin — Poulsen, pp. 34, 58, pl. I, figs. 9–10. (Descr. Figs. of cranium and free cheek.)
 1929 *Eurycare angustatum* Ang. — Strand, p. 358. (Recorded.)
 1934a *Eurycare angustatum* — Størmer, p. 333. (Listed.)
 1944a *Eurycare angustatum* Angelin — Westergård, p. 41, pl. 2, figs. 5–6. (Figs. of axial shield and free cheek.)
 1947 *Eurycare angustatum* Ang. — Westergård, p. 24. (Distribution in Sweden.)
 Non 1934 *Eurycare angustatum*, Angelin — Cobbold (= *Ctenopyge drytonensis*).

Type data:— Angelin's type material came from Andrarum, Scania, Sweden. A lectotype should be selected from this locality, and from Angelin's material.

Diagnosis:— A *Leptoplastus* species with: cephalic axis somewhat longer than wide; interocular cheeks slightly more to slightly less than half as wide as occipital ring; no preglabellar field; postocular cheeks about as wide as occipital ring; free cheeks with coarse, long spine and rounded posterior margin; thorax with 12 segments, pleural regions slightly narrower than axis; no axial macrospine; subtriangular pygidium with 3 pairs of marginal spines and 3—4 axial rings.

Norwegian material:— This agrees well with the Swedish material. The cranidia usually attain a length of 5 mm, as in the specimens from Andrarum, but some cranidia from Evjevika, Ringsaker, are as long as 5.6 mm. The free cheeks from Evjevika also differ a little from the typical *angustata* in having a slightly acute genal angle.

Occurrence:— Norway: Eiker (Stablum core), Røyken (Slemmestad), Modum, Hamar district (Løyten, Romedal), Ringsaker (Evjevika) — *Leptoplastus* zone (2c), subzone of *Leptoplastus angustatus*. Alone, or associated with *Eurycare latum*.

Leptoplastus bornholmensis (Poulsen 1923).

1923 *Ctenopyge neglecta* Westergård var. *bornholmensis* n. var. — Poulsen, p. 37, pl. I, fig. 11. (Descr. and fig. of cranidium.)

Lectotype (selected here):— The impression of a cranidium figured by Poulsen, from Læså, Bornholm, Denmark.

Diagnosis:— A *Leptoplastus* species with: interocular cheeks about three-fourths as wide as glabella at eye line; postocular cheeks somewhat less than twice as wide as occipital ring. No other parts than cranidium known.

Remarks:— This form has much wider interocular cheeks than *Leptoplastus neglectus*, and is here regarded as a distinct species. It resembles *L. intermedius*, but has wider postocular cheeks, and occurs in a higher horizon.

Occurrence:— Denmark (*Leptoplastus* zone, subzone of *Leptoplastus angustatus*. Associated with *L. angustatus*. — Bornholm.)

Leptoplastus claudicans (Moberg & Möller 1898).

Pl. 13, figs. 11—13.

1880 *Olenus*?, lik [like] *O. acanthurus* Ang. — Tullberg, p. 6. (Remarks.)

1898 *Acerocare claudicans* n. sp. — Moberg & Möller, pp. 257, 280. (Describe Tullberg's material.)

1898 *Acerocare claudicans* Mbg. & Möller — Möller, p. 314, pl. 16, figs. 1—5. (Remarks. Figs. of cranidium, free cheek, thoracic segment, and pygidium.)

- 1908a *Acerocare claudicans* Moberg — Raw, p. 513. (Assigned to *Leptoplastides*.)
1917 *Acerocare claudicans* Moberg & Möller — Westergård, p. 640. (Remarks.)
1922 *Leptoplastus claudicans* (Moberg & Möller) — Westergård, p. 147, pl. VIII, figs. 8—12. (Remarks. Suggests that the species may belong to the zone with *Leptoplastus* and *Eurycare*. Copies of Moberg & Möller's figs.)
1925 *Leptoplastus claudicans* (Moberg) — Raw, pp. 252, 263. (Remarks.)
1940 *Leptoplastus* ("*Acerocare*") *claudicans* (Moberg & Möller) — Westergård, p. 64, foot-note 1. (Suggests that the species may come from the Dictyonema Shale or some late Upper Cambrian layers.)

Type data: — As lectotype I select one of the pygidia (P. I. L. no. LO 1379) upon which Moberg's drawing is based. It comes from Andrarum, Scania, Sweden.

Remarks: — All material of *L. claudicans* comes from a loose piece of shale, which later has split into a number of tiny flakes. The stratigraphic horizon of the species is uncertain. Moberg & Möller believed it to belong to the genus *Acerocare*, and that it in all probability came from the *Acerocare* zone. Westergård (1922, p. 147) assigned it to *Leptoplastus* and suggested that it came from the *Leptoplastus* zone, like all other species assigned to *Leptoplastus* at that time. Later (1940, p. 64, foot-note 1), when describing *L. ostrogothicus* from the Dictyonema Shale (secondarily imbedded? — cf. p. 173), he found it more likely that *L. claudicans* came from Dictyonema Shale or from some layer of the late Upper Cambrian not available at Andrarum. A reexamination of the type material of *L. claudicans* has shown that the drawings published by Moberg (1898) are not quite correct, as already pointed out by Westergård (1922, p. 147). Thus the genal fields of the free cheeks are actually somewhat wider and the anterior part of the cranium rather different. The palpebral lobes are situated further back, and the preocular facial sutures are longer and less converging than shown in the drawing. A short but distinct prelabellar field is developed, and the anterior margin is slightly concave. The cranium is thus a typical *Leptoplastus* cranium. The species resembles *L. raphidophorus*, but its postocular cheeks are slightly narrower and its pygidium is entire. However, some specimens associated with the lectotype of *L. raphidophorus* also seem to have an entire pygidium. *L. claudicans* even more resembles *L. stenotus* (with entire pygidium), and it is not impossible that they are conspecific, but it is difficult to compare them, as the material of *L. claudicans* is somewhat fragmentary and not too well preserved. However, it can hardly be doubted that *L. claudicans* is very close to the *Leptoplastus* species of the *Leptoplastus* zone, and I believe it to be rather probable that it came from this zone (as may also be the case with *L. ostrogothicus*).

Occurrence: — Sweden. Horizon unknown (*Leptoplastus* zone?).

Leptoplastus crassicornes (Westergård 1944).

Pl. 4; pl. 14, figs. 1—13.

- 1944a *Eurycare angustatum crassicornes* var. n. — Westergård, p. 41, pl. 2, figs. 2—4. (Points out differences from *L. angustatus*. Figs. of dorsal shield, cranidium and free cheek.)
- 1947 *Eurycare angustatum crassicornes* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

H o l o t y p e: — By original designation, the dorsal shield figured by Westergård (1944, pl. 2, fig. 2) from Andrarum, Scania, Sweden.

D i a g n o s i s: — A *Leptoplastus* species with: elongate cephalic axis; interocular cheeks about half as wide as glabella at eye line; postocular cheeks about as wide as, or slightly wider than occipital ring; no or practically no preglabellar field; fixed cheeks with very long and very thick spine, slightly acute or right-angled genal angle, and practically straight posterior margin; thorax with 12 segments, pleural regions as wide as or slightly wider than axis, and no long axial spine; subtriangular pygidium with 4—5 axial rings and 3—4 pairs of marginal spines.

R e m a r k s: — As discussed above, this form is transferred from *Eurycare* to *Leptoplastus*. As *crassicornes* differs markedly from *angustatus* i. a. in the free cheeks, and furthermore occurs in a horizon well below that of *L. angustatus*, I prefer to regard *crassicornes* as a separate species.

N o r w e g i a n m a t e r i a l: — This consists only of detached parts of the shield. The free cheeks agree with the Swedish material in having the genal angles drawn out, and in having very coarse genal spines. The cranidia also agree very well with the type material, i. a. in having no preglabellar field.

O c c u r r e n c e: — Norway: Eiker (Krekling, Vestfossen), Røyken (Slemmestad), Hamar district, Ringsaker (Evjevika), Brummunddal. — *Leptoplastus* zone (2c), subzone of *Leptoplastus crassicornes*. Associated with *L. norvegicus*. — Sweden (same horizon), Denmark (collected by the writer at Læså, Bornholm, at "locality 6" of Poulsen, 1923).

Leptoplastus crassicornes var. Some specimens from the subzone of *Leptoplastus ovatus* apparently belong to a smaller variety with more slender cheek spines (Pl. 14, figs. 9—13). They are associated with *Leptoplastus ovatus* and *Eurycare explanatum* and come from Jønsberg in Romedal, Hamar district, Norway.

Leptoplastus intermedius (Westergård 1944).

Pl. 4.

- 1944a *Eurycare intermedium* sp. n. [partim] — Westergård, p. 41, pl. 2, figs. 7—8. (Descr. Figs. of axial shield and cranidium. Figs. 9—10 probably belong to *E. explanatum*.)
- 1947 *Eurycare intermedium* Wgård. [partim] — Westergård, p. 24. (Distribution in Sweden.)

Holotype: — The axial shield figured by Westergård (1944, pl. 2, fig. 7) from Andrarum, Scania, Sweden.

Diagnosis: — A *Leptoplastus* species with: interocular cheeks about three-fourths as wide as glabella at eye line; postocular cheeks about 1.5 times as wide as occipital ring; thorax of probably 12 segments and pleural regions up to 1.5 times as wide as axis, pygidium with 4 pairs of marginal spines. Free cheeks unknown. The most complete specimen (the holotype) is broken in front of the pygidium. This may indicate that one of the posterior thoracic segments carried a long axial spine.

Remarks: — In the holotype and a detached cranidium figured by Westergård, the interocular cheeks are about three-fourths as wide as the glabella at the eye line. Another cranidium assigned to this species by Westergård (1944, pl. 2, fig. 9), has interocular cheeks which are about as wide as the glabella, and may belong to *E. explanatum*.

Occurrence: — Sweden (*Leptoplastus* zone, subzone of *Leptoplastus ovatus?*).

Leptoplastus neglectus (Westergård 1922).

Pl. 5; pl. 17, figs. 1–7.

- 1880 *Sphærophthalmus flagellifer* Ang. [partim] — Linnarsson, p. 142 (12), pl. V (I), fig. 13. (Fig. of cranidium.)
- 1910 *Leptoplastus Bröggeri*, nov.sp. [partim] — Høltedahl, p. 13, pl. III, figs. 1, 3, 11? only. (Descr. and figs. of cranidium and free cheek. Figs. 2, 4–10 are of *Protopeltura broeggeri*.)
- 1922 *Ctenopyge neglecta* n.sp. [partim] — Westergård, p. 150, pl. X, figs. 10–17 only. (Descr. Figs. of cranidium, free cheek, pygidia, hypostoma, and larval cranidium with 8 attached thoracic segments. Fig. 18 is of *Ctenopyge postcurrens*.)
- 1922 *Leptoplastus raphidophorus* Angelin [partim] — Westergård, p. 143, pl. X, fig. 2 only. (Fig. of dorsal shield.)
- 1944a *Ctenopyge neglecta* f.typ. — Westergård, p. 42. (Mentioned.)
- 1947 *Ctenopyge neglecta* Wgård. — Westergård, p. 24. (Distribution in Sweden.)
- Non 1944a *Ctenopyge neglecta* approaching var. *postcurrens* — Westergård (= *Ctenopyge postcurrens*).

Lectotype: — By subsequent designation by Westergård (1944), a cranidium figured by Westergård (1922, pl. X, fig. 11) from Andrarum, Scania, Sweden.

Diagnosis: — A *Leptoplastus* species with: elongate cephalic axis, bluntly rounded in front; interocular cheeks about half as wide as glabella at eye line; postocular cheeks markedly wider than occipital ring; relatively well-developed preglabellar field; free cheeks with long, strong spine, straight posterior margin, and acute genal angle; thorax with 12 segments, pleural regions about one and a half times as wide as axis, and long axial spine on one of the posterior segments; pygidium with three pairs of marginal spines and three to four axial rings.

Remarks: — Westergård (1922) believed this species to be intermediate between *Leptoplastus* and *Ctenopyge*, but assigned it preliminarily to *Ctenopyge*, partly because of the *Ctenopyge*-like thorax of a specimen figured by him (1922, pl. X, fig. 18). In 1944 he included this specimen in a separate form, which he called *Ctenopyge neglecta postcurrens*. This is a typical *Ctenopyge* and is discussed below as *Ctenopyge* (*Eoctenopyge*) *postcurrens*, whereas I transfer *neglecta* to *Leptoplastus*. It is regrettable that the earliest known *Ctenopyge* thus is known as *Ct. postcurrens*, but *Leptoplastus neglectus* is a typical *Leptoplastus* species, and should not be included in *Ctenopyge*. Features of *L. neglectus* which are not known in *Ctenopyge* are i. a.: comparatively short and wide cephalic axis, well-developed preglabellar field, preocular facial sutures subparallel for a short distance in front of the palpebral lobes, and *Leptoplastus*-like pygidium. Only a young thorax of *L. neglectus* has been figured by Westergård (1922, pl. X, fig. 14). Norwegian material of *L. neglectus* shows, however, that the thorax is of the *Leptoplastus* type, with comparatively short pleural spines. This is also seen in a dorsal shield figured by Westergård (1922, pl. X, fig. 2), but assigned to *L. raphidophorus*. I believe this specimen belongs to *L. neglectus* for the following reasons: The free cheeks are more angulate and carry a coarser spine than *L. raphidophorus*, while they cannot be told from the free cheeks of *L. neglectus*. The cranidium, as well as some other cranidia on the same slab (see pl. 17, figs. 1, 5), cannot be distinguished from the cranidium of *L. neglectus*, whereas they differ from the cranidium of *L. raphidophorus* i. a. in having a distinct preglabellar field. The cranidia of these two species are, however, rather alike, and have about equally wide fixed cheeks. The axis in the dorsal shield in question is slightly narrower than in *L. raphidophorus*, and its pygidium comparatively shorter and wider than in *L. raphidophorus* (or any other *Leptoplastus* species). The slab has an attached label which seems to bear the name "Andrarum", and most probably the specimen is from this locality. It is worth noting that the fossil is preserved in limestone, as all known material of *L. raphidophorus* occurs in shale at this locality, whereas material of *L. neglectus* occurs in limestone. The limestone in this particular slab agrees with that in which *L. neglectus* occurs. It is easy to understand why Westergård did not assign the above-mentioned shield to *L. neglectus* in 1922, as he at that time included *Ctenopyge postcurrens* in this species, and figured a thorax of *Ctenopyge postcurrens*. Believing this to represent a thorax of *L. neglectus*, the dorsal shield in question was naturally too different to be assigned to *L. neglectus*.

Norwegian material: — The cranidia and free cheeks present correspond closely to those of the type material. The cranidia have rather well-developed preglabellar field, preocular sutures of the *Leptoplastus* type, and straight eye ridges. The free cheeks have a slightly acute genal angle.

In Holtedahl's material from Slemmestad in Røyken, there are similar cranidia, but also some which differ in having oblique eye ridges and some-

times shorter preglabellar field. Apart from this they agree with the others. In some other material from Slemmestad, the form with the short preglabellar field is dominating. However, only a few cranidia are present.

Occurrence: — Norway: Eiker (Stablum core), Røyken (Nærnes, Slemmestad). — Zone of *Protopeltura praecursor* (2d α), subzone of *Leptoplastus neglectus*. Alone, or associated with *Protopeltura praecursor*. — Sweden (Associated with *Protopeltura praecursor* at the type locality).

Leptoplastus norvegicus (Holtedahl 1910).

Pl. 4; pl. 15, figs. 1–10; pl. 16, figs. 1–2.

- 1910 *Eurycare angustatum*, Ang., var. *norvegicum*, nov. var. [partim] — — Holtedahl, p. 5, pl. 1, fig. 1 only. (Descr. Fig. of axial shield. Fig. 3 may be conspecific. Fig. 2 belongs to another species, possibly *Leptoplastus crassicornis*.)
- 1910 *Leptoplastus longispinus*, nov. sp. — — Holtedahl, p. 11, pl. III, figs. 12–14. (Descr. Figs. of free cheek and associated cranidium and pygidium.)
- 1922 *Eurycare angustatum norvegicum* Holtedahl [partim] — — Westergård, p. 150. (Points out its resemblance to *L. raphidophorus*.)
- 1922 *Leptoplastus longispinus* Holtedahl — — Westergård, p. 110. (Mentioned.)
- 1929 *Leptoplastus raphidophorus norvegicus* (Hltd.) — — Strand, p. 357. (Excludes the free cheek and pygidium which Holtedahl assigned to this form.)
- 1929 *Leptoplastus longispinus* Hltd. — — Strand, p. 357, pl. I, fig. 4. (Remarks. Fig. of free cheek.)

Lectotype (here selected): — The axial shield figured by Holtedahl, 1910 (P. M. O. no. 30334a; counterpiece no. 30334b), from the vicinity of Hamar, acquired for the collections by W. C. Brögger in 1889.

Diagnosis: — A *Leptoplastus* species with: elongate cephalic axis; interocular cheeks 0.5–0.7 times as wide as glabella at eye line; postocular cheeks markedly wider than occipital ring; short preglabellar field; free cheeks with long spine, acute to right-angled genal angle, and practically straight posterior margin; thorax with 12 segments, pleural regions about one and a half times as wide as axis, slender relatively long pleural spines, and probably long axial spine on 11th segment; subtriangular pygidium with 5 pairs of marginal spines and 4–6 axial rings.

Description of type material: — The cranidium of the lectotype is twice as wide as long. Cephalic axis very slightly tapering forwards, and slightly truncate in front. Two pairs of glabellar furrows in front of distinct occipital furrow. Glabellar furrows rather faint, especially S2. Short preglabellar field. Anterior border furrow distinct. Border narrow, widest axially. Anterior facial sutures cross border furrow well inside exsagittal lines through palpebral lobes, but are subparallel for a short distance in front of palpebral lobes. Postocular sutures strongly diverging backwards, very slightly sinuous. Eye ridges distinct, slightly oblique backwards. Palpebral lobes of moderate size, with centres about opposite S2. Interocular

cheeks half as wide as glabella at eye line. Postocular cheeks markedly wider than occipital ring.

The thorax of the lectotype has 12 segments, with well developed pleural spines. The thorax is broken just behind the 11th segment. As pointed out by Westergård (1922, p. 150) this indicates that *L. norvegicus* has an axial spine on this segment. As can be seen from the counterpart, the other axial rings bear no spines or tubercles.

The pygidium of the lectotype is subtriangular, with axis of three rings and end lobe of two fused rings. The counterpart clearly shows five pairs of pygidial spines. This is the number given by Høltedahl (1910, p. 7), whereas Strand (1929, p. 357) stated that there were only four pairs. The rearmost pair is, however, rather short.

The free cheek figured by Høltedahl (1910, pl. I, fig. 2) is from another area, and probably does not belong to *L. norvegicus*. Already Strand (1929, p. 357) pointed out that there are some *longispinus*-like free cheeks associated with the lectotype, and that these instead may belong to *L. norvegicus*. By splitting up the small concretion containing the lectotype, I have found more free cheeks, as well as some cranidia. There are two types of free cheeks present. The one type apparently belongs to *L. crassicornis*, which seems rather probable as one of the cranidia is similar to that of *L. crassicornis*, with no preglabellar field. The other type of free cheeks has an acute genal angle, and a long spine which is slender and curved. It seems reasonable to assume that this type belongs to *L. norvegicus*.

Two of the associated cranidia agree very well with that of the lectotype, except for being smaller. A third, rather large cranidium has wider interocular cheeks (about 0.6 times as wide as the glabella at line through centre of eyes).

Description of type material of *L. longispinus*: — Strand (1929, p. 357) suggested that *L. longispinus* probably is identical with *L. norvegicus*, and this seems the most likely.

As lectotype of *L. longispinus* is here selected the free cheek figured by Høltedahl (1910, pl. III, fig. 13), as he based the species on the free cheek, and only tentatively attributed the figured cranidium and pygidium to it. The lectotype comes from Krekling in Eiker.

The lectotype free cheek agrees with the free cheeks of *L. crassicornis* and *L. neglectus* in having an acute genal angle, but differs from *crassicornis* in having a slender spine, and from *L. neglectus* in having a more elongate genal field.

The lectotype is associated with several detached parts of other *Leptoplastus* shields. The free cheeks are either of the *longispinus* type or of the *crassicornis* type. In accordance with this, there are also two types of cranidia. One of the types agrees very well with the lectotype of *L. norvegicus*. The cranidium figured by Høltedahl (1910, pl. III, fig. 12) as probably belonging to *L. longispinus*, in reality belongs to this type. The other type

of cranidia agrees very well with that of *L. crassicorne*, i. a. in having no preglabellar field. The pygidium figured by Høltedahl (1910, pl. I, fig. 3) as belonging to *L. norvegicus*, comes from the same piece of rock. It agrees quite well with that of the lectotype of *L. norvegicus*, also in having five pairs of pygidial spines, although the rearmost pair is very small. It may possibly belong to *L. longispinus*, although it is difficult to distinguish the pygidium from that of *L. crassicorne*.

A complete dorsal shield of *L. crassicorne* has been described by Westergård (1944). As the free cheeks and cranidia of the *crassicorne*-type in the Krekling material quite agrees with these parts in the entire shield, it seems reasonable to assume that the other free cheeks (*longispinus*) and cranidia belong to one species. In that case *L. longispinus* may be regarded as a synonym of *L. norvegicus*.

Other material: — Cranidia and free cheeks of *L. norvegicus* also occur at Ringsaker, where they are associated with free cheeks and cranidia assigned to *L. crassicorne*. The Ringsaker material shows that *L. norvegicus* could attain rather a large size, and furthermore shows that the relative width of the interocular cheeks increased during growth. Whereas the interocular cheeks are about 0.5 times as wide as the glabella at the eye line in the smaller specimens, they are about 0.7 times as wide in the larger cranidia.

Free cheeks and cranidia of the *norvegicus*-type are present in some material from Andrarum in Scania, Sweden, where they are associated with parts of *L. crassicorne*, *L. intermedius*, and *Eurycare brevicauda*. When so many species are present in detached parts of the shield only, it is, however, difficult to identify the species with certainty.

Occurrence: — Norway: Eiker (Krekling, Vestfossen). Røyken (Slemmestad), Hamar district, Ringsaker (Evjevika), Brummunddalen. — *Leptoplastus* zone (2c), subzone of *Leptoplastus crassicorne*. Alone, or associated with *L. crassicorne*. — ?Sweden (same horizon).

Leptoplastus ostrogothicus Westergård 1940.

1940 *Leptoplastus ostrogothicus* sp. n. — Westergård, p. 64 (foot note 1), p. 72, figs. 8a-c. (Descr. Figs. of axial shield, cranidium, and free cheek.)

Holotype: — The axial shield figured by Westergård, from level 13.42—14.00 in core from Borghamn, Östergötland, Sweden.

Diagnosis: — A *Leptoplastus* species with: elongate cephalic axis, interocular cheeks slightly more than half as wide as glabella at eye line; postocular cheeks slightly wider than occipital ring; no or short preglabellar field; free cheeks with relatively short spine and with straight margin; thorax with 12 segments, pleural regions about as wide as axis, and no long axial spine; pygidium with 4 axial rings and apparently no marginal spines.

Remarks: — The species appears to be a true member of the genus *Leptoplastus*, and it is surprising that it apparently occurs in Dictyonema Shale (Lower Tremadocian), whereas all other species of *Leptoplastus* whose stratigraphic position is known, occur in the *Leptoplastus* zone, with the exception of *L. neglectus* from the base of the overlying zone of *Protopeltura praecursor*. Thus no *Leptoplastus* species are known from the remaining parts of the *Peltura* zones, nor from the *Acerocare* zone. However, it has been suggested that *L. claudicans*, known only from a loose piece of shale containing no other fossils, may come from the Dictyonema Shale or from some late Upper Cambrian layer (cf. Westergård, 1940, p. 64, foot note 1). In the core yielding *L. ostrogothicus*, the beds containing this fossil lie above unfossiliferous shale, probably of early or middle Upper Cambrian age (cf. diagram of core given by Westergård, 1940, p. 16). The late Upper Cambrian is apparently missing in the whole of Östergötland. There may perhaps be a possibility of the *Leptoplastus* material in the core from Borghamn having been redeposited, and that it originally might have come from the zone of *Leptoplastus*.

The detached cranidium figured by Westergård (1940, fig. 8b) differs from the cranidium of the holotype in having narrower interocular cheeks, less converging preocular facial sutures, and a short, but distinct preglabellar field, and may possibly belong to another species.

Occurrence: — Sweden: *Dictyonema* zone (secondarily imbedded??).

Leptoplastus ovatus Angelin 1854.

Pl. 4; pl. 13, figs. 8—10.

- 1854 *Leptoplastus ovatus*, n. sp. — Angelin, p. 47, pl. XXVI, fig. 3. (Inexpressive diagn. Rough sketch of dorsal shield.)
- 1882 *Leptoplastus stenotus* Ang.? — *Leptoplastus ovatus* Ang.? — Brögger, p. 117. (Brögger's material does not include *L. stenotus*, only *L. ovatus*, which agrees with his statement that the species occurs together with *Eurycare latum*.)
- 1904 *Leptoplastus ovatus* Ang. — Persson, p. 520, pl. 9, figs. 17—23. (Descr. Figs. of all parts of dorsal shield and larval cranidium.)
- 1910 *Leptoplastus ovatus*, Ang., var. *explanata* nov. var. [partim] — Høltedahl, p. 5, pl. I, figs. 1—2. (Descr. and figs. of free cheek and pygidium.)
- 1922 *Leptoplastus ovatus* Angelin — Westergård, p. 145, pl. VIII, figs. 18—21. (Remarks. Figs. of free cheeks and 2 more or less complete dorsal shields, one of which is supposed to be the specimen on which Angelin chiefly based his species.)
- 1923 *Leptoplastus ovatus* Angelin — Poulsen, p. 35, text fig. 12. (Descr. Copy of Westergård's fig. of the supposed type specimen of Angelin.)
- 1925 *Leptoplastus ovatus* — Raw, p. 263. (Remarks on larval stages described by Høltedahl, 1910.)
- 1929 *Leptoplastus minor explanatus* (Hølt.) [partim] — Strand, p. 358. (Mentions Høltedahl's material.)
- 1929 *Leptoplastus ovatus* Ang. — Strand, p. 358. (Recorded.)
- 1934a *Leptoplastus ovatus* — Stormer, p. 333. (Listed.)
- 1947 *Leptoplastus ovatus* Ang. — Westergård, p. 24. (Distribution in Sweden.)

?1952 *Leptoplastus ovatus* Angelin — Hutchinson, p. 84, pl. IV, figs. 1—2. (Remarks. Figs. of cranidia.)

Non 1910 *Leptoplastus ovatus* Ang. — — Høltedahl (= *L. raphidophorus*).

L e c t o t y p e (here selected) : — The dorsal shield figured by Westergård (1922, pl. VIII, fig. 18), supposed to be Angelin's type specimen. It is from Andrarum, Scania, Sweden.

D i a g n o s i s : — A *Leptoplastus* species with: about as long as wide cephalic axis; interocular cheeks about one-fourth as wide as glabella at eye line; postocular cheeks somewhat narrower than occipital ring; no preglabellar field; free cheeks with relatively short spine, straight posterior margin and obtuse genal angle; thorax with 12 segments, no long axial spine, and pleural regions about three-fourths as wide as axis; sub-semicircular pygidium with 3 pairs of marginal spines and 3 axial rings.

R e m a r k s : — The Canadian specimens assigned to this species do not seem to agree quite with the Swedish, as far as I can judge from the figures of two incomplete cranidia. The Canadian specimens seem to have the eyes situated somewhat farther forwards, and the whole appearance of the cranidium is more pelturoid. It is also suspicious that the Canadian form is associated with specimens assigned to *Leptoplastus minor* (i. e. *L. paucisegmentatus*), as the latter occurs well below *L. ovatus* in Scandinavia. There may perhaps be a possibility of the Canadian material belonging to *Protopeltura*.

N o r w e g i a n m a t e r i a l : — This agrees well with the Swedish material.

O c c u r r e n c e : — Norway: Eiker (Vestfossen, Stablum core), Røyken (Slemmestad), Oslo (Tøyen, Gamlebyen), Ringerike (Hval), Ringsaker (Evjevika, Steinsodden), Hamar district (Jønsberg in Romedal), Snertingdal (Rudsbekken). — *Leptoplastus* zone (2c), subzone of *Leptoplastus ovatus*. Associated with *E. latum* or *E. explanatum*. — Sweden (same horizon), Denmark (same horizon). ?Canada (Nova Scotia, *Leptoplastus* zone.)

Leptoplastus paucisegmentatus Westergård 1922.

Pl. 4.

1922 *Leptoplastus paucisegmentatus* n. sp. — Westergård, p. 146, pl. VIII, figs. 22—24. (Short descr. Figs. of axial shield, cranidium and free cheek.)

1922 *Leptoplastus minor* n. sp. — Westergård, p. 144, pl. VIII, figs. 25—29. (Descr. Figs. of cranidia, free cheek, and pygidia.)

1944a *Leptoplastus paucisegmentatus* Westergård — Westergård, p. 40, pl. 1, figs. 20—22. (Suggests that *L. minor* is in all probability synonymous with *L. paucisegmentatus*. Figs. of axial shield, dorsal shield, and free cheek.)

1947 *Leptoplastus paucisegmentatus* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

?1952 *Leptoplastus minor* Westergård — Hutchinson, p. 85, pl. IV, figs. 3—5, 6? (Descr. Figs. of cranidia, free cheek, and conspecific? pygidium.)

Non 1929 *Leptoplastus minor* Wgd. — Strand (= *L. raphidophorus*).

Lectotype: — By subsequent designation by Westergård (1944, p. 40), the axial shield from Scania, Sweden, figured by Westergård (1922, pl. VIII, fig. 22).

Diagnosis: — A *Leptoplastus* species with: elongate cephalic axis; interocular cheeks somewhat less than half as wide as glabella at eye line; postocular cheeks about as wide as occipital ring; no or very short preglabellar field; free cheeks with relatively short spine, obtuse genal angle, and straight posterior margin; thorax with 10 segments, pleural regions slightly narrower or as wide as axis, and no long axial spine; sub-semicircular pygidium with 2—3 axial rings and 2—3 pairs of marginal spines.

Remarks: — As pointed out by Westergård (1944a) this species has 10 thoracic segments, not 9 as stated in the original description. The material from Nova Scotia assigned to this species by Hutchinson (1952), is rather incomplete.

Occurrence: — Sweden (*Leptoplastus* zone, subzone of *L. paucisegmentatus*), ?Canada (Nova Scotia, *Leptoplastus* zone).

Leptoplastus raphidophorus Angelin 1854.

Pl. 4; pl. 13, figs. 1—7.

- 1854 *Leptoplastus raphidophorus*, n. sp. — — Angelin, p. 47, pl. XXVI, fig. 2. (Inexpressive diagn. Rough, partly inadequate fig. of restored dorsal shield. According to Westergård, 1922, Angelin included under this name both *L. raphidophorus* and *L. stenotus*.)
- 1864 *Olenus* (*Leptoplastus*) or *Sphaerophthalmus raphidophorus*, Angelin — — Salter, pl. 11, p. VIII, fig. 17. (Fig. of dorsal shield copied from Angelin.)
- 1910 *Leptoplastus ovatus*, Ang. — — Høltedahl, p. 8, pl. I, figs. 4—9. (Descr. of material hesitatingly assigned to *L. ovatus*. Figs. of all parts of dorsal shield and 2 larval cranidia.)
- 1922 *Leptoplastus raphidophorus* Angelin [partim] — — Westergård, p. 143, pl. VIII, figs. 13—17; pl. X, fig. 3. (Descr. Figs. of dorsal shield and all parts of dorsal shield. Pl. X, fig. 2 is of *L. neglectus*.)
- 1929 *Leptoplastus minor* Wgd. — — Strand, p. 358. (Remarks.)
- 1934 *Leptoplastus raphidophorus*, Angelin — — Cobbold, p. 351, pl. 45, fig. 18. (Figs. of free cheeks.)
- 1947 *Leptoplastus raphidophorus* Ang. — — Westergård, p. 24. (Distribution in Sweden.)

Type data: — As lectotype I select an axial shield (RM no. Ar 2114d) believed by Westergård (1922) to belong to Angelin's type material. From Andrarum, in Scania, Sweden.

Diagnosis: — A *Leptoplastus* species with: cephalic axis markedly longer than wide; interocular cheeks between half and one-third as wide as glabella at eye-line; postocular cheeks slightly to markedly wider than occipital ring; short preglabellar field; free cheeks with long spine, straight posterior margin, and slightly obtuse genal angle; thorax with 12 segments, pleural regions slightly to markedly wider than axis, and long axial spine

on 11th segment; pygidium rounded sub-triangular with 3 pairs of marginal spines and 3 axial rings.

Remarks: — I believe that the dorsal shield figured by Westergård (1922, pl. X, fig. 2) belongs to *L. neglectus* (cf. p. 169).

As to the Shropshire material assigned to *L. raphidophorus* by Cobbold (1934), the cranidia bear two occipital nodes, one behind the other, as in the Scandinavian material. The free cheeks are rather like those of Scandinavian specimens, except perhaps that their spines are slightly coarser, thus also reminding one of *L. neglectus*. However, the direction of the spines is more like that of *L. raphidophorus*, and I believe that the Shropshire material may be assigned to this species. The two fragmentary pygidia do not deviate from the pygidium of *L. raphidophorus*, but are of little help in determining the species.

Norwegian material: — The material from Stange, Hamar area, was first described by Høltedahl (1910), who hesitatingly assigned it to *L. ovatus*. Strand (1929) pointed out that it cannot belong to this species, and assigned it to *L. minor*. Westergård (1944a, p. 40) now believes that *L. minor* in all probability is synonymous with *L. paucisegmentatus*. It is obvious that the Stange form, with its narrow axis, cannot be assigned to *L. paucisegmentatus*. Comparison with the type material of *L. minor* shows that the Stange form is not conspecific with this, even if *L. minor* is not a synonym of *L. paucisegmentatus*. The glabella of the Stange form is more parallel-sided and the free cheeks are more rounded. On the other hand, the Stange material agrees in all details with the description of *L. raphidophorus*, as well as with the type material of this species. It should be remembered, however, that the number of thoracic segments is not known in the Stange form. Comparison between the outline of a part of the thorax consisting of 10 segments and another part of a thorax with attached pygidium indicates that the total number of thoracic segments has been greater than 10, probably 12 as in *L. raphidophorus* (whereas *L. paucisegmentatus* has only 10).

Specimens from Slemmestad, Røyken are rather well preserved, and agree fairly well with the Swedish specimens. The cranidia have two small axial tubercles on the occipital ring, one behind the other, or sometimes, as it seems, fused into a single elongate keel-like node. I believe to have recognized the two tubercles in the less well preserved material from Scania, Sweden, and have also seen them in the specimens from Stange. The only pygidium present in the Slemmestad material is of the triangular *Leptoplastus* type, but with narrower pleural regions than in the type material of *L. raphidophorus*.

The interocular cheeks are slightly wider in the Slemmestad material than in the type material of *L. raphidophorus* and in the Stange material. It is possible that the Slemmestad material should be regarded as a variety. The largest cranidium in the Slemmestad material is 5.1 mm long, in the Stange material 4.4 mm, and in the type material 4.2 mm long.

Occurrence: — Norway: Røyken (Slemmestad), Hamar district (Stange). — *Leptoplastus* zone (2c), subzone of *Leptoplastus raphidophorus*. Alone. — Sweden (same horizon), England (cf. p. 49).

Leptoplastus spinosus Matthew 1894.

- 1894 *Leptoplastus spinosus*, n. sp. — Matthew, p. 106, pl. 17, figs. 13a-e. (Descr. Figs. of cranidium, free cheek, thoracic segment, pygidium, and hypostoma.)
 1952 *Leptoplastus spinosus* Matthew — Hutchinson, p. 86. (Remarks.)

Type data: — As lectotype should be selected one of the specimens figured by Matthew (1894) from St. John, Nova Scotia.

Remarks: — This species seems to belong to the *raphidophorus* group. It is not impossible that it may be synonymous with one of the species described from Scandinavia, but this is difficult to judge from the description and figures alone.

Occurrence: — Canada (St. John group, division 3b. St. John, Nova Scotia.)

Leptoplastus stenotus Angelin 1854.

Pl. 2, fig. 16; pl. 4.

- 1854 *Leptoplastus stenotus*, n. sp. — Angelin, p. 47, pl. XXVI, fig. 1. (Inexpressive diagn. Rough fig. of dorsal shield.)
 1875b *Leptoplastus stenotus* Ang. — Linnarsson, p. 43, pl. V, figs. 8—10. (Descr. Figs. of pygidium, free cheek, and incomplete cranidia. The determination was doubted by Persson, 1904, because of the poor figures. Westergård, 1922, examined the material and stated that it does not differ from Angelin's species in any important features.)
 1904 *Leptoplastus stenotus* Ang. — Persson, p. 522, pl. 9, figs. 14—16. (Descr. Figs. of free cheeks and axial shields.)
 1922 *Leptoplastus stenotus* Angelin — Westergård, p. 146, pl. IX, figs. 1—6. (Remarks. Figs. of dorsal shields and all parts of dorsal shield.)
 1923 *Leptoplastus stenotus* Angelin — Poulsen, p. 36, text figs. 13—14; p. 58, text fig. 21. (Descr. Figs. of dorsal shield, free cheek, and larval cranidium.)
 1947 *Leptoplastus stenotus* Ang. — Westergård, p. 24. (Distribution in Sweden.)
 Non 1882 *Leptoplastus stenotus*, Ang.? — Brögger (= *L. ovatus*).

Type data: — A lectotype should be selected from the type locality, Andrarum in Scania, Sweden, from Angelin's material.

Diagnosis: — A *Leptoplastus* species with: elongate cephalic axis, truncate in front; short preglabellar field; interocular cheeks somewhat less than half as wide as glabella at eye line; postocular cheeks almost as wide as glabella at eye line; postocular cheeks almost as wide as occipital ring; free cheeks with slender spine, obtuse genal angle, and straight posterior margin; thorax with 12 segments, pleural regions about as wide as axis, and long axial spine in 11th segment; entire pygidium (or with small marginal points), with rounded margin and 3—4 axial rings.

Norwegian material: — This quite conforms with the Swedish material.

Occurrence: — Norway: Røyken (Slemmestad, in a single limestone lens). — *Leptoplastus* zone (2c), subzone of *Leptoplastus stenotus*. Alone. — Sweden (same horizon), Denmark (Bornholm, same horizon).

Genus *Eurycare* Angelin 1854.

Type species: — *Eurycare brevicauda* Angelin 1854, designated by Vogdes in 1925.

Diagnosis: — Leptoplastinae with: slightly tapering or almost parallel-sided cephalic axis with 2—3 pairs of glabellar furrows; moderately-sized palpebral lobes opposite L2 or S2; interocular cheeks as wide as or wider than glabella at eye line; postocular cheeks as wide as or wider than occipital ring; short preglabellar field; preocular facial sutures converging, only slightly convex; postocular facial sutures oblique, slightly sinuous; free cheeks with long and coarse spine; thorax with 12(13?)—17 segments (when number is known), short pleural spines, and no or long axial spine from 11th segment; subtriangular pygidium with marginal spines.

Included species: —

Eurycare brevicauda Angelin 1854

E. camuricorne Angelin 1854 (= *E. latum*)

E. explanatum (Holtedahl 1910) (earlier: *Leptoplastus*)

E. latum (Boeck 1838)

E. spinigerum Westergård 1922

For reasons discussed above, *Eurycare angustatum*, *E. angustatum crassicorne*, and *E. intermedium* have been transferred to *Leptoplastus*.

Occurrence: — *Leptoplastus* zone in Norway, Sweden, Denmark (Bornholm).

Phylogeny and relationships: — The *Eurycare* species may be arranged in a sequence, from *E. explanatum* with interocular cheeks about as wide as the glabella at the eye line and postocular cheeks about 1.5 times as wide as the occipital ring, through *E. spinigerum* and *E. brevicauda* with about equally wide interocular cheeks, but with postocular cheeks about as wide as the occipital ring, thus not much wider than the interocular cheeks, to *E. latum* with the interocular cheeks from about 1.2 to 1.5 times as wide as the glabella at the eye line, and postocular cheeks very slightly shorter than the interocular cheeks. This line, which also is characterized by an increase in number of thoracic segments from 12(13?) to 17, may more or less represent a phylogenetic lineage. This seems rather probable, as *Eurycare* apparently developed from the *Leptoplastus raphidophorus* group (with relatively narrower interocular cheeks and rather wide postocular

cheeks), and seems to continue a trend within this group with progressively wider interocular cheeks. The border between *Eurycare* and *Leptoplastus* has, in fact, been drawn rather arbitrarily between species with interocular cheeks less than as wide as the glabella at the eye line and species with interocular cheeks as wide as the glabella at the eye line. All the *Eurycare* species seem to occur in the subzone of *Leptoplastus ovatus*, but *E. latum* also occurs in the overlying subzone of *Leptoplastus angustatus* (lower part only?).

Eurycare brevicauda Angelin 1854.

Pl. 2, fig. 19; pl. 4.

- 1854 *Eurycare brevicauda*. n. sp. — Angelin, p. 48, pl. XXVI, fig. 4. (Diagn. Rough fig. of dorsal shield.)
 1904 *Eurycare* sp. — Persson, p. 516, pl. 8, fig. 8. (Fig. of axial shield.)
 1922 *Eurycare brevicauda* Angelin — Westergård, p. 148, pl. IX, figs. 11—12. (Descr. Figs. of axial shields.)
 1947 *Eurycare brevicauda* Ang. — Westergård, p. 24. (Distribution in Sweden.)

Type data: — Angelin's original cannot be determined with certainty, but an axial shield preserved in shale and without any accompanying label agrees so well with Angelin's figure that Westergård (1922, p. 149) believes that it probably is the original. The type locality is Andrarum, Scania, Sweden.

Diagnosis: — A *Eurycare* species with: interocular cheeks about as wide as glabella at eye line; postocular cheeks about as wide as occipital ring; thorax of 14 segments and without long axial spine.

Norwegian material: — This seems to agree with the Swedish, as far as can be judged from detached parts only.

Occurrence: — Norway: *Leptoplastus* zone (2c), subzone of *Leptoplastus ovatus*. Associated with *L. ovatus* and *Eurycare latum*. — Eiker (Vestfossen), Oslo (Gamlebyen). — Sweden (same horizon).

Eurycare explanatum (Holtedahl 1910).

Pl. 4: pl. 16, figs. 3—5.

- 1910 *Leptoplastus ovatus*, Ang., var. *explanata*, nov. var. [partim] — Holtedahl, p. 10, pl. 1, fig. 10 only. (Descr. and fig. of cranidium. Figs. 11—12 are of *Leptoplastus ovatus*.)
 1922 *Leptoplastus ovatus explanatus* Holtedahl [partim] — Westergård, p. 110. (Mentions Holtedahl's material.)
 1929 *Leptoplastus minor explanatus* (Hltd.) [partim] — Strand, p. 358. (Mentions Holtedahl's material.)
 1944a *Leptoplastus ovatus explanatus* Holtedahl [partim] — Westergård, p. 41. (Remarks.)
 1944a *Eurycare intermedium* sp. n. [partim] — Westergård, p. 41, pl. 2, figs. 9—10 only. (Figs. of cranidium and free cheek.)

Lectotype (here selected): — The cranidium (P.M.O. no. 30337a) figured by Høltedahl (1910, pl. I, fig. 10), from Jønsberg, Romedal, Hamar area, Norway.

Diagnosis: — A *Eurycare* species with: interocular cheeks as wide as glabella at eye line; postocular cheeks one and a half times as wide as occipital ring; possibly conspecific pygidium with 4 pairs of marginal spines. Thorax unknown.

Remarks: — Høltedahl (1910) based this species mainly on the cranidium, and for that reason a cranidium is selected as lectotype. Westergård (1944, p. 41) apparently doubts whether the free cheek assigned to this species by Høltedahl really belongs to it. A reexamination of the piece of limestone containing the lectotype and the free cheek figured by Høltedahl, shows that it also contains several cranidia no doubt belonging to *Leptoplastus ovatus*. It thus seems reasonable to assume that the free cheek (and pygidium) figured by Høltedahl belong to *L. ovatus*. The same piece of limestone furthermore contains several cranidia and free cheeks of the *crassicorne* type. The free cheeks are somewhat more slender than the typical *crassicorne*, and may represent a variety which is close to *Leptoplastus angustatus*. Parts of *L. ovatus* and *L. crassicorne* var. are very common in this limestone. There are only a few cranidia present of *E. explanatum*, and it is thus perhaps not so remarkable that there are no free cheeks that may be assigned to this species.

Description: — Cranidium about 2.5 times as wide as long. Largest cranidium (lectotype) 5.3 mm long. Cephalic axis with almost subparallel sides, truncate in front. Occipital ring with faint node. Occipital furrow distinct. Two pairs of glabellar furrows (S1 and S2); anterior pair rather indistinct. Short preglabellar field. Marginal border furrow distinct. Border narrow, arched in frontal view. Eye ridges distinct, transverse. Palpebral lobes small, with centres opposite S2. Interocular cheeks as wide as glabella at eye line. Postocular cheeks about 1.5 times as wide as occipital ring. Facial sutures not subparallel in front of eyes.

A large pygidium associated with the lectotype may possibly belong to *E. explanatum*. Its axis has 4 rings and an end lobe of 2 fused rings. At least 4 pairs of spines are present.

Occurrence: — Norway: Eiker-Sandsvær (Stablum core), Hamar district (Romedal), Ringsaker (Steinsodden). — *Leptoplastus* zone (2c), subzone of *Leptoplastus ovatus*. Associated with *L. ovatus* and *L. crassicorne* var. — Sweden (Associated with *L. crassicorne*. Andrarum, Scania).

Eurycare latum (Boeck 1838).

Pl. 4; pl. 16, figs. 6—9.

- 1838 *Trilobites latus* mh. — Boeck, p. 143. (Short descr.)
 1854 *Eurycare latum*. Boeck — Angelin, p. 48, pl. XXVI, fig. 6. (Diagn. Rough fig. of restored dorsal shield.)
 1854 *Eurycare camuricornis* n. sp. — Angelin, p. 48, pl. XXVI, fig. 8. (Diagn. Rough fig. of restored dorsal shield.)
 1865 *Eurycare* Ang. *latum* Boeck — Kjerulf, p. 2. (Recorded.)
 1882 *Eurycare latum*, Boeck — Brögger, p. 118, pl. XII, figs. 2, 2a-d. (Descr. Figs. of cranidium, free cheek, and pygidium.)
 1898 *Eurycare latum*, Boeck — Bjørlykke, p. 12. (Listed. Copies of Angelin's and Brögger's figs.)
 1901 *Eurycare latum* Boeck — Münster, pp. 24, 26. (Recorded.)
 1904 *Eurycare latum* Boeck — Persson, p. 513, pl. 8, figs. 1—7. (Descr. Figs. of axial shield, all parts of dorsal shield, and hypostoma.)
 1922 *Eurycare latum* (Boeck) — Westergård, p. 148, pl. IX, figs. 7—10. (Figs. of axial shield, free cheek, and cranidia.)
 1923 *Eurycare latum* Boeck — Poulsen, p. 32, pl. I, fig. 8. (Descr. fig. of cranidium.)
 1929 *Eurycare latum* (Boeck) — Strand, p. 358. (Recorded.)
 1934a *Eurycare latum* — Størmer, p. 333. (Listed.)
 1940 *Eurycare latum* (Boeck) — Størmer, p. 145. (Remarks. Cites Boeck's original description.)
 1944a *Eurycare latum* (Boeck) — Westergård, p. 41, pl. 2, figs. 11—12. (Figs. of free cheek and axial shield.)
 1947 *Eurycare latum* (Boeck) — Westergård, p. 24. (Distribution in Sweden.)
 1953 *Eurycare latum* — Høltedahl, p. 182, fig. 69 (23—24). (Fig. of cranidium and free cheeks, copied after Brögger, 1882.)

Type data: — Boeck's description (cited by Størmer, 1940) was not accompanied by any figure. Størmer (1940) decided provisionally not to select a lectotype of *E. latum*, as the specimens present in the Old Collection (from Boeck's time) were not too good, and the specimen figured by Brögger (1882), which possibly might belong to the Old Collection, had not yet been traced in the Museum. Brögger's specimen has now been found, but proved to have been collected after Boeck's time. Four pieces of dark stinkstone with *E. latum* are preserved in the Old Collection. They were collected by C. Boeck in "Oslo Alunbrud", that is the Alum Shale Quarry in Gamlebyen, Oslo, now abandoned. The material of *E. latum*, which is associated with *Leptoplastus ovatus*, consists of a few more or less incomplete cranidia, free cheeks, thoracic segments, and pygidia. As lectotype I select a rather small cranidium (P. M. O. no. 56383a), which, however, is the best preserved in the collection.

Diagnosis: — A *Eurycare* species with: interocular cheeks from 1.2 to 1.5 times as wide as glabella at eye line; postocular cheeks from 1.2 to 1.4 times as wide as occipital ring; thorax with 16—17 segments and long axial spine from the 11th segment.

Description of type material: — The lectotype cranium is 4.5 mm long (restored) and 10 mm wide. Cephalic axis with subparallel sides, and truncate in front. Occipital ring with small node. Occipital furrow distinct. Two pairs of glabellar furrows. Area in front of glabella damaged. Eye ridges distinct, slightly oblique backwards. Palpebral lobes of medium size, with centres opposite L2. Interocular cheeks about 1.4 times as wide as glabella at eye line. Postocular cheek about 1.4 times as wide as occipital ring. A larger, but not so well preserved cranium appears to have been about 10 mm long. It shows a distinct, but short preglabellar field, and also very faint traces of S3.

Remarks: — Other material from the same locality as the lectotype agrees with this, but shows a variation in the width of the interocular cheeks from 1.4 to 1.5 times the width of the glabella at the eye line. Axial shields figured by Persson (1904) and Westergård (1922, 1944) show that *E. latum* had 16 or 17 thoracic segments.

As suggested by Brögger (1882) and discussed by Persson (1904), *E. camuricorne* most probably is an immature specimen of *E. latum*.

Occurrence: — Norway: *Leptoplastus* zone (2c), subzone of *Leptoplastus ovatus* and subzone of *Leptoplastus angustatus* (lower part only?). Associated with *Leptoplastus ovatus* \pm *Eurycare brevicauda*, or *Leptoplastus angustatus*. — Eiker (Vestfossen, Stablum core), Røyken (Slemmestad), Oslo (Gamlebyen), Modum (Fure), Ringsaker (Evjevika), Hamar district (Fura in Løyten), Brummunddalen. — Sweden (same horizon), Denmark (Bornholm, same horizon).

Eurycare spinigerum Westergård 1922.

1922 *Eurycare spinigerum* n. sp. — Westergård, p. 149, pl. IX, figs. 13–14; pl. X, fig. 1. (Descr. Figs. of axial shield and posterior part of axial shields.)

1947 *Eurycare spinigerum* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Lectotype (selected here): — The axial shield figured by Westergård (1922, pl. IX, fig. 13) from Andrarum in Scania, Sweden.

Diagnosis: — A *Eurycare* species with: interocular cheeks about as wide as glabella at eye line; postocular cheeks slightly wider than occipital ring; thorax of 12 (or 13?) segments and with long axial spine on 11th segment.

Remarks: — *E. spinigerum* differs from *E. brevicauda* apparently only in having an axial spine on the 11th segment, and in having one or two segments less. Westergård (1922, p. 142) believes, however, that the differences indicate specific differences rather than e.g. sexual dimorphism, since no specimens without axial spine have been found in other leptoplastids

(as *Leptoplastus stenotus*) where a great number of specimens with axial spines have been examined.

Occurrence: — Sweden (*Leptoplastus* zone, subzone of *Leptoplastus ovatus*.)

Genus *Ctenopyge* Linnarsson 1880.

Type species: — *Olenus (Sphaerophthalmus) pecten* Salter 1864, designated by Vogdes (1890).

Diagnosis: — Leptoplastinae with: long, sub-parallel or tapering cephalic axis; very short, or, usually, no preglabellar field; medium-sized palpebral lobes moderately close to or remote from glabella and opposite L2 or L1; interocular and postocular cheeks narrow to wide; free cheeks with long spine; hypostoma with or without expanded marginal brim; thorax with long or very long, round or flattened pleural spines; pygidium (unknown in most species) with marginal spines and prominent axial spine.

Subgenera: — The genus *Ctenopyge* may be divided into three subgenera; *Eoctenopyge* n. subgen., *Mesoctenopyge* n. subgen., and the nominal subgenus *Ctenopyge*, which stratigraphically appear in this order.

Subgenus *Eoctenopyge* nov. Type species: — *Sphaerophthalmus flagellifer* Angelin 1854. Diagnosis: — As for genus, but with hypostoma without expanded posterior brim.

Subgenus *Mesoctenopyge* nov. Type species: — *Ctenopyge spectabilis* Brögger 1882. Diagnosis: — As for genus, but hypostoma with expanded posterior brim, and pleural spines always round.

Subgenus *Ctenopyge* Linnarsson 1880. Type species: — As for genus. Diagnosis: — As for genus, but hypostoma without expanded posterior brim, and pleural spines always flattened.

Species included in the genus *Ctenopyge*: —

Ctenopyge (Eoctenopyge) acadica Matthew 1894 (= *Ct. flagellifera*)

Ct. (Eoct.) angusta Westergård 1922

Ct. (Eoct.) drytonensis Cobbold 1933

Ct. (Eoct.) flagellifera (Angelin 1854)

Ct. (Eoct.) fusiformis Lake 1913 (= ? *Ct. flagellifera*)

Ct. (Eoct.) modesta n. sp.

Ct. (Eoct.) parabola (Cobbold 1933) (= ? *Ct. drytonensis*)

Ct. (Eoct.) postcurrens Westergård 1944

Ct. (Mesoctenopyge) erecta Westergård 1922

Ct. (Mesoct.) similis n. sp.

Ct. (Mesoct.) spectabilis Brögger 1882

Ct. (Mesoct.) tumida Westergård 1922

Ct. (Mesoct.) tumidoides n. sp.

Ct. (Ctenopyge) affinis affinis Westergård 1922

Ct. (Ct.) affinis gracilis n. subsp.

- Ct. (Ct.) bisulcata* (Philips 1848)
Ct. (Ct.) concava Linnarsson 1880 (= *Ct. pecten*)
Ct. (Ct.) directa Lake 1919
Ct. (Ct.) falcifera Lake 1913
Ct. (Ct.) fletcheri (Matthew 1901) (earlier: *Sphaerophthalmus*)
Ct. (Ct.) laticornis Westergård 1944 (= *Ct. fletcheri*)
Ct. (Ct.) linnarssoni Westergård 1922
Ct. (Ct.) pauper (Phillips 1848) (= ? *Ct. bisulcata*)
Ct. (Ct.) pecten (Salter 1864)
Ct. (Ct.) teretifrons (Angelin 1854)
and possibly also:
Ct. ? expansa Lake 1913
Ct. ? oelandica Westergård 1922

Ct. neglecta Westergård 1922 is transferred to *Leptoplastus* (cf. p. 169), whereas *Ct. neglecta postcurrens* Westergård 1944 is regarded as a species of *Ctenopyge*, and referred to as *Ct. (Eoct.) postcurrens*.

Ct. elachista Harrington (1938, p. 205, pl. VII, fig. 5) is probably a larval olenid, as suggested by its long palpebral lobes. Its late appearance (Tremadocian) makes it improbable that it should belong to *Ctenopyge*. It seems reasonable to assume that it may be a larval form of one of the associated olenid species.

Remarks on the pygidium: — Adult pygidia are known in only three *Ctenopyge* species; *Ct. (Eoct.) flagellifera*, *Ct. (Mesoct.) erecta*, and *Ct. (Ct.) pecten*. This is rather surprising, since other parts of the many species with unknown adult pygidium may occur in great numbers. Only a single pygidium of *Ct. (Eoct.) flagellifera* has been described (Westergård, 1922, p. 152). It is not too well preserved, and is slightly displaced from the rest of the axial shield. It apparently consists of only two segments. The anterior segment has an axial ring with a long axial spine and narrow pleural areas with a pair of marginal spines. The posterior segment seems to correspond only to the end lobe in more conventional pygidia. The pygidium of *Ct. (Mesoct.) erecta* (described below) consists of more segments, but likewise carries a prominent axial spine on the anterior segment. Both this and the following segment have well-developed pleural areas with marginal spines. The posterior part of the pygidium consists of an axis of three rather short and fused rings and extremely narrow pleural areas with tiny marginal points. The pygidium of *Ct. (Ct.) pecten* (which gave the genus its name) is of a different type. Its 6–7 axial rings are delimited from each other by furrows only on the two lateral thirds of the axis. One of the posterior rings carries a long axial spine. The pleurae are wide and equipped with long pleural spines. Behind the last segment is a small terminal plate. Lake (1946, p. 342) suggested that the pleurae were united to each other, but that the union was very weak and easily broken. The Swedish specimens, preserved in lime-

stone, seem to show that the pleurae really were free, as stated by Linnarsson (1880, p. 146), Moberg (1892, p. 351), and Westergård (1922, p. 161). The few Norwegian pygidia are very fragmentary and not sufficiently well preserved to add any additional information. Since *Sphaerophthalmus* developed from *Ctenopyge*, it is of interest that the pygidium is known in *Sph. humilis*, *Sph. majusculus*, and *Sph. major*. The *Sphaerophthalmus* pygidium resembles the posterior part of the pygidium of *Ct. (Mesoct.) erecta*, except for the furrows between the axial rings being well developed.

The pygidia of the three above-mentioned *Ctenopyge* species are all rather different, but have in common a prominent axial spine. The pygidia of the other *Ctenopyge* species (at least the better known) can hardly have been of the size of the pygidia of *Ct. (Mesoct.) erecta* and *Ct. (Ct.) pecten*, or they would undoubtedly have been found. In the cases where the thoracic shields of these species are known, they, too, suggest that the pygidia were small. It is probable that they carried a long axial spine, like the known pygidia. It is well known in e. g. *Leptoplastus* that the thoracic shields often broke near a segment which carried a long axial spine, probably because of the spine causing the segment to turn over. Similarly, a small pygidium with long axial spine would easily turn over and become imbedded with the pygidium proper normal to the bedding surface. This could explain both why the pygidia had become detached from the rest of the shield and why the pygidia are not found. It is possible that most of the unknown pygidia resemble that of *Ct. (Eoct.) flagellifera*, of which, characteristically enough, only a single specimen seems to be known, in spite of the great material of the other parts of this species. It is noteworthy in this connection that the known pygidia of *Sphaerophthalmus* have no axial spine, whereas a spine probably belonging to the otherwise unknown pygidium of *Sph. alatus* (Boeck, non auctorum) has been described by Westergård (1922, p. 164, as *Sph. major*).

Larval shields of *Ctenopyge* often are found with their posterior part preserved (cf. Westergård, 1922).

Occurrence: — Zones of *Protopeltura praecursor*, *Peltura minor*, and *Peltura scarabaeoides* in Norway, Sweden, Denmark, Great Britain, and E. Canada. Zone of *Peltura minor* in Poland.

Phylogeny and relationships: — Subgenus *Eoctenopyge* is the earliest subgenus of *Ctenopyge* to appear, and its earliest member is *Ct. (Eoct.) postcurrens*, index fossil of a subzone of the zone of *Protopeltura praecurrens* in Scandinavia. *Ct. (Eoct.) postcurrens* apparently developed from *Leptoplastus neglectus*, of which it was originally regarded as a subspecies (hence the unfitting name *postcurrens*), and with which it is connected by intermediate forms. However, whereas *Leptoplastus neglectus* is a true *Leptoplastus*, *Ct. (Eoct.) postcurrens* is a typical *Ctenopyge* species. *Ct. (Eoct.) flagellifera*, index fossil of the following subzone, is apparently close to *Ct. (Eoct.) postcurrens*, but differs i. a. in having wider pleural

regions and the cheek spines rather far forwards. *Ct. (Eoct.) drytonensis* may occur associated with *Ct. (Eoct.) flagellifera*, and is no doubt closely related to it, although it differs somewhat in the shape of the free cheeks. *Ct. (Eoct.) modesta* n. sp. from the next subzone (subzone of *Ct. similis* at the base of the zone of *Peltura minor*) is apparently close to the earlier members of *Eoectenopyge*, but differ i. a. in having a rather convex anterior lateral margin of the free cheeks. In this feature it differs also from its probable descendent, *Ct. (Eoct.) angusta* of the overlying subzone of *Ct. spectabilis*, but there appear to be intermediate forms between them. *Ct. (Eoct.) angusta* resembles rather much the slightly younger *Sphaerophthalmus alatus* Boeck (non auctorum), also in its small size, and probably gave rise to it. *Ct. (Eoct.) angusta* is the latest known member of *Eoectenopyge*. It is possible that the insufficiently known *Ct.? oelandica* from the zone of *Peltura minor* also belongs to *Eoectenopyge*, if it does not belong to *Sphaerophthalmus*.

The earliest known members of the subgenus *Mesoectenopyge* are *Ct. (Mesoct.) similis* n. sp. and *Ct. (Mesoct.) erecta* from the subzone of *Ct. similis*. They resemble *Ct. (Eoct.) flagellifera*, and *Mesoectenopyge* apparently developed from *Eoectenopyge*, but the species of *Mesocenopyge* are larger and have a hypostoma with an expanded posterior brim. *Ct. (Mesoct.) erecta* is probably closely related to *Ct. (Mesoct.) similis*, but has wider postocular cheeks and pleural regions, the eyes situated slightly further back, and a different shape of the free cheeks. *Ct. (Mesoct.) spectabilis* and *Ct. (Mesoct.) tumidoides* are both from the following subzone of *Ct. spectabilis* and may both have developed from *Ct. (Mesoct.) similis*. *Ct. (Mesoct.) spectabilis* differs in attaining a larger size, in having a slightly different shape of the free cheeks, and in having a hypostoma with a pair of wing-like posterior projections. *Ct. (Mesoct.) tumidoides* n. sp. has postocular facial sutures which are oblique, but which cut the margins slightly further forwards, and is thus intermediate between *Ct. (Mesoct.) similis* and the markedly proparian *Ct. (Mesoct.) tumida* with transverse postocular facial sutures. *Ct. (Mesoct.) tumida*, from the zone of that name, is the latest known member of *Mesoectenopyge*.

Subgenus *Ctenopyge* is the latest to appear of the three subgenera of *Ctenopyge*, and its earliest known representatives are *Ct. (Ct.) affinis affinis* and *Ct. (Ct.) affinis gracilis* n. subsp. from the subzone of *Ct. affinis*, the uppermost subzone of the zone of *Peltura minor*. It is difficult to say whether the subgenus *Ctenopyge* developed from *Eoectenopyge* or *Mesoectenopyge*. On the whole, the cranium of *Ct. (Ct.) affinis* resembles more that of *Ct. (Eoct.) angusta* than those of the late *Mesoectenopyge* species. Furthermore, the pleural spines of *Ct. (Eoct.) angusta* are slightly flattened, although not so wide and prominent as in *Ct. (Ct.) affinis* and other members of the subgenus *Ctenopyge* (where the thorax is known), whereas the pleural spines of *Mesoectenopyge* always seem to be round. At present it thus appears more

probable that the subgenus *Ctenopyge* developed from *Eoctenopyge* than from *Mesoctenopyge*. The two subspecies of *Ct. (Ct.) affinis* differ from each other mainly in the shape of the glabella. The next species to appear, *Ct. (Ct.) bisulcata*, from the subzone of that name at the base of the zone of *Peltura scarabaeoides*, is probably close to *Ct. (Ct.) affinis*, but differs i. a. in the shape of the free cheeks and in having wider fixed cheeks. A number of species occur in the following subzone of *Ct. pecten*, the latest subzone known to contain *Ctenopyge* species. *Ct. (Ct.) pecten* itself seems to be closely related to *Ct. (Ct.) affinis*, but has wider pleural regions and postocular cheeks, a slightly different shape of the free cheeks, and a peculiar pygidium. The four other species known from this subzone in Scandinavia, *Ct. (Ct.) fletcheri*, *Ct. (Ct.) directa*, *Ct. (Ct.) linnarssoni*, and *(Ct.) teretifrons*, seem to be rather closely related, and may have developed from *Ct. (Ct.) bisulcata*. They all four have a glabella with rather distinct S1, whereas the other glabellar furrows are extremely short or missing. The species differ i. a. in the width of the interocular and postocular cheeks. *Ct. (Ct.) fletcheri*, with the narrowest fixed cheeks, is remarkable because of its flat and unusually wide cheek spines. *Ct. (Ct.) teretifrons* and *Ct. (Ct.) directa* have very wide interocular cheeks and may be regarded as a parallel to *Eurycare*. The exact stratigraphic position of *Ct. (Ct.) falcifera*, reported only from Great Britain, is not known. It is possible that it is rather close to, if not synonymous with *Ct. (Ct.) linnarssoni*, but different preservation of the two species makes it difficult to compare them in detail.

Ctenopyge (Eoctenopyge) angusta Westergård 1922.

Pl. 5; pl. 19, figs. 11—16, 18.

- 1882 *Ctenopyge spectabilis*, n. sp. [partim] — Brögger, p. 120, pl. II, fig. 12c. (Fig. of young free cheek.)
- 1922 *Ctenopyge flagellifera angusta* n. var. [partim] — Westergård, p. 153, pl. XI, figs. 2—5, 8. (Diagn. Figs. of axial shield without pygidium, cranidia, and free cheek. Figs. 6—7 are here referred to *Ct. modesta* n.sp.)
- 1923 *Ctenopyge flagellifera* Angelin var. *angusta* Westergård — Poulsen, p. 39. (Descr.)
- 1927a *Ctenopyge flagellifera* var. *angusta* Westergård — Czarnocki, p. 198. (Recorded from Poland.)
- 1927b *Ctenopyge flagellifera* var. *angusta* Westergård — Czarnocki, p. 11. (Recorded from Poland.)
- 1947 *Ctenopyge angusta* Wgård. — Westergård, p. 24. (Distribution in Sweden.)
- Non 1934 *Ctenopyge flagellifera angusta*, Westergård — Cobbold. (= *Ct. drytonensis*.)

Type data: — As lectotype I select a cranidium figured by Westergård (1922, pl. XI, fig. 3). It is from Andrarum, Scania, Sweden, and is associated with other parts of the same species and with *Ct. tumida*.

Diagnosis: — A *Ctenopyge* species with: slightly tapering glabella; 2 pairs of glabellar furrows; oblique eye ridges; centres of palpebral lobes

opposite S1; interocular cheeks between half and three-fourths as wide as glabella at eye line; postocular cheeks about as wide as occipital ring; free cheeks with long slender round spine, with posterior lateral margin straight or only very slightly convex and shorter than convex anterior lateral margin, and with obtuse genal angle; thorax with pleural regions (excluding spines) about as wide as axis and with long posterior pleural spines. Pygidium unknown.

Norwegian material: — This agrees well with the Swedish, and shows that the hypostoma is of the same type as in *Ct. flagellifera* and *Ct. modesta* n. sp.

Occurrence: — Norway: Røyken (Slemmestad), Oslo (Tøyen), Ringsaker (Steinsodden). — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge spectabilis*. Alone, or associated with *Ct. spectabilis*. — Sweden (same horizon), Denmark (Bornholm, same horizon), Poland (Upper Cambrian).

Ctenopyge (Eoctenopyge) drytonensis Cobbold 1934.

Pl. 5; pl. 18, figs. 5—14.

- 1934 *Ctenopyge drytonensis*, sp. nov. — Cobbold, p. 352, pl. 45, figs. 9, 15a, 19. (Descr. and figs. of cranidia.)
 1934 *Ctenopyge flagellifera* (Angelin) — Cobbold, p. 351, pl. 45, figs. 15b, 16. 17. (Figs. of cranidia and free cheek.)
 1934 *Ctenopyge flagellifera angusta*, Westergård — Cobbold, p. 351, pl. 45, figs. 14, 15c, 15d. (Figs. of cranidia and free cheek.)
 1934 *Eurycare angustatum*, Angelin — Cobbold, p. 351, pl. 45, figs. 7—8. (Figs. of cranidium and free cheek.)
 1934 *Sphaerophthalmus*(?) *parabola* sp. nov. — Cobbold, p. 353, pl. 45, figs. 11—13. (Descr. and figs. of cranidia.)
 1934 Free cheeks. *Eurycare*, *Ctenopyge*, *Sphaerophthalmus* (?) — Cobbold, p. 355, pl. 45, figs. 7, 10, 14, 16. (Figs. of free cheeks.)

H o l o t y p e: — By original designation, a cranidium figured by Cobbold (refigured here: pl. 18, fig. 8), from "Block A", Dryton Brook, Rushton area, Shropshire, England.

D i a g n o s i s: — A *Ctenopyge* species with: tapering glabella, 3 pairs of glabellar furrows; eye ridges slightly oblique; palpebral lobes opposite L2; interocular cheeks about half as wide as glabella at eye line; postocular cheeks slightly wider than occipital ring; free cheeks with round slender spine with base only slightly closer to anterior than to posterior end of genal field, slightly convex anterior border, posterior border somewhat more convex, and slightly obtuse genal angle. Thorax, pygidium, and hypostoma unknown.

R e m a r k s: — The cranidium of *Ct. drytonensis* is described in detail by Cobbold. I should like to add that the axial furrow is rather shallow at the anterior corners of the glabella. The area around the anterior part of the glabella thus has a characteristic uneven appearance. The holotype cranidium

is larger than any other of the cranidia in the loose blocks examined by Cobbold. It is fairly well preserved, except that its anterior border is missing in front of the glabella.

I believe that the associated cranidia determined by Cobbold as *Eury-care angustatum*, *Ctenopyge flagellifera*, and *Ct. flagellifera angusta* all belong to *Ct. drytonensis*, and that their apparent differences were due to the varying degree to which they had been cleaned from the matrix. The cranidia described by him as *Sphærophthalmus? parabola* may likewise belong to *Ct. drytonensis*. The holotype cranidium of *Sph.? parabola* is not very well preserved, especially not in the anterior region. The glabella bends more strongly downwards in front than the holotype of *Ct. drytonensis*. However, some better preserved cranidia which show the same strong curvature of the glabella in front, otherwise agree completely with the holotype of *Ct. drytonensis*. Similar differences occur within other species of *Ctenopyge*, and I believe that *Sph.? parabola* should be regarded as a synonym of *Ct. drytonensis*. In any case, *parabola* should be assigned to *Ctenopyge* and is at least very closely related to *Ct. drytonensis*. It is important that the associated free cheeks are all of the same type. This is not so evident from the drawings published by Cobbold (1934, pl. 45, figs. 7, 10, 14, 16), but is suggested by the photographs of the same specimen reproduced here (pl. 11, figs. 11—14).

Norwegian material: — A few free cheeks from Gamlebyen, Oslo, agree very well with the Shropshire specimens. They are associated with numerous cranidia and free cheeks of *Ct. flagellifera*.

Affinities: — *Ct. drytonensis* is no doubt very close to *Ct. flagellifera*, but differs especially in the free cheeks. Thus the genal angle is less obtuse, and the posterior lateral margin of the free cheek is about as long as the anterior lateral margin, whereas the posterior lateral margin is considerably longer in *Ct. flagellifera*, and also more convex.

Occurrence: — Norway: Oslo (Gamlebyen). — Zone of *Protopeltura praecursor* (2d α), subzone of *Ctenopyge flagellifera*. Associated with *Protopeltura praecursor* and *Ctenopyge flagellifera*. — England (Shropshire. Not associated with any other species.)

Ctenopyge (Eoctenopyge) flagellifera (Angelin 1854).

Pl. 2; fig. 17; pl. 5; pl. 18, figs. 1—4.

- 1854 *Sphærophthalmus flagellifer*. n. sp. — Angelin, p. 49, pl. XXVI, fig. 7. (Diagn. Rough fig. of restored dorsal shield.)
- 1880 *Sphærophthalmus flagellifer* Ang. [partim] — Linnarsson, p. 12 (142), pl. I(V), figs. 14—17 only. (Descr. Figs. of free cheeks and parts of thoraces, one with attached incomplete cranidium. Fig. 17 is of *Leptoplastus neglectus*.)
- 1884 *Ctenopyge flagellifera*, Ang. — Brögger, p. 257. (Recorded.)
- ?1892 *Ctenopyge flagellifer*, Ang. var. — Matthew, p. 56, pl. XIII, figs. 12a-b. (Descr. Rough figs. of cranidium and free cheek.)

- 1892 *Ctenopyge spectabilis*. Brög. var. — Matthew, p. 57, pl. XIII, figs. 13a-b. (Descr. Rough figs. of cranidium and free cheek.)
- 1894 *Ctenopyge acadica*, n. sp. — Matthew, p. 109, pl. 17, figs. 13a-e. (Descr. Figs. of cranidium, free cheek, thoracic segment, and hypostomae.)
- ?1913 *Ctenopyge fusiformis*, sp. n. — Lake, p. 80, pl. VIII, fig. 14. (Descr. Fig. of cranidium and attached part of thorax.)
- 1922 *Ctenopyge flagellifera* (Angelin) — Westergård, p. 152, pl. X, 19—23; pl. XI, fig. 1. (Descr. Figs. of cranidium, free cheek, thoracic segments, hypostoma, and 2 axial shields without pygidium.)
- 1923 *Ctenopyge flagellifera* Angelin — Poulsen, p. 38, text-fig. 15, pl. I, figs. 12—13. (Descr. Figs. of cranidia, one with 7 attached thoracic segments, and copy of Westergård's fig. of axial shield without pygidium.)
- ?1946 *Ctenopyge fusiformis*, Lake — Lake, p. 342. (Remarks.)
- 1947 *Ctenopyge flagellifera* (Ang.) — Westergård, p. 24. (Distribution in Sweden.)
- 1952 *Ctenopyge flagellifera* (Angelin) — Hutchinson, p. 87, pl. IV, fig. 11. (Descr. and fig. of cranidium.)
- 1952 *Ctenopyge flagellifera* Angelin — Hupé, p. 117, fig. 78. (Diagram showing position of macropleurae.)
- Non 1864 *Olenus* (*Sphaerophthalmus*) *flagellifer*.? — Salter (= *Ct. linnarssoni*?); 1866 *Olenus* (*Sphaerophthalmus*) *flagellifer*, Angelin? — Salter (= *Ct. linnarssoni*?); 1882 *Ctenopyge flagellifera*, Ang. — Brögger (= *Ct. modesta* n. sp.); 1910 *Ctenopyge* (*Sphaerophthalmus*) *flagellifera*, Ang. — Høltedahl (= *Ct. modesta* n. sp.); 1934 *Ctenopyge flagellifera* (Angelin) — Cobbold (= *Ct. drytonensis*).

Type data: — Angelin's type specimen cannot be traced with certainty (Westergård, 1922, p. 153). One of Linnarsson's types from the same locality, Andrarum in Scania, Sweden, is selected here as neotype, namely the free cheek figured by him (1880, pl. I, fig. 14) and re-figured by Westergård (1922, pl. X, fig. 20).

Diagnosis: — A *Ctenopyge* species with: tapering glabella; 3 pairs of glabellar furrows; eye ridges slightly oblique; centres of palpebral lobes opposite S2; interocular cheeks slightly more than half as wide as glabella at eye line; postocular cheeks as wide as occipital ring; postocular facial sutures oblique and sinuous; free cheeks with long and slender round spine with base almost normal to lateral margin, and with posterior lateral margin rather convex and somewhat longer than slightly convex anterior lateral margin; thorax with at least 10 segments, slightly flattened pleural spines, the posterior ones being rather long; pleural regions (excluding spines) up to somewhat wider than axis; axial rings with spines, the posterior ones being long; small and imperfectly known pygidium apparently with 1 axial ring and an end lobe.

Remarks: — The most characteristic part of *Ct. flagellifera* is the free cheek with the spine situated rather far forwards. The genal angle is very obtuse; at the type locality from 140° to almost 180°.

Matthew (1892) referred some Canadian specimens to *Ctenopyge flagellifera* var. They are stated to differ from the Swedish form in having no preglabellar field, and from the Norwegian form described by Brögger,

in the position of the cheek spine. Brögger's form belongs, however, to *Ct. modesta* n. sp., and the Swedish type material likewise shows no preglabellar field. The Canadian form thus does not differ from *Ct. flagellifera* in these two features. Nevertheless, it may not belong to this species. The cheek spine is less curved than in *Ct. flagellifera*, and the glabella less tapering, as far as can be judged from the drawing of the cranidium. Moreover, the Canadian form is distinguished by Matthew (1892) from another Canadian form, which he referred to as *Ctenopyge spectabilis* var. and later (1894) gave the name *Ct. acadica*, which no doubt is a synonym for *Ct. flagellifera*. Both the cranidium and free cheek figured by Matthew (1892, pl. XIII, figs. 13a-b) agree very well with *Ct. flagellifera*. The cheek spine differs from that in *Ct. spectabilis* i. a. in not continuing the curve of the anterior lateral margin. I have further examined some specimens (nos. Ar. 32344—45) at the Swedish State Museum of Natural History, which were collected by G. F. Matthew and determined by him as *Ct. spectabilis* var. This material belongs to *Ct. flagellifera*, which is recorded from Canada also by Hutchinson (1952).

Ct. fusiformis described by Lake (1913) from England, was suggested by Westergård (1922, p. 153) probably to be a synonym of *Ct. flagellifera*. Lake (1946, p. 342) doubted this, but admitted that the differences might be apparent and only due to the preservation. It is difficult to settle this question as long as the free cheeks of *Ct. fusiformis* are unknown. However, it is certain that *Ct. flagellifera* occurs in England (cf. p. 49).

Norwegian material: — This agrees entirely with the Swedish, except for some free cheeks having a less obtuse genal angle (about 120°).

Occurrence: — Norway: Skien-Brevik district (Saltboden core), Eiker-Sandsvær (Stablum core), Røyken (Slemmestad), Oslo (Gamlebyen). — Zone of *Protopeltura praecursor* (2d α), subzone of *Ctenopyge flagellifera*. Alone, or associated with *Protopeltura praecursor* \pm *Ctenopyge drytonensis*. — Sweden (same horizon), Denmark (Bornholm, same horizon), England (Upper Cambrian), E. Canada (New Brunswick, Nova Scotia, *Peltura* zone).

Ctenopyge (Eoctenopyge) modesta n. sp.

Pl. 5; pl. 19, figs. 1—10.

- 1882 *Ctenopyge flagellifera*, Ang. [partim] — Brögger, p. 120, pl. II, figs. 15, 17. (Figs. of young cranidium and restored cephalon.)
 1910 *Ctenopyge (Sphaerophthalmus) flagellifera*, Ang. — Holtedahl, p. 21, pl. II, fig. 14. (Figs. of larval cranidium, which is associated with parts of *Ct. modesta* only.)
 1922 *Ctenopyge flagellifera angusta* n. var. [partim] — Westergård, p. 185, pl. XI, figs. 6—7. (Figs. of cranidium and free cheek.)

Name: — The name *modesta* is given as this species hitherto has not attracted due attention.

Holotype: — A free cheek (P. M. O. no. 29497a), associated with other parts of the dorsal shield. Collected on an excursion in 1880 at Slemmestad in Røyken.

Diagnosis: — A *Ctenopyge* species with: almost parallel-sided glabella; 2 pairs of glabellar furrows; rather oblique eye ridges; centres of eyes opposite S1; interocular cheeks about three-fourths as wide as glabella at eye line; postocular cheeks as wide as or slightly wider than occipital ring; postocular facial sutures oblique and sinuous; free cheeks with long round spine, posterior lateral margin short and straight, anterior lateral margin long and very convex, almost angular, genal angle very obtuse; thorax with pleural regions slightly wider than axis and with moderately long pleural spines. Pygidium unknown.

Description: — This is based on a great number of detached parts of the shield. The cranidia reach a length of 3.5 mm.

Cranidium strongly bent down in front. Glabella almost parallel-sided, rather convex, strongly bent down in front. Occipital ring with keel-like node, sometimes giving the impression of being composed of two nodes, one behind the other. Apparently no occipital spine. Occipital furrow very distinct, deepest a short distance from axial furrow. S1 also deepest a short distance from axial furrow, and united across glabella. Very faint impressions of S2 may sometimes be seen as a pair of pits near axial furrow. Anterior border raised up in front, concave in dorsal view, convex in front view. Eye ridges rather oblique. Interocular cheeks about three-fourths as wide as glabella at eye line. Postocular cheeks distinctly as wide as or wider than occipital ring. Palpebral lobes flexed upwards, and with centres opposite S1. Palpebral furrows distinct.

Free cheek with long, curved round spine, much closer to posterior than to anterior end of marginal border. Posterior lateral margin almost straight and comparatively short. Anterior lateral margin long and strongly curved. Eye strongly convex and slightly elongate. Well-preserved specimens show that it bears a great number of facets.

Hypostoma. Rather like that of *Ct. flagellifera*, with entire posterior margin.

Thorax. Parts of thoraces with up to 7 segments have been found. At least the anterior segments have wider pleurae than axis. Axial rings with node. Pleurae with moderately long pleural spines.

Pygidium unknown. The posterior part of larval shields have, however, been found. They are of the type usual in olenids.

Affinities: — *Ct. modesta* n. sp. seems to be related both to *Ct. flagellifera* and *Ct. angusta*, and may occupy an intermediate position between these. The cranidium of *Ct. modesta* n. sp. reminds one most of that of *Ct. angusta* with the eyes set far back and with oblique eye ridges, but its

postocular cheeks are wider, almost as wide as in *Ct. flagellifera*. The pleurae are about as wide as in *Ct. flagellifera*. In the free cheek the genal angle is rather obtuse, but not as much as in *Ct. flagellifera*, and on the whole the free cheek of *Ct. modesta* n. sp. reminds one more of that of *Ct. angusta*, with the spine in the posterior half, and a straight margin behind the spine. However, the margin in front of the spine is more convex than in *Ct. angusta*.

Occurrence: — Norway: Røyken (Slemmestad; Nærnes), Oslo (Tøyen; Nedre Slottsgate). — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge similis*. Alone, or associated with *Ctenopyge similis* \pm *Parabolina mobergii* \pm *Protopeltura bidentata*. — Sweden (same horizon).

Ctenopyge (Eoctenopyge) postcurrens Westergård 1944.

Pl. 5; pl. 17, figs. 8—10.

- 1922 *Ctenopyge neglecta* n. sp. [partim] — Westergård, p. 150, pl. X, fig. 18 only. (Fig. of cranium with 9 attached thoracic segments.)
 1944a *Ctenopyge neglecta postcurrens* var. n. — Westergård, p. 42, pl. 2, figs. 15—17. (Diagn. Figs. of cranidia and free cheek.)
 1944a *Ctenopyge neglecta* Westergård, a form approaching var. *postcurrens*. — Westergård, p. 42, pl. 2, figs. 13—14. (Figs. of cranium and free cheek.)
 1947 *Ctenopyge neglecta postcurrens* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Holotype: — A cranium figured by Westergård (1944, pl. 2, fig. 15), from a boring at Andrarum, Scania, Sweden. (S. G. U.)

Diagnosis: — A *Ctenopyge* species with: almost parallel-sided or slightly tapering glabella; no or very short preglabellar field; slightly oblique eye ridges; centres of palpebral lobes opposite L2; interocular cheeks as wide as or slightly wider than glabella at eye line; postocular cheeks markedly wider than occipital ring; free cheeks with long round spine, almost right-angled genal angle, straight posterior lateral margin and markedly longer and convex anterior lateral margin; thorax with at least one long axial spine, long round pleural spines, and pleural regions (excluding spines) about as wide as axis. Pygidium unknown.

Remarks: — I have transferred *Ctenopyge neglecta* to *Leptoplastus* for reasons given above (p. 169). *Ctenopyge neglecta postcurrens* is, however, a true member of *Ctenopyge*, and is referred to here as *Ctenopyge (Eoctenopyge) postcurrens*. Typical *Ctenopyge* features are the facial sutures converging in front of the eyes, the very long pleural spines, and one might also add, the absence of any pygidia in the material of this form.

The holotype cranium has a comparatively long and narrow glabella, and a short preglabellar field. Another cranium figured by Westergård (1944a, pl. 2, fig. 17) has a relatively shorter and wider glabella, and no preglabellar field. Both types occur associated in the material from the type locality. A cranium figured by Westergård (1944a, pl. 2, fig. 13) as a form

of *Ctenopyge neglecta* approaching var. *postcurrens*, also has a rather short and *Leptoplastus*-like glabella, but has only a short preglabellar field. As its facial sutures converge in front of the eyes, I believe that this form should be regarded as a variety of *Ctenopyge postcurrens* rather than of *Leptoplastus neglectus*. However, it seems to be intermediate between these two species, and the reference to the one or the other is uncertain as long as only its cephalon is known.

Norwegian material: — This is rather scarce. The Slemmestad specimens agree with the holotype, having a narrow and long glabella and a short preglabellar field. The border is not concave, and thus more *Leptoplastus*-like than in the Swedish specimens. The Hjellum material has a relatively shorter and more tapering glabella and practically no preglabellar field, thus agreeing better with the other cranidium figured by Westergård (1944, pl. 2, fig. 17.)

Occurrence: — Norway: Røyken (Slemmestad), Hamar area (Hjellum). — Zone of *Protopeltura praecursor* (2d α), subzone of *Ctenopyge postcurrens*. Alone, or associated with *Protopeltura praecursor*. — Sweden (same horizon.)

Ctenopyge (Mesoctenopyge) erecta Westergård 1922.

Pl. 5; pl. 20, figs. 1—9.

1922 *Ctenopyge erecta* n. sp. [partim] — Westergård, p. 156, pl. XI, figs. 21—25. (Descr. Figs. of cranidia, free cheek, and thoracic segments. The hypostoma in fig. 27 may belong to *Ct. similis* n. sp.)

1947 *Ctenopyge erecta* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Type data: — As lectotype I select a cranidium figured by Westergård (1922, pl. XI, fig. 21) from Nygård, Hunneberg, Västergötland, Sweden.

Diagnosis: — A *Ctenopyge* species with: slightly tapering glabella; 3—4 glabellar furrows not united across glabella; slightly oblique eye ridges; centres of palpebral lobes opposite L2 or S2; interocular cheeks somewhat narrower than, to as wide as glabella at eye line; postocular cheeks from somewhat less to slightly more than twice as wide as occipital ring; wide free cheeks with long slender round spine, obtuse genal angle, and straight posterior lateral margin, markedly shorter than convex anterior lateral margin; thorax with pleural regions (excluding spines) up to 2.5 times as wide as axis; pygidium with 2 axial rings (anterior ring with long axial spine), end lobe of 3 fused rings, and at least 2 pairs of marginal spines; hypostoma with large posterior brim and convex posterior margin.

Remarks: — As discussed below (p. 196), the hypostoma assigned to *Ct. erecta* by Westergård (1922) probably belongs to *Ct. similis* n. sp. However, the hypostomae of these two species are rather similar.

Norwegian material: — This consists of a few cranidia, free cheeks, and isolated thoracic segments, which agree very well with those described by Westergård from Sweden. Furthermore a few hypostomae and two pygidia are present. The hypostoma of *Ct. erecta* has a large posterior brim and very much resembles that of *Ct. similis*. The pygidia are of special interest, both because they are of an unusual type and because the pygidium is known in only two other *Ctenopyge* species: *Ct. flagellifera* (imperfectly known) and *Ct. pecten*. The two pygidia present are isolated, but may fairly safely be assigned to *Ct. erecta* since they are too large to belong to the only other *Ctenopyge* species (*Ct. modesta* n. sp.) associated with them.

In describing the pygidium of *Ct. erecta*, one may distinguish between the anterior and the posterior part. The anterior part has an axis with two rings and well-developed pleural areas with two pairs of marginal spines. Furthermore the anterior axial ring carries an axial spine. Only the base of this is preserved in the two specimens present, but as it is rather prominent, it is likely that the spine was quite long. In the posterior part of the pygidium, the axis consists of three rather short and fused axial rings. The pleural areas of this posterior part are extremely narrow, and appear to be provided with one or two pairs of small marginal points. (For comparison with pygidia of related species, see p. 184.)

Occurrence: — Norway: Oslo (Tøyen, Drammensveien at Parkveien). — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge similis*. Associated with *Ct. modesta* n.sp. \pm *Ct. similis* n.sp. and *Parabolina mobergi*. — Sweden (same horizon).

Ctenopyge (Mesoctenopyge) similis n. sp.

Pl. 5; pl. 20, figs. 10—14.

1922 *Ctenopyge erecta* n.sp. [partim] — Westergård, p. 156, pl. XI, figs. 26—27. (Figs. of part of thorax and hypostoma.)

Name: — The name *similis* is given as this species reminds one of several other *Ctenopyge* species, especially *Ct. tumida*, *Ct. spectabilis*, and *Ct. flagellifera*.

Holotype: — A cranidium (P. M. O. no. S 481) associated with other parts of the same species and parts of *Ct. modesta* sp. n. and *Parabolina mobergi*. Collected in Hadeland by L. Størmer in 1919.

Diagnosis: — A *Ctenopyge* species with: strongly tapering glabella; 4 pairs of glabellar furrows; eye ridge slightly oblique; centres of palpebral lobes opposite S2; interocular cheeks about as wide as glabella at eye line; postocular cheeks almost 1.5 times as wide as occipital ring; postocular facial sutures oblique; narrow free cheeks with coarse, flattened long spine with (usually furrowed) keel-like ridge on both sides, about right-angled inner spine angle, convex posterior lateral margin, markedly longer than almost straight anterior lateral margin; at least some thoracic segments

with long spine; hypostoma with entire posterior margin and well-developed posterior brim. Pygidium unknown.

Description: — This is based on numerous detached parts of the shield. The largest cranidium present (the holotype) is 4 mm long and fully 8 mm wide.

Cranidium with tapering glabella. Occipital ring with short axial spine. Occipital ring distinct. 4 pairs of glabellar furrows, not united across the glabella. S1 oblique backwards, S2 shorter, fainter and almost transverse, S3 and S4 very short, close together, and directed obliquely forwards. Border upturned, concave in dorsal view, convex in front view. Eye lines distinct, slightly oblique. Palpebral lobes upturned, relatively small, with centres opposite S2. Interocular cheeks only slightly narrower than glabella at eye line. Postocular cheeks about $\frac{4}{3}$ as wide as occipital ring. Postocular facial suture oblique.

Free cheeks narrow, with long and curved spine, round near base, but somewhat flattened further out, and provided with axial ridge (on both sides) which may be divided into two parallel ridges by a furrow (as in *Ct. fletcheri*). Anterior margin almost straight, and distinctly shorter than posterior lateral margin, which is almost straight near the spine (with which it forms a slightly acute angle) and is convex posteriorly.

Hypostoma tongue-shaped. Anterior lobe of middle body strongly convex, tapering rearwards. Posterior lobe less convex, rather large. Anterior margin slightly convex. Anterior wings triangular, flexed ventral. Lateral margins with convex border. Posterior margin with flatter border, flexed slightly ventral axially.

Thorax known only from detached segments. Axial rings with axial node (or spine). Pleurae with long, round, curved spines.

Pygidium unknown.

Remarks: — The hypostoma described by Westergård (1922, p. 156, pl. XI, fig. 27) as probably belonging to *Ct. erecta*, occurs in a small block together with similar hypostomae as well as cranidia and free cheeks of *Ct. similis* n. sp., but no parts of *Ct. erecta*. As the hypostoma is exactly like those associated with *Ct. similis* in the Norwegian material, I believe that it should be assigned to this species. So should probably also the fragment of a thorax from the same block (Westergård, 1922, pl. XI, fig. 26).

Variations and affinities: — The cranidium of *Ct. similis* n. sp. resembles those of *Ct. spectabilis* and *Ct. tumida*. The postocular facial suture may be more or less oblique, in the latter case approaching the transverse suture of *Ct. tumida*. There seems to be an even transition, at least in the cranidium, from *Ct. similis* n. sp. through *Ct. tumoides* n. sp. with slightly oblique postocular facial suture, to *Ct. tumida* itself. *Ct. similis* n. sp. may also be regarded as being intermediate between *Ct. flagellifera* and *Ct. spectabilis*. The free cheeks of *Ct. similis* resemble those of *Ct. flagellifera* in having a posterior lateral margin which is curved, at least posteriorly, but

it is almost straight near the spine. In *Ct. spectabilis* the whole of the posterior margin is straight. The acute angle between the posterior margin and the spine resembles that of *Ct. spectabilis*. The posterior brim in the hypostoma is rather large, and larger than in *Ct. tumida*.

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad), Oslo (Tøyen), Hadeland. Zone of *Peltura minor* (2d β), subzone of *Ctenopyge similis*. Associated with *Ct. modesta* n. sp. \pm *Parabolina mobergi* \pm *Protopeltura planicauda* \pm *Protopeltura bidentata*. — Sweden (same horizon.)

Ctenopyge (Mesoctenopyge) spectabilis Brögger 1882.

Pl. 2, fig. 20; pl. 5; pl. 21, figs. 1—7.

- 1882 *Ctenopyge spectabilis*, n. sp. [partim] — Brögger, p. 120, pl. II, figs. 18, 18a-b; pl. XII, figs. 12a-b. (Descr. Figs. of cranidium, free cheeks, thoracic segment, and hypostoma. Fig. 12 is a fragment of a pygidium of a *Protopeltura* sp., and fig. 12c is of a young free cheek belonging to the associated *Ct. angusta*.)
- 1922 *Ctenopyge spectabilis* Brögger — Westergård, p. 154, pl. XI, figs. 9—14. (Descr. Figs. of cranidia, free cheek, thorax, and hypostoma.)
- 1929 *Ctenopyge spectabilis* Br. — Strand, p. 359. (Recorded.)
- 1934a *Ctenopyge spectabilis* — Stormer, p. 332. (Listed.)
- 1947 *Ctenopyge spectabilis* Brögg. — Westergård, p. 24. (Distribution in Sweden.)
- 1953 *Ctenopyge spectabilis* — Høltedahl, p. 182, fig. 69 (27). Fig. of cranidia and free cheeks, copied from Brögger, 1882.)
- Non 1892 *Ctenopyge spectabilis* Brög. var. — Matthew (= *Ct. flagellifera*).

Type data: — I select as lectotype the cranidium (P.M.O. no. 2981a) figured by Brögger (1882, pl. II, fig. 18). Collected by Brögger in 1879 at Slemmestad in Røyken, Norway.

Diagnosis: — A *Ctenopyge* species with: strongly tapering glabella, 3—4 pairs of glabellar furrows; oblique, somewhat curved eye ridges; centres of palpebral lobes opposite L2; interocular cheeks slightly more than three-fourths as wide as glabella at eye line; postocular cheeks from six-fifths to eight-fifths as wide as occipital ring; narrow free cheeks with long, coarse spine, posterior lateral margin slightly convex and markedly longer than slightly convex anterior lateral margin, spine almost confluent with anterior lateral margin, inner spine angle acute; thorax with long pleural spines and pleural regions (excluding spines) somewhat wider than axis; hypostoma with posterolateral extensions and large posterior brim. Pygidium unknown.

Description: — This is based on numerous detached parts of the shield. The largest cranidium from the type locality is 6.8 mm long. A cranidium from Steinsodden, Ringsaker, Norway, is 8.1 mm long.

Cranidium with tapering glabella. Occipital ring with small and slender spine. Occipital furrow deepest a little inside axial furrow. Four pairs of glabellar furrows, which do not unite across the glabella. S1 oblique backwards; each branch with deep pit-like impression about halfway between

axial furrow and axial line. S2 pair only slightly oblique backwards. S3 short, oblique forwards. S4 represented by faint impressions rather close to the S3, and directed even more forwards. Border flexed obliquely upwards; concave in dosal view, slightly convex in front view. Eye lines distinct, long, oblique backwards, slightly curved. Palpebral lobes of medium size, narrow, flexed upwards, with centres opposite S1. Interocular cheeks about 7/9 as wide as glabella at eye line. Postocular cheeks about 6/5 as wide as occipital ring.

Free cheeks narrow, with long, coarse and curved spine. Posterior lateral margin straight, and shorter than slightly curved anterior lateral margin. Genal angle obtuse. Acute inner spine angle.

Hypostoma subrectangular in outline. Middle body strongly convex, semi-ovoid. Anterior border slightly convex. Anterior wings triangular, bent dorsal. Lateral borders prominent, slightly concave. Posterolateral corners protruded into rounded triangular wings. Posterior margin concave. Brim rather wide and slightly inflated.

Thorax known only from single segments in the Norwegian material. They have axial node, and long pleural spines. A fragment of the thorax, consisting of 10 segments, has been figured by Westergård (1922, pl. IX, fig. 13) from Sweden. The pleurae (excluding spines) of the anterior segments are markedly wider than the axial ring.

Pygidium unknown.

Remarks: — The specimen figured by Brögger (1882, pl. XII, fig. 12a) as a pygidium of *Ct. spectabilis*, is the axial part of a pygidium of a pelturine. The specimen figured by Brögger (1882, pl. XII, fig. 12c) as a young free cheek of *Ct. spectabilis*, does not belong to this species, as already suggested by Westergård (1922, p. 154). It belongs to the associated *Ct. angusta*.

Occurrence: — Norway: Røyken (Slemmestad), Ringsaker (Steinsodden). — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge spectabilis*. Associated with *Ct. angusta*, *Ct. tumidoides*, *Peltura minor*, *Parabolina* sp. — Sweden (same horizon).

Ctenopyge (Mesoctenopyge) tumida Westergård 1922.

Pl. 5; pl. 20, fig. 16.

- 1880 *Ctenopyge?* sp. indet. — Linnarsson, p. 26 (156), pl. II(VI), fig. 15. (Descr. and fig. of part of thorax.)
- 1922 *Ctenopyge tumida* n. sp. [partim] — Westergård, p. 155, pl. XI, figs. 15–18. (Descr. Figs. of cranidia and free cheek. Figs. 19–20 are of *Ct. tumidoides* n. sp.)
- 1923 *Ctenopyge tumida* Westergård [partim] — Poulsen, p. 39, pl. I, fig. 14. (Descr. Fig. of cranidium. Text fig. 16 is of *Ct. tumidoides* n. sp.)
- 1947 *Ctenopyge tumida* Wgård. [partim] — Westergård, p. 24. (Distribution in Sweden, including that of *Ct. tumoides*.)
- Non 1953 *Ctenopyge tumida* Westergård — Hupé (= *Ct. tumidoides* n. sp.).

Type data: — As lectotype I select a cranidium figured by Westergård (1922, pl. XI, fig. 16), from Andrarum, Scania, Sweden, and associated with i. a. *Sphacrophthalmus alatus*.

Diagnosis: — A *Ctenopyge* species with: tapering glabella; four pairs of glabellar furrows; transverse or slightly oblique eye ridges; centres of palpebral lobes opposite S2; interocular cheeks somewhat narrower than, to as wide as glabella at eye line; postocular cheeks almost 1.5 times as wide as occipital ring; facial sutures proprian, postocular facial suture transverse; free cheeks with long spine, straight posterior lateral margin shorter than convex anterior lateral margin, and obtuse genal angle; thorax with long pleural spines and pleural regions (excluding spines) almost as wide as axis. Hypostoma and pygidium unknown.

Remarks: — Westergård (1922) included in *Ct. tumida* two different forms. In one of the forms the postocular facial suture is transverse, and in the other it runs obliquely backwards. The name *Ct. tumida* is retained for the form with transverse suture, whereas the other form is described below as *Ct. tumidoides* n.sp. The cranidium of *Ct. tumida*, as restricted here, differs from that of *Ct. tumidoides* n.sp. also in having wider posterior cheeks. The hypostoma figured and described by Westergård (1922) apparently belongs to *Ct. tumidoides* n.sp., and the hypostoma of *Ct. tumida* is thus not known. A part of the thorax of *Ct. tumida* figured by Westergård (1922, pl. XI, fig. 18) shows that the pleurae are provided with long spines, and that the pleural regions are about as wide as the axis, whereas the pleural regions in *Ct. tumidoides* n.sp. (Westergård, 1922, pl. XI, fig. 19) are slightly narrower than the axis (excluding pleural spines).

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad), Oslo (Rosenkranzgate, Tøyen), Hadeland. — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge tumida*. Associated with *Sphacrophthalmus alatus*, \pm *Protopeltura planicauda*, \pm *Peltura acutidens*, \pm *P. minor*. — Sweden (same horizon), Denmark (Bornholm, same horizon).

Ctenopyge (*Mesoctenopyge*) *tumidoides* n. sp.

Pl. 5; pl. 20, fig. 15.

- 1922 *Ctenopyge tumida* n. sp. [partim] — Westergård, p. 155, pl. XI, figs. 17–20. (Figs. of cranidium with 5 attached thoracic segments, and of hypostoma.)
- 1923 *Ctenopyge tumida* Westergård [partim] — Poulsen, p. 39, text fig. 16. (A reproduction of Westergård's fig. of a cranidium with attached thoracic segments.)
- 1947 *Ctenopyge tumida* Wgård. [partim] — Westergård, p. 24. (Distribution in Sweden of *Ct. tumida*, including that of *Ct. tumidoides* n.sp.)
- 1953 *Ctenopyge tumida* Westergård — Hupé, p. 117, fig. 78, B, I. (Lists first thoracic segment of this form as macropleural.)

Name: — The name *tumidoides* is given to suggest the resemblance to *Ct. tumida*.

Holotype: — As holotype I select the cranidium with 5 attached thoracic segments figured by Westergård (1922, pl. XI, fig. 19) from Andrarum, Scania, Sweden. It is associated with detached parts of *Ct. angusta*.

Diagnosis: — A *Ctenopyge* species with: tapering glabella; 3 pairs of glabellar furrows; slightly oblique, almost transverse eye ridges; centres of palpebral lobes opposite L3; interocular cheeks slightly narrower than glabella at eye line; postocular cheeks as wide as, or slightly wider than occipital ring; thorax with very long, round pleural spines and pleural regions somewhat narrower than axis; hypostoma with entire posterior border and distinct, but not very large posterior brim. Free cheeks and pygidium unknown.

Description: — Cranidium rather similar to that of *Ct. tumida*, but the postocular facial sutures run slightly obliquely backwards in *Ct. tumidoides*, whereas they are transverse in *Ct. tumida*. In this feature *Ct. tumidoides* reminds one of *Ct. similis* n. sp., which, however, has wider postocular cheeks. The postocular cheeks are about as wide as the occipital ring in *Ct. tumidoides*, whereas they are about $\frac{4}{3}$ the width of the occipital ring in *Ct. similis* n. sp. The occipital ring in *Ct. tumidoides* is provided with a spine, as in *Ct. similis* n. sp. and *Ct. tumida*.

Free cheeks unknown.

The hypostoma figured by Westergård (1922, pl. XI, fig. 20) comes from the same block as the holotype of *Ct. tumidoides*, and most probably belongs to this species. It reminds one of that of *Ct. similis* n. sp., but its posterior brim is not so extended.

The 5 thoracic segments in the holotype show that the pleural regions are rather narrow (narrower than the axis), but the pleurae are provided with long, curved spines. The spines of the first segment appear to be longer than those of the others, and Hupé (1953, p. 117) regards this segment as macropleural.

Remarks: — *Ct. tumidoides* n. sp. is slightly earlier than *Ct. tumida*, which occurs in the following subzone together with i. a. *Sphaerophthalmus alatus*.

Occurrence: — Norway: Røyken (Slemmestad), Ringsaker (Steinsodden) — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge spectabilis*. Associated with *Ct. spectabilis*, *Ct. angusta*, *Peltura* cf. *minor*, *Parabolina* sp. — Sweden (Scania, same horizon).

Ctenopyge (*Ctenopyge*) *affinis affinis* Westergård 1922.

Pl. 5; pl. 19, fig. 22.

1922 *Ctenopyge affinis* n. sp. [partim] — Westergård, p. 157, pl. XII, figs. 1–6, 14. (Descr. Figs. of cranidia, free cheeks, and thoracic segments. Figs. 7–13 are here referred to *Ct. affinis gracilis* n. subsp., fig. 15 to *Ct. pecten*?)

- 1923 *Ctenopyge affinis* Westergård — Poulsen, p. 41, pl. II, fig. 5. (Descr. Fig. of cranidium.)
 1947 *Ctenopyge affinis* Wgård. [partim] — Westergård, p. 24. (Distribution in Sweden of this form and *Ct. affinis gracilis* n.subsp.)
 Non 1929 *Ctenopyge affinis* Wgd. — Strand (= *Ct. affinis gracilis* n.subsp.).

Lectotype — A cranidium from Andrarum, Scania, Sweden, figured by Westergård (1922, pl. XII, fig. 1). Designated by Poulsen (1923, p. 42).

Diagnosis: — A *Ctenopyge* subspecies with: tapering glabella; four pairs of glabellar furrows; rather oblique eye ridges; centres of palpebral lobes opposite S1; interocular cheeks about half as wide as glabella at eye line; postocular cheeks as wide as or slightly wider than occipital ring; postocular facial sutures oblique and rather straight; free cheeks with long slender spine, straight posterior lateral margin much shorter than convex anterior lateral margin, and acute genal angle; thorax with pleural regions markedly wider than axis and with long pleural spines, some of which flattened and longitudinally grooved. Hypostoma and pygidium unknown.

Remarks: — Westergård (1922) included two different forms under the name *Ct. affinis*. They are easily distinguished, as one of the forms has a decidedly tapering glabella, which appears more robust than the parallel-sided glabella of the other form. These forms are regarded here as distinct subspecies. The lectotype of *Ct. affinis* belongs to the subspecies with tapering glabella, and this subspecies must consequently be called *Ct. affinis affinis*. This is also the form on which Westergård based his description of *Ct. affinis*. The other subspecies is given the name *Ct. affinis gracilis* (cf. below).

The Norwegian material agrees very well with the Swedish. The largest cranidia are about 5 mm long. In Danish material the cranidia may be well over 10 mm long.

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad). — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge affinis*. Associated with *Sphaerophthalmus alatus* and *Peltura minor*, \pm *Ct. affinis gracilis* n. subsp. — Sweden (same horizon), Denmark (Bornholm, same horizon).

Ctenopyge (Ctenopyge) affinis gracilis n. subsp.

Pl. 5; pl. 19, figs. 17, 19—21.

- 1922 *Ctenopyge affinis* n. sp. [partim] — Westergård, p. 157, pl. XII, figs. 7—13 only. (Figs. of cranidia, free cheek, thoracic segments, and hypostoma.)
 1929 *Ctenopyge affinis* Wgd. — Strand, p. 359. (Recorded.)

Name: — The name *gracilis* is given as this subspecies appears more graceful than the rather robust *Ct. affinis affinis*.

Holotype: — A cranidium (P. M. O. no. 19993a) collected by W. C. Brøgger in 1880 at Slemmestad, Røyken. It is associated with other

parts of the same form, as well as of *Ct. affinis affinis*, *Sphaerophthalmus alatus*, and *Peltura minor*.

Diagnosis: — Differs from *Ctenopyge affinis affinis* in having a narrower glabella with sub-parallel sides.

Description: — This is based on detached parts of the shield. The holotype cranidium is 3.3 mm long; other cranidia reach a length of 4 mm. This form is thus smaller than the main form of *Ct. affinis*, as already pointed out by Westergård (1922). I would like to emphasize that also equal-sized cranidia of the two subspecies clearly show the characteristic differences.

Cranidium with parallel-sided glabella. Occipital ring with very short axial spine. Occipital furrow distinct. S1 united to form a continuous furrow, rather shallow and not so well defined in middle part. Glabella in front of S1 rather convex, and with only very short impressions of additional glabellar furrows on the sides. S2 clearly seen, but S3 and S4 short and very narrow and best seen from the side. Glabella bends ventrad rather steeply in front. Border slightly upturned, slightly concave, almost straight in dorsal view, and slightly arched upwards in front view. Eye ridges distinct, oblique backwards. Interocular cheek about 2/3 as wide as glabella at eye line. Postocular cheeks about 4/3 as wide as occipital ring. Postocular part of facial suture oblique backwards.

Free cheeks relatively narrow, with long and slightly curved spine. Posterior lateral margin straight and short, almost normal to spine. Anterior lateral margin long and curved. Facetted eyes often preserved.

Hypostoma (probably belonging to this form) tongue-shaped, rather narrow, but with two triangular anterior wings bent only slightly ventrad. Middle body rather convex, long, and tapering backwards. Brim rather flat, but flexed somewhat ventrad, forming platform for anterior lobe. Lateral borders distinct and sub-parallel, posterior border less pronounced and curved. No posterior wings.

Thorax known only from parts of segments. Pleurae with long curved pleural spines. The spines are flat, with a median ridge on both sides. The median ridge may be divided into two ridges by a faint median furrow, at least near the base of the spine. Some straight, flat spines, also with a median ridge on both sides, appear to be axial spines. In at least one specimen traces of the axial ring appear to be preserved at the base of such a spine.

Pygidium unknown.

Affinities: — *Ct. affinis gracilis* n. subsp. is close to *Ct. affinis affinis*, and they have the same type of pleural spines and free cheeks. *Ct. spectabilis*, like several other late *Ctenopyge* species, also has this type of pleural spines, but differs from *Ct. affinis gracilis* i. a. in the shape of the free cheeks. Nevertheless, they may be rather closely related.

Occurrence: — Norway: Røyken (Slemmestad), Ringsaker (Evjevika) — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge affinis*. Associated with *Sphaerophthalmus alatus* and *Peltura minor*, \pm *Ct. affinis*. — Sweden (same horizon).

Ctenopyge (*Ctenopyge*) *bisulcata* (Phillips 1848).

Pl. 5.

- 1848 *Olenus bisulcatus*, n. s. [partim] — Phillips, p. 55, fig. 1, p. 346. (Descr. Fig. of cranium. Fig. 2 is suspected by Lake, 1913, to be of *Ct. pecten*.)
- 1864 *Olenus bisulcatus*, Phillips [partim] — Salter, p. 8. (Not fig. 6, pl. VIII, according to Lake, 1913.)
- ?1866 *Olenus* (*Sphaerophthalmus*) *alatus*, Beck — Salter, p. 302, pl. IV, fig. 3. (Remarks. Figs. of cranium and cheek spines.)
- 1868 *Sphaerophthalmus bisulcatus*, Phil. — Belt, p. 10. (Suggests that this species and Salter's *Olenus pecten*, *O. flagellifer*, and *O. alatus* are synonyms, and that this species is not identical with Boeck's *Sph. alatus*.)
- 1871 *Olenus bisulcatus*. Phillips — Phillips, p. 68, fig. 7. (Inaccurate fig. of cranium.)
- ?1871 *Olenus pauper* n. sp. — Phillips, p. 68, fig. 4. (Fig. of poorly preserved dorsal shield with no pygidium.)
- 1873 *Olenus* (*Sphær.*) *bisulcatus*, Phillips — Salter, p. 12. (Remarks.)
- 1880 *Ctenopyge bisulcata* Phill. sp. — Linnarsson, p. 23 (153), pl. I (V), figs 18—19; pl. II (VI), figs. 1—2. (Descr. Figs. of crania, free cheek, and thoracic segments.)
- 1913 *Ctenopyge bisulcata* (Phillips) — Lake, p. 81, pl. VIII, figs. 15—19; pl. IX, figs. 1—4. (Descr. Figs. of crania, free cheek, parts of thorax, and hypostoma.)
- 1922 *Ctenopyge bisulcata* (Phillips) — Westergård, p. 159, pl. XII, figs. 19—25. (Remarks. Figs. of crania, free cheek, and thoracic segments.)
- 1923 *Ctenopyge bisulcata* Phillips — Poulsen, p. 46, pl. II, fig. 4. (Descr. Fig. of cranium.)
- 1938 *Ctenopyge bisulcata* (Phillips) — Stubblefield, p. 29. (Remarks on type material.)
- 1947 *Ctenopyge bisulcata* (Phillips) — Westergård, p. 24. (Distribution in Sweden.)
- ?1949 *Olenus pauper* Phillips — Edmonds, p. 59. (Selects holotype.)
- 1952 *Ctenopyge bisulcata* (Phillips) — Hutchinson, p. 87, pl. IV, figs. 9—10. (Remarks. Figs. of cranium and free cheek.)

Type data: — A lectotype should be chosen from the type stratum and locality, the Black Shales of Whiteleaved Oak, Malvern Hills, Shropshire, England, from the material collected by J. Phillips.

Diagnosis: — A *Ctenopyge* species with: almost parallel-sided glabella; S1 strong, usually united across glabella, other glabellar furrows very short; oblique eye ridges; centres of palpebral lobes opposite S1 or L2; interocular cheeks somewhat narrower than glabella at eye line; postocular cheeks slightly less to slightly more than 1.5 times as wide as occipital ring; free cheeks with long flattened spine, obtuse genal angle, and straight posterior lateral margin slightly shorter than convex anterior lateral margin; thorax with pleural regions (excluding spines) somewhat wider than axis

and long flat pleural spines (at least posteriorly); hypostoma with relatively short brim. Pygidium unknown.

Remarks: — Westergård (1922, p. 159) remarked that the Swedish form deviates slightly from the British form (as described and illustrated by Lake, 1913), which has more oblique eye ridges. In material from Malvern Hills there are, however, cranidia which have no more oblique eye ridges than the Swedish (and Norwegian) specimens. The Norwegian material consists of only a few cranidia and imperfect free cheeks.

Occurrence: — Norway: Modum (Engelstad). — Zone of *Peltura scarabaeoides*, lower part (2dγ), subzone of *Ctenopyge bisulcata*. Associated with *Peltura scarabaeoides scarabaeoides*, *Sphaerophthalmus humilis* and *Sph. majusculus*. — Sweden (same horizon), Denmark (Bornholm, same horizon), England (Upper Lingula Flags), Nova Scotia (*Peltura* zone).

Ctenopyge (Ctenopyge) directa Lake 1919.

Pl. 5.

1913 *Ctenopyge directa*, sp. nov. — Lake, pl. X, fig. 11. (Fig. of cranidium.)

1919 *Ctenopyge directa*, sp. nov. — Lake, p. 89, pl. XI, fig. 1. (Descr. Fig. of cranidium.)

1922 *Ctenopyge directa* Lake [partim] — Westergård, p. 158, pl. XII, fig. 16. (Descr. Fig. of cranidium. Fig. 17 is of *Ct. fletcheri*.)

1947 *Ctenopyge directa* Lake — Westergård, p. 24. (Distribution in Sweden.)

Non 1923 *Ctenopyge directa* Lake — Poulsen (= *Ct. fletcheri*).

Type data: — As lectotype I select a cranidium figured by Lake (1919, pl. XI, fig. 1), from Dolgelley Beds, Dolgelley, Wales.

Diagnosis: — A *Ctenopyge* species with: slightly tapering glabella; S1 united across glabella, practically no other glabellar furrows; oblique eye ridges; centres of palpebral lobes opposite L2; interocular cheeks as wide as or slightly wider than glabella at eye line; postocular cheeks slightly wider than occipital ring. Other parts than cranidium unknown.

Occurrence: — Sweden (associated with *Sphaerophthalmus humilis* and *Peltura scarabaeoides scarabaeoides*), England (Upper Lingula Flags), Wales (Upper Lingula Flags).

Ctenopyge (Ctenopyge) falcifera Lake 1913.

1913 *Ctenopyge falcifera*, sp. nov. — Lake, p. 84, pl. IX, figs. 5–6. (Descr. Figs. of hypostoma and dorsal shield with no pygidium.)

Type data: — I select as lectotype the dorsal shield without pygidium, figured by Lake (1913, pl. IX, fig. 5), from the Upper Lingula Flags, Rhiwfelyn.

Diagnosis: — A *Ctenopyge* species with: tapering glabella; slightly oblique eye ridges, centres of palpebral lobes opposite S1; interocular cheeks

about as wide as glabella at eye line; postocular cheeks somewhat wider than occipital ring; postocular facial sutures oblique and sinuous; free cheeks with long flattened spine almost normal to lateral margin and long convex posterior lateral margin, apparently longer than anterior lateral margin; thorax with pleural regions (excluding spines) somewhat wider than axis and very wide pleural spines; hypostoma with moderately large posterior brim. Pygidium unknown.

Occurrence: — England (Upper Lingula Flags), Wales (Upper Lingula Flags).

Ctenopyge (*Ctenopyge*) *fletcheri* (Matthew 1901).

Pl. 5; pl. 22, figs. 1—6.

- 1880 *Ctenopyge*? sp. indet. — Linnarsson, p. 26, pl. 2, fig. 14. (Descr. and fig. of free cheek.)
- 1894 *Sphaerophthalmus alatus*, Boeck, var. *Canadensis*, n. var. The narrow form. — Matthew, p. 108, pl. 17, figs. 12a-b. (Descr. and fig. of cranidium and free cheek.)
- 1901 *Ctenopyge* n. sp. — Lindström, p. 29, pl. III, figs. 28—30. (Figs. of free cheek and surface of eye.)
- 1901 *Sphaerophthalmus Fletcheri* [partim] — Matthew, p. 280, pl. V, figs. 7d. (Descr. and fig. of free cheek. The cranidium, pygidium, and hypostoma described and figured, belong to *Sph. humilis*.)
- 1903 *Sphaerophthalmus Fletcheri* [partim] — Matthew, p. 227, pl. XVII, fig. 7d. (Descr. and fig. of free cheek. The cranidium, pygidium and hypostoma described and figured, belong to *Sph. humilis*.)
- 1913 *Sphaerophthalmus alatus* var. *canadensis* Matthew, "narrow form" [partim] — Lake, p. 76. (Remarks.)
- 1922 *Ctenopyge directa* Lake [partim] — Westergård, p. 159, pl. 12, fig. 17. (Fig. of cranidium.)
- 1922 *Ctenopyge teretifrons* (Angelin) [partim] — Westergård, p. 162, pl. 13, figs. 7—8. (Descr. and figs. of free cheeks.)
- 1923 *Ctenopyge directa* Lake — Poulsen, p. 45, pl. III. (Descr. Figs. of cranidium and free cheeks.)
- 1944a *Ctenopyge laticornis* sp. n. — Westergård, p. 42, pl. 3, figs. 1—2. (Remarks on species. Figs. of cranidium and free cheek.)
- 1947 *Ctenopyge laticornis* Westergård — Westergård, p. 17. (Free cheek compared with that of *Sphaerophthalmus Fletcheri*), p. 24. (Distribution in Sweden.)
- 1952 *Sphaerophthalmus fletcheri* Matthew [partim] — Hutchinson, p. 89. (Remarks on species.)
- 1952 *Sphaerophthalmus major* Lake — Hutchinson, p. 90, pl. IV, figs. 16—17. (Descr. and figs. of cranidia.)

Type data: — As lectotype I select the free cheek figured by Matthew (1901, pl. IV, fig. 7d, and 1903, pl. XVII, fig. 7d), from Band C 3b, Escasonie Shore, East Bay, Nova Scotia.

Diagnosis: — A *Ctenopyge* species with: almost parallel-sided glabella; S1 unied across glabella, other glabellar furrows very short; oblique eye ridges; centres of palpebral lobes opposite L2; interocular cheeks about three-fourths as wide as glabella at eye line; postocular cheeks about as wide

as occipital ring; free cheeks with unusually wide, flattened spine with longitudinal rib (or pair of ribs) on both sides, acute genal angle, and slightly convex anterior and posterior lateral margins. Thorax, pygidium, and hypostoma unknown.

Remarks: — The characteristic free cheek of this species was first described and figured by Linnarsson (1880) as *Ctenopyge?* sp. indet. The same type of free cheek was tentatively assigned to *Ct. teretifrons* by Westergård (1922). Poulsen (1923) showed that the free cheek really belonged to a type of cranium which was assigned to *Ct. directa* by Westergård (1922). In 1944 Westergård erected the species *Ct. laticornis* for this type of free cheeks and crania. Similar free cheeks were included in a new species, *Sphaerophthalmus Fletcheri*, by Matthew (1901), together with crania, hypostomae, and pygidia of the *Sphaerophthalmus* type. Lake (1913, p. 76) and Westergård (1922, pp. 165, 203) suggested that this species was based on the misassociation of crania, hypostomae, and pygidia of *Sphaerophthalmus alatus* and free cheeks of some species of *Ctenopyge*. This view was supported by Hutchinson (1952, p. 89), who examined Matthew's material. Already Matthew (1894, p. 108; 1903, p. 228) pointed out the resemblance between the free cheek of his *Sph. Fletcheri* and the free cheek figured by Linnarsson in 1880. In 1947 (p. 17) Westergård compared the free cheeks of *Ct. laticornis* and *Sph. fletcheri*, and stated that they are of the same characteristic shape, but that the aperture of the eye seems to be slightly farther forward in the Swedish form than in the Canadian. However, this difference is very small and probably of no great significance. I believe that the free cheeks of *Sph. fletcheri* and *Ct. laticornis* are conspecific. A cast of a slab of Matthew's material furthermore shows that free cheeks of the *fletcheri* type are associated with crania of the *laticornis* type, as well as i. a. parts of *Sphaerophthalmus humilis* (= *Sph. alatus* auct.). Since Matthew did not select any holotype, it depends on the choice of the lectotype whether *Sph. Fletcheri* should become a synonym of *Sph. humilis*, or be a valid species (with *Ct. laticornis* as a synonym). Since the free cheeks were considered the distinguishing feature of this species, I have found it correct to choose the figured free cheek as lectotype.

Crania from Norway quite agree with the Canadian and Swedish crania. Free cheeks from Norway are also of the same type as the Canadian and Swedish, with a prominent, curved spine, which is flat and with ribs transversing the spine on both sides. The free cheeks from Norway, however, show some variation. Large free cheeks have very wide flat areas outside the rib, at least proximally, and the rib is divided by a furrow into two ribs. Distally, the two ribs unite to form one ridge on each side of the spine. The flat lateral areas decrease in width, and eventually disappear, so that the distal part of the spine corresponds to the ridges in the proximal part. In other specimens the furrow dividing the ridge does not seem to be developed, not even near the base of the spine, and in some specimens the

flat areas are relatively narrower. It is interesting that the spine is similar in structure to the pleural spines of several other *Ctenopyge* species, as e. g. *Ct. affinis*.

Occurrence: — Norway: Røyken (Slemmestad), Oslo (Tøyen), Ringerike (Viul). — Zone of *Peltura scarabaeoides*, lower part (2dγ), subzone of *Ctenopyge linnarssoni*. Associated with *Peltura scarabaeoides scarabaeoides*, *Sphaerophthalmus humilis*, *Sph. majusculus*, ± *Ct. linnarssoni*. — — Sweden (same horizon), Denmark (Bornholm, same horizon), Canada (associated with *Peltura scarabaeoides scarabaeoides*, *Sph. humilis*, *Parabolina dawsoni*, etc.)

Ctenopyge (Ctenopyge) linnarssoni Westergård 1922.

Pl. 5; pl. 22, fig. 8.

- 1880 *Ctenopyge pecten* Salt. sp. [partim] — Linnarsson, p. 16 (146), pl. II (VI), figs. 3—4, 8?, 9. (Descr. Figs. of crania and free cheeks.)
 ?1903 *Ctenopyge pecten*, Salter [partim] — Matthew, p. 229, pl. 17, fig. 5a. (Fig. of cranium.)
 1922 *Ctenopyge linnarssoni* n. sp. Westergård, p. 162, pl. XIII, figs. 2—5. (Descr. Figs. of crania and free cheeks.)
 1923 *Ctenopyge linnarssoni* Westergård — Poulsen, p. 45, pl. 1, fig. 17. (Descr. and fig. of cranium.)
 1947 *Ctenopyge linnarssoni* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

Type data: — As lectotype I select a cranium figured by Westergård (1922, pl. XIII, fig. 2), from Andrarum, Scania, Sweden.

Diagnosis: — A *Ctenopyge* species with: almost parallel-sided glabella; S1 united across axis, other glabellar furrows very short; straight transverse eye ridges; centres of palpebral lobes opposite S2; interocular cheeks as wide as glabella at eye line; postocular cheeks almost 1.5 times as wide as occipital ring; postocular sutures oblique; free cheeks with long curved and flattened spine, slightly convex posterior lateral margin slightly shorter than almost straight anterior lateral margin. Other parts of shield unknown.

Remarks: — A few crania and free cheeks from Norway agree well with the Swedish specimens. The largest cranium is 3.8 mm long. One cranium has wider fixed cheeks and seems to approach *Ct. teretifrons*, which I have not found in Norwegian material.

A cranium figured by Matthew (1903, pl. 17, fig. 5a) as belonging to *Ct. pecten*, may belong to *Ct. linnarssoni* or some related species (cf. Westergård, 1922, p. 114).

Occurrence: — Norway: Røyken (Slemmestad). — Zone of *Peltura scarabaeoides*, lower part (2dγ), subzone of *Ctenopyge linnarssoni*. Associated with *Peltura scarabaeoides scarabaeoides*, *Sphaerophthalmus humilis*, *Sph. majusculus*, ± *Ct. fletcheri*, ± *Ct. pecten*. — — Sweden (same horizon), Denmark (Bornholm, same horizon), Canada (*Peltura* zone).

Ctenopyge (Ctenopyge) pecten (Salter 1864).

Pl. 2, fig. 18; pl. 5; pl. 22, figs. 9—10.

- 1848 *Olenus bisulcatus*. n. s. [partim] — Phillips, p. 55, fig. 2, p. 346. (Fig. of cranidium, suggested to belong to *Ct. pecten* by Lake, 1913.)
- 1864 *Olenus (Sphær.) pecten*. [partim] — Salter, p. 9, pl. VIII, fig. 12. (Descr. Fig. of pygidium. Fig. 13 shows the thorax of another *Ctenopyge* species.)
- 1864 *Olenus bisulcatus* Phillips [partim] — Salter, p. 8, pl. VIII, fig. 6. (Fig. of young cranidium.)
- 1865 *Olenus (Sphærophthalmus) pecten*. [partim] — Salter, p. 482, figs. 4—5. (Figs. of pygidium and cranidium with 7 attached thoracic segments.)
- 1871 *Sphærophthalmus pecten*. Salter — Phillips, p. 68, fig. 3. (Fig. of pygidium.)
- 1873 *Olenus (Sphær.) pecten*, Salter — Salter, p. 12. (Remarks, fig. of restored dorsal shield.)
- 1880 *Ctenopyge pecten* Salt. sp. — Linnarsson, p. 16 (146), pl. II (VI), figs. 5—7. (Descr. Figs. of 3 pygidia. Figs. 3—4, 8?, 9 are probably of *Ct. linnarssoni*.)
- 1880 *Ctenopyge concava* n. sp. — Linnarsson, p. 21 (151), pl. II (VI), figs. 10—11. (Descr. Figs. of cranidium.)
- 1892 *Ctenopyge pecten* Salter sp. — Moberg, p. 351, figs. 1—2. (Descr. and figs. of pygidia.)
- 1892 ?*Ctenopyge pecten* Salt. — Matthew, p. 58.
- 1901 *Ctenopyge pecten* Salter — Lindström, p. 29, pl. III, figs. 26—27. (Figs. of free cheek with eyes and restored cephalon.)
- 1903 *Ctenopyge pecten*, Salter — Matthew, p. 229, pl. 17, fig. 5b. (A copy of one of Linnarsson's figs. of a pygidium. Fig. 5a is of a cranidium of the *Ct. linnarssoni* group.)
- 1913 *Ctenopyge pecten* (Salter) — Lake, p. 85, pl. IX, figs. 7—9; pl. X, figs. 1—7. (Descr. Figs. of all parts of dorsal shield.)
- 1922 *Ctenopyge pecten* (Salter) — Westergård, p. 160, pl. XII, figs. 26—33; pl. XIII, fig. 1. (Discussion of pygidium. Figs. of cranidia, free cheek, and pygidia.)
- ?1922 *Ctenopyge affinis* n. sp.?? — Westergård, p. 157, pl. XII, fig. 15. (Fig. of cranidium.)
- 1923 *Ctenopyge pecten* Salter — Poulsen, p. 42, pl. II, figs. 1—3. (Descr. Figs. of cranidium and 2 dorsal shields with the cephalon missing.)
- 1946 *Ctenopyge pecten* (Salter) — Lake, p. 342. (Remarks on pygidium.)
- 1947 *Ctenopyge pecten* (Salter) — Westergård, pp. 17, 24, pl. 3, fig. 12. (Fig. of almost complete dorsal shield. Distribution in Sweden.)
- 1952 *Ctenopyge pecten* (Salter) — Hutchinson, p. 86, pl. IV, figs. 7—8. (Remarks. Figs. of two cranidia which may belong to this species.)

Type data: — As lectotype should be chosen one of Salter's specimens from the Upper Lingula Flags at Malvern, England.

Diagnosis: — A *Ctenopyge* species with: slightly tapering or almost parallel-sided glabella; S1 united across glabella, other glabellar furrows short; oblique eye ridges; centres of palpebral lobes opposite S1 or L2; interocular cheeks from about three-fourths as wide to as wide as glabella at eye line; postocular cheeks from 1.5 times to twice as wide as occipital ring; free cheeks with long flattened spine, short concave posterior lateral margin, and markedly longer, slightly convex anterior lateral margin; thorax

with long flattened pleural spines, and pleural regions (excluding spines) up to three times as wide as axis; pygidium with about 7 axial rings, long axial spine, and pleurae (not united with each other?) with long flattened pleural spines. Hypostoma unknown.

Remarks: — The most remarkable feature of this species is the pygidium (cf. p. 184). Linnarsson (1880) assigned the cranidium of *Ct. linnarssoni* to *Ct. pecten*, and erected a new species, *Ct. concava*, for the cranidium of *Ct. pecten* (cf. Westergård, 1922, p. 160). *Ct. concava* is thus a synonym of *Ct. pecten*.

The cranidia from Nova Scotia assigned to *Ct. pecten* by Hutchinson (1952, pl. IV, figs. 7—8) do not show the characteristic wide postocular cheeks, but this may possibly be due to the preservation. In any case, the characteristic pygidium of *Ct. pecten* has been recorded from Canada by Matthew (1903, p. 229).

Occurrence: — Norway: Eiker (Stablum core), Ringerike (Viul). — Zone of *Peltura scarabaeoides*, lower part (2dγ), subzone of *Ctenopyge linnarssoni*. Associated with *Peltura scarabaeoides scarabaeoides*, *Ctenopyge linnarssoni*, *Sphaerophthalmus humilis*, and *Sph. majusculus*. — Sweden (same horizon), Denmark (Bornholm, same horizon), England (Upper Lingula Flags), E. Canada (*Peltura* zone).

Ctenopyge (Ctenopyge) teretifrons (Angelin 1854).

Pl. 5.

- 1854 *Sphaerophthalmus teretifrons*. n. sp. — — Angelin, p. 49, pl. XXVI, fig. 10. (Brief diagn. Fig. of restored dorsal shield.)
- 1880 *Ctenopyge teretifrons* Ang. sp. — — Linnarsson, p. 152 (22), pl. VI (II), figs. 12—13. (Descr. and fig. of cranidium.)
- 1913 *Ctenopyge teretifrons* (Angelin) — — Lake, p. 88, pl. X, figs. 9—10. (Descr. and figs. of cranidia.)
- 1922 *Ctenopyge teretifrons* (Angelin) — — Westergård, p. 162, pl. XIII, fig. 6. (Fig. of cranidium. The free cheeks tentatively assigned to this species, belong to *Ct. fletcheri*.)
- 1923 *Ctenopyge teretifrons* Angelin — — Poulsen, pp. 44, 46, pl. I, fig. 16. (Descr. and fig. of cranidium.)
- 1944a *Ctenopyge teretifrons* (Angelin) — — Westergård, p. 42. (Remarks.)
- 1947 *Ctenopyge teretifrons* (Ang.) — — Westergård, p. 26. (Distribution in Sweden.)
- 1949 *Ctenopyge teretifrons* (Angelin) — — Edmonds, p. 59. (Listed.)

Type data: — As lectotype should be chosen a cranidium from Andrarum, Scania, Sweden, and from Angelin's material.

Diagnosis: — A *Ctenopyge* species with parallel-sided glabella; S1 united across axis, other glabellar furrows very short; straight, almost transverse eye ridges; centres of palpebral lobes opposite S2; interocular cheeks almost 1.5 times as wide as glabella at eye line; postocular cheeks

about twice as wide as occipital ring; postocular facial sutures oblique and slightly transverse. Other parts than cranium unknown.

Remarks: — The free cheeks which tentatively were assigned to this species by Westergård (1922) were shown by Poulsen (1923) to belong to another *Ctenopyge* species which Westergård later (1944a) gave the name *Ct. laticornis* (here regarded as a synonym of *Ct. fletcheri* Matthew 1901). The cranium of *Ct. teretifrons* resembles that of *Ct. linnarssoni*, and it seems probable that also their free cheeks are of the same type.

Occurrence: — Sweden (Zone of *Peltura scarabaeoides*, subzone of *Ctenopyge linnarssoni*. Associated with *Peltura scarabaeoides scarabaeoides*, *Ct. pecten*, *Ct. linnarssoni*, *Ct. fletcheri*, and *Sph. humilis*), Denmark (Bornholm, same horizon), England (Upper Lingula Flags), Wales (Upper Lingula Flags).

Ctenopyge? expansa (Salter 1873).

1873 *Olenus* (*Sphaer.*) *expansus*, n. sp. — Salter, p. 12. (Short descr. of thorax.)

1877 *Olenus* (*Sphaerophthalmus*) *expansus*, Salter — Woodward, p. 47. (Listed.)

1891 *Olenus* (*Sphaerophthalmus*) *expansus*, Salter — Woods, p. 149. (Listed.)

1900b *Olenus* (*Ctenopyge?*) *expansus*, Salter — Reed, p. 306, pl. XII, figs. 2—3. (Descr. and figs. of parts of thoraces, one with attached pygidium.)

1913 *Ctenopyge? expansa* (Salter) — Lake, p. 87, pl. X, fig. 8. (Descr. and fig. of part of thorax.)

1922 *C[tenopyge] expansa* Lake — Westergård, p. 156. (Remarks.)

Type data: — As lectotype should be chosen one of the two specimens on which Salter founded this species (figured by Reed, 1900, pl. XII, figs. 2—3). They were found in the Upper Lingula Flags at Moel Gron.

Diagnosis — A *Ctenopyge?* species with: thorax with pleural regions up to 3 times as wide as glabella and short broad-based pleural spines; pygidium with wide pleural regions, resembling that of Burlingiidae.

Remarks: — Reed (1900, p. 307) remarked that "it is extremely doubtful to what subgenus or even genus this imperfect fossil should be ascribed" and included it tentatively in *Ctenopyge*. Lake (1913, p. 88) agreed in referring this species to *Ctenopyge*, as the peculiar pleurae of the species reminded him more of those of *Ct. pecten* than those of any other trilobite with which he was acquainted.

The pleurae of *Ct.? expansa* apparently end in short recurved points, and thus differ from the long spines in all other known *Ctenopyge* species. The pygidium (Reed, 1900, pl. XII, fig. 2) is also rather peculiar, reminding one more of the pygidium of the Burlingiidae. Both thorax and pygidium somewhat resemble the ceratopygid(?) *Hedinaspis*. For the time being, the species can be referred to as *Ctenopyge? expansa*.

Occurrence: — Wales (Upper Lingula Flags).

Ctenopyge? oelandica Westergård 1922.

1922 *Ctenopyge oelandica* n. sp. — Westergård, p. 158, pl. XII, fig. 18. (Descr. and fig. of cranidium.)

1947 *Ctenopyge oelandica* Wgård. — Westergård, p. 24. (Distribution in Sweden.)

H o l o t y p e (by monotypy): — The cranidium figured by Westergård (1922) from Degerhamn, S. Möckleby, Öland, Sweden.

R e m a r k s: — Only the cranidium is known of this species, and it is uncertain to which subgenus it belongs, if it does not belong to *Sphaerophthalmus*.

D i a g n o s i s: — A *Ctenopyge?* species with: almost parallel-sided glabella; S1 united across glabella, other glabellar furrows very short; eye ridges oblique and curved; centres of palpebral lobes opposite L1; interocular cheeks about as wide as glabella at eye line; postocular cheeks slightly wider than occipital ring. No other parts than the cranidium known.

O c c u r r e n c e: — Sweden (zone of *Peltura minor*.)

Genus *Sphaerophthalmus* Angelin 1854.

T y p e s p e c i e s: — *Trilobites alatus* Boeck 1838, designated by Linnarsson, 1880.

D i a g n o s i s: — Leptoplastinae with: slightly tapering glabella; distinct occipital furrow and continuous S1 (may be shallow in middle part), other glabellar furrows very short; slightly to strongly oblique, straight or slightly convex eye ridges; centres of palpebral lobes opposite L1 to opposite L2; interocular cheeks less than half as wide as, to almost as wide as glabella at eye line; postocular cheeks less than half as wide as, to as wide as occipital ring; free cheeks with slender and relatively short spine; thorax with relatively short pleural spines; pygidium (when known) small and sub-triangular (or sub-semicircular?) with very narrow pleural regions.

R e m a r k s: — Linnarsson (1880) erected the genus *Ctenopyge* for a group of species which had earlier been included in *Sphaerophthalmus*, but retained *Sph. flagellifer* Angelin in *Sphaerophthalmus*. Brögger (1882) included the species in *Ctenopyge*, and this has since become the practice. *Ctenopyge angusta* Westergård 1922 is intermediate between *Ctenopyge* and *Sphaerophthalmus*. Its reference to *Ctenopyge*, which is maintained here, means that the necessarily rather arbitrary border between these genera is drawn between this species and *Sph. alatus* (= *Sph. major* of Scandinavian authors), which probably developed from *Ct. angusta*.

I n c l u d e d s p e c i e s: —

Sphaerophthalmus alatus (Boeck 1838)

Sph. alatus canadensis Matthew 1894 (= *Sph. alatus*)

Sph. humilis (Phillips 1848)

Sph. major Lake 1913

Sph. majusculus Linnarsson 1880

Sph. sphaenopygus (Angelin 1854) (= *Sph. humilis*)

The insufficiently known *Ctenopyge*? *oelandica* may possibly belong to *Sphaerophthalmus*.

Sph. fletcheri Matthew 1903 is included in *Ctenopyge*, and so is *Sph.?* *parabola* Cobbold 1934.

Occurrence: — Zone of *Peltura minor* in Norway, Sweden, Denmark; zone of *Peltura scarabaeoides* in Norway, Sweden, Denmark, Poland, England, Wales, E. Canada.

Phylogeny and relationships: — The earliest known *Sphaerophthalmus* species in Scandinavia, *Sph. alatus* (Boeck, non auctorum) from the upper part of the zone of *Peltura minor*, most probably developed from the slightly earlier *Ctenopyge* (*Eoctenopyge*) *angusta*, which differs only in minor features, such as in having more prominent pleural spines, fixed cheeks with wider genal fields, and wider postocular cheeks in relation to the interocular cheeks. The next *Sphaerophthalmus* species to appear in Scandinavia, *Sph. humilis* (= *Sph. alatus* auctorum, non Boeck) in the two lower zones of the zone of *Peltura scarabaeoides*, is apparently a descendant of *Sph. alatus*, but differs i. a. in having the eyes further back, and the cheek spine further forwards. It is often accompanied by *Sph. majusculus*, which likewise has the eyes rather far back, but attains a greater size and has wider fixed cheeks. *Sph. majusculus* is no doubt very close to *Sph. alatus*; it is not impossible that they represent dimorphs of the same species. *Sph. major* in Great Britain is not very well known, and its exact horizon is uncertain.

Sphaerophthalmus alatus (Boeck 1838).

Pl. 2, fig. 15; pl. 5; pl. 22, figs. 18—26.

- 1838 *Trilobites alatus* mh. — — Boeck, p. 143. (Short descr., cited by Stormer, 1940.)
- 1857 *Sphaerophthalmus alatus* Boeck — — Kjerulf, p. 92. (Listed.)
- 1865 *Sphaerophthalmus* Ang. *alatus* Boeck — — Kjerulf, p. 2. (Listed.)
- 1882 *Sphaerophthalmus alatus*, Boeck [partim] — — Brögger, p. 119. (Most of Brögger's material belongs to *Sph. humilis*.)
- ?1913 *Sphaerophthalmus major*, sp.n. — — Lake, p. 77, pl. VIII, figs. 7—9, 10?, 11?, 12—13. (Descr. Figs. of all parts of dorsal shield.)
- 1922 *Sphaerophthalmus major* Lake — — Westergård, p. 163, pl. XIII, figs. 9—19. (Descr. Figs. of cranidia, free cheeks, and thorax.)
- 1923 *Sphaerophthalmus major* Lake — — Poulsen, p. 47, text figs. 17a-b; pl. I, fig. 15. (Descr. Figs. of cranidium, free cheek, and hypostoma.)
- 1929 *Sphaerophthalmus major* Lake — — Strand, p. 359. (Listed.)
- 1934a *Sphaerophthalmus major* — — Stormer, p. 332. (Listed.)
- 1940a *Sphaerophthalmus alatus* (Boeck) — — Stormer, p. 144, pl. 1, figs. 16—17. (Descr. and figs. of lectotype cranidium.)
- 1947 *Sphaerophthalmus major* Lake? — — Westergård, p. 26. (Distribution in Sweden.)
- Non 1866 *Olenus* (*Sphaerophthalmus*) *alatus*, Bæck — — Salter (= *Ctenopyge bisulcata*.) (See further under *Sph. humilis* for material erroneously assigned to *Sph. alatus*.)

Type data: — The lectotype (selected by Størmer, 1940a, p. 145) is a cranidium (P.M.O. no. 56371) from the old alum shale quarry in Gamlebyen in Oslo, Norway.

Diagnosis: — A *Sphaerophthalmus* species with: centres of eyes opposite L2 or S1; interocular cheeks slightly more than half as wide as glabella at eye line; postocular cheeks about two-thirds as wide as occipital ring; free cheeks with spine in posterior part, posterior lateral margin slightly convex, almost straight and shorter than slightly convex anterior lateral margin; thorax with pleural regions about two-thirds as wide as axis, short pleural spines and at least some axial spines. Pygidium unknown.

Remarks: — A restudy of the lectotype and associated fossils has unfortunately shown that Boeck's species is specifically distinct from the *Sphaerophthalmus* species referred to as *Sph. alatus* by all authors after Boeck, except Kjerulf and Størmer, who deal with Boeck's type material. Thus *Sph. alatus* (Boeck) does not have the eyes situated as far back as "*Sph. alatus auctorum*", and consequently its eye ridges are less oblique. The free cheeks associated with the lectotype are all of the type belonging to a species referred to as *Sph. major* by Westergård and other Scandinavian authors, not of the type with rather anteriorly situated spine as in "*Sph. alatus auctorum*". Furthermore, by splitting up the little piece of rock containing the lectotype, I have found parts of *Peltura minor* and *Ctenopyge tumida*, which shows that it occurs in a lower horizon than "*Sph. alatus auctorum*". It is obvious that what has been called *Sph. major* by Scandinavian authors, really is *Sph. alatus* (Boeck). "*Sph. alatus auctorum*" (non Boeck) is conspecific with *Olenus humilis* Phillips. This name, which was discarded under the false apprehension that it was a junior synonym of *Sph. alatus*, must now be revived. Whereas the true *Sph. alatus* Boeck (= *Sph. major* of Scandinavian authors) occurs in the upper part of the zone of *Peltura minor*, *Sph. humilis* (Phillips) (= "*Sph. alatus auctorum*") occurs in the succeeding zone of *Peltura scarabacoides*.

The confusion arose when Linnarsson (1880) declared that his material of *Sphaerophthalmus* undoubtedly belonged to Boeck's *Trilobites alatus* (after having seen Boeck's type material). Linnarsson's material, however, belongs to *Sph. humilis*. His mistake is understandable, as the cranidia of the two species resemble each other, and he probably did not see the difference in the free cheeks. As a matter of fact, I had to clean some free cheeks in the type material in order to ascertain that they were not of the *humilis* type. Furthermore, Boeck mentioned some material from Andrarum in Scania, Sweden, as well as the material from Opslo (= Gamlebyen in Oslo) (from which the lectotype was selected), and it is not impossible that this material belonged to the same species as Linnarsson's material. Linnarsson examined Boeck's material mainly to control Angelin's reconstruction of *Sph. alatus*, which is quite misleading. Incidentally, this reconstruction

caused Salter (1866) to believe that *Olenus bisulcatus* Phillips (i. e. *Ctenopyge bisulcata*) was conspecific with *Sph. alatus*.

Although the Scandinavian specimens attributed to *Sph. major* really belong to *Sph. alatus* (Boeck), this does not necessarily imply that the British species *Sph. major* Lake is a synonym of *Sph. alatus* (Boeck). Thus it is not certain that the true *Sph. alatus* occurs in Great Britain. In this connection it is of interest to note that none of the other olenid species associated with *Sph. alatus* in Scandinavia, have so far been recorded from Great Britain, such as *Ctenopyge tumida*, *Ct. affinis*, *Peltura minor*, and *P. acutidens*.

Hutchinson (1952) recorded *Sph. major* from Nova Scotia. As it occurs comingled with "*Sph. alatus*" (i. e. *Sph. humilis*), it is probably not conspecific with the true *Sph. alatus*.

Description of Norwegian material: — This is based on Boeck's material from the type locality and stratum (subzone of *Ctenopyge tumida*), when nothing else is stated.

Cranidium with faintly tapering glabella in adult specimens and almost parallel-sided glabella in young specimens. Occipital ring with short axial spine. Occipital furrow distinct, deepest at the sides. S1 well defined, united across glabella, but rather shallower at middle than at sides. S2 represented by a pair of faint impressions at sides of glabella. Cephalic axis well raised above fixed cheeks, and rather convex, especially in anterior part, which bends rather steeply down in front. Border upturned, slightly concave in dorsal view, convex in front view. Eye ridges oblique backwards, apparently more so in adult specimens than in young ones. Palpebral lobe slightly bent up. Centres of eyes slightly in front of transverse line through anterior ends of S2. Interocular cheeks about 2/3 as wide as glabella at eye line. Postocular cheeks about as wide as occipital ring. At least in some specimens the cranidium is very finely granulate.

Free cheeks rather narrow, with spine probably no longer than genal field. Posterior lateral margin straight, and shorter than convex anterior lateral margin. Round eye often preserved, usually showing facets.

Hypostoma elongate with rather convex area in middle, tapering backwards, and resting as it seems, on a platform which bends dorsad ("down") posteriorly. A fine border can be seen on both sides. Triangular anterior wings.

The thorax is preserved in a specimen collected in a loose lens (subzone of *Ctenopyge tumida*) at Vippetangen in Oslo. It consists of 9 segments, but the posterior segment is somewhat broken, and turned slightly upwards. It is possible that it carried a long axial spine. Most of the other axial rings are also damaged in the middle, but in one the axial tubercle (base of spine?) is preserved. Thorax widest at 3rd segment. Pleural regions (excluding spines) are narrower than axis. Pleural spines directed obliquely backwards, outwards, and upwards. This specimen agrees well with a specimen from

Sweden figured by Westergård (1922, pl. XIII, fig. 19). The Swedish specimen is provided with a long axial spine on the 9th segment.

Pygidium unknown, but as far as can be judged from the thorax it must be very small, possibly similar to the pygidium of *Ctenopyge flagellifera*, which apparently consists of only two segments.

Specimens from the subzone of *Ctenopyge affinis* seem to agree rather well with those described above, except that the postocular cheeks of the cranidia appear to be bent more strongly ventrad, in this respect approaching *Sph. humilis*.

The cranidia of *Sph. alatus* seem to reach a length of 4 mm.

Occurrence: — Norway: Skien—Brevik district (Rognstrand core, Ombordsnes), Eiker—Sandsvær (Teigen core, Stablum core), Røyken (Nærsnes, Slemmestad), Oslo (Gamlebyen, Tøyen), Modum, Ringerike, Hadeland, Ringsaker (Evjevika, Steinsodden), Snertingdal. — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge tumida* and subzone of *Ctenopyge affinis*. Associated either with *Ctenopyge tumida* \pm *Peltura minor* \pm *P. acutidens* \pm *Protopeltura planicauda*, or with *Ct. affinis* \pm *Peltura minor*. — Sweden (same horizon), Denmark (Bornholm, same horizon), ?Canada.

Sphaerophthalmus humilis (Phillips 1848).

Pl. 5; pl. 22, figs. 7, 11—15.

- 1848 *Olenus humilis*. n. s. — Phillips, p. 55, figs. 4—6, p. 347. (Figs. of 3 cranidia, one with 4 attached thoracic segments. Descr.)
- 1854 *Olenus sphæropygus*. n. sp. — Angelin, p. 43, pl. XXV, fig. 3. (Descr. and fig. of pygidium.)
- 1854 *Anopocare pusillum*. n. sp. [partim] — Angelin, p. 50, pl. XXVII, figs. 1—2, non 1a. (Incorrect figs. of young cranidia. The pygidium belongs to *Peltura scarabaeoides*.)
- 1864 *Olenus (Sphæroph.) humilis*, Phill. — Salter, dec. XI, part VIII, pl. VIII, figs. 9—11, p. 7. (Descr. Figs. of 2 cranidia based on Phillips' figs., and fig. of axial shield.)
- 1866 *Olenus (Sphaerophthalmus) humilis*, Phill. — Salter, p. 302, pl. V, fig. 12. (Figs. of axial shield, pleural ends, and pygidium.)
- 1871 *Olenus humilis*. Phillips — Phillips, p. 68, fig. 8. (Fig. of axial shield.)
- 1873 *Olenus (Sphær.) humilis*, Phillips — Salter, p. 12. (Remarks.)
- 1880 *Sphaerophthalmus alatus* Boeck sp. — Linnarsson, p. 7 (137), pl. I (V), figs. 6—10. (Descr. Figs. of cranidia, free cheek, and pygidium.)
- 1882 *Sphaerophthalmus alatus*, Boeck [partim] — Brögger, p. 119, pl. II, figs. 14, 14a. (Figs. of cranidium and pygidium copied from Linnarsson. Some of Brögger's specimens belong to *Sph. alatus*.)
- 1884 *Sphaerophthalmus alatus*, Boeck — Brögger, p. 257. (Recorded.)
- 1890 *Sphaerophthalmus alatus* Boeck — Pompeckj, p. 89, pl. IV, figs. 27, 27a. (Descr. and figs. of cranidium.)
- 1894 *Sphaerophthalmus alatus*, Boeck, var. *Canadensis* n. var. [partim] — Matthew, p. 107, pl. XVII, figs. 11a-b. (Descr. Figs. of cranidia and free cheek. Figs. 12a-b = *Ctenopyge fletcheri*.)
- 1898 *Sphaerophthalmus alatus* — Bjorlykke, p. 12. (Recorded.)

- 1901 *Sphaerophthalmus alatus* Ang. [sic!] — Lindström, p. 29, pl. III, figs. 31—34. (Figs. of cephalon, free cheek, and sections of eyes.)
- 1902 *Sphaerophthalmus alatus* — Schiøtz, pp. 17, 38. (Recorded.)
- 1903 *Sphaerophthalmus Fletcheri* [partim] — Matthew, p. 227, pl. XVII, figs. 7a-b, 7e-f. (Descr. and figs. of cranidium, pygidium, and probably conspecific hypostoma. The free cheek belongs to *Ctenopyge fletcheri*.)
- 1910 *Sphaerophthalmus alatus* — Goldschmidt, p. 5, fig. 4. (Fig. of cranidium.)
- 1913 *Sphaerophthalmus alatus* (Boeck) — Lake, p. 74, pl. VIII, figs. 1—5. (Descr. Figs. of all parts of dorsal shield. The pygidium in fig. 6 may belong to *Sph. majusculus*.)
- 1922 *Sphaerophthalmus alatus* (Boeck) — Westergård, p. 165, pl. XIII, figs. 20—22. (Figs. of all parts of dorsal shield.)
- 1923 *Sphaerophthalmus alatus* Boeck — Poulsen, p. 49. (Descr.)
- 1927a *Sphaerophthalmus alatus* Boeck — Czarnocki, p. 12. (Recorded from Poland.)
- 1927b *Sphaerophthalmus alatus* Boeck — Czarnocki, p. 119. (Recorded from Poland.)
- 1929 *Sphaerophthalmus alatus* (Boeck) — Strand, p. 359. (Recorded.)
- 1938 *Sphaerophthalmus alatus* (Boeck) — Stubblefield, p. 29. (Remarks on type material of *Sph. humilis*.)
- 1946 *Sphaerophthalmus alatus* (Boeck) — Lake, p. 341. (Remarks.)
- 1947 *Sphaerophthalmus alatus* (Boeck) — Westergård, p. 26. (Distribution in Sweden.)
- 1952 *Sphaerophthalmus alatus* (Boeck) — Hutchinson, p. 88, pl. IV, figs. 12a-c, 13—15. (Remarks. Figs. of cranidia, free cheek and pygidium.)
- 1953 *Sphaerophthalmus alatus* Angelin [sic!] — Hupé, p. 78, fig. 32:4. (Fig. of section through eye, copied from Lindström, 1901.)

Type data: — As lectotype should be selected a specimen from the type locality, between Fowlet Farm and Whiteleaved Oak, Malvern Hills, Great Britain; namely one of the cranidia figured by Phillips in 1848.

Diagnosis: — A *Sphaerophthalmus* species with: centres of palpebral lobes opposite L1, just behind S1; interocular cheeks slightly less than half as wide as glabella at eye line; postocular cheeks about half as wide as occipital ring; free cheeks with spine in anterior part, posterior lateral margin convex and longer than convex anterior lateral margin; thorax with pleural regions about two-thirds as wide as axis, no(?) pleural spines, but axial nodes; triangular pygidium with pleural regions half as wide as axis, or less.

Remarks: — As discussed above, the true *Sph. alatus* (Boeck) is slightly earlier than, and not conspecific with *Sph. humilis*. For a long time *Sph. humilis* was believed to be a synonym of *Sph. alatus*. Since this is not the case, the name *Sph. humilis* is revived. *Olemus sphæropygus* Angelin 1854 is based on the pygidium of *Sph. humilis* (Phillips 1848), and is thus a younger synonym. As pointed out by Linnarsson (1880), *Anopocare pusillum* Angelin 1854 is based on young cranidia of *Sph. alatus* (i. e. *Sph. humilis*) and a small pygidium of *Peltura scarabaeoides*. Lake (1913) and Westergård (1922) suggest that *Sph. alatus canadensis* Matthew may be identical with *Sph. alatus* (i. e. *Sph. humilis*), and this is verified by Hutchinson (1952, p. 89), who has examined Matthew's type material.

Matthew's "narrow form" of *Sph. alatus canadensis* apparently belongs to *Ctenopyge fletcheri*.

Sph. humilis has been described in detail by Lake in 1913 (under the name *Sph. alatus*). Good illustrations of it has also been given by Westergård in 1922 (likewise under the name *Sph. alatus*). The Norwegian specimens quite agree with the British and Swedish specimens.

Well preserved cranidia show a minute granulation on the surface, except in the furrows. The occipital ring was probably always furnished with a spine, although this is often broken off, especially in limestone specimens. There is a tiny node in front of the spine, but it is only seen in well preserved specimens. The largest cranidia in the Norwegian material are about 3 mm long.

The hypostoma which probably belongs to this species, is tongue-shaped, with the central convexity forming a rather narrow median ridge. This type of hypostoma is rather common in samples containing *Peltura scarabaeoides*, *Ctenopyge* species and *Sphaerophthalmus* species. It cannot belong to *Peltura*, which has a larger and quite different hypostoma. It probably does not belong to any of the associated *Ctenopyge* species, as these are comparatively rare, whereas the *Sphaerophthalmus* species occur abundantly. As *Sphaerophthalmus humilis* on the whole is more common than *Sph. majusculus*, it seems reasonable to assume that *Sph. humilis* had this type of hypostoma. It is, however, quite possible that *Sph. majusculus* had a rather similar hypostoma, perhaps not even distinguishable from that of *Sph. humilis*. Unfortunately, no hypostomae have been found in situ in these species.

O c c u r r e n c e: — Norway: Skien—Brevik district, Eiker, Sandsvær, Røyken, Oslo, Modum, Ringerike, Hadeland, Valdres, Hamar district, Ringsaker, Brummunddalen, Østerdalen (Glomstad, Ulvåen). — Zone of *Peltura scarabaeoides*, lower part (2dγ), subzone of *Ctenopyge bisulcata* (associated with *Peltura scarabaeoides scarabaeoides*, *Sph. majusculus*, and *Ctenopyge bisulcata*), and subzone of *Ctenopyge linnarssoni* (associated with *Peltura scarabaeoides scarabaeoides*, ± *Ct. linnarssoni*, ± *Ct. pecten*, ± *Ct. fletcheri*). — Sweden (same horizons), Denmark (Bornholm, same horizon), Poland (Upper Cambrian), England (Upper Lingula Flags), Wales (Upper Lingula Flags), E. Canada (*Peltura* zone.)

Sphaerophthalmus major Lake 1913.

- 1913 *Sphaerophthalmus major*, sp. n. — Lake, p. 77, pl. VIII, figs. 7—13. (Descr. Figs. of all parts of dorsal shield.)
 1949 *Sphaerophthalmus major* Lake — Edmonds, p. 60. (Listed.)
Sphaerophthalmus major Lake of Westergård (1922, 1947), Poulsen (1923), Strand (1929), and Størmer (1934) belongs to *Sph. alatus* (Boeck).

Type data: — As lectotype should be selected one of the specimens described by Lake (1913) from the Upper Lingula Flags in Great Britain.

Remarks: — The exact stratigraphic position of *Sph. major* is unfortunately not known. It is possible that the specimens figured by Lake (1913, pl. VIII, figs. 7—13) do not at all belong to one species, so that the concept of the species thus depends on the choice of lectotype. His fig. 7 shows a cranidium which may belong to *Sph. alatus* (Boeck). Fig. 9 shows a dorsal shield without pygidium. Its free cheek has a long and convex posterior margin, thus reminding one of *Sph. humilis*. Fig. 12 is of an incomplete dorsal shield without pygidium. The spine of the free cheek is longer than in *Sph. alatus* and *Sph. humilis* and reminds one more of *Ctenopyge*. Fig. 10 shows a thorax with attached pygidium. This specimen differs from the thoraces in figs. 9, 12, and 13 in showing no pleural or axial spines, but this may possibly be due to the preservation. Its pygidium differs from those of *Sph. humilis* and *Sph. majusculus*.

Matthew's "narrow form" of *Sph. alatus canadensis* was assigned to *Sph. minor* by Hutchinson (1952, p. 90), who also assigned some more cranidia to *Sph. minor*. Both Matthew's and Hutchinson's specimens seem to belong to *Ctenopyge fletcheri*.

Occurrence: — England (Upper Lingula Flags), Wales (Upper Lingula Flags).

Sphaerophthalmus majusculus Linnarsson 1880.

Pl. 5; pl. 22, figs. 16—17.

- 1880 *Sphaerophthalmus majusculus* n. sp. — Linnarsson, p. 11 (141), pl. I (V), figs. 11—12. (Descr. and figs. of cranidium and pygidium.)
- 1882 *Sphaerophthalmus majusculus*, Linnr.? — Brögger, p. 120. (Recorded.)
- 1913 *Sphaerophthalmus alatus* (Boeck) [partim] — Lake, p. 74, pl. VIII, fig. 6 only. (Fig. of pygidium suggested to belong to *Sph. majusculus* by Westergård, 1922, p. 166. Cf. also Lake, 1946, p. 341.)
- 1922 *Sphaerophthalmus majusculus* Linnarsson — Westergård, p. 166, pl. XIII, figs. 30—35. (Descr. and figs. of cranidia and pygidia.)
- 1929 *Sphaerophthalmus majusculus* Linnr. — Strand, p. 359. (Recorded.)
- 1934a *Sphaerophthalmus majusculus* — Störmer, p. 332. (Listed.)
- 1946 *Sphaerophthalmus majusculus* Linnarsson — Lake, p. 341. (Remarks.)
- 1947 *Sphaerophthalmus majusculus* Linnr. — Westergård, p. 26. (Distribution in Sweden.)

Type data: — The species is based on the pygidium, and as lectotype I select the pygidium figured by Linnarsson (1880) and refigured by Westergård (1922, pl. XIII, fig. 33), from Andrarum, Scania, Sweden.

Diagnosis: — Differs from *Sphaerophthalmus alatus* in having wider fixed cheeks (width at eye line about three-fourths that of glabella) and pygidium with wider pleural regions (up to as wide as axis). Free cheeks and thorax unknown.

Remarks: — The pygidium of *Sph. majusculus* resembles that of *Sph. humilis*, but has markedly wider pleural areas. As long as no axial or dorsal shields of *Sph. majusculus* have been found, it is not certain that the type of cranidium attributed to this species really belongs to it, but, as discussed by Westergård (1922, p. 166), this is most probably the case. The cranidium attributed to *Sph. majusculus* resembles that of *Sph. humilis*, but, as in the pygidium, the lateral areas (fixed cheeks) are wider. Furthermore the glabella of *Sph. majusculus* is less convex and less raised above the fixed cheeks than in *Sph. humilis*. It differs from *Sph. humilis* also in having no occipital spine, but a tiny node corresponding to the tiny node in front of the occipital spine in *Sph. humilis*. In some specimens the surface is finely granulate, as in *Sph. humilis*.

The differences between the pygidia and cranidia of *Sph. majusculus* and *Sph. humilis* are not greater than that one might suspect them to be sexual rather than specific. The free cheeks of *Sph. majusculus* are still unknown, but in a stinkstone lens from Viul, Ringerike, Norway, containing pygidia and cranidia of both *Sph. majusculus* and *Sph. humilis* (and in addition only *Peltura scarabaeoides scarabaeoides* and *Ctenopyge fletcheri*), I have found two different kinds of free cheeks. Their eyes are set far back, and apparently both belong to *Sphaerophthalmus*. One of the types has the spine far forwards, and also agrees in other features with the free cheek assigned to *Sph. humilis*. The other type has the spine near the eye. It is possible that this second type of free cheeks belongs to *Sph. majusculus*, which in that case is more distinct from *Sph. humilis* than shown by the pygidium and cranidium.

The free cheeks here attributed to *Sph. majusculus*, resemble those of *Sph. alatus*, with a relatively long spine far back. It differs from that of *Sph. alatus* in having a relatively larger eye, placed even further back, and in having a narrower genal field. The border is wider than in *Sph. alatus*, and in this feature approaching *Sph. humilis*. The facets of the eye can often plainly be seen. The genal field inside the border is finely granulate, just as the cranidium.

The thorax and hypostoma of *Sph. majusculus* are unknown, but it is possible that the hypostoma resembles that of *Sph. humilis* so much that some of the hypostomae assigned to the latter really belong to *Sph. majusculus*.

An unusually large cranidium in the Norwegian material is 4.5 mm long and 7.5 mm wide.

Occurrence: — Norway, Røyken (Slemmestad), Oslo, Modum, Ringerike (Viul), Hamar district (Romedal), Snertingdal, Ringsaker (Evjevika), Brummunddalen. — Zone of *Peltura scarabaeoides*, lower part (2dy), subzone of *Ctenopyge bisulcata* (associated with *Peltura scarabaeoides scarabaeoides*, *Sph. humilis*, \pm *Ct. bisulcata*), and subzone of *Ctenopyge linnarsoni* (associated with *Peltura scarabaeoides scarabaeoides*, *Sph. humilis*, \pm *Ctenopyge fletcheri*). — Sweden (same horizons), ?England (Upper Lingula Flags, cf. Westergård, 1922, p. 166).

Subfamily Pelturinae Corda 1847.

Pl. 2, figs. 1—14.

Type genus: — *Peltura* Milne Edwards 1840.

Diagnosis: — Olenidae with free cheeks without spine. Exceptions: *Protopeltura* and some species of *Peltura* with straight spine deviating from course of lateral margin, but with typical pelturoid cranium.

Remarks: — Corda (1847, p. 118) erected a family Pelturides: A subfamily Pelturinae was erected by Harrington & Leanza (1952, p. 195). Jujuyaspinae (recte Jujuyaspidinae) Hupé (1953, p. 207) is regarded here as a synonym.

Genus *Protopeltura* Brögger 1882.

Type species: — When Brögger erected *Protopeltura* as a subgenus of *Peltura*, he included in it only one species, which he believed to be conspecific with *Olenus? acanthurus* Angelin 1854, and which he consequently referred to as *Protopeltura acanthura* Angelin. Moberg & Möller (1898, p. 265) were the first to discover that Brögger's material did not belong to Angelin's species, and that the latter is a *Parabolina* species. Westergård later (1909) gave the name *Peltura praecursor* to Brögger's species. In 1922 (p. 168) Westergård revived the name *Protopeltura* for a pelturine genus, and regarded *P. praecursor* (Westergård) (= *P. acanthura* Brögger non Angelin) as type species. As *P. acanthura* Angelin was the only species assigned to *Protopeltura* by Brögger, it should strictly be regarded as the type species. I have proposed to the International Commission on Zoological Nomenclature to designate *P. praecursor* as type species, since this is the species Brögger had at hand, and to prevent *Protopeltura* from becoming a synonym of *Parabolina* (Bull. Zool. Nomencl., 12, pt. 1, pp. 31—32).

Diagnosis: — Pelturinae with: glabella rounded or truncated in front; glabellar furrows not united across glabella; short or no preglabellar field; small palpebral lobes far forwards and close or moderately close to glabella; fixed cheeks from about one-half to about three-fourths as wide as occipital ring; free cheeks with spine which deviates slightly from course of lateral margin, and with straight posterior margin; thorax with 10(?) to 12 segments, pleural spines, and pleural regions three-fourths as wide to slightly wider than axis; sub-triangular to sub-semicircular pygidium with or without marginal spines.

Remarks: — Brögger erected *Protopeltura* for a subgenus of *Peltura* with cheek spines, and transverse pygidium with marginal spines. Lake (1919) regarded *Protopeltura* as a synonym of *Peltura*. Westergård did the same at first (1909), but later, when *Protopeltura praecursor* was better known, and related species had been described, he (1922) regarded *Protopeltura* as a distinct genus, which has since been the general practice. Lake

(1919, p. 96) pointed out that a subdivision of *Peltura* and allied genera according to the presence or absence of marginal spines in the pygidium does not lead to a satisfactory grouping, and Westergård (1922) included species with entire pygidium in *Protopeltura*. According to Westergård's diagnosis, *Protopeltura* differs from *Peltura* also in having a preglabellar field in front of the glabella. Now that *P. bidentata* and *P. planicauda* are included in *Protopeltura*, this difference does not apply any more; the main difference being that *Protopeltura* has a well developed cheek spine, deviating only slightly from the lateral margin, whereas *Peltura* has no spine or a small spine almost at right angle to the lateral margin.

Included species and subspecies: —

Protopeltura aciculata aciculata (Angelin 1854)

P. aciculata pusilla Westergård 1922

P. bidentata (Brögger 1882) (earlier: *Peltura*)

P. broeggeri (Holtedahl 1910) (earlier: *Leptoplastus*)

P. holtedahli n. sp.

P. intermedia Westergård 1922

P. planicauda (Brögger 1882) (earlier: *Peltura*)

P. praecursor Westergård 1922

and possibly also

P.? *solitaria* (Westergård 1922) (earlier: *Beltella*)

A *Protopeltura* sp. is recorded from the Upper Cambrian in Poland by Czarnocki (1927a, p. 11; 1927b, p. 198).

Protopeltura praecursor Westergård var.? described from Siberia (Vologdin, 1940) may possibly be a *Protopeltura* species, but resembles also *Parabolina*, as far as can be judged from the figures (l. c., pl. XLIX, figs. 5, 5a-c).

P. acanthura tetracanthura Matthew 1892 is a *Parabolina* species, and is now referred to as *Parabolina tetracanthura*. *Protopeltura granulosa* Harrington 1938 was declared a synonym of *Parabolinopsis* (here: *Leptoplastides*) *mariana* Hoek 1912 by Harrington & Leanza (cf. Harrington & Kay, 1951, p. 662).

Occurrence: — *Parabolina* zone in Norway and Sweden; *Leptoplastus* zone in Sweden; zone of *Protopeltura praecursor* in Norway and Sweden; zone of *Peltura minor* in Norway, Sweden, and England (cf. p. 48). Upper Cambrian in Poland.

Phylogeny and relationships: — As discussed above (p. 114), the earliest known *Protopeltura* species, *P. aciculata*, is very close to the earliest known *Parabolina* species, *P. brevispina*. They occur at the base of the *Parabolina spinulosa* zone, in the subzone of *Parabolina brevispina* just above the *Olenus* zone, and belong to a stock which no doubt developed from *Olenus*. *Protopeltura aciculata* is divided into two subspecies, *aciculata* and the succeeding *pusilla*, which differ only in minor details. The

only *Protopeltura* species known from the overlying *Leptoplastus* zone is *P. intermedia*, which differs from *P. aciculata* i. a. in having shorter preglabellar field and narrower fixed cheeks. *P. holtedahli* n. sp. and *P. broeggeri* both come from the transitional beds between the *Leptoplastus* zone and the zone of *Protopeltura praecursor*, although they are not associated. *P. broeggeri* is interesting because it has rather wide interocular and postocular cheeks, thus recalling *Olenus*. Nevertheless, it is no doubt closely related to other *Protopeltura* species, and thus shows that the typical *Peltura*-cranidium of the other *Protopeltura* species and of succeeding genus *Peltura* had not yet become quite stabilized. *Protopeltura holtedahli* n. sp. is close both to the preceding *P. intermedia* and the succeeding *P. praecursor*, although it differs from both in having wider fixed cheeks. *P. praecursor* (from the zone of that name) differs from all the earlier species in having a pygidium with marginal spines, but is obviously very close to them and must have developed from a form with entire pygidium. Like all the earlier species, *P. praecursor* has a preglabellar field, but it is very short, and its closely related successor, *P. bidentata* from the base of the zone of *Peltura minor*, has no preglabellar field at all. Whereas *P. praecursor* has 2—4 pairs of marginal spines in the pygidium, *P. bidentata* has a pygidium with 1—2 pairs of marginal spines, and, as a new feature, flattened border. The latest known *Protopeltura* species, *P. planicauda*, appears slightly after *P. bidentata* and is connected with it through intermediate forms. *P. planicauda* agrees with *P. bidentata* in most features, thus also in having no preglabellar field, but its pygidium has a more expanded flattened border. *P. planicauda* occurs associated with species of the genus *Peltura*, which no doubt developed from *Protopeltura* (cf. p. 232).

Protopeltura aciculata aciculata (Angelin 1854).

Pl. 3.

- 1854 *Olenus aciculatus*. n. sp. — Angelin, p. 44, pl. XXV, fig. 6. (Inexpressive diagnosis. Rough, partly inadequate fig. of dorsal shield.)
 1922 *Protopeltura aciculata* (Angelin) — Westergård, p. 169, pl. XIV, figs. 3—13. (Descr. Figs. of axial shield, cranidia, free cheeks, fragments of thoraces, pygidia, and hypostoma.)
 1947 *Protopeltura aciculata* (Ang.) — Westergård, p. 26. (Distribution in Sweden.)

Type data: — Westergård (1922) pointed out that Angelin's type specimen is missing. As lectotype I select the axial shield figured by Westergård (1922, pl. XIV, fig. 6), from Andrarum, Scania, Sweden.

Diagnosis: — A *Protopeltura* species with: cephalic axis well rounded in front; relatively long preglabellar field; S1 and S2 distinct; interocular cheeks about half as wide as glabella at eye line; postocular cheeks about as wide as occipital ring; free cheeks with slightly acute to slightly obtuse inner spine angle; 12 thoracic segments; pygidium sub-semicircular, entire or with one pair of small marginal spines.

Remarks: — The hypostoma tentatively assigned to this species by Westergård (1922, pl. XIV, fig. 13), probably belongs to it, as it is rather like the hypostoma of the closely related *P. aciculata pusilla*.

Occurrence: — Sweden: *Parabolina spinulosa* zone, subzone of *Parabolina brevispina*. Alone, or associated with *Parabolina brevispina* and/or *Orusia lenticularis*.

Protopeltura aciculata pusilla Westergård 1922.

Pl. 3; pl. 23, figs. 1—6.

1922 *Protopeltura aciculata pusilla* n. var. — Westergård, p. 171, pl. XIV, figs. 14—17. (Diagnosis. Figs. of cranium, free cheek, and pygidia.)

1947 *Protopeltura aciculata aciculata* Wgård. — Westergård, p. 26. (Distribution in Sweden.)

Type data: — As lectotype I select the cranium figured by Westergård (1922, pl. XIV, fig. 14), from a local boulder, Funäs, Myssjö parish, Jämtland, Sweden.

Diagnosis: — Differs from *Protopeltura aciculata aciculata* in being smaller, having truncate glabella, wider free cheeks, and rounded subtriangular pygidium.

Remarks: — The Norwegian specimens conform well with the Swedish specimens described by Westergård (1922), but include also more or less entire axial and dorsal shields and hypostomae. The thorax resembles much that of *P. aciculata aciculata*, having 12 segments with pleurae protruded into short spines, and with short axial spines. The axial spines are often broken off, but may be seen in external impressions. The large size of one axial shield (with detached pygidium) might suggest that it belonged to *P. aciculata aciculata*. Its pygidium is incomplete (and preserved as an impression), and does not give any clue as to which subspecies the specimen belongs. The cranium has a rather truncated glabella, which suggests *P. aciculata pusilla*. As the specimen furthermore is associated with numerous detached parts of *P. aciculata pusilla*, I believe that it belongs to this form. The cranium of this specimen is 4.3 mm long. The associated, and no doubt conspecific hypostomae, are, as one might expect, rather similar to that assigned to *P. aciculata aciculata* by Westergård (1922), and resembles also the hypostoma of *Parabolina brevispina*.

Occurrence: — Norway: Sandsvør (Gjørefoss), Røyken (Slemestad, Bødalen), Oslo (Gamlebyen, Prinsensgate), Ringerike (S of Hvalsmoen), Hadeland (Boulder at Mæna): Zone of *Parabolina spinulosa* (2b), subzone of *Parabolina spinulosa*. Alone, or associated with *Parabolina spinulosa*, and/or *Orusia lenticularis*. — Sweden (same horizon).

Protopeltura bidentata (Brögger 1882).

Pl. 6; pl. 24, figs. 6—10.

- 1882 *Peltura bidentata*, n. sp. — Brögger, p. 106, pl. II, figs. 7, 7a. (Short descr. Figs. of axial shield and cranidium.)
1922 *Protopeltura praecursor* (Westergård)? — Westergård, p. 172, pl. XIV, fig. 30. (Remarks. Fig. of pygidium.)

Type data: — As lectotype I select the axial shield (P.M.O. no. H2721) figured by Brögger (1882, pl. II, fig. 7). It is associated with *Ctenopyge modesta* n. sp. and was collected by Brögger in 1880 at Slemmestad in Røyken, Norway.

Remarks: — The free cheeks of this species were earlier not known. They have now been found, and proved to have a spine, for which reason the species is transferred to *Protopeltura*.

Diagnosis: — A *Protopeltura* species with: no prelabellar field; S1 and S2 distinct, S3 and S4 faintly impressed or obsolete; palpebral lobes far forwards and close to glabella; postocular cheeks about half as wide as occipital ring, which carries small axial node; thorax with 12 segments and relatively long pleural spines; pygidium with flattened border, 1—2 pairs of marginal spines, 3 axial rings and semi-conical prolongation of axis reaching posterior border.

Description: — This is based on detached parts and two axial shields preserved in limestone. The largest cranidia are 7 mm long.

Cranidium with cephalic axis tapering slightly forwards. Glabella truncated in front, but with rounded corners. Occipital ring with small axial node. Occipital furrow distinct. S1 bent obliquely backwards, with geniculum. S2 directed less backwards, without geniculum. S3 developed as faint and short furrow midway between axial furrow and sagittal line. No prelabellar field. Eye ridges faint, short, and directed obliquely backwards. Palpebral lobes small, opposite S3. Interocular cheeks small, width about one-fifth of that of glabella at eye line. Postocular cheeks about half as wide as occipital ring. Surface appears smooth, but is very finely granulated.

Free cheeks with well developed spine. Inner spine angle obtuse. Genal caeca may be present.

Hypostoma unknown.

Thorax with 12 segments. Axis wider than pleural regions anteriorly, about as wide as pleural regions posteriorly. Fulcrum closer to axial furrow than to pleural ends. Pleurae with slender, but not very long spines. Axial rings with axial node.

Pygidium sub-semicircular. Axis with two rings and end lobe. A semi-conical prolongation of axis reaches posterior margin. Border flattened. One pair of marginal spines, and a pair of "bends" of margin behind the spines. In a pygidium with two pairs of spines, the posterior pair corresponds to the

"bends" in the others. The pygidium with two pairs of spines occur associated with the same species as *Protopeltura bidentata*, and I do not think it is necessary to assign it to a separate species or subspecies.

Occurrence: — Norway: Røyken (Slemmestad), Oslo (Tøyen). — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge similis*. Associated with *Ctenopyge similis* n. sp., *Ct. modesta* n. sp. \pm *Parabolina mobergi*. — Sweden (Västergötland, same horizon).

Protopeltura broeggeri (Holtedahl 1910).

Pl. 6; pl. 23, figs. 7—15.

- 1910 *Leptoplastus Bröggeri*, nov. sp. [partim] — Holtedahl, p. 18, pl. III, figs. 2, 4—10. (Descr. Figs. of part of cranium, part of thorax, pygidium, hypostoma, larval axial shield, larval cranium and larval pygidium.)
 1922 *Leptoplastus Bröggeri* Holtedahl — Westergård, pp. 110, 111, 151. (Remarks.)

Type data: — As lectotype I select a pygidium, figured by Holtedahl (1910, pl. III, fig. 6). It is associated with other detached parts of this species in a stinkstone lens, collected by Holtedahl in 1908 at Slemmestad, Røyken, Norway.

Remarks: — Holtedahl (1910) based his description of *Leptoplastus Bröggeri* on two different species (excluding the cranium in his pl. III, fig. 11, which probably belongs to neither of them), namely a *Leptoplastus* species and a *Protopeltura* species. His description of the cranium suits both species, and he figured a cranium of each of them. The free cheek described belongs to *Leptoplastus*, whereas the thorax and pygidium belong to *Protopeltura*. Since Holtedahl assigned his species to *Leptoplastus* (although with some doubt), it would perhaps have been most natural to retain Holtedahl's name for the *Leptoplastus* species. As the *Leptoplastus* species has been described by Westergård (1922) as *Ctenopyge neglecta* and the *Protopeltura* species has not been named by any others, I have found it most practical to retain Holtedahl's name for the *Protopeltura* species, thus avoiding that *Leptoplastus neglectus* becomes a synonym. Eight of Holtedahl's illustrations are of *Protopeltura broeggeri*, only two are of *Leptoplastus neglectus*.

Diagnosis: — A *Protopeltura* species with: relatively long preglabellar field; S1 and S2 distinct; interocular cheeks about half as wide as glabella at eye line; postocular cheeks slightly wider than occipital ring; widest pleurae up to 1.5 times as wide as axis; with entire, rounded subtriangular pygidium with 3 axial rings and end lobe. Number of thoracic segments unknown (probably 12).

Description: — This is based on detached parts of the dorsal shield, and an incomplete young dorsal shield, all preserved in limestone. The cranidia reach a length of 4.5 mm.

Cranidium slightly more than twice as wide as it is long. Cephalic axis tapering only very slightly forwards, rounded and somewhat truncated in front. Occipital ring with two nodes, one in front of the other. Occipital furrow distinct, deepest halfway between sagittal line and axial furrow. S1 clearly seen, but not so deep as occipital furrow. Outer parts straight, inner parts curved somewhat backwards, just reaching inner third of glabella. S2 rather similar, but even less well impressed, and less curved backwards. S3 missing, or developed as faint impressions midway between axial furrow and sagittal line. Preglabellar field well developed. Border narrow, widest at sagittal line. Eye ridges distinct, transverse, or running slightly backwards. Palpebral lobes small, flexed slightly upwards, and with centres opposite S3. Width of interocular cheeks about one half of that of glabella at eye line. Postocular cheeks somewhat wider than occipital ring. Surface appears smooth, but may be seen to be granulated on a very small scale in some specimens. Faint genal caeca cross the prelabellar field in some specimens.

Free cheeks of pelturoid type, and with a small and slender spine. Border well developed. Genal angle obtuse. Genal caeca are often seen.

Hypostoma with rather convex central body with a pair of maculae posteriorly. Border moderately wide, bent dorsal ("down") posteriorly. Posterior margin convex and entire.

Thorax known from parts only. In a small dorsal shield where the posteriormost part is missing, there are 10 or 11 thoracic segments. Another specimen consists of the 7 anterior segments. The 4th segment from the front is the widest, with pleurae about one and a half time as wide as axial ring. Pleural spines short and broad-based. External impressions of detached segments show that the axial ring had a small spine or node.

Pygidium sub-triangular, entire, slightly more than twice as wide as long. Axis with two rings and end lobe of two fused rings.

A f f i n i t i e s: — The cranidium of *Protopeltura broeggeri* is not very pelturine-like with its well-developed prelabellar field and rather wide postocular cheeks. However, its free cheeks, thorax, pygidium and small eyes betray the pelturine, although the pleural regions are wider than usual in early pelturines. *P. broeggeri* is no doubt close to *P. aciculata*, which has narrower pleural regions. It is easy to understand how Høltedahl could mix *P. broeggeri* and *Leptoplastus neglectus*, as their cranidia are rather similar and of about equal size. The cranidium of *L. neglectus* differs i. a. in having larger palpebral lobes and consequently shorter postocular cheeks.

O c c u r r e n c e: — Norway: Eiker (Stablum core), Røyken (Slemmestad). — Exact horizon uncertain, but somewhere between beds with *Leptoplastus angustatus* and beds with *Leptoplastus neglectus*. It occurs alone, and may possibly belong to the subzone of *Leptoplastus stenotus*. Since it has never been found together with *L. stenotus*, it seems more probable that it occurs above this subzone, and is tentatively placed at the base of the *Peltura* zones in its own subzone.

Protopeltura holtedahli n. sp.

Pl. 6; pl. 23, figs. 16—22.

1910 *Peliura præcursor*, Westergård [partim] — Holtedahl, p. 14, pl. II, figs. 3—4, 6—10. (Figs. of parts of thoraces with attached pygidium, young free cheek, pygidium, and cranidia.)

N a m e: — The name is given in honour of Professor, Dr. O. Holtedahl, who first depicted this species.

H o l o t y p e: — A cranidium (P. M. O. no. 29251) collected at Slemmestad in Røyken; Norway, by O. Holtedahl, 1908. Preserved in stinkstone.

D i a g n o s i s: — A *Protopeltura* species with: short preglabellar field; S1 and S2 distinct; postocular cheeks about three-fourths as wide as occipital ring; interocular cheeks about one-fourth as wide as glabella at eye line; free cheeks with relatively wide border and long spine; thorax apparently with 10 segments; entire pygidium.

D e s c r i p t i o n: — This is based on detached parts of the shield, and dorsal shields without cephalon. The largest cranidium is 5 mm long and 7 mm wide.

Cranidium with slightly tapering cephalic axis, rounded and somewhat truncated in front. Occipital ring with axial ridge, apparently formed by two fused nodes. Occipital furrow distinct. Glabellar furrows not joined across glabella. S1 transverse in its outer parts, curved obliquely backwards in its inner parts. S2 less oblique and fainter. S3 present as faint impression half-way between sagittal line and axial furrows. Preglabellar field short but distinct. Anterior border furrow distinct. Border shaped as very low and broad-based triangle. Eye ridges short, directed obliquely backwards, and rather indistinct. Palpebral lobes small, convex (exs.). Eye line well in front of S3. Interocular cheeks about one-fourth as wide as glabella at eye line. Postocular cheeks about three-fourths as wide as occipital ring. Surface appears smooth, but is very finely granulated. Faint genal caeca traverse preglabellar field.

Free cheeks of the pelturoid type, and with relatively long spine, almost as long as cheek plate. Borders well developed, unusually wide. Genal caeca usually present.

Hypostoma tongue-shaped. Central body strongly convex, tapering backwards, truncated posteriorly. Two nodes (maculae) posteriorly. Brim and borders well developed. Anterior wings with spine-like extension.

Thorax with 10 segments in two specimens where apparently only the cephalon is missing. Pleural regions somewhat wider than axis. Pleurae ending in short, broad-based spines. Axial rings with axial nodes (or short spines). Fulcrum midway between pleural end and axial furrow.

Pygidium sub-semicircular. Entire, but with very slightly undulating border. Axis occupies about three-sevenths of total width of pygidium anteriorly.

Affinities: — *Protopeltura holtedahli* n. sp. is rather close to *P. aciculata*, from which it differs in having narrower postocular cheeks and wider borders in the free cheeks. It also resembles *P. intermedia* and *P. praecursor*, but has a longer preglabellar field, wider postocular cheeks, and wider borders in the free cheeks. Its entire pygidium distinguishes it readily from *P. praecursor*. In many ways *P. holtedahli* n. sp. appears to be intermediate between *P. aciculata* and *P. praecursor*.

Occurrence: — Norway: Røyken (Slemmestad) — Exact horizon unknown, probably at the base of the zone of *Protopeltura praecursor* (cf. p. 38). Occurs alone.

Protopeltura intermedia Westergård 1922.

Pl. 4.

1922 *Protopeltura intermedia* n. sp. — — Westergård, p. 171, pl. XIV, figs. 18–22. (Descr. Figs. of cranidia, free cheek, and pygidia.)

1947 *Protopeltura intermedia* Wgård. — — Westergård, p. 26. (Distribution in Sweden.)

Type data: — As lectotype I select a pygidium figured by Westergård (1922, pl. XIV, fig. 21), from Kloxåsen, Näs parish, Jämtland, Sweden.

Diagnosis: — A *Protopeltura* species with: very short preglabellar field; glabella bluntly rounded in front; S1 and S2 distinct; eyes rather close to glabella; postocular cheeks slightly more than half as wide as occipital ring; free cheeks with short and slender spine; pygidium sub-semicircular, entire. Thorax unknown.

Occurrence: — Sweden (zone of *Leptoplastus* and *Eurycare*; subzone of *Leptoplastus paucisegmentatus* and subzone of *Leptoplastus ovatus*.)

Protopeltura planicauda (Brögger 1882).

Pl. 6; pl. 24, figs. 11–13.

1882 *Peltura planicauda*, n. sp. — — Brögger, p. 107, pl. II, fig. 8 (Short descr. Fig. of pygidium.)

1922 *Peltura planicauda* Brögger — — Westergård, p. 173, pl. XV, fig. 2. (Descr. and fig. of specimen consisting of 10 thoracic segments and pygidium.)

1947 *Peltura planicauda* Brögg. — — Westergård, p. 26. (Distribution in Sweden.)

Type data: — As lectotype I select the pygidium (P. M. O. no. H 2715a) figured by Brögger (1882, pl. II, fig. 8). It is associated with *Peltura acutidens*, *Sphaerophthalmus alatus*, and *Ctenopyge tumida* (not *Ct. spectabilis* as stated by Brögger). It was collected by Brögger at Slemmestad in Røyken, Norway, in 1880.

Remarks: — Brögger (1882) believed this species to have free cheeks without spine, and consequently assigned it to *Peltura*. There is a free cheek of this type on the slab containing the lectotype, but by splitting up

the slab I found other free cheeks with spine, as well as a pygidium of *Peltura acutidens*. When pygidia of *P. acutidens* occur without being accompanied by pygidia of *Protopeltura planicauda*, they are associated with free cheeks of the spineless *Peltura* type only. It is thus rather certain that the free cheeks with spine in the above-mentioned slab are conspecific with the pygidium of *planicauda*, and this species is referred here to *Protopeltura*. This is probable also because of the great likeness between the pygidia of *P. planicauda* and *P. bidentata*. Some pygidia are almost intermediate between the two species. Also the thorax of *P. planicauda* suggests *Protopeltura* rather than *Peltura*, having relatively wide pleural regions.

Diagnosis: — A *Protopeltura* species with: thorax with at least 10 segments and relatively long pleural spines; pygidium with flattened and expanded border, 2 pairs of marginal spines (posterior pair rudimentary), and axis with three rings and tumid post-axial ridge. Cranidium unknown.

Description: — Cranidium not known with certainty, as the cranidia associated with the lectotype pygidium are rather incomplete, and may as well belong to *Peltura acutidens*.

Free cheeks with spine. Unfortunately no well-preserved free cheek has been found.

Hypostoma unknown.

Thorax with at least 10 segments (cf. Westergård, 1922, pl. XV, fig. 2). Pleurae with slender spine, and axial rings with axial node.

Pygidium rather similar to that of *P. bidentata*, but more expanded at the border. Faint terrace lines form a Bertillion pattern on axis of lectotype.

Occurrence: — Norway: Røyken (Slemmestad). — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge similis* and subzone of *Ctenopyge tumida*. Associated with *Ct. similis* and *Ct. angusta*, or with *Ct. tumida* and *Peltura acutidens*. — Sweden (same horizon).

Protopeltura praecursor (Westergård 1909).

Pl. 2, fig. 2; pl. 6; pl. 24, figs. 1—5.

- 1882 *Protopeltura acanthura*, Ang. — Brögger, p. 106, pl. I, figs. 14, 14a-c; pl. II, figs. 13, 13a. (Remarks. Figs. of incomplete cranidium, free cheek, parts of pleurae, pygidium, and hypostoma.)
- 1884 *Protopeltura acanthura*, Ang. — Brögger, p. 257. (Recorded.)
- 1898 *Protopeltura acanthura* — Moberg & Möller, p. 265. (Point out that Brögger's species is not conspecific with Angelin's *Olenus? acanthurus*, which is a *Parabolina* species.)
- 1909 *Peltura praecursor* n. sp. — Westergård, p. 48. (Gives this name to Brögger's species, which is distinct from *Parabolina acanthura*.)
- 1910 *Peltura praecursor*, Westergård [partim] — Høltedahl, p. 14, pl. II, figs. 1, 2, 5? only. (Figs. of cranidium, free cheek, and hypostoma. The other specimens figured belong to *Protopeltura høltedahli* n. sp.)
- 1922 *Protopeltura praecursor* (Westergård) — Westergård, p. 171, pl. XIV, figs. 23—29, 31; pl. XV, fig. 1. (Descr. Figs. of dorsal shield, cranidia, free cheek,

pygidia, and hypostoma. The pygidium in fig. 30, tentatively assigned to this species, probably belongs to *P. bidentata*.)

1929 *Protopeltura praecursor* (Wgd.) — Strand, p. 359. (Recorded.)

1934a *Protopeltura praecursor* — Stormer, p. 332. (Listed.)

1947 *Protopeltura praecursor* (Wgård.) — Westergård, p. 26. (Distribution in Sweden.)

1955 *Protopeltura praecursor* (Westergård) — Tjernvik, p. 209, text-fig. 1 A. (Sketch of cranidium.)

Type data: — As lectotype I select the pygidium (P. M. O. no. H 2715a) figured by Brögger (1882, pl. I, fig. 14c). It is associated with other parts of the same species and parts of *Ctenopyge postcurrens*, and occurs in a stinkstone slab collected by Brögger in 1880 at Nærsnes in Røyken, Norway.

Diagnosis: — A *Protopeltura* species with: very short, practically no glabellar field; S1 and S2 distinct, S3 very faintly impressed or obsolete: palpebral lobes far forwards and close to glabella: postocular cheeks somewhat more than half as wide as occipital ring, which carries two axial nodes behind each other; free cheeks with spine; thorax with 12 segments and short pleural spines; pygidium with 2—4 pairs of marginal spines and 3—4 axial rings.

Remarks: — *Protopeltura praecursor* occurs in three subzones, but I have not been able to detect any significant differences between specimens from different subzones.

Occurrence: — Norway: Skien—Brevik district (Ombordsnes), Eiker (Stablum core), Røyken (Nærsnes, Slemmestad), Oslo (Gamlebyen) — Zone of *Protopeltura praecursor* (2d α), subzone of *Leptoplastus neglectus* (associated with *L. neglectus*), subzone of *Ctenopyge postcurrens* (associated with *Ct. postcurrens*), and subzone of *Ctenopyge flagellifera* (associated with *Ct. flagellifera* \pm *Ct. drytonensis*). — Sweden (same horizons).

Protopeltura? solitaria (Westergård 1922).

Pl. 3.

1922 *Beltella solitaria* n. sp. — Westergård, p. 140, pl. XIV, fig. 1 only. (Descr. Fig. of axial shield without pygidium. Fig. 2 is probably of a *Protopeltura* sp.)

1947 *Beltella solitaria* Wgård. — Westergård, p. 25. (Distribution in Sweden.)

1952 *Beltella solitaria* Westergård — Harrington & Leanza, p. 193. (Remarks.)

1954 *Beltella solitaria* Westergård — Wilson, p. 276. (Remarks.)

Type data: — As lectotype I select the axial shield without pygidium figured by Westergård (1922, pl. XIV, fig. 1), from Andrarum, Scania, Sweden.

Remarks: — Besides the lectotype, which is rather a small and apparently young individual, Westergård assigned, with some doubt, only one more specimen to this species. This specimen is an almost complete

dorsal shield (Westergård, 1922, pl. XIV, fig. 2), apparently of an adult individual. It was suggested to be a somewhat deformed specimen of *Protopeltura aciculata* by Harrington & Leanza (1952, p. 193). However, it differs from this species in minor features probably not due to deformation, such as having at least two pairs of marginal spines in the pygidium. Nevertheless, it is most probably closely related to *Protopeltura aciculata*, and may fairly safely be included in *Protopeltura*. If the lectotype is conspecific with it, *solitaria* should be referred to *Protopeltura*. However, some features, especially the relative size and position of the palpebral lobes, are more different than one might expect of a young and adult specimen of the same species, and it is possible that the two specimens represent two species. If so, the generic reference of *solitaria* is uncertain. Its cranidium appears to be more or less intermediate between that of *Olenus* and that of *Protopeltura*. For the time being, I assign *solitaria* tentatively to *Protopeltura*.

Occurrence: — Sweden: *Parabolina spinulosa* zone, subzone of *Parabolina brevispina* and *Protopeltura aciculata*.

Genus *Peltura* Milne Edwards 1840.

Type species: — *Entomostracites scarabæoides* Wahlenberg 1821, designated by Corda (Hawle & Corda, 1847, p. 127), and by Miller (1889).

Synonym: — *Anthes* Goldfuss 1843 (type species: *Entomostracites scarabæoides* Wahlenberg 1821, selected here.)

Remarks on the name: — The name of the genus was spelt *Peltoura* by Milne Edwards, but Burmeister (1843, p. 83) altered it to *Peltura*. I agree with Dr. C. J. Stubblefield who has proposed to the ICZN to validate the familiar spelling *Peltura*, on grounds of over a hundred years' universal usage. Furthermore, this spelling agrees with that of *Protopeltura*.

Diagnosis: — Pelturinae with: small palpebral lobes far forwards and close to glabella; postocular cheeks with more or less convex outer margin and not wider than half as wide as occipital ring; cephalic axis slightly longer than wide, slightly tapering forwards and bluntly rounded in front; glabellar furrows (when present) not united across glabella; free cheeks with evenly curved lateral margin, with or without slender spine almost normal to margin and situated far back; thorax with 12 segments (when number is known) and pleural ends with short broad-based spines; pygidium sub-semicircular or sub-semielliptical, entire, or with marginal spines.

Included species and subspecies: —

Peltura acutidens Brögger 1882

P. cornigera Westergård 1909 (= *P. transiens*)

P. costata (Brögger 1882)

P. malvernus (Phillips 1871) (earlier: *Conoccephalus*) (= *P. scarabæoides*)

P. minor (Brögger 1882)

- P. paradoxa* (Moberg & Möller 1898)
P. scarabaeoides scarabaeoides (Wahlenberg 1821)
P. scarabaeoides obesus (Salter 1864) (= *P. scarabaeoides scarabaeoides*)
P. scarabaeoides octacantha Linnarsson 1880 (= *P. scarabaeoides scarabaeoides*)
P. scarabaeoides westergårdi n. subsp.
P. transiens (Brögger 1882).

Peltura bidentata Brögger 1882 and *P. planicauda* Brögger 1882 have both been transferred to *Protopeltura*. *Peltura punctata* Crosfield & Skeat 1896 has been transferred to *Triarthrus*. *Acerocare norvegicum* Moberg & Möller 1898 and *Conocoryphe? olenoides* Salter 1886, which both have been included in *Peltura*, are here transferred to the new genus *Peltocare*. *Peltura(?)* sp. indet. Harrington 1937 probably is a *Parabolinella* species. *Peltura? jarillana* Rusconi 1953 is insufficiently known (cf. p. 25). *Peltura? inflata* and *Peltura??* sp. described from the Lower Cambrian of Sardinia by Bornemann (1891) are not well known, but may safely be excluded from the Olenidae.

Occurrence: — Zone of *Peltura minor* in Norway and Sweden; zone of *Peltura scarabaeoides* in Norway, Sweden, Denmark, Poland, England, Wales, and E. Canada; zone of *Acerocare* in Norway and Sweden. ?France (?Upper Cambrian).

Phylogeny and relationships: — The early *Peltura* species differ from *Protopeltura* mainly in having free cheeks without spine, and there can be no doubt that *Peltura* developed from *Protopeltura*. The two earliest *Peltura* species, *P. acutidens* and *P. minor*, appear in the subzone of *Ctenopyge tumida*. They seem to be closely related, but *P. minor* has an entire pygidium without flattened border, whereas that of *P. acutidens* has 3 pairs of prominent marginal spines and a flattened border reminding one of the borders of *Protopeltura planicauda* and *Protopeltura bidentata*. *Peltura minor* also occurs in the following subzone of *Ctenopyge affinis*, and it is possible that its range slightly overlaps that of *P. scarabaeoides scarabaeoides* in the zone of *Peltura scarabaeoides*. The pygidium of *P. scarabaeoides scarabaeoides* resembles that of the closely related *P. acutidens*, but its border is not flattened and its marginal spines are smaller and with a greater distance between the posterior pair of spines. *P. scarabaeoides scarabaeoides* apparently gave rise to *P. scarabaeoides westergårdi*, which succeeds it, and which has a pygidium with longer marginal spines and the posterior pair of spines closer together, although not as close as in *P. acutidens*. Furthermore, its pygidium is not as wide as that of *P. acutidens*. Above *P. scarabaeoides westergårdi* comes *P. paradoxa* (in the subzone of that name), which has an entire pygidium and which differs from all the earlier species of *Peltura* in having free cheeks with a spine. The spine differs from the spine of *Protopeltura* in being shorter and slender and in being

situated far back and almost normal to the border. The succeeding species, *P. transiens* (= *P. cornigera*), in the subzone of that name, has a similar spine in the free cheeks, but a pygidium with short marginal spines. *P. costata*, which appears next (in the subzone of that name), is the latest known representative of the genus *Peltura*. It has again an entire pygidium and free cheeks without spine. On the whole, the genus *Peltura* is rather conservative, the eyes, for instance, having more or less the same position in all its known species. However, *Peltura* apparently gave rise, directly and indirectly, to all the later pelturine genera. *Nericiaspis*, *Acerocarina*, and possibly *Pelturina* seem to have developed from *Peltura*.

Peltura acutidens Brögger 1882.

Pl. 6; pl. 25, figs. 1, 3, 4, 7, 9, 11.

- 1882 *Peltura scarabæoides*, Wahlenb. var. *acutidens* — Brögger, p. 108, pl. II, fig. 9. (Descr. and fig. of pygidium.)
 1922 *Peltura scarabæoides acutidens* Brögger — Westergård, p. 175, pl. XV, figs. 14—17. (Descr. of pygidium. Figs. of cranidium, free cheek, pygidium, and hypostoma.)
 1929 *Peltura scarabæoides acutidens* Br. — Strand, p. 360. (Recorded.)
 1934a *Peltura scarabæoides acutidens* — Størmer, p. 332. (Listed.)
 1947 *Peltura acutidens* Brögg. — Westergård, p. 26. (Distribution in Sweden.)

Type data: — A lectotype I select the pygidium (P.M.O. no. H 2720) figured by Brögger (1882, pl. II, fig. 9). It is associated with *Sphaerophthalmus alatus* and *Ctenopyge tumida* (not *Ct. spectabilis* as stated by Brögger), and was collected by Brögger in 1880 at Slemmestad in Røyken, Norway.

Diagnosis: — A *Peltura* species with: S1 and S2 distinct, S3 and S4 faintly impressed or obsolete; fixed cheeks slightly less than half as wide as occipital ring, which carries faint axial node; free cheeks without spine; thorax with short pleural spines; pygidium with flattened and expanded border, 3 axial rings and 3 pairs of broad-based, well-developed marginal spines; distance between axes of posterior pair of spines somewhat shorter than width of terminal axial ring.

Description of Norwegian material: — The largest cranidium encountered is about 10 mm long and 16 mm wide. Cephalic axis tapering forwards, bluntly rounded in front. Occipital ring with rather small and low axial node. Occipital furrow distinct. S1 and S2 rather shallow, geniculated. S3 developed as very faint impression halfway between axial furrow and sagittal line. No preglabellar field. Border rather narrow. Eye ridges oblique backwards, not very distinct. Palpebral lobes small with centres opposite S3. Interocular cheeks small, about one-sixth as wide as glabella at eye line. Postocular cheeks slightly less than half as wide as occipital ring.

Free cheeks narrow, without spine.

Hypostoma with convex central body, tapering backwards and truncated posteriorly, where a pair of maculae are developed at the corners. Brim rather wide laterally, and with a pair of small spines posteriorly. Anterior wings present.

Thorax known from detached segments only. Axis without node or spine, pleurae with short pleural spine.

Pygidium with relatively wide pleural regions. Border area flattened and expanded, and provided with 3 pairs of rather long, acute spines. Surface with terrace lines.

Occurrence: — Norway: Røyken (Slemmestad), Ringsaker (Steinsodden, Evjevika) — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge tumida*. Associated with *Ct. tumida* and *Sphaerophthalmus alatus* \pm *Peltura minor*. — Sweden.

Peltura costata (Brögger 1882).

Pl. 7; pl. 27, figs. 1—5, 7, 9.

1882 *Cyclognathus costatus*, n. sp. — Brögger, p. 110, pl. I, figs. 5a—d. (Descr. Figs. of restored cephalon, thoracic segment, and pygidium.)

1898 *Acerocare costatum* Brögger — Moberg & Möller, p. 242. (Remarks.)

1919 "*Cyclognathus*" *costatus* Brögger — Lake, pp. 95, 96, 101. (Remarks. Suggests that the species should be assigned to *Peltura*.)

?1922 *Peltura costata* (Brögger) — Westergård, p. 177. (Records the species with uncertainty from Sweden.)

1934a *Peltura costata* — Stormer, p. 332. (Listed.)

1944a *Peltura* ("*Cyclognathus*") *costata* (Brögger) — Westergård, p. 43. (Remarks.)

1952 *Cyclognathus costatus* Brögger — Hutchinson, p. 95. (Compared with *C. rotundifrons* Matthew.)

1953 *Acerocare?* *costatus* — Høltedahl, p. 182, text fig. 69: figs. 28—29. (Figs. of restored cephalon, thoracic segment, and pygidium.)

Type data: — As lectotype I select a pygidium (P.M.O. no. 29017) figured by Brögger (1882, pl. I, figs. 5c—d). It was collected by W. C. Brögger in 1879 at Vestfossen, Eiker, Norway.

Diagnosis: — A *Peltura* species with: obsolete glabellar furrows in adult cranidia; fixed cheeks somewhat less than half as wide as occipital ring; free cheeks without spine; thorax apparently without axial nodes, otherwise insufficiently known; pygidium entire and with axis with 2 rings and end lobe.

Description: — This is based on detached parts of the shield. Largest cranidium present about 10 mm long. Cranidium pelturoid. Cephalic axis slightly longer than wide, tapering slightly forwards, bluntly rounded in front. Occipital ring with faint occipital node and faint composite furrow. Two pairs of very faint glabellar furrows, practically invisible in larger cranidia. Anterior border furrow very indistinct. Oblique eye ridges hardly

visible. Interocular cheeks small and narrow, about one-sixth as wide as glabella at eye line. Postocular cheeks almost half as wide as occipital ring. Facial sutures converge moderately in front of eyes, and diverge moderately behind eyes.

Free cheeks pelturoid, without spine. Border relatively wide. Doublure as wide as border, longitudinally striate.

Hypostoma rather like that of *P. scarabaeoides* and *P. transiens*.

Thorax known only from detached segments. Pleural ends rounded and with small spine. Axial rings apparently without node.

Pygidium sub-semicircular, about twice as wide as long. Pleural regions somewhat narrower than axis anteriorly. Axis with two rings and end lobe. Two pairs of distinct pleural furrows, and a third posterior pair which is rather indistinct and short. Border distinct, subtubular. Doublure about as wide as border. Surface with terrace lines.

Occurrence: — Norway: Eiker (Vestfossen), Røyken (Slemmestad), Oslo (Tøyen), Brumunddalen — *Acerocare* zone (2de), subzone of *Peltura costata*. Associated with *Parabolina heres heres* ± *Eoorthis*? sp. — Sweden (same horizon).

Peltura minor (Brögger 1882).

Pl. 6; pl. 25, figs. 2, 5.

- 1882 *Cyclognathus costatus* n.sp. var. *minor* — Brögger, p. 110, pl. II, figs. 10—11. (Descr. Figs. of 2 pygidia.)
1922 *Peltura minor* (Brögger) — Westergård, p. 175, pl. XV, figs. 3—11. (Descr. Figs. of cranidia, free cheek, pygidia, hypostoma, and thorax with attached pygidium.)
1934a *Peltura minor* — Størmer, p. 332. (Listed.)
1947 *Peltura minor* (Brögger) — Westergård, p. 26, pl. 2, fig. 12. (Fig. of axial shield. Distribution in Sweden.)

Type data: — As lectotype I select a pygidium (P.M.O. no. H 2713a) figured by Brögger (1882, pl. II, fig. 10). It is associated with *Sphaerophthalmus alatus* and *Ctenopyge tumida*, and was collected by Brögger in 1880 at Slemmestad in Røyken, Norway.

Diagnosis: — A *Peltura* species with: S1 and S2 distinct; fixed cheeks slightly less than half as wide as occipital ring; free cheeks without spine; thorax with 12 segments and pleural ends with short spines; entire pygidium with 3—4 axial rings.

Remarks: — The Swedish material described by Westergård (1922) agrees with the Norwegian, except that the hypostomae associated with the Norwegian material do not show so well-developed posterior projections as the hypostoma figured by Westergård (1922, pl. XV, fig. 11). The surface of the cranidium appears smooth, but is faintly and very finely granulated. The free cheeks may show faint genal cacca. The pygidium usually shows rather distinct terrace lines, and so does the border of the hypostoma.

Occurrence: — Norway: Røyken (Slemmestad, Nærnes), Oslo, Ringerike, Ringsaker (Evjevika, Steinsodden), Snertingdal — Zone of *Peltura minor* (2d β), subzone of *Ctenopyge tumida* (associated with *Ct. tumida*, *Sphaerophthalmus alatus* \pm *Peltura acutidens*) and subzone of *Ctenopyge affinis* (associated with *Ct. affinis* and *Sphaerophthalmus alatus*). — Sweden (same horizons and base of zone of *Peltura scarabaeoides*).

Peltura paradoxa (Moberg & Möller 1898).

Pl. 7; pl. 26, figs. 3—6.

- 1898 *Acerocare paradoxum* n.sp. — Moberg & Möller, p. 251, pl. 11, figs. 10—13, 14? (Descr. Figs. of free cheek, part of thorax, pygidia, and associated hypostoma.)
 1908a *Acerocare paradoxum* Moberg — Raw, p. 513. (Assigned to *Leptoplastides*.)
 1919 *Acerocare paradoxum* Moberg & Möller — Lake, p. 92. (Mentioned.)
 1922 *Peltura paradoxa* (Moberg & Möller) — Westergård, p. 177, pl. XVI, figs. 1—4, 5? (Remarks. Copies of Moberg & Möller's figs.)
 ?1944a ?*Peltura paradoxa* (Moberg & Möller) — Westergård, p. 42, pl. 3, fig. 5. (Remarks. Fig. of cranidium.)
 1947 *Peltura paradoxa* (Mob. & Möll.) — Westergård, p. 26. (Distribution in Sweden.)

Type data: — As lectotype I select a pygidium figured by Moberg & Möller (1898, pl. 11, fig. 13), from Åkarpsmölla, Scania, Sweden.

Diagnosis: — A *Peltura* species with: obsolete glabellar furrows; fixed cheeks about half as wide as occipital ring; free cheeks with small spine far back and almost normal to margin; pygidium entire, with 2 axial rings and end lobe. Thorax insufficiently known.

Remarks: — The type material of this species is rather poor. Unfortunately the Norwegian material, from a single stinkstone lens, is not much better preserved, and likewise consists of detached parts.

Description of Norwegian material: — Cranidium pelturoid. Cephalic axis only slightly longer than wide, tapering slightly forwards, and bluntly rounded in front. Occipital ring with small axial node. Occipital furrow rather shallow. Three pairs of glabellar furrows of the pelturoid type are rather faintly impressed. Very faint anterior border furrow. Eye ridges hardly distinguishable. Palpebral lobes small, opposite S3. Postocular cheeks about half as wide as occipital ring. Facial sutures subparallel just in front of eyes, moderately diverging and convex behind eyes.

Free cheeks pelturoid, elongate, and with small spine almost normal to margin near posterior end of cheek. Eyes with facets.

Hypostoma not found.

Thorax only known from fragments of segments. Apparently without axial node.

Pygidium with entire border. Pleural regions about as wide as axis in front. Axis with two rings and end lobe. Two distinct and a posterior, rather indistinct pair of pleural furrows.

Occurrence: — Norway: Modum (Furetangen). — *Acerocare* zone (2de), subzone of *Peltura paradoxa*. Associated with *Parabolina megalops*? — Sweden (same horizon).

Peltura scarabaeoides scarabaeoides (Wahlenberg 1821).

Pl. 2, fig. 1; pl. 6; pl. 25, figs. 6, 13—14; pl. 26, figs. 1—2.

- 1821 *Entomostracites scarabaeoides* — Wahlenberg, p. 41, pl. I, fig. 2. (Descr. Rough, inadequate fig. of axial shield.)
- 1822 *Paradoxides scarabaeoides* — Brongniart, p. 34, pl. III, fig. 5. (Copy of Wahlenberg's descr. and fig.)
- 1827 *Trilobites scarabaeoides* — Boeck, p. 36, fig. 24. (Remarks on cranidium. Fig. of cranidium.)
- 1827 *Olenus scarabaeoides* — Dalman, p. 72 (257). (Short descr.)
- 1837 *Olenus scarabaeoides* — Hisinger, 19, pl. IV, fig. 4. (Diagn. Copy of Wahlenberg's fig.)
- 1838 *Trilobites scarabaeoides* Wahlb. — Boeck, p. 144. (Listed.)
- 1840 *Peltura scarabaeoides* — Milne Edwards, vol. III, p. 344. (Descr.)
- 1843 *Anthes scarabaeoides* Wahlenberg — Goldfuss, p. 544. (Listed.)
- 1847 *Peltura scarabaeoides* — Hawle & Corda, p. 127, pl. VI, fig. 68. (Descr. Fig. of restored dorsal shield.)
- 1848 *Olenus spinulosus*? — Phillips, p. 55, fig. 3, p. 347. (Descr. and fig. of cranidium.)
- 1854 *Peltura scarabaeoides*. Wahl. — Angelin, p. 45, pl. XXV, fig. 8. (Fig. of dorsal shield.)
- 1854 *Anopocare pusillum* [partim] — Angelin, p. 50, pl. XXVII, fig. 1a only. (According to Linnarsson, 1880, the pygidium belongs to *P. scarabaeoides*.)
- 1857 *Peltura scarabaeoides* Boeck [sic!] — Kjerulf, p. 284 (92). (Listed.)
- 1864 *Olenus scarabaeoides* var. *obesus*. — Salter, dec. XI, pl. VIII, figs. 1—4, p. 5. (Descr. Figs of axial shield, cranidium, and pygidium.)
- 1865 *Peltura* M. Edw. *scarabaeoides* Wahl. — Kjerulf, p. 2. (Listed.)
- 1866 *Olenus scarabaeoides*, Wahl. — Salter, p. 301, pl. V, figs. 2—5. (Remarks. Figs. of 2 axial shields, cranidium, and pygidium.)
- 1871 *Conocephalus Makvernius* n. sp. — Phillips, p. 68, fig. 5. (Fig. of dorsal shield.)
- 1871 *Olenus scarabaeoides*. Wahlenberg. — Phillips, p. 68, fig. 6. (Fig. of small cranidium.)
- 1873 *Olenus (Peltura) scarabaeoides*, Wahl. — Salter, p. 11. (Listed.)
- 1880 *Peltura scarabaeoides* Wahlenb. sp. — Linnarsson, p. 134 (4), pl. V (I), figs. 1—4. (Descr. Figs. of all parts of dorsal shield.)
- 1880 *Peltura scarabaeoides* var. *octacantha* — Linnarsson, p. 135 (5), pl. V (I), fig. 5. (Descr. and fig. of pygidium with 4 pairs of marginal spines.)
- 1882 *Peltura scarabaeoides*, Wahlenb. — Brögger, p. 107, pl. I, figs. 7—9, pl. II, fig. 12. (Descr. Figs. of all parts of dorsal shield.)
- 1884 *Peltura scarabaeoides*, Wahlenb. — Brögger, p. 257. (Listed.)
- 1892 *Peltura scarabaeoides*. Wahl. — Matthew, p. 53, pl. XIII, figs. 9a—b. (Figs of cranidium and pleurae.)

- 1898 *Peltura scarabæoides*, Wahlenb. — — Bjørlykke, p. 12. (Listed.)
- 1901 *Peltura scarabæoides* Wahlenb. — — Lindström, pp. 29, 64, pl. III, figs. 35—42. (Figs. of cephalon, free cheek, eyes, and hypostoma.)
- 1901 *Peltura scarabæoides* Wahlb. — — Münster, p. 25. (Recorded.)
- 1902 *Peltura scarabæoides* — — Schiøtz, pp. 17, 38. (Recorded.)
- 1903 *Peltura scarabæoides*, Wahlenb. — — Matthew, p. 230. (Listed.)
- 1910 *Peltura scarabæoides* — — Goldschmidt, p. 4, figs. 1—3. (Figs. of pygidium and thoracic segment.)
- 1919 *Peltura scarabæoides* (Wahlenberg) — — Lake, p. 97, pl. XI, figs. 9—12. (Descr. Figs. of dorsal and axial shields.)
- 1922 *Peltura scarabæoides* (Wahlenberg) — — Westergård, p. 173, pl. XV, figs. 12—13, 18. (Remarks. Figs. of pygidium, axial shield, and dorsal shield.)
- 1923 *Peltura scarabæoides* Wahlenberg — — Poulsen, p. 50, text fig. 18, pl. II, figs. 6—7; p. 58, text fig. 22. (Descr. Figs. of cranidia and free cheeks, and copy of Westergård's fig. of a dorsal shield. Descr. and figs. of larval cranidia.)
- 1927a *Peltura scarabæoides* Wahlenb. — — Czarnocki, p. 12. (Recorded.)
- 1927b *Peltura scarabæoides* Wahlenb. — — Czarnocki, p. 199. (Recorded.)
- 1929 *Peltura scarabæoides* (Wahlenb.) — — Strand, p. 359. (Recorded.)
- 1934a *Peltura scarabæoides* — — Størmer, p. 332. (Listed.)
- 1937 *Peltura scarabæoides* (Wahl.) — — Richter, p. 418, text fig. 2. (Orientation in sediments.)
- 1942 *Peltura scarabæoides* (Wahlenberg) — — Størmer, p. 89. (Mentions Poulsen's material of larval cranidia.)
- 1947 *Peltura scarabæoides* (Wahl.) — — Westergård, p. 26. (Distribution in Sweden, including also that of *P. scarabæoides westergårdi* n. subsp.)
- 1952 *Peltura scarabæoides* (Wahlenberg) — — Hutchinson, p. 93, pl. V, figs. 1—6. (Descr. Figs. of cranidia, free cheeks, and pygidia.)
- 1953 *Peltura scarabæoides* — — Høltedahl, p. 182, text fig. 69, figs. 25—26. (Figs. of free cheek, cranidium, thoracic segment, and pygidium.)

Type data: — As lectotype should be chosen one of Wahlenberg's specimens from Sweden.

Diagnosis: — A *Peltura* subspecies with: S1 and S2 distinct or somewhat effaced; fixed cheeks somewhat less than half as wide as occipital ring; free cheeks without spine, thorax with 12 segments and well-developed pleural spines; pygidium with 2—3 axial rings and 3 pairs of marginal spines, distance between posterior pair slightly longer than width of anterior axial ring in pygidium.

Remarks: — The Norwegian material quite agrees with the Swedish. The largest cranidium found in Norway is 30 mm wide (restored) and 15 mm long. A form with long marginal spines in the pygidium is separated below as *P. scarabæoides westergårdi* n. subsp..

Occurrence: — Norway: Skien—Brevik district (Ombordsnes), Eiker—Sandsvær (Sandbakk core, Teigen core, Stablum core, Krekling), Røyken (Nærsnes, Slemmestad), Oslo, Modum, Ringerike, Hadeland, Hamar district (Romedal), Ringsaker (Evjevika), Brumunddal, Valdres (Tonsåsen), Snertingdal, Østerdalen (Glomstad, Ulvåen). — Zone of *Peltura scarabæoides*, lower part (2dγ), subzone of *Ctenopyge bisulcata*

(associated with *Sphaerophthalmus humilis* \pm *Ct. bisulcata*) and subzone of *Ctenopyge linnarssoni* (associated with *Sph. humilis* \pm *Ct. linnarssoni* \pm *Ct. fletcheri* \pm *Ct. pecten*). — Same horizons in Sweden, Denmark (Bornholm), Poland, Great Britain, Canada.

Peltura scarabaeoides westergårdi n. subsp.

Pl. 7; pl. 25, figs. 8, 10, 12, 15—17.

- 1898 *Parabolina megalops* n.sp. [partim] — Moberg & Möller, p. 275, pl. 13, fig. 9 only. (Fig. of pygidium, cf. Westergård, 1942.)
 1942 *Peltura scarabaeoides* (Wahlenberg) — Westergård, p. 14. (Points out that the pygidium figured by Moberg & Möller, 1898, pl. 13, fig. 9, as *Parabolina megalops*, belongs to a form of *Peltura scarabaeoides* predominant in the subzone of *Parabolina longicornis* and immediately underlying strata.)
 1944a *Peltura scarabaeoides* (Wahlenberg) — Westergård, p. 40, pl. 3, fig. 3. (Fig. of pygidium.)
 1947 *Peltura scarabaeoides* (Wahl.) [partim] — Westergård, p. 26. (Distribution in Sweden of *Peltura scarabaeoides*, including also *P. scarabaeoides westergårdi* n. subsp.)

N a m e: — The name *westergårdi* is given in honour of Fil. Dr. A. H. Westergård.

H o l o t y p e: — A cranidium figured by Westergård (1944, pl. 3, fig. 3), from a limestone boulder, Åkarpsmölla, Scania, Sweden. It is associated with *Parabolina lobata* [= *P. longicornis*].

D i a g n o s i s: — Differs from *Peltura scarabaeoides scarabaeoides* in having longer and straighter marginal spines in pygidium; distance between posteroir pair of spines almost equal to width of end lobe.

D e s c r i p t i o n: — This is based on detached parts only. Cranidium similar to that of *P. scarabaeoides scarabaeoides*. A fragment of a cranidium suggests that the cranidia of *P. scarabaeoides westergårdi* attained at least a length of 13 mm. The same fragment shows well-developed S4.

Free cheeks seem to differ from those in main subspecies in being somewhat narrower. Faint genal caeca may be present.

Hypostoma similar to that of main subspecies, and usually showing terrace lines.

Thorax known from fragments of thoracic segments only. As in main subspecies apparently without axial nodes.

Pygidium resembles that of main subspecies, but differs in not having border and marginal spines bent down, and in having longer marginal spines and a greater distance between posterior pairs of spines.

A f f i n i t i e s: — *P. scarabaeoides westergårdi* is no doubt very close to *P. scarabaeoides scarabaeoides*, from which it most probably has developed. The pygidium of *P. scarabaeoides westergårdi* resembles somewhat that of *P. acutidens*, which likewise has rather long spines, but is easily distinguished from it as it has much narrower pleural areas, and the bases

of the spines on a more curved line. Furthermore the posterior pair of spines are set much further apart than in *P. acutidens*.

Occurrence: — Norway: Eiker (Vestfossen), Røyken (Slemmestad), Oslo. — Zone of *Peltura scarabaeoides*, upper part (2d8), subzone of *Parabolina lobata* (associated with *Parabolina lobata praecurrens* or with *Parabolina lobata lobata* \pm *Agnostus rudis holmi* \pm *Eoorthis?* sp.) — Sweden (same horizon).

Peltura transiens (Brögger 1882).

Pl. 7; pl. 26, figs. 7—13.

- 1882 *Cyclognathus transiens*, n. sp. — Brögger, p. 109, pl. 1, fig. 6. (Descr. Fig. of pygidium.)
- 1898 *Acerocare transiens* Brögger — Moberg & Möller, pp. 242, 253. (Compared with *Peltura paradoxa*.)
- 1909 *Peltura cornigera* n. sp. — Westergård, p. 47, pl. I, figs. 2—4. (Descr. Figs. of cranium, free cheek, and pygidium.)
- 1922 *Peltura cornigera* Westergård — Westergård, p. 176, pl. XV, figs. 19—23. (Descr. Figs. of cranium, free cheeks, and pygidium.)
- 1922 *Peltura* ("Cyclognathus") *transiens* (Brögger) — Westergård, p. 176. (Remarks.)
- 1934a *Peltura* (= *Cyclognathus*) *transiens* — Størmer, p. 332. (Listed.)
- 1944a *Peltura cornigera* Westergård — Westergård, p. 43, pl. 13, fig. 4. (Fig. of pygidium with rudimentary marginal spines.)
- 1944a *Peltura cornigera* Wgård. — Westergård, p. 26. (Distribution in Sweden.)

Type data: — As lectotype I select the pygidium (P. M. O. no. 19947a) figured by Brögger (1882, pl. I, fig. 6). It is associated with other parts of the same species, and was collected by Brögger in 1879 at Vestfossen in Eiker, Norway.

Diagnosis: — A *Peltura* species with: obsolete glabellar furrows in adult crania; postocular cheeks somewhat more than half as wide as occipital ring; narrow free cheeks with slender spine almost normal to margin; pygidium with 3 pairs of short marginal spines and axis with 2 rings and end lobe. Thorax insufficiently known.

Remarks: — Brögger (1882) remarked that the head shield of *P. transiens* is very like that of *P. scarabaeoides*, but did not particularly mention the free cheek. A restudy of Brögger's material showed that the free cheeks have spines as in *P. cornigera*. This is also seen in additional material collected at the type locality. Westergård (1922, p. 176) compared *P. cornigera* with *P. transiens* (as described by Brögger) and stated that the latter differed in having no cheek spine, in having one, rarely two pairs of pleural furrows in the pygidium, and having apparently more rudimentary marginal spines in the pygidium. As *P. transiens* does have free cheeks with spine and the pleural furrows in the pygidium proved to be developed exactly as in *P. cornigera*, I believe that *P. cornigera* should be considered a synonym of *P. transiens*. The third difference noted by Westergård, namely that the

spines in *P. transiens* are more rudimentary than in *P. cornigera*, is rather insignificant, as the spines in both cases are rather small. Furthermore, Westergård later (1944a) included in *P. cornigera* a pygidium with rudimentary marginal spines. In the type material of *P. transiens* the spines are more or less damaged, and may not have been shorter than in the pygidium of *P. cornigera* figured by Westergård in 1922 (pl. XV, fig. 23). The cranidium figured by Westergård in 1922 (pl. XV, fig. 19) differs from those described below in having smaller postocular cheeks. Cranidia of the same type as those described below occur, however, at the type locality of *P. cornigera* (Grönhögen, Öland, Sweden).

Description of Norwegian material: — This is based on detached parts of the shield. The largest cranidium present is about 10 mm long. Cephalic axis slightly longer than wide, tapering slightly forwards, bluntly rounded in front. Occipital ring with faint node. Two pairs of very faint glabellar furrows. No anterior border furrow. Eye ridges oblique and indistinct. Interocular cheeks narrow. Postocular cheeks somewhat wider than half the width of occipital ring.

Free cheeks pelturoid, elongate, with relatively wide border and a slender cheek spine almost normal to the margin, and situated far back. The spine is slightly curved.

Hypostoma rather like that of *P. scarabaeoides*.

Thorax known only from fragments of segments.

Pygidium sub-semicircular. Axis with two rings and end lobe. Pleural regions about as wide as axis in front. Two pairs of distinct and one indistinct pair of short posterior pleural furrows. Three pairs of short marginal spines. Terrace lines usually seen.

Occurrence: — Norway: Eiker (Vestfossen), Røyken (Slemmestad) — *Acerocare* zone (2d ϵ), subzone of *Peltura transiens*. Associated with *Parabolina heres heres*. — Sweden (same horizon).

Genus *Nericiaspis* Tjernvik 1955.

Type species: — *Jujuyaspis*(?) *robusta* Tjernvik 1953, by original designation.

Diagnosis: — Pelturinae with: *Peltura*-like cranidium, but with prominent intergenal spines; sub-elliptical pygidium with few segments. Thorax and free cheeks unknown.

Occurrence: — Sweden, zone of *Peltura scarabaeoides*.

Relationships: — The type species is the only known species. *Nericiaspis* most probably developed from *Peltura* (cf. Tjernvik, 1955).

Nericiaspis robusta (Tjernvik 1953).

Pl. 2, fig. 6; pl. 6.

- 1953 *Jujuyaspis*(?) *robusta* sp. n. — Tjernvik, p. 75, text fig. 2. (Descr. and fig. of incomplete cranidium.)
1955 *Nericiaspis robusta* (Tjernvik) — Tjernvik, p. 210, pl. II, figs. 1—4; text-fig. 1 B. (Descr. Figs. of cranidia and pygidia.)

Holotype: — By monotypy the incomplete cranidium figured by Tjernvik (1953), from Lanna, Nerike, Sweden.

Diagnosis: — A *Nericiaspis* species with: postocular cheeks somewhat narrower than occipital ring; small palpebral lobes opposite S3; interocular cheeks about one-fourth as wide as glabella at eye line; S1 and S2 distinct, S3 indistinct. No other parts than cranidium known.

Occurrence: — Sweden: *Peltura* zone, subzone of *Peltura scarabaeoides* and *Sphaerophthalmus humilis*.

Genus *Acerocare* Angelin 1854.

Type species: — *Acerocare ecorne* Angelin 1854, by monotypy.

Diagnosis: — Pelturinae with: rather anteriorly situated palpebral lobes (opposite S3), short but distinct pre-glabellar field; rather wide postocular cheeks; more or less distinct glabellar furrows; free cheeks pelturoid, without spine; thorax with 12 or more segments; pleural ends truncated, but may be provided with small spines; pygidium with 6 or more axial rings, and with fine terrace lines sub-parallel to margin.

Remarks: — Angelin (1854) erected this genus for *Acerocare ecorne*. Moberg & Möller (1898) added *A. tullbergi*, as well as a number of species which later have been transferred to other genera (*Acerocarina*, *Westergårdia*, *Peltura*, and *Leptoplastus*).

Included species: —

Acerocare ecorne Angelin 1854.

A. tullbergi Moberg & Möller 1898.

Occurrence: — *Acerocare* zone, Norway, Sweden.

Phylogeny and relationships: — *Acerocare* resembles, and is no doubt close to *Acerocarina* and late *Peltura* species, but it is difficult to judge from which of these genera it developed. It is unfortunate that the exact stratigraphic position of *A. tullbergi* is not known. It differs from *A. ecorne* i. a. in having wider fixed cheeks, wider pleural regions, marginal spines in the pygidium, and at least 2 more thoracic segments. On the whole, *A. tullbergi* appears more advanced, and probably developed from the closely related *A. ecorne*.

Acerocare ecorne Angelin 1854.

Pl. 2, fig. 3; pl. 7; pl. 30, figs. 1—8; pl. 31.

- 1854 *Acerocare ecorne*. n. sp. — Angelin, p. 46, pl. XXV, fig. 10. (Descr. Fig. of restored dorsal shield.)
- 1898 *Acerocare ecorne* Ang. — Moberg & Möller, p. 231, pl. 10, figs. 1—10. (Descr. Figs. of all parts of the dorsal shield, immature cranidia, and hypostoma.)
- 1922 *Acerocare ecorne* Angelin — Westergård, p. 178, pl. XVI, figs. 6—14. (Fig. of axial shield and copies of Moberg & Möller's figs.)
- 1925 *Acerocare ecorne* — Raw, pp. 262, 264. (Remarks.)
- 1947 *Acerocare ecorne* Ang. — Westergård, p. 26. (Distribution in Sweden.)
- 1955 *Acerocare ecorne* Angelin — Tjernvik, p. 209, text-fig. 1 C. (Sketch of cranidium.)

Type data: — A lectotype should be selected from material from Sandby, Sweden; and from Angelin's specimens.

Diagnosis: — An *Acerocare* species with: fixed cheeks about three-fourths as wide as occipital ring; palpebral lobes close to glabella, two small tubercles near anterior corners of cranidium; four pairs of faint glabellar furrows; a pair of anterior pits may be developed; free cheeks pelturoid, without spine; thorax with 12 segments, axial nodes, and truncated pleural ends with tiny spine in posterior corner; pygidium entire with 6—7 axial rings and terrace lines subparallel to margin.

Remarks: — Some cranidia from Sweden show rather distinct muscle marks, which are described above (p. 92).

Norwegian material: — This conforms with the Swedish material but shows that their pleural ends have a tiny posterior spine, corresponding to that in *A. tullbergi*. A bedding surface almost covered with more or less complete immature shields (4—8 mm long) is described above (p. 71).

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad). — *Acerocare* zone (2d ϵ), subzone of *Acerocare ecorne*. Associated with *Parabolina acanthura* and *Pelturina punctifera* n. sp. — Sweden (same horizon).

Acerocare tullbergi (Moberg & Möller 1898).

Pl. 7; pl. 30, figs. 9—11.

- 1880 *Acerocare* sp. — Tullberg, p. 6. (Mentioned.)
- 1898 *Acerocare Tullbergi* n. sp. — Moberg & Möller, p. 254, pl. 14, figs. 6—9. (Descr. Figs. of cranidium, free cheek, hypostoma, and thorax with pygidium.)
- 1922 *Acerocare Tullbergi* Moberg & Möller — Westergård, p. 178, pl. XVI, figs. 15—18. (Remarks. Figs. of cranidium, free cheek, and hypostoma, copied from Moberg & Möller, and fig. of thorax with pygidium.)
- 1925 *Acerocare Tullbergi* Moberg & Möller — Raw, p. 264. (Remarks.)
- 1947 *Acerocare tullbergi* Mob. & Möll. — Westergård, p. 26. (Distribution in Sweden.)

Type data: — As lectotype I select the cranium figured by Moberg & Möller (1898, pl. 14, fig. 6), from Andrarum, Scania, Sweden.

Diagnosis: — An *Acerocare* species with: practically no preglabellar field; interocular cheeks about one-fourth as wide as glabella at eye line; fixed cheeks markedly wider than occipital ring and with distinct intersutural spines; thorax with (at least) 14 segments; truncate pleural ends with 2 small spines; pygidium with 4 pairs of marginal spines.

Remarks: — Raw (1925) suggested that the hypostoma, thorax, and pygidium figured by Moberg & Möller (1898) do not belong to *Acerocare*, but to another genus, perhaps *Parabolinella*. However, there is no reason to doubt that they are conspecific with the cranium and free cheek figured by Moberg & Möller. Admittedly, no axial or dorsal shields have been found to prove this, but there are numerous detached parts in the type material, and no traces of any other species. The thorax assigned to *A. tullbergi* differs from that of *A. ecorne* i. a. in being wider, but the cranium of *tullbergi* is correspondingly wider than that of *A. ecorne*. Furthermore the surface ornamentation of the thorax of *A. tullbergi* agrees with that of the cranium.

As pointed out by Westergård (1922) the pleural ends of *A. tullbergi* have each two small spines, one from the posterior corner and a smaller one from the middle of the lateral margin of the pleural end. The marginal spines in the pygidium seem to correspond to the smaller anterior pleural spines. It supports the reference of the thorax to *A. tullbergi* that small pleural spines, corresponding to the posterior pleural spines in *A. tullbergi*, have now been observed also in *A. ecorne*.

The intergenal spines in *A. tullbergi* are rather distinct (pl. 22, fig. 11). Anterior pits may be well developed in larger crania, which furthermore show 4 pairs of glabellar furrows. *A. tullbergi* carries, like *A. ecorne*, a pair of small bosses in the frontal area, one near each anterior corner.

Occurrence: — Sweden: *Acerocare* zone.

Genus *Saltaspis* Harrington & Leanza 1952.

Type species: — *Jujuyaspis steinmanni* Kobayashi 1936, by original designation.

Diagnosis: — Pelturinae with: medium-sized palpebral lobes close to glabella, and rather anteriorly situated; proparian facial sutures; postocular cheeks with a pair of long and strong spines; thorax with 12 segments and fusiform axis; pleurae with fulcra close to axis, and with short pleural spines; semi-circular, entire pygidium.

Remarks: — This genus was erected for *Jujuyaspis steinmanni* by Harrington & Leanza, who pointed out that it has a proparian facial suture, whereas *Jujuyaspis keideli*, type species of *Jujuyaspis*, which had also been attributed a proparian facial suture actually is opisthoparian (cf. postscript).

Saltaspis differs from *Jujuyaspis* i. a. in having a more *Peltura*-like thorax, with fulcra rather close to the axis and short pleural spines.

Included species: —

Saltaspis steinmanni (Kobayashi 1937).

S. viator Tjernvik 1956.

S. sp. — Tjernvik, 1955, 1956.

Occurrence: — Lower Tremadocian: Bolivia, Argentina. Upper Tremadocian: Sweden, ?Norway. Lowermost Arenigian: Sweden.

Phylogeny and relationships: — *Saltaspis* apparently is close to the earlier genus *Acerocarc*, with which it shares well-developed intergenal spines. The spines are especially prominent in *Saltaspis*. The known species of *Saltaspis* are no doubt closely related.

Saltaspis steinmanni (Kobayashi 1937).

Pl. 2, fig. 11.

- 1937a *Jujuyaspis steinmanni*, new species. — Kobayashi, p. 176, text figs. 1—5. (Descr. Figs. of cranidia, free cheek, part of thoracic segment, and pygidia.)
 1937c *Jujuyaspis steinmanni* Kobayashi — Kobayashi, p. 480, pl. IV, figs. 1—5. (Remarks. Figs. of cranidia, free cheek, part of thoracic segment, and pygidia.)
 1938 *Jujuyaspis steinmanni* Kobayashi — Harrington, p. 206. (Mentioned.)
 1952 *Saltaspis steinmanni* (Kobayashi) — Harrington & Leanza, p. 198, pl. I, figs. 1—2, 7. (Descr. Figs. of cephalon, dorsal shield, and fragmentary dorsal shield.)
 1953 *Jujuyaspis steinmanni* Kobayashi — Tjernvik, p. 75. (Mentioned.)

Type data: — As lectotype I select a cranidium figured by Kobayashi (1937a, text fig. 1; 1937c, pl. IV, fig. 1) from Guanacuno, Bolivia.

Diagnosis: — A *Saltaspis* species with: postocular cheeks slightly wider than occipital ring; palpebral lobes relatively large; thorax with 12 segments, proximal fulcra, fusiform axis, and very short pleural spines; entire pygidium.

Occurrence: — Lower Tremadocian. Bolivia, Argentina (zone of *Kainella meridionalis*).

Saltaspis viator Tjernvik 1956.

- 1956 *Saltaspis viator* n. sp. — Tjernvik, p. 201, text-fig. 30; pl. II, figs. 1—3. (Descr. Figs. of cranidium, free cheek, and pygidium.)

Holotype: — A cranidium figured by Tjernvik (1956, pl. II, fig. 1), from Västergötland, Sweden.

Diagnosis: — Differs from the type species in having: longer postocular cheeks; palpebral lobes nearer to the anterior margin; converging preocular facial sutures; and very much wider pygidial border.

Occurrence: — Sweden: Lowermost Arenigian (zone of *Plesio-megaspis armata*).

Saltaspis sp.

Pl. 8.

1955 *Saltaspis* sp. — Tjernvik, text-fig. 1 D. (Drawing of cranidium.)1956 *Saltaspis* sp. — Tjernvik, p. 203, pl. II, fig. 4. (Remarks, fig. of cranidium.)

Remarks: — According to Tjernvik (1956), the cranidium (the only part known) differs from that of *S. viator* in the following features: the palpebral lobes are situated further back, the preocular facial sutures seem to be subparallel, and the postocular cheeks are shorter. In all these features the species agrees better with the type species than with *S. viator*.

Norwegian material: — A single fragment of a cranidium may possibly belong to this species.

Occurrence: — Sweden: Upper Tremadocian zone of *Apatokephalus serratus*. ?Norway: Upper Tremadocian Ceratopyge Limestone (3aγ) at Slemmestad, Røyken.

Genus *Peltocare* n. gen.

Name: — From Greek *πελτη* (= crescent-shaped shield) and *καρπ* (= head). The name suggests the likeness to *Peltura* and *Acerocare*.

Type species: — *Acerocare norvegicum* Moberg & Möller 1898.

Diagnosis: — Pelturinae with: small palpebral lobes close to glabella and far forwards, almost on line with preglabellar furrow; short frontal area; glabellar furrows faint or missing; free cheeks pelturoid, without spine; ()-sided thorax with 12 segments (where number is known); entire pygidium with terrace lines.

Included species: —

Peltocare glaber (Harrington 1938) (earlier *Cyclognathus*)
(= ?*P. norvegicum*)

P. norvegicum (Moberg & Möller 1898) (earlier: *Acerocare*, *Peltura*)

P. olenoides (Salter 1866) (earlier: *Conocoryphe*?, *Peltura*)

P. rotundifrons (Matthew 1893) (earlier: *Cyclognathus*).

Occurrence: — Upper Tremadocian in Norway, Sweden, Wales, E. Canada, Argentina.

Phylogeny and relationships: — *Peltocare* resembles late *Peltura* species like *P. costata*, but differs i. a. in having wider fixed cheeks and postocular facial sutures which cut the cephalic margin further forward. *Peltocare* shares these features with *Acerocare* and *Saltaspis*, and it is probable that it is closest related to these two genera, although it differs in having the palpebral lobes set further forwards, thus resembling *Acerocarina*. All species assigned to *Peltocare* seem to be close to each other, and differ only in minor details.

Peltocare norvegicum (Moberg & Möller 1898).

Pl. 2, fig. 9; pl. 8; pl. 27, figs. 6, 8, 10—14.

- 1882 *Cyclognathus micropygus*, Linrs. — Brögger, p. 111, pl. I, figs. 3, 3a, 3c, 4. (Descr. Figs. of dorsal shield, cranidium, and free cheek. The hypostoma in fig. 3b does not belong to this species.)
- 1898 *Acerocare norvegicum* n.sp. — Moberg & Möller, p. 243. (Point out differences between this species and Linnarsson's *Cyclognathus micropygus*.)
- 1905a *Acerocare norvegicum* Mbg. — Wiman, p. 63, pl. III, figs. 19—30. (Descr. Figs. of cranidia, thoracic segments, and pygidia.)
- 1906 *Acerocare norvegicum* Moberg & Möller — Moberg & Segerberg, p. 82, pl. IV, figs. 27—28. (Figs. of cranidium and pygidium, copied after Wiman, 1902.)
- 1908 *Acerocare norvegicum* Moberg — Raw, p. 513. (Included in *Leptoplastides*.)
- 1919 *Acerocare norvegicum* Moberg & Möller — Lake, p. 92. (Mentioned.)
- 1920 *Acerocare norvegicum* Mbg. — Størmer, p. 8, pl. I, figs. 5, 6, 10. (Additional description. Figs. of axial shield and larval cranidia.)
- 1920 *Acerocare?* sp. — Størmer, p. 14, pl. II, fig. 9. (Descr. and fig. of hypostoma.)
- 1934a *Peltura norvegicum* — Størmer, p. 332. (Listed.)
- 1938 *Acerocare norvegicum* Moberg — Harrington, p. 213. (Mentioned.)
- ?1938 *Cyclognathus glaber* sp. nov. — Harrington, p. 212, pl. IX, figs. 1, 5, 12. (Descr. Figs. of dorsal shields.)
- 1953 *Acerocare?* *norvegicum* — Høltedahl, p. 189, fig. 70: figs. 2—3. (Figs. of cranidium and pygidium.)

Type data: — As lectotype I select a cranidium (P. M. O. no. H 2619) figured by Brögger (1882, pl. I, fig. 3), from Vekkerø, Oslo, Norway. It comes from 3aα (erroneously printed as 3cα in the explanation of Brögger's plate.)

Remarks: — Brögger (1882) included this form in *Cyclognathus micropygus* Linnarsson, but Moberg & Möller (1898) pointed out that it differed from this, and gave Brögger's form the name *Acerocare norvegicum*. Raw (1908) included it in *Leptoplastus* (*Leptoplastides*), but Lake (1919) could not see any reasons for placing it either in *Leptoplastus* or *Leptoplastides*. Størmer (1934) assigned it to *Peltura*, whereas other authors have retained it in *Acerocare*. Although the species resembles both *Acerocare* and *Peltura*, it differs from both, and I propose to include it in a new genus, *Peltocare*.

Diagnosis: — A *Peltocare* species with fixed cheeks somewhat more than half as wide as occipital ring; thorax with 12 segments; pygidium with 4 axial rings and strong terrace lines.

Description: — The dorsal shield figured by Brögger (1882, pl. I, fig. 4) is fully 40 mm long, the cranidium being 13 mm and the pygidium 7 mm long. The largest cranidia present are about 15 mm long.

Cranidium pelturoid. Cephalix axis slightly longer than wide, slightly tapered forwards, and bluntly rounded in front. Occipital ring with axial node. Occipital furrow shallow, faintly tripartite. Two practically invisible

pairs of glabellar furrows. No anterior border furrow. Frontal area slightly convex, almost flat, and downsloping. Eye ridges absent. Palpebral lobes small, far forwards, and close to glabella. Eye line only very slightly behind preglabellar furrow. Interocular cheeks very small. Postocular cheeks somewhat more than half as wide as occipital ring. Facial sutures converge in front of eye and diverge strongly just behind eyes, but diverge less further back.

Free cheeks pelturoid, without cheek spine. Eyes with facets. Border distinct, convex.

Hypostoma found in situ in one specimen. Subquadrate with rounded corners. Central body almost triangular, tapering strongly backwards. Brim downsloping. Border distinct, somewhat expanded at posterior corners, and with terrace lines subparallel to border.

Thorax with 12 segments. Anterior axial rings about twice as wide as posterior rings. Axial rings without axial node. Pleural regions narrower than axis. No pleural ends are well preserved, but they seem to be of the *Peltura* type with broad-based short spines.

Pygidium more than twice as wide as long, with rounded and entire posterior border. Axis occupies about one-third of the entire width of the pygidium anteriorly, and tapers markedly backwards. Axis with three rings and end lobe. Pleural regions with rather faint furrows, except anterior pair which is rather distinct. Surface traversed by distinct terrace lines. Border distinct, convex.

A f f i n i t i e s : — *P. glaber* (Harrington 1938) is no doubt very close to *P. norvegicum*, and, as far as can be judged from the illustrations and description, appears to be conspecific. The cephalon seems to agree with that of *norvegicum*, but the posterior facial suture is not seen so well in the specimens figured by Harrington (1938, pl. IX, figs. 1 and 12), as they may be more or less covered by the free cheeks. Nevertheless, the course of the facial suture appears to be the same in both forms. The thorax consists of 12 segments and has also the same outline as in *P. norvegicum*. The pygidium appears to be identical with that of *P. norvegicum*. *P. glaber* reaches at least the same size as *P. norvegicum*, as can be seen from the specimen figured by Harrington in plate IX, figure 5.

P. rotundifrons (Matthew 1893) is also close to *P. norvegicum*, but appears to be a smaller species.

O c c u r r e n c e : — Norway: Oslo (Lysaker, Kampen, Tøyen), Ringes-rike (Klekken), Hadeland (Jaren), Østerdalen (Glomstad). — Zone of *Symphysurus incipiens* (3aα). Associated with *Bienwillia tetragonalis broegeri* n. subsp. and non-olenids. — Sweden (same horizon). ?Argentina (Tremadocian).

Peltocare olenoides (Salter 1866).

- 1886 *Conororyphe?* *olenoides*, n.sp. — Salter, p. 308, pl. 8, fig. 6. (Descr. and sketch of restored cephalon.)
1919 *Peltura olenoides* (Salter) — Lake, p. 100, pl. XII, figs. 4—5. (Descr. Figs. of Salter's specimen and imperfect dorsal shield.)

Type data: — Holotype (by monotypy) is the imperfect cephalon described by Salter, and upon which his restoration of the cephalon was based. The specimen was figured by Lake (1919). It is from the Upper Tremadocian at Garth, Minffordd, Portmadoc, Wales.

Remarks: — The species has the palpebral lobes set far forwards and apparently belongs to *Peltocare*. Unfortunately the number of thoracic segments is not definitely known; it was suggested by Lake (1919) to be 11. It may be very close to *P. norvegicum*, but as far as can be judged from the two imperfect specimens known, it may have narrower fixed cheeks.

Occurrence: — Wales (Upper Tremadocian).

Peltocare rotundifrons (Matthew 1893).

- 1893 *Cyclognathus rotundifrons*, Matt. — Matthew, p. 107, pl. VII, figs. 16a-b. (Descr. Schematic drawing of cranium with some attached thoracic segments and of free cheek.)
1952 *Cyclognathus rotundifrons* Matthew — Hutchinson, p. 94, pl. V, figs. 7—9. (Descr. Figs. of dorsal shield, cephalon, and free cheek.)

Type data: — As lectotype should be selected one of Matthew's specimens from Division 3d at the Suspension Bridge, St. John, New Brunswick, Canada.

Diagnosis: — A *Peltocare* species with: fixed cheeks about half as wide as occipital ring; thorax with 12 segments; pygidium with 2 axial rings.

Occurrence: — Canada (Division 3d at St. John, New Brunswick, McLeod formation in Nova Scotia).

Genus *Pelturina* n. gen.

Name: — The name *Pelturina* alludes to the likeness to *Peltura*.

Type species: — *Pelturina punctifera* n.sp.

Diagnosis: — *Pelturinae* resembling *Peltura*, but with palpebral lobes further back (opposite S2).

Remarks: — The type species is the only known species assignable to *Pelturina*.

Occurrence: — *Accrocare* zone; Norway, Sweden.

Affinities: — The genus *Pelturina* seems to be close to *Peltura*, from which it may have developed. In this connection the cranidium of *Peltura cornigera* (= *P. transiens*) figured by Westergård (1922, pl. XV, fig. 19) is of interest, as its eyes are placed further back than usual in *Peltura*, and thus seems to point towards *Pelturina*.

Pelturina punctifera n. gen. & sp.

Pl. 2, fig. 5; pl. 7; pl. 28, figs. 1–4.

1944a *Peltura* (*paradoxa*?) — Westergård, p. 44. (Three small cranidia recorded)

Name: — The name *punctifera* alludes to the finely punctate surface of the cranidium.

Holotype: — A cranidium (P.M.O. no. 66806) collected by H. Rosendahl in 1931 near Brummundsagen, Brummunddalen, Norway. It is associated with *Parabolina heres lata* and *Westergårdia lata*.

Diagnosis: — A *Pelturina* species with: eye line crossing the axial line at about one-third of the axial line from the anterior margin to the posterior margin of the cranidium; postocular cheeks markedly less than half as wide as occipital ring; surface of cranidium finely punctate; pygidium with 2 axial rings and end lobe of two fused rings and 2 pairs of marginal spines. Free cheeks and thorax unknown.

Description: — This is based on 12 cranidia and two pygidia. The pygidia are considered conspecific, as they apparently agree in size with the cranidia, and cannot belong to any of the associated species.

The largest cranidia are about 6 mm long. Posterior two-thirds of cephalic axis almost parallel-sided, anterior third markedly tapering, truncated in front, although with rounded corners. Occipital ring with two axial nodes, one behind the other. Occipital furrow well developed, composite. Glabellar furrows not united across glabella. S1 and S2 rather distinct. S3 and S4 shorter and faint. S1 oblique backwards, sinuous; S2 curved oblique backwards. S3 oblique, straight, not reaching axial furrow, outer end close to middle part of S4, as if branching from it. S4 oblique forwards, curved, reaches axial furrow. Periglabellar area in front of palpebral lobes forms narrow band of equal width curving round the front of the glabella. Palpebral lobes small. Eye ridges absent. Eye line through S2 and crossing sagittal line of cranidium about one-third of the way from anterior to posterior border. Postocular cheeks pelturoid, markedly narrower than half the width of occipital ring. Interocular cheeks very narrow. Facial sutures converging in front of palpebral lobes, diverging moderately behind palpebral lobes. Surface finely punctate.

Free cheeks, hypostoma, and thorax unknown.

Probably conspecific pygidia not well preserved. 2 pairs of marginal spines. Pleural regions downsloping, with two pairs of distinct furrows. Axis with two rings and end lobe of two fused rings.

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad), Brummunddalen (near Brummundsagen) — *Acerocare* zone (2de), subzone of *Westergårdia* (associated with *Westergårdia* species and *Parabolina heres lata*) and subzone of *Acerocare ecorne* (associated with *Acerocare ecorne* and *Parabolina acanthura*). — Sweden (subzone of *Westergårdia*).

Genus *Acerocarina* Poulsen 1952.

Synonym: — *Cyclognathus* Linnarsson 1875 non St. Hillaire 1833.

Type species: — *Cyclognathus micropygus* Linnarsson 1875, by original designation.

Diagnosis: — Pelturinae with: pelturoid cranidium; small palpebral lobes close to glabella and far forwards, almost on line with preglabellar furrow; no glabellar furrows; free cheeks pelturoid, without spine; 10 thoracic segments; posterior half of thorax rapidly narrowing backwards; pleural ends truncate, with or without minute spine in posterior corner; small, entire pygidium, with strong terrace lines sub-parallel to posterior margin.

Remarks: — Linnarsson (1875) erected the genus *Cyclognathus* for the two species *C. micropygus* and *C. granulatus*. Brögger (1882) included some species which have later been transferred to *Peltura* (*Peltura costata*, *P. minor*, *P. transiens*), and identified as *Cyclognathus micropygus* a form which is now referred to as *Peltocare norvegicum*. Moberg & Möller (1898) regarded *Cyclognathus* as a synonym of *Acerocare*. Lake (1919, p. 97) revived the name *Cyclognathus* for *C. micropygus* and *C. granulatus* (and similar species). Poulsen (1952) pointed out that *Cyclognathus* Linnarsson 1875 is a homonym of *Cyclognathus* St. Hillaire 1833, and gave the new name *Acerocarina* to Linnarsson's genus.

Included species: —

Acerocarina granulata (Moberg & Möller 1898)

A. micropyga (Linnarsson 1875).

Occurrence: — *Acerocare* zone; Norway, Sweden.

Phylogeny and relationships: — *Acerocarina* probably developed from *Peltura* and is probably ancestral to *Westergårdia*. *Acerocarina micropyga* is, no doubt closely related to *A. granulata*, which differs i. a. in having narrower and tuberculate pleural regions.

Acerocarina granulata (Moberg & Möller 1898).

Pl. 7.

- 1898 *Acerocare granulatum* n. sp. [partim] — Moberg & Möller, p. 244, pl. XI, figs. 1—9. (Descr. Figs. of imperfect dorsal shield, axial shield, cranidium, free cheek, hypostoma, thoracic segment, immature cranidium, and restored dorsal shield. Pl. XIV, figs. 1—5 are of *Westergårdia illaenopsis*.)
- 1898 *Acerocare granulatum* Mbg. & Möller var. — Moberg, pl. 16, fig. 6. (Fig. of almost complete dorsal shield.)
- 1922 *Cyclognathus granulatus* (Moberg & Möller) — Westergård, p. 179, pl. XVI, figs. 26—32. (Remarks. Figs. of cranidium, free cheek, hypostoma, thoracic segment, pygidium, and immature cranidium, all copied from Moberg & Möller, and fig. of axial shield.)
- 1947 *Cyclognathus granulatus* (Mob. & Möll.) — Westergård, p. 26. (Distribution in Sweden.)

Type data: — As lectotype I select the axial shield figured by Moberg & Möller (1898, pl. 11, fig. 1), from Sandby, Scania, Sweden.

Diagnosis: — An *Acerocarina* species with: fixed cheeks almost three-fourths as wide as occipital ring; pleurae up to three-fourths as wide as axial rings, and with rows of tubercles at anterior and posterior margin; pygidium with anterior part of pleural regions about three-fourths as wide as anterior axial rings, well defined axis, and truncate or indented posterior margin.

Norwegian material: — This consists only of a few detached parts, but seems to agree quite with the Swedish material.

Occurrence: — Norway: Eiker (Teigen). — *Acerocare* zone (2d ϵ). Associated with *Parabolina heres heres*, i. e. from the subzone of *Peltura transiens* or the subzone of *Peltura costata*. — Sweden (same zone).

Acerocarina microphyga (Linnarsson 1875).

Pl. 2, fig. 10; pl. 7; pl. 28, fig. 5.

- 1875 *Cyclognathus micropygus* n. gen. & n. sp. — Linnarsson, p. 500, pl. XXII, figs. 8—10. (Descr. Figs. of dorsal shield, thoracic segment, and pygidium.)
- 1898 *Acerocare micropygum* Linrs. sp. — Moberg & Möller, p. 237, pl. 10, figs. 11—18. (Descr. Figs. of axial shield, cranidium, free cheek, hypostoma, thoracic segment, pygidium, immature cranidium, and restored dorsal shield.)
- 1922 *Cyclognathus micropygus* Linnarsson — Westergård, p. 178, pl. XVI, figs. 19—25. (Remarks. Figs. of cranidium, free cheek, hypostoma, thoracic segment, pygidium, and immature cranidium, all copied from Moberg & Möller, and fig. of dorsal shield.)
- 1947 *Cyclognathus micropygus* Linrs. — Westergård, p. 26. (Distribution in Sweden.)
- 1952 *Cyclognathus micropygus* Linnarsson — Poulsen, p. 442. (Cited as type species of *Acerocarina*.)
- Non 1882 *Cyclognathus micropygus*, Linrs. — Brögger (= *Peltocare norvegicum*.)

Type data: — As lectotype I select the dorsal shield figured by Linnarsson (1875, pl. 22, fig. 8), from Åkarpsmölle, Scania, Sweden.

Diagnosis: — An *Acerocarina* species with: fixed cheeks slightly more than half as wide as occipital ring; pleurae up to as wide (tr.) as axial rings and without tuberculation; pygidium with anterior part of pleural regions about as wide as anterior axial ring, with axis not well defined posteriorly, and rounded posterior margin.

Norwegian material: — This apparently agrees quite with the Swedish.

Occurrence: — Norway: Oslo (Gamlebyen). — *Acerocare* zone (2de), ?subzone of *Peltura costata*. Associated with parts of a *Parabolina* species (probably *P. heres heres*) and free cheeks probably of *Peltura costata*. — Sweden (same zone).

Genus *Westergårdia* Raymond 1924.

Type species: — *Boeckia scanica* Westergård 1909, by original designation.

Diagnosis: — Pelturinae with: palpebral lobes relatively far from glabella and occupying an anterior, posterior, or intermediate position; free cheeks without spine; thorax with 9 segments (where number is known) and pyriform outline; pleural ends truncate and with minute spine in posterior corner; pygidium with more or less trapezoidal outline, without border, and traversed by terrace lines.

Synonym: — *Sphaerophthalmoides* Hutchinson 1952 with type species *Leptoplastus latus* Matthew 1892 is no doubt a synonym of *Westergårdia*. In a letter (dated April 23., 1954) Dr. R. D. Hutchinson has kindly informed me that he realized that *Sphaerophthalmoides* was a synonym of *Westergårdia* shortly after his paper was published.

Included species: —

Westergårdia illaenopsis (Westergård 1909) (= *W. lata*)

W. intermedia Westergård 1944

W. lata (Matthew 1892) (transferred here from *Sphaerophthalmoides*)

W. ornata (Hutchinson 1952) (transferred here from *Sphaerophthalmoides*)
(possible syn. of *W. lata*)

W. scanica (Westergård 1909)

W.? *inornata* Harrington & Kay 1951 from the Lower Tremadocian in Eastern Colombia is incompletely known, and it is rather doubtful whether it should be included in this genus.

Occurrence: — *Acerocare* zone; Norway, Sweden, Canada.

Phylogeny and relationships: — It seems rather certain that *Westergårdia* developed from the slightly earlier genus *Acerocarina*. The genera agree in many features, thus also in having a thorax with pyri-

form outline, a rather rare feature among olenids. The main difference is that the palpebral lobes are situated far forward and close to the glabella in *Acerocarina*, whereas they are more or less removed from the glabella in *Westergårdia*. They have a rather anterior position in *Westergårdia scanica*, although not so extremely as in *Acerocarina*. They are placed further back in *W. intermedia* and as far back as opposite S1 in *W. lata*. It is very interesting that *Westergårdia scanica*, which morphologically is closest to *Acerocarina*, appears slightly earlier than the others in Scania. Apparently the palpebral lobes acquired a progressively more posterior position during the phylogeny of *Westergårdia*. The evolution seems to have been rather rapid, thus *W. scanica*, *W. intermedia*, and *W. lata* occur together in Norway.

Westergårdia intermedia Westergård 1944.

Pl. 7.

- 1944a *Westergårdia intermedia* sp. n. — Westergård, p. 44, pl. 3, figs. 13–14. (Desc.: Figs. of cranidia.)
 1947 *Westergårdia intermedia* Wgård. — Westergård, p. 26. (Distribution in Sweden.)

Holotype: — A cranidium figured by Westergård (1944a, pl. 3, fig. 14), from a boring at S. Sandby, Scania, Sweden.

Diagnosis: — A *Westergårdia* species with: intermediate position of palpebral lobes; interocular cheeks about three-fourths as wide as glabella at eye line.

Norwegian material: — A few cranidia, which agree with those figured by Westergård.

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad). — *Acerocare* zone (2d ϵ), subzone of *Westergårdia*. Associated with *Westergårdia scanica*, *W. lata*, *Parabolina heres lata*, and *Pelturina punctifera* n.sp. — Sweden (same horizon).

Westergårdia lata (Matthew 1891).

Pl. 7; pl. 28, figs. 7–10.

- 1880 *Cyclognathus* — Tullberg, p. 6. (Mentioned.)
 1882 *Cyclognathus* — Tullberg, p. 23. (Mentioned.)
 1891 *Leptoplastus latus* N. sp. — Matthew, p. 462, text figs. 1–3. (Short description. Figs. of cranidium, free cheek, and thorax with pygidium.)
 1892 *Leptoplastus latus*, Matt. — Matthew, p. 54, pl. XIII, figs. 10a–c. (Desc. New figs. of cranidium, free cheek, and thorax with pygidium.)
 1893 *Boeckia hirsuta* Brögger — Segerberg, p. 692. (Recorded.)
 1898 *Acerocare granulatum* n. sp. var. — Moberg & Möller, p. 248, pl. 14, figs. 1–5. (Figs. of axial shield, cranidia, and pygidia.)
 1909 *Boeckia? illænopsis* n. sp. — Westergård, p. 49, pl. I, figs. 14–20. (Copies of Moberg & Möller's figs. and figs. of two cranidia.)
 1919 *Acerocare granulatum*, var. — Lake, p. 96, foot note 2. (Remarks.)

- 1922 *Boeckia*(?) *illaenopsis* Westergård — — Westergård, p. 179, pl. 16, figs. 33—39.
(Copies of figs. in preceding paper.)
- 1929 *Boeckia illaenopsis* Wgd. — — Strand, p. 360. (Recorded.)
- 1934a *Boeckia illaenopsis* — — Stormer, p. 332. (Listed.)
- 1944a *Westergårdia illaenopsis* (Westergård) — — Westergård, p. 44, pl. 3, figs. 15—22.
(Descr. Figs. of cranidia, free cheeks, and pygidia.)
- 1947 *Westergårdia illaenopsis* (Wgård.) — — Westergård, p. 26. (Distribution in Sweden.)
- 1952 *Sphaerophthalmoides latus* (Matthew) — — Hutchinson, pp. 90, 92. (Remarks. Designated type species of *Sphaerophthalmoides*.)
- ?1952 *Sphaerophthalmoides ornatus*, sp. nov. — — Hutchinson, p. 91, pl. IV, figs. 18—25.
(Descr. Figs. of cranidia, free cheeks, and pygidia.)

Type data: — As lectotype should be selected one of Matthew's specimens from black shale of Division 3b at Navy Island, St. John Harbour, New Brunswick, Canada.

Diagnosis: — A *Westergårdia* species with: palpebral lobes far back, opposite S1; interocular cheeks about half as wide as occipital ring; cephalon partly or wholly covered with small tubercles; thorax ornamented with tubercles; pygidium sub-trapezoidal.

Remarks: — *Westergårdia lata* was originally assigned to *Leptoplastus*, but Hutchinson (1952, p. 92) pointed out that Matthew had oriented the free cheek reversely. The point which Matthew interpreted as the genal spine is actually the anterior prolongation of the border. The species was designated type species of *Sphaerophthalmoides* by Hutchinson, but this genus may be regarded as a synonym of *Westergårdia*. *W. lata* has the palpebral lobes placed just as far back as the Swedish species *W. illaenopsis*. I have examined a few cranidia of *W. lata* in the collections of the Swedish State Museum of Natural History (Paleozoological Department), Stockholm. The cranidia are from St. John, and were collected and identified by G. F. Matthew. They are rather poorly preserved, but suggested that *W. lata* might be a synonym of *W. illaenopsis*. However, according to Matthew's sketch of the thorax of *W. lata* ("*Leptoplastus latus*"), it appeared to have more thoracic segments (12?) than *W. illaenopsis*, which has at least 8, probably 9 (cf. Westergård, 1944a, p. 45), and furthermore to have rather distinct pleural spines, whereas *W. illaenopsis* was stated to have truncate pleural ends. As I was interested in obtaining more information on *W. lata*, Dr. Madeleine A. Fritz of the Royal Ontario Museum of Zoology and Palaeontology in Toronto very kindly had casts made for me of all Matthew's cotypes (Royal Ontario Museum of Palaeontology, no. 333). The casts showed that the most complete fragment of an axial shield consisted of the posterior part of the cranidium and 9 thoracic segments. The 9th segment is represented by a part of the axial ring only. However, from the outline of the thorax it appears improbable that there could have been more thoracic segments behind the 9th, at least not as many as 2 or 3 more. It is possible that Matthew's restoration of the dorsal shield of the species was influenced

by his concept of it belonging to *Leptoplastus* (usually with 12 segments). The thoracic segments of *W. lata* display the same tuberculate ornamentation as *W. illaenopsis*, and some of the cranidia show faint granulation in the posterior part, just as in some specimens of *W. illaenopsis*. As to the pleural spines in *W. lata*, they are not very conspicuous, and some of the pleural ends appear truncate. I therefore believe that *W. illaenopsis* should be considered a junior synonym of *W. lata*. In this connection it is of interest that the associated *Parabolina heres lata* occurs both in Canada and Scandinavia.

Hutchinson (1952) erected the species *Sphaerophthalmoides ornatus* (i. e. *Westergårdia ornata*), which was stated to differ from *S. latus* (i. e. *W. lata*) in lacking the second glabellar furrow (S2), and in the ornamentation of the cephalon. However, these differences may only be apparent. In Scandinavian material of *W. lata* (= *illaenopsis*) it is seen that the glabellar furrows are hardly visible in well-preserved specimens with test, whereas they are rather distinct in more or less flattened specimens. The tuberculation of the cephalon may be more or less distinct, possibly due to preservation. Internal moulds do not show any tuberculation. As furthermore a faint tuberculation is seen in the posterior part of some of the cranidia of the type material of *W. lata*, it is possible that *W. ornata* is a synonym of *W. lata*.

Westergård (1944a, p. 45) suggested that the two cranidia which he figured in 1909 (pl. I, figs. 18—19) and in 1922 (pl. 16, figs. 33—34) may possibly belong to an independent species, as their fixed cheeks are narrower than in the type material of *W. illaenopsis*. In the Norwegian material there appears to be intermediate forms as well, and it is possible that the variations should be considered as intraspecific.

Norwegian material: — This consists of detached parts of the dorsal shield. Cranidia with test preserved show a tuberculation which is more distinct than in *W. scanica*. As in this species, the cranidia are provided with a pair of minute intergenal points, and the occipital ring has a small keel-like axial node, which in some specimens is seen to be formed by two tiny tubercles, the one behind the other. The occipital furrow seems to be straighter and with deeper lateral parts than in *W. scanica*. A well-preserved free cheek with eye shows that the eye has facets, and that the border is ornamented with terrace lines parallel to the margin.

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad), Brummundalen. — *Acerocare* zone (2de), subzone of *Westergårdia*. Associated with *Parabolina heres lata*, *Pelturina punctifera* n. sp., and *Westergårdia intermedia* ± *W. scanica*. — Sweden (same subzone), Canada (New Brunswick, *Peltura* zone, *Westergårdia ornata* in Nova Scotia, *Peltura* zone of the MacNeil formation).

Westergårdia scanica (Westergård 1909).

Pl. 2, fig. 4; pl. 7; pl. 28, fig. 6.

- 1909 *Boeckia scanica* n. sp. — Westergård, p. 50, pl. I, figs. 9—13. (Descr. Figs. of axial shield, cranidium, and free cheek.)
- 1922 *Boeckia scanica* Westergård — Westergård, p. 179, pl. XVI, figs. 40—43. (Copies of the figs. in Westergård, 1909.)
- 1924 *Westergårdia scanica* (Westergård) — Raymond, p. 402. (Species discussed and selected as type species of *Westergårdia*.)
- 1944a *Westergårdia scanica* (Westergård) — Westergård, p. 44, pl. 3, figs. 6—12. (Remarks. Figs. of axial shield, cranidia — including holotype —, and probably conspecific pygidium.)
- 1947 *Westergårdia scanica* (Wgård.) — Westergård, p. 26. (Distribution in Sweden.)

Type data: — Lectotype (selected by Westergård, 1944a) is a cranidium, figured by Westergård (1909, pl. I, fig. 11; 1922, pl. 16, fig. 41; 1944a, pl. 3, fig. 6). It is from Andrarum, Scania, Sweden.

Diagnosis: — A *Westergårdia* species with: palpebral lobes far forwards; interocular cheeks about half as wide as glabella at eye line; thorax with 9 segments; pygidium rounded sub-trapezoidal.

Norwegian material: — This consists of detached parts, which agree quite with the Swedish material. Well-preserved cranidia show faint granulation, as also observed by Westergård. Furthermore they show a pair of minute intergenal intersutural spines and that the occipital ring has a keel-like node, which is formed by two small nodes, one behind the other. In some specimens the keel-like node is almost absent. The occipital furrow is composite; the middle, curved part is deepest, and the slightly oblique lateral parts may in some specimens be obsolete.

Occurrence: — Norway: Røyken (Nærsnes, Slemmestad), Oslo (Tøyen). — *Acerocare* zone (2de), subzone of *Westergårdia*. Associated with *Parabolina heres lata* and *Pelturina punctifera* n. sp. ± *Westergårdia intermedia* and *W. lata*. — Sweden (same horizon).

Genus *Boeckaspis* Henningsmoen 1955.

Name: — *Boeckaspis* was given as a new name for *Boeckia* Brögger 1882, non Malm 1870.

Type species: — *Boeckia hirsuta* Brögger 1882, by monotypy.

Diagnosis: — Pelturinae with: palpebral lobes opposite middle or posterior third of glabella and moderately remote from glabella; no preglabellar field; pelturoid free cheeks without spine; thorax with long, falcate spines; sub-trapezoidal pygidium with one pair of marginal posterolateral

spines and pleural areas densely covered with fine terrace lines subparallel to margin.

Included species: — Brögger erected the genus *Boeckia* for the one species *B. hirsuta*. Wiman (1905) added the species *B. mobergi*. In 1909 Westergård described two species as *B. scanica* and *B. ? illænopsis*, but they were later transferred to a new genus, *Westergardia*, by Raymond (1924). Størmer erected the species *B. jarensis* in 1922, but this turned out to be a synonym of *B. mobergi*, which at first was erroneously described as having a genal spine. *B. ? descensus* Clark 1924 probably is no olenid (cf. p. 22). *Boeckaspis* thus includes the following species:

Boeckaspis hirsuta (Brögger 1882)

B. jarensis (Størmer 1922) (subj. syn. of *B. mobergi*)

B. mobergi (Wiman 1905).

Occurrence: — *Dictyonema* zone (Lower Tremadocian); Norway, Sweden.

Phylogeny and relationships: — *Boeckaspis* and the closely related genera *Sphaerophthalmella* (cf. postscript) and *Jujuyaspis* undoubtedly developed from late pelturines, most probably from *Westergardia*, from which they differ mainly in having long pleural spines. *Boeckaspis mobergi* apparently is a descendant of the slightly earlier *B. hirsuta* which has slightly wider interocular cheeks and the eyes set slightly farther forwards.

Boeckaspis hirsuta (Brögger 1882).

Pl. 2, fig. 8; pl. 8; pl. 29, figs. 1—8.

1882 *Boeckia hirsuta*, n. sp. — Brögger, p. 122, pl. II, figs. 6, 6a-d. (Descr. Figs. of pygidia, thoracic segments, and restored cephalon.)

1909 *Boeckia hirsuta* Brögger — Westergård, pp. 49, 51. (Mentioned.)

1922 *Boeckia hirsuta* Brögger — Westergård, pp. 110, 179. (Mentioned.)

1922a *Boeckia hirsuta* Brögger — Størmer, pp. 6, 7. (Mentioned.)

Non 1893 *Boeckia hirsuta* Brögger — Segerberg, p. 692 (= *Westergardia lata*.)

Type data: — As lectotype I select a pygidium (P.M.O. no. H 2712), figured by Brögger (1882, pl. II, fig. 6b). It is associated with other parts of the same species, and was collected by W. C. Brögger in 1880 at Nærsnes in Røyken, Norway.

Diagnosis: — A *Boeckaspis* species with: centres of palpebral lobes opposite S2; interocular cheeks slightly more than half as wide as glabella at eye line; posterior part of cranidium tuberculate; rather wide free cheeks; thoracic axis and pleurae with rows of tubercles; pygidium with one pair of posterior marginal spines, and 4 axial rings and end lobe.

Description: — This is based on a great number of detached parts of the shield. The largest cranidia are about 7 mm long.

Cranidium about twice as wide as long. Cephalic axis slightly longer than wide, slightly tapering forward, bluntly rounded in front. Occipital ring with axial spine. Occipital furrow composite, deepest at the ends of the middle curved part. Two glabellar furrows (S1 and S2), which are rather faint and in some cranidia almost invisible. Preglabellar furrow just reaches anterior border furrow axially, so that there is no preglabellar field. Border narrow, rather short. Eye ridges distinct, slightly oblique, almost transverse, long. Palpebral lobes of medium size, upsloping with centres opposite S1. Interocular cheeks about half as wide as glabella at eye line. Postocular cheeks about two-thirds as wide as occipital ring. Preocular facial sutures rather convex, converging strongly. Postocular facial sutures diverging very strongly, but turn round and become almost parallel at the rounded tip of the postocular cheeks. The tips are flexed ventrad. Surface of cranium smooth, except for distinct tubercles on both sides of the posterior furrows and on occipital ring, and a pair of tubercles in front of the eye ridges.

Free cheeks pelturoid, without spine. Rather wide, and dropping rather steeply down from narrow ocular half-ring. Border distinct, with terrace lines subparallel to margin.

Hypostoma with lateral margins diverging slightly backward. Central body very strongly convex, tapering backwards to produce a triangular outline. Brim sloping ventrad. Border forms a pair of rounded lobes at posterior corners, so that posterior margin is incurved.

Thorax known from parts only, the largest part consisting of 8 segments. Axial rings with axial spine. Pleurae with very long pleural spines, except perhaps the anterior pleurae, which appear to have shorter spines. Axial rings and pleurae with tubercles. Segments partly imbedded in the matrix show that the tubercles are really short spines.

Pygidium trapezoidal. Posterior width about one-third of anterior width. Axial length about half the maximum width of pygidium. Axis wider than pleural regions. Axis with 5 rings with axial node (spine?) and end lobe. Posterior corners produced into spines. Surface covered with fine terrace lines.

Occurrence: — Norway: Røyken (Nærsnes). — *Dictyonema* zone, base of subzone of *Dictyonema flabelliforme sociale* (2 α). Associated with *Parabolina acanthura*.

Boeckaspis mobergi (Wiman 1905).

Pl. 8; pl. 29, figs. 9—12.

1905b *Boeckia Mobergi* n. sp. [partim] — Wiman, p. 81, pl. V, figs. 9, 11?, 12—14. (Descr. Figs. of cranidia and pygidia. According to Westergård, 1917, fig. 10 shows a free cheek of *Bienvillia? wimani* and fig. 11 either a genal spine of *B.? wimani*, or more probably, a pleural spine of *B. mobergi*.)

1906 *Boeckia Mobergi* Wiman — Moberg & Segerberg, p. 82. (Remarks.)

- 1909 *Boeckia Mobergi* Wiman [partim] — Westergård, p. 55, pl. II, figs. 6, 8—9. (Reproductions of Wiman's figs. of cranidium and pygidia. Fig. 7, also reproduced from Wiman, is of a free cheek of *Bienwillia? wimani*.)
- 1917 *Boeckia Mobergi* Wiman — Westergård, p. 637, pl. 7, figs. 1—9. (Descr. Figs. of cranidium, free cheeks, hypostoma, fragments of thoracic segments, and pygidia.)
- 1922a *Boeckia Jarensis* n. sp. — Størmer, p. 4, pl. I, figs. 1—10, pl. II, figs. 1a-b. (Descr. Figs. of cranidia, free cheeks, pygidia, one with posterior part of thorax attached, larval cranidium, and larval pygidium.)
- 1922b *Boeckia Mobergi* Wiman — Størmer, p. 231. (Assumes that *B. jarensis* is a synonym.)
- 1929 *Boeckia mobergi* Wiman — Strand, p. 361. (Recorded.)
- 1933 *Boeckia Mobergi* Wiman — Thorslund, p. 7. (Remarks.)
- 1934a *Boeckia mobergi* — Størmer, p. 332. (Listed.)
- 1934 *Boeckia jarensis* (Størmer) (*B. mobergi* Wiman) — Ruedemann, p. 38, pl. 25, figs. 5—6. (Discussed as planktonic form. Copies of Størmer's figs. of cranidium, and pygidium with attached thoracic segments.)

Type data: — As lectotype I select a cranidium figured by Wiman (1905, pl. V, fig. 12), from Tåsjöberget, Ångermanland, Sweden.

Diagnosis: — A *Boeckaspis* species with: centres of palpebral lobes opposite L2; interocular cheeks about half as wide as glabella at eye line; relatively narrow free cheeks; thorax with flattened pleural spines; pygidium with 3 axial rings and 1 pair of marginal spines; test of dorsal shield without tubercles.

Remarks: — As pointed out by Westergård (1917), Wiman assigned to *B. mobergi* a free cheek of *Parabolinella* (here: *Bienwillia?*) *wimani*. Størmer (1922a), who was not aware of Westergård's revised description, gave the name *B. Jarensis* to a form without cheek spine, which no doubt is conspecific with *B. mobergi* (cf. Størmer, 1922b). Also Thorslund (1933) remarked that the free cheeks he found together with *B. mobergi* differed from the free cheek assigned to this species by Wiman.

As observed by Størmer (1922a, p. 5) there is a small tubercle on each of the eye ridges, almost on the middle of the ridge. The pair of tubercles may correspond to that in *B. hirsuta* and *Acerocare ecorne*, which, however, is situated in front of the eye ridges.

Norwegian material: — This agrees quite with the Swedish.

Occurrence: — Norway: Hadeland (Jaren), Hamar district (Fura in Løyten), Ringsaker (Steinsodden, Stein), Østerdalen (Øksna). *Dictyonema* zone, subzone of *Dictyonema flabelliforme flabelliforme* (2eβ). Associated with *Bienwillia? wimani* and *Dictyonema flabelliforme flabelliforme*. — Sweden (same horizon).

Genus *Jujuyaspis* Kobayashi 1936.

Type species: — *Jujuyaspis keideli* Kobayashi 1936, by original designation.

Diagnosis: — Pelturinae with: palpebral lobes opposite middle or posterior third of glabella and rather close to glabella; posterior facial sutures strongly diverging, almost transverse behind eyes; no preglabellar field; pelturoid free cheeks; without spine; thorax with long pleural spines, at least on the posterior segments; sub-trapezoidal or sub-triangular pygidium with faint pleural segmentation and without spines.

Included species: — Kobayashi erected this genus for the one species *J. keideli*, but soon after he also included *J. steinmanni*. Harrington & Leanza (1952) made the latter the type species of a new genus, *Saltaspis*. Two new forms are assigned below to *Jujuyaspis*, which now includes:

Jujuyaspis angusta n. sp.

J. borealis Kobayashi 1955 (cf. postscript)

J. harringtoni Kobayashi 1955 (cf. postscript)

J. keideli keideli Kobayashi 1936

J. keideli norvegica n. subsp.

Affinities: — *Jujuyaspis* is no doubt very close to *Boeckaspis* and differs mainly in having the eyes closer to the glabella. *Jujuyaspis angusta* n. sp. appears somewhat later than *J. keideli* and differs in having the eyes further back and in having much narrower postocular cheeks.

Occurrence: — Lower Tremadocian; Norway, Argentina.

Jujuyaspis angusta n. sp.

Pl. 8; pl. 28, figs. 11–15.

Name: — The name *angusta* alludes to the narrowness of the postocular cheeks.

Holotype: — A cranidium (P. M. O. no. 35674) from Evjevika in Ringsaker, collected by O. E. Schiøtz in 1904.

Diagnosis: — A *Jujuyaspis* species with: palpebral lobes relatively far back, opposite S1; narrow postocular cheeks; pygidium about two-thirds as long as wide, and with indented posterior margin. Number of thoracic segments unknown.

Description: — This is based on detached parts of the dorsal shield. The cranidia are up to about 3 mm long.

Cephalic axis about three-fourths as wide as long, slightly tapering forward, truncate in front, but with rounded corners. Occipital ring with axial spine. Occipital furrow distinct, composite, deepest at the ends of the curved middle part. Two pairs of faint glabellar furrows (S1 and S2). No

preglabellar field. No eye ridges. Palpebral lobes of moderate size, close to glabella, and situated opposite S1. Facial sutures in front of eyes converging, forming a rounded corner before crossing faint border furrow. Postocular cheeks broken in all cranidia present. However, the facial suture can be seen in the free cheeks, and shows that the postocular cheeks must be rather short and narrow.

Free cheeks pelturoid, without spine, and rather wide. Genal field downsloping from narrow ocular socket. Border and border furrow distinct.

Thorax known only from parts of detached segments. At least some segments carry long, falcate pleural spines, which are rather wide and flat, with narrow rim on both edges. At least some axial rings with axial spine.

Pygidium sub-trapezoidal, two-thirds as long as wide, and about half as wide posteriorly as anteriorly. Axis about as wide as pleural regions. Axis with 3 rings and end lobe. Faint pleural furrows. Border narrow, flat, and not well defined. Posterior border of pygidium incurved. Surface covered with fine terrace lines.

A f f i n i t i e s : — *Jujuyaspis angusta* n. sp. is probably rather close to *J. keideli*, in spite of having the eyes further back and narrower postocular cheeks. Its morphologic position to this species quite corresponds to that of *Boeckaspis mobergi* (palpebral lobes far back, narrow postocular cheeks) as compared with *B. hirsuta* (palpebral lobes further forwards, wider postocular cheeks).

O c c u r r e n c e : — Norway: Ringsaker (Evjevika). — *Dictyonema* zone, subzone of *Dictyonema flabelliforme flabelliforme* (2eß). The species is known from a single stinkstone lens, which also contains a free cheek, probably of *Bienwillia? wimani*.

Jujuyaspis keideli keideli Kobayashi 1936.

Pl. 2, fig. 7.

- 1936a *Jujuyaspis keideli*, new species. — Kobayashi, p. 90, pl. XVI, figs. 5—9. (Descr. Figs. of cranidia, free cheeks, and more or less entire dorsal shields.)
 1937a *Jujuyaspis keideli* Kobayashi — Kobayashi, p. 176, text fig. 6. (Remarks)
 1937b *Jujuyaspis keideli* Kobayashi — Kobayashi, p. 13. (Listed.)
 1937c *Jujuyaspis keideli* Kobayashi — Kobayashi, p. 480. (Remarks.)
 1938 *Jujuyaspis keideli* Kobayashi — Harrington, p. 206, pl. IX, figs. 2—4, 10. (Remarks. Figs. of more or less complete dorsal shields.)
 1943a *Jujuyaspis keideli* — Harrington & Leanza, p. 219. (Remarks on occurrences.)
 1943b *Jujuyaspis keideli* Kobayashi — Harrington & Leanza, p. 352, pl. II, figs. 2, 7. (Remarks. Figs. of dorsal shield and cephalon.)
 1952 *Jujuyaspis keideli* Kobayashi — Harrington & Leanza, p. 196, pl. I, fig. 8. (Remarks. Fig. of cranidium.)
 1953 *Jujuyaspis keideli* Kobayashi — Tjernvik, p. 74. (Mentioned.)

T y p e d a t a : — As lectotype should be selected one of Kobayashi's specimens from the *Parabolinella* zone in Quebrada de Humahuaca, Province of Jujuy, Argentina.

Diagnosis: — A *Jujuyaspis* species with: palpebral lobes about twice as close to anterior as to posterior margin of cranidium; postocular cheeks about as wide as occipital ring; thorax with 13 segments; pleural regions (excluding spines) narrower than axis; pleural ends with spines, posterior segments with very long pleural spines; entire pygidium with 4—5 axial rings and convex posterior margin.

Remarks: — This species was at first suggested to be proparian (Kobayashi, 1936), but as shown by Harrington & Leanza (1952) it is opisthoparian (cf., however, postscript).

Occurrence: — Lower Tremadocian; Argentina, Bolivia.

Jujuyaspis keideli norvegica n. subsp.

Pl. 8; pl. 28, figs. 16—21.

1953 *Jujuyaspis* n. sp. — Henningsmoen in Tjernvik, p. 74. (Mentioned.)

1954 *Jujuyaspis* — Bulman, p. 27. (Mentioned.)

Name: — The name *norvegica* alludes to its occurrence in Norway.

Holotype: — A cranidium (P.M.O. no. 35878c) from Stein, Ringsaker, collected by T. Strand in 1925.

Diagnosis: — Differs from *Jujuyaspis keideli keideli* in having the palpebral lobes slightly further back and consequently also slightly shorter postocular cheeks.

Description: — Most unfortunately the material of this form is poorly preserved and consists only of detached parts of the dorsal shield. The larger cranidia are between 5 and 6 mm long.

Cephalic axis slightly tapering forwards, bluntly rounded in front. Frontal area slightly longer than in *J. keideli*. Preocular facial sutures subparallel or slightly diverging. Interocular cheeks about one-fourth as wide as glabella at eye line. Eye line slightly further back than in *J. keideli*, cutting sagittal line at a point whose distance from anterior end of cephalic axis equals 0.43 of total sagittal length of cephalic axis (as compared to 0.31 in *J. keideli*). Postocular cheeks almost as wide as occipital ring, slightly narrower than in *J. keideli*.

Free cheeks as in *J. keideli*, but with incurving for eye slightly further back.

Thorax known from fragments only. The pleural ends of at least some segments carry long spines.

Pygidium rounded sub-triangular. Axis distinct, with 4 rings and small end lobe. Faint pleural furrows. Surface with fine terrace lines, subparallel to outer margin.

Affinities: — This form seems to be very close to *J. keideli keideli*, but differs slightly in the features mentioned above.

Occurrence: — Norway: Røyken (Nærsnes), Ringsaker (Stein, in a loose local stinkstone lens). — *Dictyonema* zone, subzone of *Dictyonema flabelliforme sociale* (Zea), lower part (beds with *Dictyonema flabelliforme parabola*).

Genus *Leptoplastides* Raw 1908.

Synonyms: — *Parabolinopsis* Hoek 1912 (type species: *P. mariana* Hoek 1912), *Andesaspis* Kobayashi 1935 (type species: *A. argentinensis* Kobayashi 1935).

Type species: — *Conocoryphe Salteri* Callaway 1877, by original designation.

Diagnosis: — Pelturinae with: cephalic axis *Peltura*-like or more parabolic in outline; faint glabellar furrows; short preglabellar field; small palpebral lobes, situated rather far forwards and rather close to glabella; facial sutures more or less convex between eyes and anterior furrow, diverging and slightly convex behind eyes; free cheeks with spine which diverges slightly outwards from lateral cheek margin; thorax with 12 segments, spinose pleural ends, axial rings with axial nodes or spines; pygidium entire or with marginal spines.

Remarks: — *Leptoplastides* was erected by Raw (1908) as a subgenus of *Leptoplastus*. Besides the type species, he included in it three other species, which are now assigned to other genera, i. e. *Leptoplastus claudicans* (Moberg & Möller), *Peltocare norvegicum* (Moberg & Möller) and *Peltura paradoxa* (Moberg & Möller).

I prefer to regard *Leptoplastides* as a separate genus, especially as I believe that it belongs to the Pelturinae rather than the Leptoplastinae. It is true that *L. salteri* resembles *Leptoplastus*, but it shows some features which remind one more of the Pelturinae. The outline of the axial shield is more like that of e. g. *Peltura* than that of *Leptoplastus*. Its axis is widest anteriorly and tapers markedly backwards as in *Peltura*, whereas it is more or less spindle-like in *Leptoplastus*. Its glabella is more dominating than in *Leptoplastus*, and may be quite *Peltura*-like in adult specimens (cf. Raw, 1925, pl. XVIII, figs. 20 and 22). Its palpebral lobes are smaller and situated further forwards than in *Leptoplastus*, and in this respect agreeing well with e. g. *Peltura*. The convex preocular margin of the cranium is a feature which is otherwise not known either in the Leptoplastinae or Pelturinae, whereas the slightly convex course of the facial sutures behind the eyes agrees only with the Pelturinae. The free cheek has a spine which deviates outwards from the course of the cheek margin. This is a feature known both from the Leptoplastinae and Pelturinae, but the shape of the genal field resembles more that of pelturines. On the whole, *Leptoplastides* reminds one more of the Pelturinae than of the Leptoplastinae, but its position is not quite certain before it can be shown from which genus it branched off.

Parabolinopsis, which I regard as a synonym of *Leptoplastides*, and *Beltella*, which I believe is very close to *Leptoplastides*, were both assigned to the subfamily Pelturinae by Harrington & Leanza (1952).

Prof., Dr. H. J. Harrington has been kind enough to send me very good photographs of two almost complete dorsal shields of *Parabolinopsis mariana*. This species agrees so well with *Leptoplastides salteri* that I do not doubt that they are congeneric. Its cranidium and free cheeks resemble strongly those of *L. salteri*, and so does its thorax, having 12 segments, axial nodes (spine bases?), pleural spines, and the fulcra rather near the axis. *Parabolinopsis mariana* has slightly wider pleural regions and a pygidium which differs from that of *Leptoplastides salteri* in having marginal spines. As the two species otherwise agree well, I do not think this prevents them from being regarded as congeneric, especially as other olenid genera contain species both with and without marginal spines, and as it is only the largest pygidia of *Leptoplastides salteri* which do not have at least one pair of marginal spines. *Parabolinopsis mariana* is the type species (and only certain species) of *Parabolinopsis*, which becomes a junior synonym of *Leptoplastides*, as does also *Andesaspis* which apparently is based on the same species as *Parabolinopsis*.

Beltella depressa (type species) resembles *Leptoplastides* in practically all features, except in having truncate pleural ends and no axial nodes or spines in the thorax. It is possible that *Beltella*, too, may be considered a synonym of *Leptoplastides*, especially as the differences are no greater than the differences between species of some other olenid genera.

Included species: —

Leptoplastides argentinensis (Kobayashi 1935) (earlier: *Andesaspis*, *Parabolinopsis*) (= *L. marianus*)

L. granulosus (Harrington 1938) (earlier: *Protopeltura*) (= *L. marianus*)

L. marianus (Hoek 1912) (earlier: *Parabolinopsis*)

L. mitchinsoni (Thomas 1900) (= *L. salteri*)

L. salteri (Callaway 1877)

and possibly also

L.? *spiniferus* (Lake 1912) (earlier: *Beltella*).

The pygidia described by Harrington & Kay (1952, p. 662, pl. 96, figs. 13, 15—16) from Colombia as *Parabolinopsis?* sp. may perhaps also belong here.

Occurrence: — Tremadocian in England, Argentina, Bolivia, and ?Colombia.

Leptoplastides marianus (Hoek 1912).

- 1912 *Parabolinopsis mariana* n.g.n.sp. — Hoek in Steinmann & Hoek, p. 226, pl. VII, figs. 1—3. (Descr. Figs. of dorsal shields.)
- 1935b *Andesaspis argentinensis* n.sp. [partim] — Kobayashi, p. 67, pl. XI, figs. 1—2. (Descr. and figs. of cranidium and free cheek.) (Non figs. 3—4, = pygidia of *Pseudokainella lata*, cf. Harrington & Leanza, 1952.)
- 1937c *Parabolinopsis mariana* Hoek — Kobayashi, p. 479, pl. IV, figs. 15—17. (Remarks. Figs. of dorsal shields.)
- 1937 *Andesaspis argentinensis* Kobayashi — Harrington, p. 111, pl. VII, figs. 8—10. (Remarks. Figs. of free cheeks and incomplete cranidium.)
- 1938 *Protopeltura granulosa* sp. nov. — Harrington, p. 213, pl. VIII, figs. 13, 18, 21; pl. V, fig. 12. (Descr. Figs. of dorsal and axial shields.)
- 1938 *Andesaspis argentinensis* Kobayashi [partim] — Harrington, p. 204, pl. VIII, figs. 10, 14, 15. (Descr. and figs. of cranidia.) (Figs. 8—9, 16 are of pygidia of *Pseudokainella lata*, cf. Harrington & Leanza, 1952.)
- 1951 *Parabolinopsis mariana* Hoek — Harrington & Kay, p. 662. (Mentioned.)
- 1951 *Protopeltura granulosa* Harrington — Harrington & Kay, p. 662. (State that Harrington & Leanza have been able to prove that it is identical with *Parabolinopsis mariana*. Descr. of pygidium.)
- 1952 *Parabolinopsis mariana* Hoek — Harrington & Leanza, p. 196. (Mentioned.)
- 1952 *Andesaspis argentinensis* Kobayashi — Harrington & Leanza, p. 196. (Regard it as a synonym of *Parabolinopsis mariana*.)
- Non 1954 *Andesaspis argentinensis* Kobayashi — Wilson, p. 279, pl. 26, figs. 3, 6. (= *Angelina?* sp.).

Type data: — As lectotype I select the dorsal shield figured by Hoek (1912, pl. VII, fig. 1), from Cuesta de Escayache at Calama near Tarija, Bolivia.

Diagnosis: — A *Leptoplastides* species with: slightly obtuse genal angle; pleural regions (excluding spines) about four-fifths as wide as axis; pygidium with 3 pairs of marginal spines.

Remarks: — Harrington and Leanza regard *Protopeltura granulosa* as a synonym of *Parabolinopsis mariana* (cf. Harrington & Kay, 1951, p. 662). *Andesaspis argentinensis* is based on cranidia and free cheeks of *Parabolinopsis mariana* and pygidia of *Pseudokainella lata* according to Harrington & Leanza (1952, p. 196), who selected a cranidium as lectotype of *Andesaspis argentinensis*, which thus becomes a junior synonym of *Parabolinopsis mariana*. As discussed above, I transfer this species to *Leptoplastides*, as it seems to be very close to *Leptoplastides salteri*.

Some cranidia from Texas were assigned to *Andesaspis argentinensis* by Wilson (1954, p. 279). However, they have rather a long preglabellar field and probably do not belong to *Leptoplastides*. They may possibly be related to the associated *Angelina? latifrons*.

Occurrence: Bolivia (Tremadocian), Argentina (Tremadocian).

Leptoplastides salteri (Callaway 1877).

Pl. 2, fig. 14.

- 1874 *Conocoryphe Salteri* — Callaway, p. 196. (Mentioned as new species.)
 1877 *Olenus Salteri*, Call. — Callaway, p. 666, pl. XXIV, fig. 5. (Descr. Fig. of dorsal shield.)
 1900 *Olenus Mitchinsoni*, sp. nov. — Thomas, p. 619, pl. XXXV, figs. 5—6. (Descr. Fig. of incomplete axial shield and thoracic segment.)
 1908b *Leptoplastides Salteri*, Call. — Raw, p. 513. (Remarks on the development.)
 1919 *Leptoplastus salteri* (Callaway) — Lake, p. 90, pl. XI, figs. 2—5. (Descr. Figs. of dorsal shields and thorax.)
 1925 *Leptoplastus salteri* (Callaway) — Raw, p. 227, text figs. A—B (p. 249), pl. XV, fig. 1; pl. XVI, figs. 1—7; pl. XVII, figs. 8—17; pl. XVIII, figs. 18—24. (Detailed descr. of all known stages. Figs. of all parts of dorsal shield, including larval stages, and of hypostoma.)
 1927 *Leptoplastus salteri* (Callaway) — Raw, p. 25, text fig. 1 (p. 12), text figs. 6—11 (p. 24). (Descr. of known stages. Figs. of larval dorsal shields and cranidium, and of adult cephalon, thoracic segment, and pygidium.)
 1942 *Leptoplastus salteri* (Callaway) — Størmer, p. 89, pl. 1, fig. 31. (Remarks on ontogeny. Fig. of larval dorsal shield copied from Raw.)
 1946 *Leptoplastus salteri* (Callaway) — Lake, p. 342. (Remarks.)

Type data: — As lectotype should be selected one of Callaway's specimens from the Shineton Shales at Shineton, Shropshire, England.

Diagnosis: — A *Leptoplastides* species with: very obtuse genal angle; pleural regions (excluding spines) about two-thirds as wide as axis; entire pygidium.

Remarks: — All the known stages of this species have been described in great detail by Raw (1925).

Occurrence: — England (Tremadocian).

Leptoplastides? spiniferus (Lake 1932).

- 1931 *Beltella spinifera*, sp. nov. — Lake, pl. XVIII, figs. 9—10. (Figs. of cranidia.)
 1932 *Beltella spinifera*, sp. nov. — Lake, p. 149. (Descr. of cranidium.)

Type data: — As lectotype I select the larger of the cranidia figured by Lake (1931, pl. XVIII, fig. 10), from the Shineton Shales, Shineton, England.

Remarks: — As long as its thorax is unknown, it is uncertain whether the species should be assigned to *Beltella* or *Leptoplastides*. However, the cranidia agree very well with larger cranidia of *L. salteri*, also in possessing a long axial spine (not known in *Beltella*). *L.? spiniferus* may be rather close to *L. salteri*, but apparently differs in having a markedly tapering glabella.

Genus *Beltella* Lake 1919.

Type species: — *Ellipsocephalus depressus* Salter 1859, designated by Vogdes (1925).

Diagnosis: — Differs from *Leptoplastides* in having truncate pleural ends and thorax with no axial spines or nodes. Pygidium entire.

Included species: —

Beltella depressa (Salter 1859)

and possibly also:

B.? *ulrichi* (Kayser 1897)

B.? *verisimilis* (Salter 1866).

A cephalon and thorax described as *Beltella*(?) sp. by Hutchinson (1952, p. 83, pl. 3, fig. 16) may possibly belong to this genus.

Some rather poorly known species were assigned to *Beltella* by Lake (1919), viz. *Conocoryphe vexata* Salter 1868 (suggested by Lake to be a synonym of *Beltella depressa*), *C.?* *verisimilis* Salter 1866, *C.?* *bucephala* Belt 1868, and *C. williamsoni* Salter 1873 non Belt (regarded as a synonym of *Beltella bucephala* by Lake.) Only *verisimilis* is tentatively retained in *Beltella*, whereas *vexata* has been transferred, with doubt, to *Angelina*, and *bucephala* (and *williamsoni*), likewise with doubt, to *Olenus*.

B. solitaria Westergård 1922 has tentatively been assigned to *Protopeltura*; *B. latifrons* Wilson 1954 with doubt to *Angelina*, and *B. spinifera* Lake 1932 with doubt to *Leptoplastides*.

Relationships: — As discussed above, *Beltella* may be very close to, if not congeneric with *Leptoplastides*.

Occurrence: — Lower Tremadocian in England, Wales, ?E. Canada, ?Bolivia and ?Argentina.

Beltella depressa (Salter 1859).

Pl. 2, fig. 12.

- 1859 *Ellipsocephalus depressus*, n. sp. — Salter, p. 47, foss. 7, fig. 2.
- 1866 *Conocoryphe (Solenopleura) depressa*, Salter — Salter, p. 307, pl. 6, figs. 1—3. (Descr. Figs. of restored dorsal shield, axial shield, and thorax with attached pygidium.)
- 1873 *Conoryphe depressa*, Salter — Salter, p. 15. (Remarks.)
- 1898 *Conoryphe depressa*, Salter — Brögger, p. 198. (Suggests that it belongs to *Cyclognathus*.)
- 1898 *Cyclognathus*(?) *depressus*, Salt. — Brögger, p. 210. (Listed.)
- 1900a *Conocoryphe (Solenopleura) depressa*, Salter — Reed, p. 253. (Remarks.)
- 1919 *Beltella depressa* (Salter) [partim] — Lake, p. 104, pl. XII, figs. 6—8. (Descr. Figs. of axial shield, greater part of damaged dorsal shield, and of thorax with attached pygidium.) (Figs. 9—10 = *Angelina?* *vexata*.)
- 1933 *Beltella depressa* (Salter) — Stubblefield, p. 366, pl. XXXIV, figs. 1, 9—11. (Descr. Figs. of axial shield, free cheeks, and incomplete cephalon.)

- 1938 *Beltella depressa* (Salter) — — Harrington, p. 203. (Mentioned.)
1946 *Beltella depressa* (Salter) — — Lake, p. 343. (Remarks.)
1954 *Beltella depressa* (Salter) — — Wilson, p. 276. (Remarks.)

Type data: — Lectotype is a thorax and pygidium, which was figured by Salter (1859). A new figure of it was given by Lake (1919, pl. XII, fig. 7) and it comes from the Lower Tremadocian at Penmorfa, Wales.

Remarks: — As pointed out by Stubblefield (1933, p. 367), the genal spine does not continue the curve of the lateral cheek margin (as in Salter's restoration), but deviates slightly outwards.

The pleural tips of the type specimens seem to be truncate. Lake (1919) believed that they were produced into spines and that the truncate appearance was due to the preservation. Stubblefield (1933) described some specimens from another locality, which appear to have truncate pleural tips. He suggested that Lake had been brought to his conclusion by including within the species specimens of "*Beltella*" *vexata*, which was suggested by Lake to be a synonym of *L. depressus*, but is regarded as a distinct species by Stubblefield, as it differs as to morphology and comes from a higher stratigraphic horizon. Lake (1946) is disposed to accept that Stubblefield's specimens have truncate pleural ends, but is not altogether convinced about the type specimens, because their pleural ends are lost beneath the plane along which the rock has split.

Occurrence: — Wales (Lower Tremadocian), England (Lower Tremadocian).

Beltella? ulrichi (Kayser 1897).

- 1897 *Liostracus Ulrichi* n. sp. — — Kayser, p. 277, pl. VII, figs. 1, 1a, 4. (Descr. Figs. of cranidium and pygidia.)
1935b "*Liostracus*" *ulrichi* Kayser — — Kobayashi, p. 67. (Listed.)
1937b "*Liostracus*" *ulrichi* Kayser — — Kobayashi, p. 13. (Listed.)
1938 *Beltella ulrichi* (Kayser) — — Harrington, p. 201, pl. VII, figs. 9, 13—18. (Descr. Figs. of incomplete cephalon with a few attached thoracic segments, cranidia, free cheeks, and pygidia.)
1943b *Beltella ulrichi* (Kayser) — — Harrington & Leanza, p. 351, pl. II, fig. 5. (Remarks. Fig. of incomplete dorsal shield.)

Type data: — As lectotype I select the cranidium figured by Kayser (1897) from the sandstone at Iruya, province of Salta, Argentina.

Remarks: — The thorax of this species has not been described, but the incomplete dorsal shield figured by Harrington & Leanza (1943, pl. II, fig. 5) suggests that the pleural ends are truncate.

Occurrence: — Argentina (Lower Tremadocian), Bolivia (Lower Tremadocian).

Beltella? verisimilis (Salter 1866).

- 1866 *Conocoryphe? verisimilis*, n. sp. — Salter, p. 308, pl. 6, fig. 13. (Descr. Fig. of restored dorsal shield.)
1868 *Conocoryphe? verisimilis*, Sal. — Belt, p. 10. (Suggests that it is a synonym of *L. depressus*.)
1873 *Conocoryphe verisimilis*, Salter — Salter, p. 15. (Remarks.)
1882 *Conocoryphe(?) verisimilis*, Salter — Brögger, p. 111. (Suggests that it may belong to *Cyclognathus*.)
1898 *Conocoryphe verisimilis*, Salt. — Brögger, p. 199 (separate copies, 1896, p. 36). (Suggests that it probably belongs to *Cyclognathus*.)
1900a *Conocoryphe? verisimilis*, Salter — Reed, p. 256. (Referred to *Angelina*.)
1919 *Beltella verisimilis* (Salter) [partim] — Lake, p. 107, pl. XIII, figs. 1–3 only. (Descr. Figs. of more or less damaged dorsal and axial shields, including the type specimen. Figs. 4–5 are here assigned to *Olenus? bucephalus*.)
1954 *Beltella verisimilis* (Salter) — Wilson, p. 276. (Remarks.)

Type data: — As lectotype I select the incomplete dorsal shield figured by Lake (1919, pl. XIII, fig. 1). This is the specimen upon which Salter's restoration was based. It comes from the Lower Tremadocian, Penmorfa Village, Wales.

Remarks: — This species may be rather close to *B. depressa*. It apparently differs from it (and from *Leptoplastides*) in having a genal spine which continues the course of the lateral margin. As far as can be judged from the figure of the lectotype, this difference may possibly not be real, but due to the preservation. If so, the species may possibly be a synonym of *L. depressus*, as suggested already by Belt (1868). Some specimens which were assigned to *L.? verisimilis* by Lake (1919), are here transferred to *Olenus? bucephalus*.

Occurrence: — Wales (Lower Tremadocian).

Genus *Paenebeltella* Ross 1951.

Type species: — *Paenebeltella vultulata* Ross 1951, by original designation.

Diagnosis: — Differs from *Beltella* and *Leptoplastides* in having convergent instead of divergent preocular facial sutures, which do not become inframarginal, and in having no preglabellar furrows (except in larval cranidia).

Remarks: — This genus may be related to *Beltella* and *Leptoplastides*. However, its thoracic shield is not known. The type species and *P. convexa* Kobayashi 1955 (cf. postscript) are the only known species.

Paenebeltella vultulata Ross 1951.

Pl. 2, fig. 13.

- 1951 *Paenebeltella vultulata* Ross, n. sp. — — Ross, p. 79, pl. 18, figs. 1—2, 5—6, pl. 19, fig. 10? or figs. 5?, 7? (Descr. and figs. of cranidia and free cheeks. Figs. of two types of pygidia, one of which may belong to this species.)

H o l o t y p e: — Cranidium with free cheek glued in place (Peabody Museum of Natural History, Yale University, no. 18063).

D i a g n o s i s: — As for genus.

O c c u r r e n c e: — Garden City formation (Zone E, = Roubidoux interval?), NE Utah.

Postscript

In a recent paper Jaanusson (1956, p. 37) has introduced the same symbols for lateral glabellar furrows (S1—S4) and lobes (L1—L4) as proposed above (p. 12).

In another paper which I received when the present paper was sent to the press, Kobayashi (1955) has described several olenids, all new, from the McKay Group in British Columbia, Western Canada. They occur in the three earlier of the eight faunal assemblages recognized by Kobayashi, namely in the *Symphysurina* fauna (*Parabolinella bisulcata*, *Sphaerophthalmella inexpectans*, *Jujuyaspis borealis*), the *Robsonoceras*?-*Apatokephalus* faunules (*Peltura pacifica*, *P. canadensis*), and in the *Evansaspis*-*Kainella* fauna (*Paenebeltella convexa*). The faunas are assumed to have appeared in this order.

It is uncertain whether *Parabolinella bisulcata* belongs to *Parabolinella* as defined above, and should perhaps rather be referred to as *Parabolinella*? *bisulcata*. *Sphaerophthalmella inexpectans* was made the type species of the new genus *Sphaerophthalmella*, which was assigned to the Leptoplastinae by Kobayashi. The holotype of *S. inexpectans* is a cranidium. The cranidium seems to be closer to *Boeckaspis* than to *Sphaerophthalmus*. A pygidium assigned to this species was compared with that of *Sphaerophthalmus*. However, it does not agree with the rather aberrant pygidium of that genus, but resembles the pygidium of later pelturines, and is quite similar to that of *Jujuyaspis*. It is perhaps possible that the pygidium really belongs to the associated *Jujuyaspis* species. In any case, I believe that *Sphaerophthalmella* is closest to genera like *Boeckaspis*, and should be transferred to the subfamily Pelturinae. *Sphaerophthalmella* differs from *Boeckaspis* in having the eyes situated slightly further back, and if the pygidium is correctly assigned to *Sphaerophthalmella*, it differs in having a rounded posterior border. If the pygidium does not belong to *Sphaerophthalmella*, it is a question whether the slightly different position of the eyes warrants the separation of the genera, especially as the position varies within *Boeckaspis*. If they are regarded as synonyms, the name *Sphaerophthalmella* should be retained for the genus, since this name was published in September 1955, whereas *Boeck-*

aspis was proposed in November 1955. *Peltura pacifica* apparently is close to *Triarthrus punctatus*, and should be referred to as *Triarthrus pacificus*. Neither should *Peltura canadensis* be assigned to *Peltura*. It may possibly belong to *Bienwillia* and may provisionally be referred to as *Bienwillia? canadensis*.

The *Symphysurina* beds of the McKay Group were regarded as Lower Tremadocian by Kobayashi, who furthermore correlated them with zones B—C of the Pogonip Group and zones A—C of the Garden City Formation. The occurrence of *Jujuyaspis* and a genus close to *Boeckaspis* certainly strongly suggests an Early Tremadocian age. Since the zones A—D of the Garden City Formation are of Gasconade age (Ross, 1951, p. 32), it is possible that the lower boundary of the Tremadocian approximately corresponds to the lower boundary of the Canadian in North America.

Kobayashi (1955, p. 567) furthermore introduced the name *Jujuyaspis harringtoni* for the specimens assigned to *J. keideli* by Harrington & Leanza (1952). He maintained that the true *J. keideli* is proparian and regarded *Salteraspis* (recte: *Saltaspis*) as a synonym of *Jujuyaspis*.

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 Pianaspis — 22
 pirquoensis (*Mendoparabolina*) — 25
 planicauda (*Peltura*, *Protopeltura*) — 228
 Plantii (*Olenus*, *Parabolinites*) — 129, 131
 Plesioparabolina — 19
 Plicatolina — 152
 Porterfieldia — 152
 postcurrents (*Ctenopyge*) — 193
 posthuma (*Parabolinella*?) — 141
 praecursor (*Peltura*, *Protopeltura*) — 229
 praecursor var.? (*Protopeltura*) — 221
 Proaulacopleura — 22, 27, 30
 Proceratopyge — 28
 Proetus — 20
 Protopeltura — 220
 punctatus (*Peltura*, *Triarthrus*) — 149
 punctifera (*Pelturina*) — 250
 punctolineata (*Angelina*) — 156
 — (*Parabolinella*?) — 141
 pusillum (*Anopocare*) — 215, 237
 pygmaeus (*Triarthrus*) — 152
 Pyraustocranium — 19

 quadrisulcata (*Parabolina*?) — 128

 raphidophorus (*Leptoplastus*) — 175
 reedi (*Triarthrus*) — 152
 Remopleuridae — 29
 Rhodonaspis — 21
 Richardsonellidae — 29
 Richardsonellinae — 29
 robusta (*Jujuyaspis*, *Nericiaspis*) — 242
 rotundatus (*Olenus*) — 107
 rotundifrons (*Cyclognathus*, *Peltocare*) — 249
 rugosa (*Parabolinella*) — 137

 Saltaspis — 244
 saltensis (*Keidelaspis*) — 155, 157
 salteri (*Conocoryphe*, *Olenus*, *Lepto-*
plastus, *Leptoplastides*) — 267
 Samsonowicz (Beltella) — 46
 Sao — 22
 scanica (*Boeckia*, *Westergårdia*) — 257
 scanicus (*Olenus*) — 108
 scarabaeoides (*Entomostracites*, *Paradox-*
ides, *Trilobites*, *Olenus*, *Anthes*, *Pel-*
tura) — 237
 — obesus (*Olenus*) — 237
 — octacantha (*Peltura*) — 237
 — westergårdi (*Peltura*) — 239

- sedgwickii (Angelina) — 157
 serratus (Parabolina) — 126
 sexdentata (Parabolina) — 127
 shinetonensis (Triarthrus, Bienvillia) — 144
 similis (Ctenopyge) — 195
 simplex (Conocoryphe?, Parabolinella?) — 141
 skutensis (Triarthrus) — 152
 solitaria (Beltella, Protopeltura?) — 230
 spectabilis (Ctenopyge) — 197
 sphaenopygus (Sphaerophthalmus) — 215
 Sphaerophthalmella — 272
 Sphaerophthalmoides — 253
 Sphaerophthalmus — 211
 spiniferus (Beltella, Leptoplastides) — 267
 spiniger (Leptoplastus) — 162
 spinigerum (Eurycare) — 182
 spinosus (Leptoplastus) — 177
 — (Triarthrus) — 152
 — rougensis (Triarthrus) — 152
 spinulosa (Entomostracites, Paradoxides, Olenus) — 126
 steinmanni (Jujuyaspis, Saltaspis) — 245
 — (Liostracus, Angelina) — 157
 stenotoides (Leptoplastus) — 162
 stenotus (Leptoplastus) — 177
 subarmata (Angelina) — 157

 Taenicephalus — 28
 tellecheai (Olenus?) — 24
 teretifrons (Sphaerophthalmus, Ctenopyge) — 209
 terranova (Bienvillia, Leiobienvillia) — 160
 tetracanthura (Protopeltura, Parabolina) — 128

 tetragonalis (Parabolinella, Triarthrus, Bienvillia) — 144
 — broeggeri (Bienvillia) — 145
 Tostonia — 19
 transiens (Cyclognathus, Acerocare, Peltura) — 240
 transversus (Olenus) — 108
 triangulatus (Olenus?) — 24
 triarthra (Olenus, Parabolinella) — 138
 Triarthroides — 19
 triarthroides (Parabolinella) — 139
 Triarthropsis — 24
 Triarthrus — 147
 triarthrus (Triarthrus) — 152
 truncatus (Trilobus, Olenus) — 109
 tullbergi (Acerocare) — 243
 tumida (Ctenopyge) — 198
 tumidoides (Ctenopyge) — 199

 ulrichi (Liostracus, Beltella) — 269

 variscorum (Triarthrus?) — 150
 verisimilis (Conocoryphe, Beltella) — 270
 vexata (Conocoryphe, Parabolinella, Beltella, Angelina?) — 158
 viator (Saltaspis) — 245
 vultulata (Paenebeltella) — 271

 wahlenbergi (Olenus) — 110
 Westergårdia — 253
 Westergårdites — 154
 williamsoni (Conocoryphe) — 111
 williamsonii (Conocoryphe?, Parabolinella, Parabolinites?) — 131
 wilsoni (Olenus?) — 111
 wimani (Parabolinella, Bienvillia?) — 146
 Zacampsus — 22

CHART 1. *Geographic distribution of Upper Cambrian and Tremadocian olenids.*

Geographic distribution of Upper Cambrian and Tremadocian olenids (T = Tremadocian forms)	Districts in Norway																							
	1a Skien-Brevik	1b Eiker-Sandsvør	1c Oslo-Asker	1d Modum	1e Ringerike	1f Hadeland	1g Hamar	1h Ringsaker	1i Valdres-Vardal	1j Østerdalen	1 Norway	2 Sweden	3 Denmark	4 Poland	5 England	6 Wales	7 Germany	8 E. maritime Canada	9 N. America elsewhere	10 S. America	11 Siberia	12 Central Asia	13 Korea	14 Australia
<i>Olenus</i> alpha n. sp.	+	.	.	+
asiaticus
attenuatus	+	+	+	+	+	+	.
cataractes	+
dentatus
gibbosus	+	+	.	.	+	.	.	+	+	+	+	+	+	.	.	+
micrurus	+
mundus	+
rotundatus	+
scanicus	+
transversus	+	.	+	+	+
truncatus	+	.	.	+	+	.	+	+	+	.	.	+
wahlenbergi	+	+	.	.	+	+	+
? bucephalus	+
? wilsoni n. sp.	+
? sp.	+
<i>Parabolina</i> acanthura	+	+	+	+	+
argentina (incl. andina) T	+
brevispina	+	+	+

Parabolina dawsoni		-	+	+	-	-	-	+	-	+	+	-	-	-	-	+	-	-	-	-	-
heres heres		-	+	+	-	-	-	+	-	+	+	-	-	-	-	+	-	-	-	-	-
heres lata		-	-	+	-	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	-
frequens T		-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
jemtlandica		-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
kinnekullensis		-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
lapponica		-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
lobata lobata		-	+	-	-	-	+	-	-	+	+	+	?	-	-	-	-	-	-	-	-
lobata praecurrens		-	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-
megalops		-	-	-	+	-	-	?	-	+	+	-	-	-	-	-	-	-	-	-	-
mobergi		-	-	+	-	+	-	-	-	+	+	-	?	-	-	-	-	-	-	-	-
spinulosa		+	+	+	+	+	+	+	-	+	+	+	-	+	+	-	+	-	-	-	-
tetracanthura		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
? quadrisulcata n. sp.		-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
<hr/>																					
Parabolinites laticaudus		-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
? leptoplastorum		-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
? longispinus		-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
? williamsonii		-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<hr/>																					
Parabolinella argentinensis T		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
lata n. sp. T		-	-	+	-	+	-	-	-	+	-	-	-	-	-	?	-	-	-	-	-
limitis T		-	-	+	-	+	+	-	-	+	-	-	-	?	-	?	-	-	-	-	-
rugosa T		-	+	?	-	-	-	-	-	+	-	-	-	?	-	-	-	-	-	-	-
triarthra (incl. quadrata) T		-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-
triarthroides T		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	+	-	-	-
? bisulcata T		-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-
? caesa		-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
? incerta T		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
? posthuma		-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
? punctolineata		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
? simplex		-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-

CHART 1 (cont.).

Geographic distribution of Upper Cambrian and Tremadocian olenids (T = Tremadocian forms)	Districts in Norway									1 Norway	2 Sweden	3 Denmark	4 Poland	5 England	6 Wales	7 Germany	8 E. maritime Canada	9 N. America elsewhere	10 S. America	11 Siberia	12 Central Asia	13 Korea	14 Australia
	1a Skien-Brevik	1b Eiker-Sandsvør	1c Oslo-Asker	1d Modum	1e Ringerike	1f Hadeland	1g Hamar	1h Ringsaker	1i Valdres-Vardal	1j Østerdalen													
<i>Bienvillia corax</i>	T	+
<i>micula</i>	T	+
<i>shinetonensis</i>	T	+
<i>tetragonalis tetragonalis</i>	T	+
<i>tetragonalis broeggeri</i> n. subsp.	T	.	.	+	+	+
? <i>canadensis</i>	T	+
? <i>wimani</i>	T	+	+	+	.	.	+	+
<i>Trizarthrus angelini angelini</i>	T	.	+	+	.	+	.	.	+	.	+	+	.	.	.	?
<i>angelini rectifrons</i>	T	+
<i>pacifica</i>	T	+	.	.	+
<i>punctatus</i>	T
? <i>belli</i>	T	+
? <i>variscorum</i>	T	+
<i>Plicatolina kindlei</i>	T	+
<i>pheidolopyge</i>	T	+
<i>Westergårdites pelturaeformis</i>	T?	+	.	.
<i>Angelina punctolineata</i>	T	+
<i>sedgwickii</i>	T	+

[illegible]

CHART 1 (cont.)

Geographic distribution of Upper Cambrian and Tremadocian olenids (T = Tremadocian forms)	Districts in Norway										1 Norway	2 Sweden	3 Denmark	4 Poland	5 England	6 Wales	7 Germany	8 E. maritime Canada	9 N. America elsewhere	10 S. America	11 Siberia	12 Central Asia	13 Korea	14 Australia
	la Skien-Brevik	lb Eiker-Sandsvær	lc Oslo-Asker	ld Modum	le Ringerike	lf Hadeland	lg Hamar	lh Ringsaker	li Valdres-Vardal	lj Østerdalen														
<i>Ctenopyge erecta</i>			+								+	+	+	+	+	+								
<i>falclifera</i>																								
<i>flagellifera</i>	+	+																						
<i>fletcheri</i>			+																					
<i>linnaeasoni</i>			+																					
<i>modesta</i> n. sp.			+																					
<i>pecten</i>		+																						
<i>postcurrentis</i>			+				+																	
<i>similis</i> n. sp.			+																					
<i>spectabilis</i>			+																					
<i>teretifrons</i>																								
<i>tumida</i>			+																					
<i>tumidoides</i> n. sp.			+																					
<i>?expansa</i>																								
<i>?oelandica</i>																								
<i>Sphaerophthalminus alatus</i>	+	+										+	+	+										
<i>tumilis</i>			+																					
<i>major</i>			+																					
<i>maiusculus</i>																								

Protopeltura aciculata aciculata	-	-	-	-	-	-	-	-	-
aciculata pusilla	-	+	+	-	+	+	-	-	-
bidentata	-	-	+	-	-	-	-	-	-
broeggeri	-	+	+	-	-	-	-	-	-
holtedahli n. sp.	-	-	+	-	-	-	-	-	-
intermedia ?.....	-	-	-	-	-	-	-	-	-
planicauda	-	-	+	-	-	-	-	-	-
praecursor	+	+	+	-	-	-	-	-	-
spp.	-	-	-	-	-	-	-	+	+
? solitaria	-	-	-	-	-	-	-	-	-
? sp.	-	-	-	-	-	-	-	-	+
Peltura acutidens	-	-	+	-	-	-	+	-	-
costata	-	+	+	-	-	-	+	-	-
minor	-	+	+	-	+	-	-	+	-
paradoxa	-	-	-	+	-	-	-	-	-
scarabaeoides scarabaeoides	+	+	+	+	+	+	+	+	+
scarabaeoides westergårdi n. subsp. ...	-	+	+	-	-	-	-	-	-
transiens	-	+	+	-	-	-	-	-	-
Nericiaspis robusta	-	-	-	-	-	-	-	-	-
Acerocare ecorne	-	-	+	-	-	-	-	-	-
tullbergi	-	-	-	-	-	-	-	-	-
Saltaspis steinmanni T	-	-	-	-	-	-	-	-	+
sp. T	-	-	?	-	-	-	-	-	-
Peltochore norvegicum (incl. glaber)... T	-	-	+	-	+	+	-	-	+
olenoides T	-	-	-	-	-	-	-	+	-
rotundifrons	-	-	-	-	-	-	-	+	-
Pelturina punctifera	-	-	+	-	-	-	+	-	-
Acerocarina granulata	-	+	-	-	-	-	-	-	-
micropyga	-	-	+	-	-	-	-	-	-

CHART 1 (cont.)

Geographic distribution of Upper Cambrian and Tremadocian olenids (T = Tremadocian forms)	Districts in Norway										1 Norway	2 Sweden	3 Denmark	4 Poland	5 England	6 Wales	7 Germany	8 E. maritime Canada	9 N. America elsewhere	10 S. America	11 Siberia	12 Central Asia	13 Korea	14 Australia
	la Skien-Brevik	lb Eiker-Sandsvør	lc Oslo-Asker	ld Modum	le Ringerike	lf Hadeland	lg Hamar	lh Ringsaker	li Valdres-Vardal	lj Østerdalen														
Westergårdia intermedia	+	+	+
lata (incl. illaenopsis)	+	+	.	.	+	+	+
scanica	+	+	+
Böeckaspis hirsuta T	.	.	+	+	+
mobergi T	+	+	+	.	+	+	+
Sphaeroplithahnella inexpectans T	+
Jujuyaspis angusta n. sp. T	+	.	.	+
borealis T	+
keideli keideli T	+
keideli norvegica n. subsp. T	.	.	+	+	.	.	+	+
Leptoplastides marianus T	+
salteri T	+
?spinifera T	+
Beltella depressa T	+	+
?ulrichi T	+
?verisimilis T	+
Paenebeltella convexa T	+
vultulata T	+

Zones	Sub-zones	CHART 2. <i>Stratigraphic occurrence of olenids in the Olenid Series in Norway</i>			
Acerocare 2dε	ecor. West. cost. trans.	Parabolina acanthura Par. heres lata Par. heres heres Par. heres heres	Acerocare ecorne Westergårdia spp.	Pelturina punctifera Pelturina punctifera	Peltura costata Pelt. transiens
Peltura scarabaeoides 2dγ-δ	parad. lob. linn. bis.	Par. megalops Par. lobata lobata, Par. lobata praecurrens Ct. linnarssoni, Ct. fletcheri, Ct. pecten Ct. bisulcata	?Acerocarina granulata Sph. humilis, Sph. majusculus Sph. humilis, Sph. majusculus		Pelt. paradoxa Pelt. scarabaeoides westergårdi Pelt. scarabaeoides scarabaeoides Pelt. scarabaeoides scarabaeoides
Peltura minor 2dβ	aff. tum. spect. sim.	Ct. affinis affinis, Ct. affinis gracilis Ct. tumida Ct. spectabilis, Ct. tumidoides, Ct. angusta Par. mobergi Ct. similis, Ct. modesta	Sph. alatus Sphaerophthalmus alatus	Prot. planicauda Prot. bidentata	Pelt. minor Pelt. minor, Pelt. acutidens
Protopeltura praecursor 2dα	flag. postc. negl. ?holt. ?broeg.	Ct. flagellifera, Ct. drytonensis Ctenopyge postcurrens Leptoplastus neglectus		Prot. praecursor Prot. praecursor Prot. praecursor Prot. holtedahli Prot. broeggeri	
Leptoplastus 2c	sten. ang. ovat. crass. raph. [pauc.]	L. stenotus L. angustatus L. ovatus, L. crassicorne var., E. explanatum, E. latum, E. brevicauda L. crassicorne, L. norvegicus L. raphidophorus	E. latum		
Parabolina spinulosa 2b	spin. brev.	Par. spinulosa Par. brevispina	Protopeltura aciculata pusilla		
Olenus & Agnostus obesus 2aβ	[scan.] [dent.] att. wahl. trunc. gibb.	Olenus attenuatus O. wahlenbergi O. truncatus O. gibbosus, O. transversus	? in front of a name indicates that the exact stratigraphic horizon is uncertain. [] indicates that the subzone has not been recognized in Norway, but is known in Sweden.		
Agnostus pisiformis 2aα		O. alpha			

? in front of a name indicates that the exact stratigraphic horizon is uncertain.
[] indicates that the subzone has not been recognized in Norway, but is known in Sweden.

CHART 3. *Zones and subzones in the Olenid Series and their known occurrences.*

<i>Zones</i> I—VI = proposed international symbols Norwegian symbols in brackets		<i>Subzones</i> Dotted line = a subzone within this range	Norway	Sweden	Denmark	Poland	G. B.	E. Canada	Correlation with Westergård's subzones:	
									1922	1947
Acerocare VI (2dε)		Acerocare ecorne Westergårdia spp. Peltura costata Peltura transiens	+	+	?			+	6	6d 6c ? 6b ? 6a
Peltura zones V (2dα-δ)	Peltura scarabaeoides Vc (2dγ-δ)	Peltura paradoxa Parabolina lobata Ctenopyge linnarssoni Ctenopyge bisulcata	+	+		+		+	5d 5c	? 5f 5e 5d
			+	+	+		+	+		
	Peltura minor Vb (2dβ)	Ctenopyge affinis Ctenopyge tumida Ctenopyge spectabilis Ctenopyge similis	+	+	+				5b	5c
	Protopeltura praecursor Va (2dα)	Ctenopyge flagellifera Ctenopyge postcurrens Leptoplastus neglectus ? Protopeltura holtedahli } position ? Protopeltura broeggeri } uncertain	+	+	+		+	+	5a	5b 5a
Leptoplastus IV (2c)		Leptoplastus stenotus Leptoplastus angustatus Leptoplastus ovatus Leptoplastus crassicorne Leptoplastus raphidophorus Leptoplastus paucisegmentatus	+	+	+				4	4e 4d 4c 4b 4a
Parabolina spinulosa III (2b)		Parabolina spinulosa Parabolina brevispina	+	+	+		+	+	3	3b 3a
Olenus zones I—II (2a)	Olenus and Agnostus obesus II (2aβ)	Olenus scanicus Olenus dentatus Olenus attenuatus Olenus wahlenbergi Olenus truncatus Olenus gibbosus		+	+				2	2f 2e 2d 2c 2b 2a
		I (2aα) Agnostus pisiiformis	+	+	+		+	+	1	1

CHART 4. *Distribution of Tremadocian olenids. (? in front of name denotes uncertain stratigraphic position.)*

Upper Tremadoc.	Norway (+ = also Sweden)	England	Wales	New Brunswick, Nova Scotia	
	Parabolina lata Parabolinella rugosa Triarthrus angelini+ Saltaspis sp.+	Leptoplastides salteri Parabolinella triarthra Bienvillia shinetonensis	{ Angelina sedgwicki Peltocare olenoides Angelina? vexata	Triarthrus? belli Parabolinella triarthra Parabolinella limitis? Leptoplastides? sp. Angelina? sp.	
	Triarthrus angelini+ Parabolinella limitis		? { Parabolinella rugosa? Triarthrus punctatus		
Bienvillia tetragonalis broeggeri Peltocare norvegicum+					
Lower Tremadoc.	? Jujuyaspis angusta { Boeckaspis mohergi+ { Bienvillia? wimani+	Germany Parabolina frequens Triarthrus? variscorum	Beltella depressa Beltella? verisimilis	Newfoundland ? { Leiobienvillia terranovica Leiobienvillia laevigata ? Parabolinella argentinensis	
	Jujuyaspis keideli norvegica				
	Boeckaspis hirsuta Parabolina acanthura				
Upper Tremadoc.	South America	Texas (Marathon uplift)	Vermont	Yukon	British Columbia
	{ Triarthrus angelini rectifrons { Parabolinella triarthroides { Parabolinella argentinensis { Peltocare glaber	Parabolinella triarthroides?	Parabolinella triarthroides? Plicatolina kindlei	Parabolinella punctolineata	Paenebeltella convexa
Lower Tremadoc.	Saltaspis steinmanni Parabolinella argentinensis Bienvillia pheidelopyge Leptoplastides marianus Beltella ulrichi Angelina steinmanni Angelina punctolineata	? { Leptoplastides marianus Beltella latifrons	? Bienvillia micula	Quebec ? { Parabolinella? incerta Bienvillia corax	{ Triarthrus pacificus Bienvillia? canadensis { Parabolinella? bisulcata Sphaerophthalmella inexpectans Jujuyaspis borealis
	Parabolinella argentinensis Bienvillia tetragonalis Parabolina argentina Jujuyaspis keideli				

CORRELATION CHART OF UPPER CAMBRIAN AND LOWERMOST ORDOVICIAN BIOSTRATIGRAPHY IN THE ACADO-BALTIC AND NORTH AMERICAN PROVINCES							
ACADO-BALTIC PROVINCE				Faunal connections	NORTH AMERICAN PROVINCE		
TREMADOCIAN	Upper Tremadocian				Symphysurina - Hystricurus	LOWERMOST CANADIAN	
	Lower Tremadocian (Dictyonema flabelliforme)		 ? ? .. ? or ?	Saukia	TREMP. EALEAU.	
UPPER CAMBRIAN (OLENID SERIES)	Acerocare		VI	... ? ...	Prosaukia - Ptychaspis		FRANCONIAN
	Peltura scarabaeoides	Vc	Peltura V				
	Peltura minor	Vb					
	Protopeltura praecursor	Va					
	Leptoplastus		IV	... ? .. or ?	Conaspis		
	Parabolina spinulosa		III		Irvingella major		
	Olenus & Agnostus obesus	II	Olenus I-II		Elvinia		
	Agnostus pisiformis	I			Aphelaspis		
TOP OF M. CAMBR.	Lejopyge laevigata			... ? ...	Crepicephalus		DRESBACHIAN
	Solenopleura brachymetopa				Cedaria		

CHART 5.

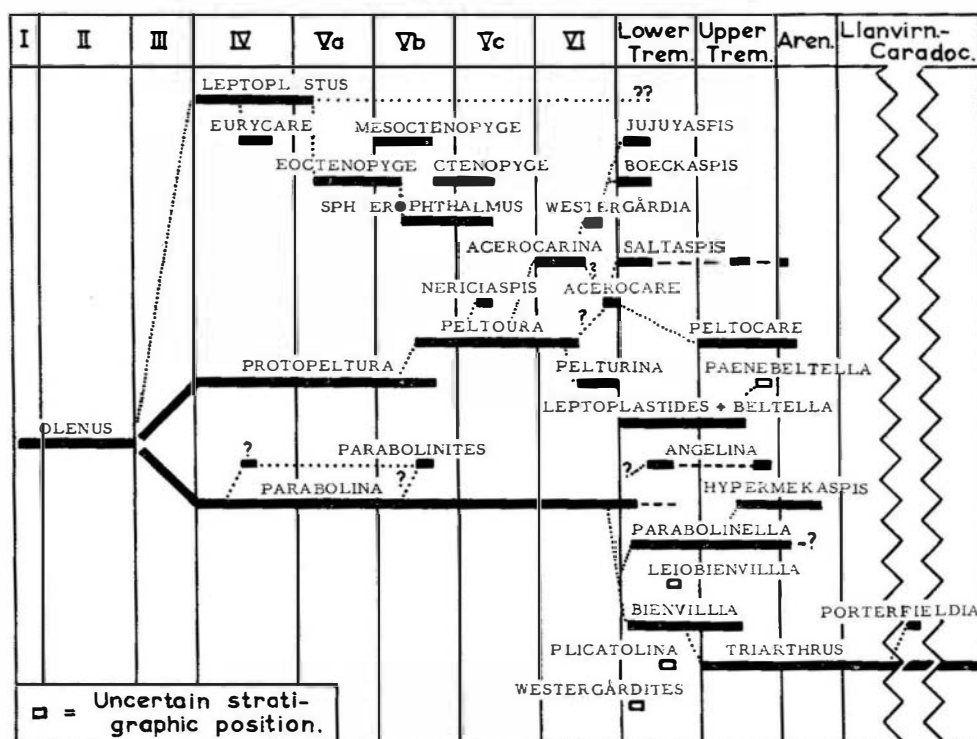


CHART 6.

Stratigraphic range and suggested relationships of olenid genera and subgenera.

For *Peltoura* read *Peltura*. *Hypermekaspis* (nomen nudum) indicates an undescribed genus related to *Parabolinella* (cf. p. 137).

PLATES 1—2

Outline drawings of the dorsal shields of the type species of the olenid genera and subgenera. The drawings are based on illustrations given by various authors.

All about 1.8 times. Although probably all the shields belong to holaspid specimens, they may not represent the very largest instar in each species.

To facilitate a comparison of the cranidia, only the left free cheek is drawn in the species where the free cheeks are known. To facilitate a comparison of the free cheeks, they are drawn as if lying on a flat surface, even when they were more or less tilted in their natural position.

PLATE 1

Oleninae. All are type species, except fig. 7. C. $\times 2$.

- Fig. 1. *Olenus gibbosus* (Wahlenberg 1821).
» 2. *Parabolina spinulosa* (Wahlenberg 1821).
» 3. *Triarthrus beekii* Green 1832.
» 4. *Westergårdites pelturaeformis* Troedsson 1937.
» 5. *Leiobienvillia laevigata* Rasetti 1954.
» 6. *Bienvillia corax* (Billings 1865).
» 7. *Bienvillia shinetonensis* (Lake 1913) (for comparison).
» 8. *Parabolinella limitis* Brögger 1882.
» 9. *Parabolinites laticaudus* (Westergård 1922).
» 10. *Angelina sedgwickii* Salter 1859.
» 11. *Plicatolina kindlei* Shaw 1951.
» 12. *Porterfieldia coccigenus* (Raymond 1920).

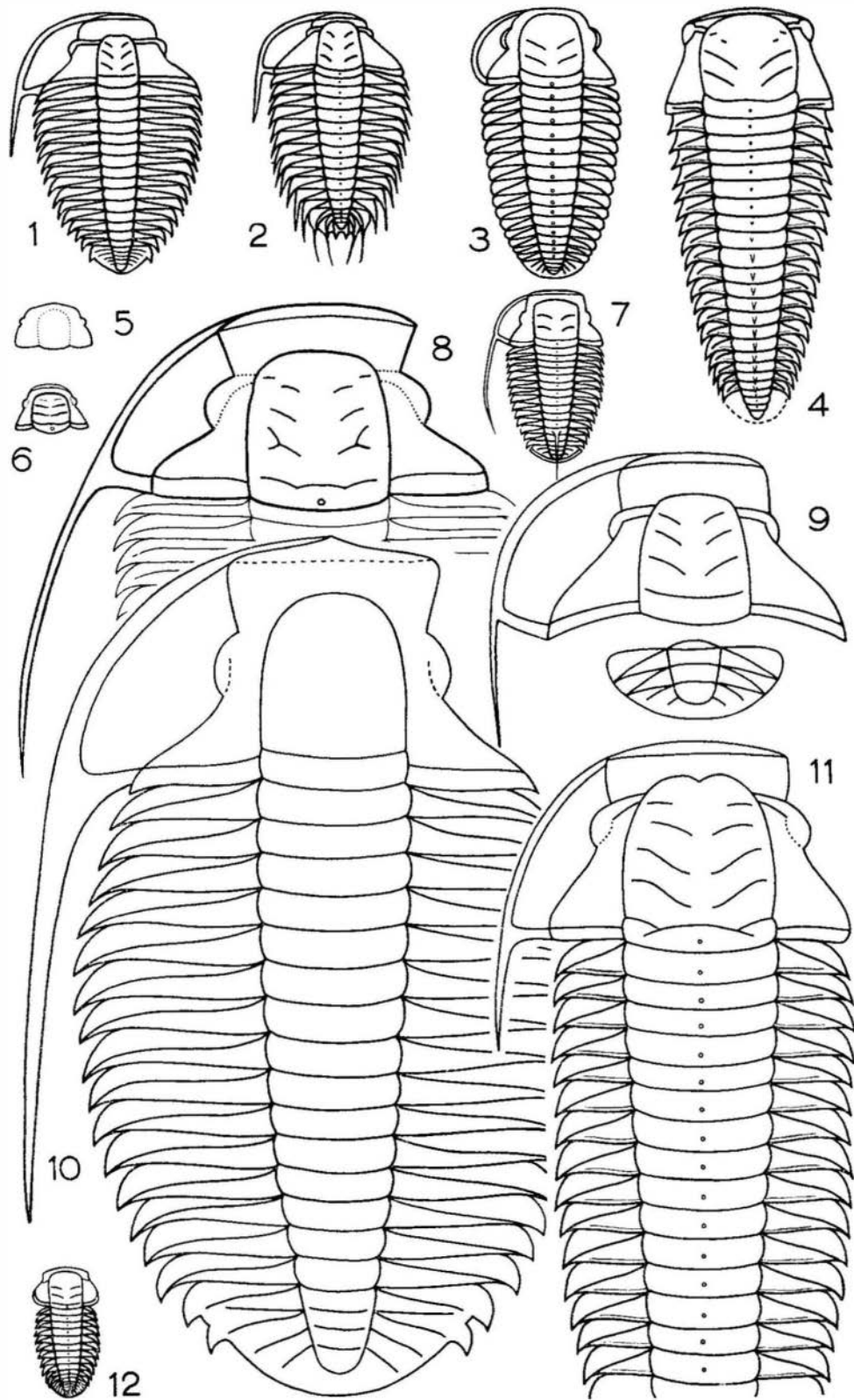


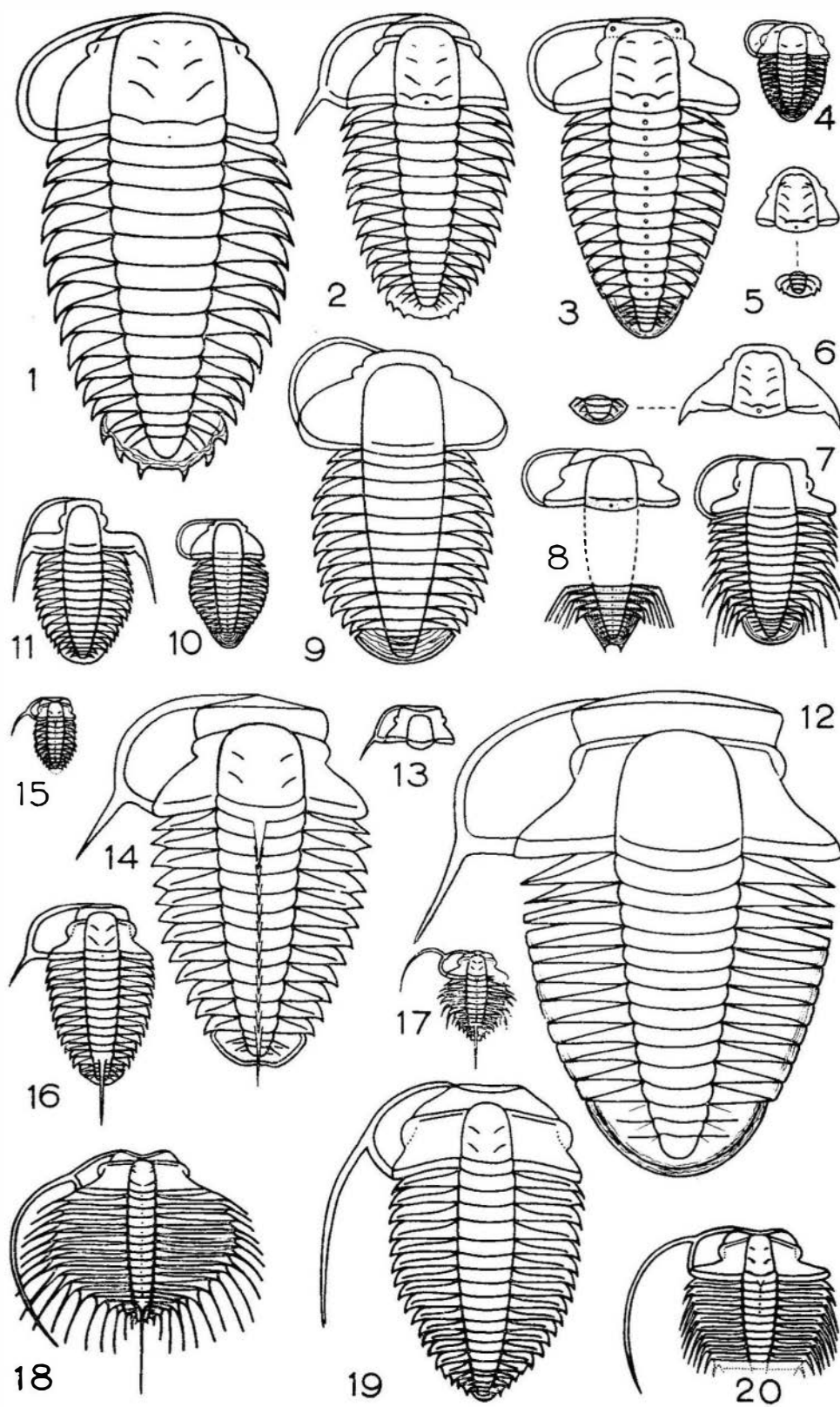
PLATE 2

Pelturinae. Type species. C. \times 2.

- Fig. 1. *Peltura scarabaeoides* (Vahlenberg 1821).
» 2. *Protopeltura praeursor* (Westergård 1909).
» 3. *Acerocare ecorne* Angelin 1854.
» 4. *Westergårdia scanica* (Westergård 1909).
» 5. *Pelturina punctifera* n. sp.
» 6. *Nericiaspis robusta* (Tjernvik 1953).
» 7. *Jujuyaspis keideli* Kobayashi 1936.
» 8. *Boeckaspis hirsuta* (Brögger 1882).
» 9. *Peltocare norvegicum* (Moberg & Möller 1898).
» 10. *Acerocarina micropyga* (Linnarsson 1875).
» 11. *Saltaspis steinmanni* (Kobayashi 1937).
» 12. *Beltella depressa* (Salter 1859).
» 13. *Paenebeltella vultulata* Ross 1951.
» 14. *Leptoplastides salteri* (Callaway 1877).

Leptoplastinae. Type species. C. \times 2.

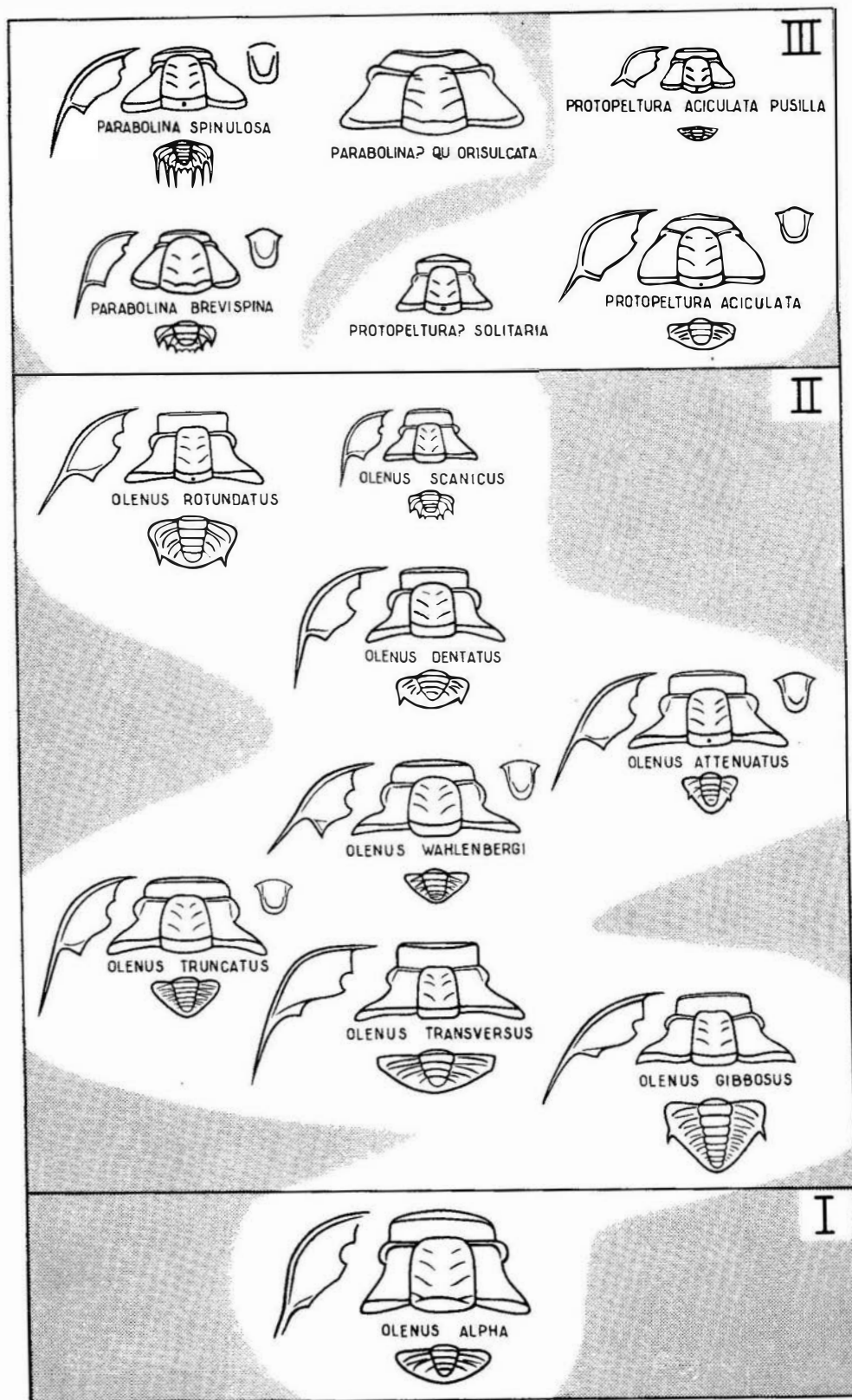
- Fig. 15. *Sphaerophthalmus alatus* (Boeck 1838).
» 16. *Leptoplastus stenotus* Angelin 1854.
» 17. *Ctenopyge* (*Eoctenopyge*) *flagellifera* (Angelin 1854).
» 18. *Ctenopyge* (*Ctenopyge*) *pecten* (Salter 1864).
» 19. *Eurycare brevicauda* Angelin 1854.
» 20. *Ctenopyge* (*Mesoctenopyge*) *spectabilis* Brögger 1882.



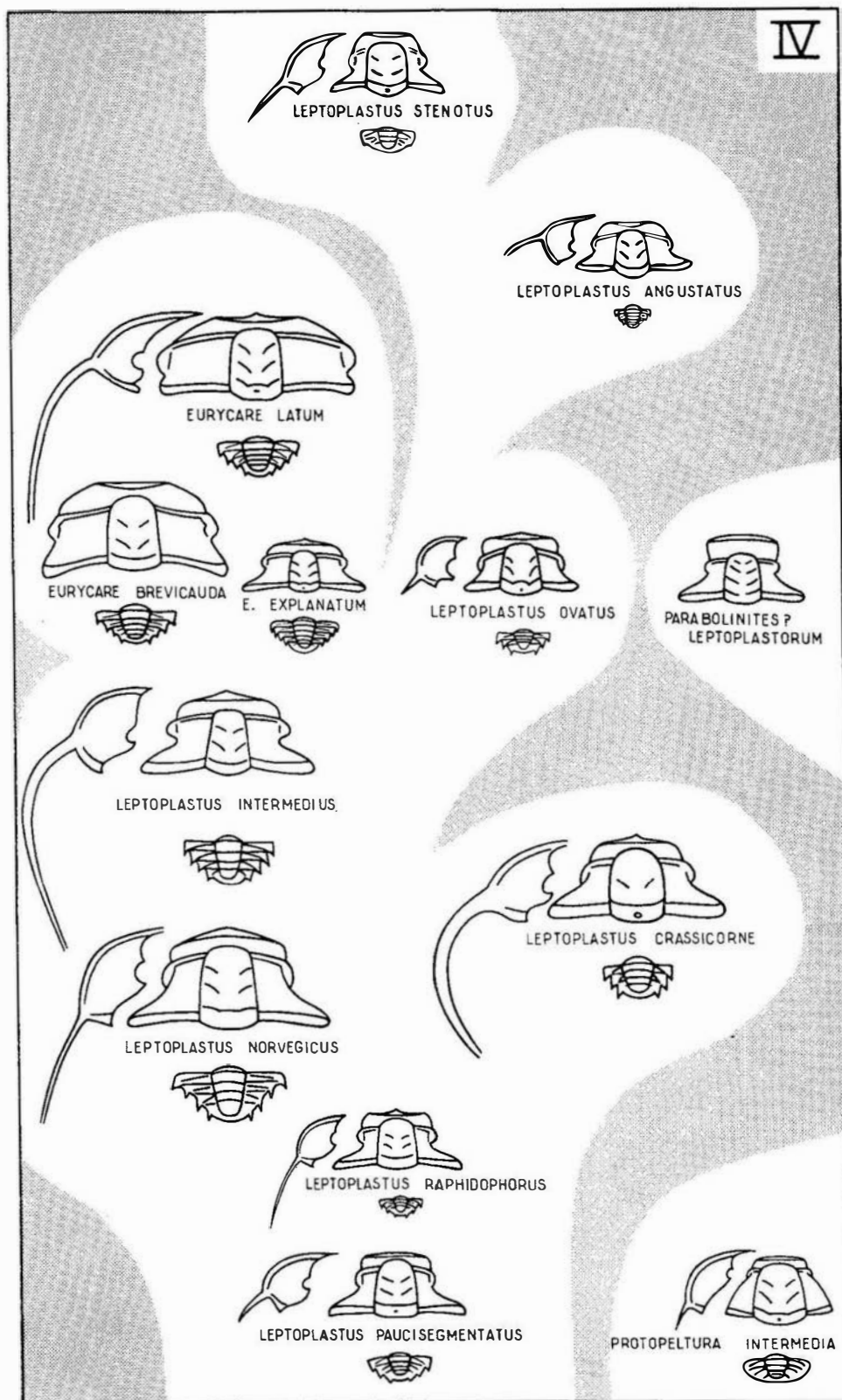
PLATES 3—8

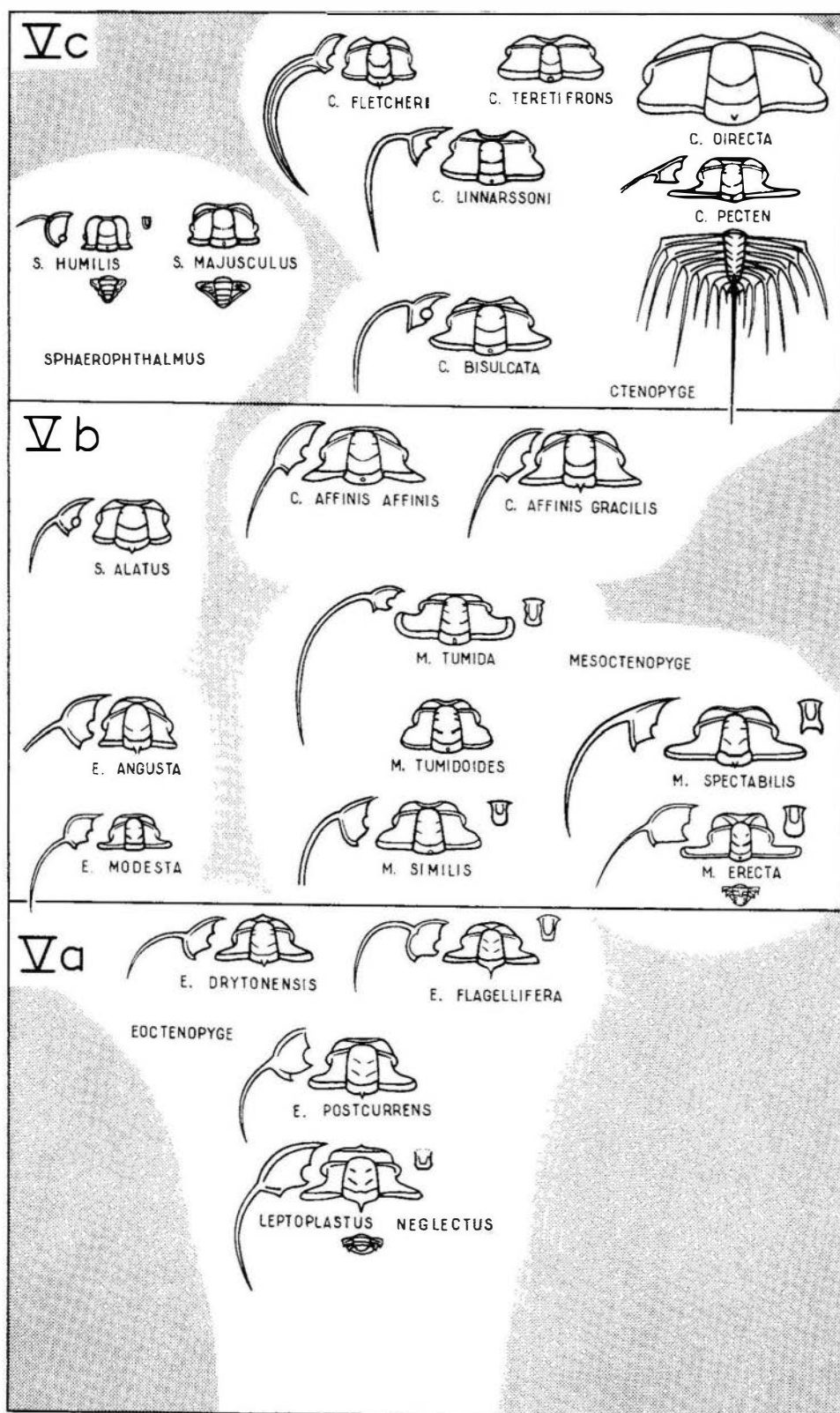
Outline drawings of free cheeks, cranidia, hypostomae, and pygidia of almost all the Upper Cambrian and Tremadocian olenids in Scandinavia, arranged in stratigraphic order (cf. also charts 2—4).

The drawings are based on photographs published by Westergård (1922, 1944a, 1947) and on photographs in this paper. All the drawings show the parts of the shields at about twice the natural size. In species where complete axial or dorsal shields are not known, the pygidium may possibly belong to a slightly smaller or larger specimen than the cranidium. Since specimens with the hypostoma in situ are very rare, the hypostoma, too, may not correspond exactly in size to the cranidium.

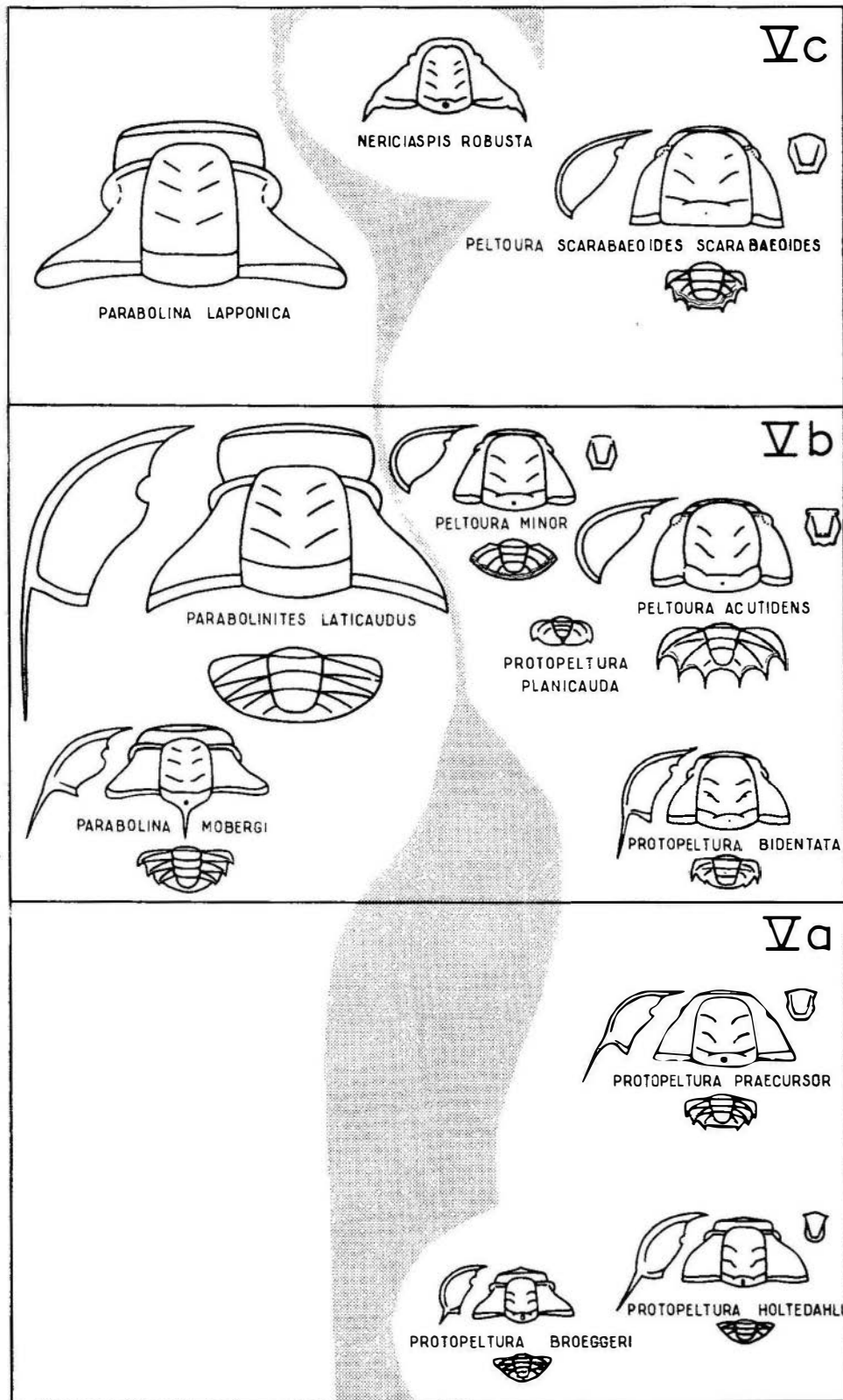


Pl. 3. Olenids in the Upper Cambrian zones I—III (all c. $\times 2$).

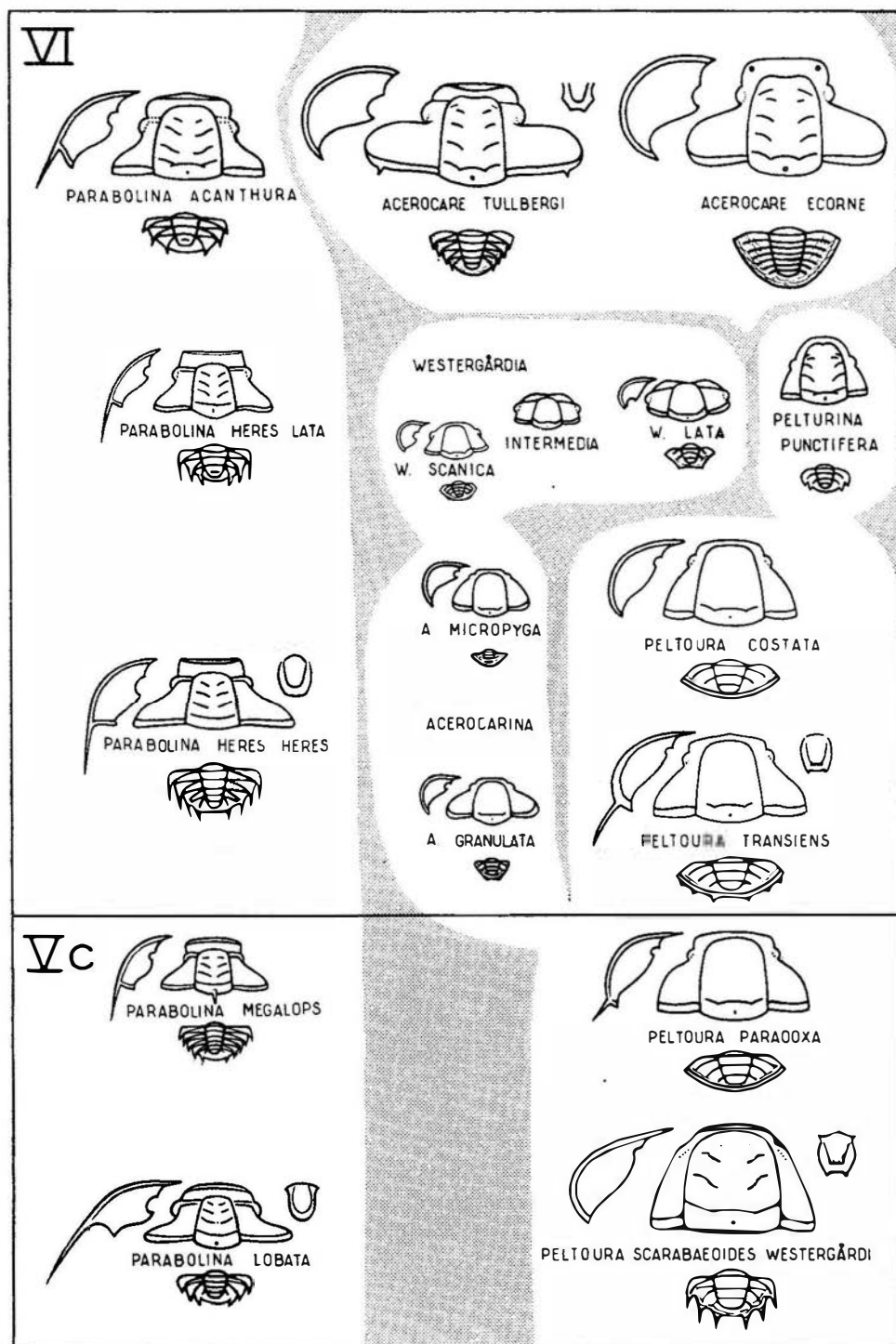
Pl. 4. ●lenids in the Upper Cambrian zone IV (all c. $\times 2$).



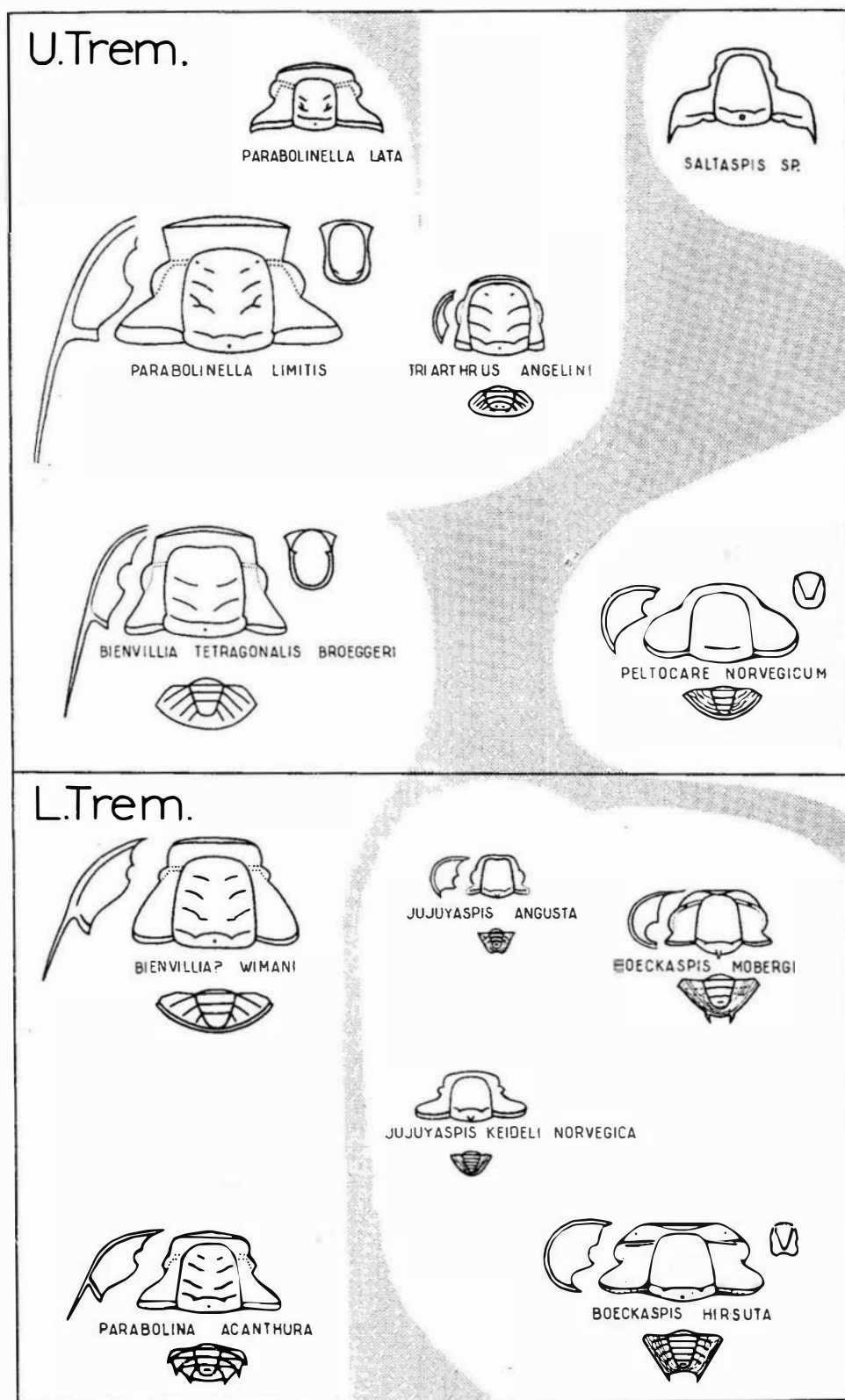
Pl. 5. Lepto-plastines in the Upper Cambrian zones Va-b and the lower part of the zone Vc (all c. $\times 2$).



Pl. 6. Olenines and pelturines in the Upper Cambrian zones Va, Vb, and Vc (lower part) (all c. $\times 2$). For *Peltoura* read *Peltura*.



Pl. 7. Olenids in the Upper Cambrian zones Vc (upper part) and VI (all c. $\times 2$).
For *Peltoura* read *Peltura*.

Pl. 8. Lower and Upper Tremadocian olenids (all c. $\times 2$).

PLATES 9—31

The photographs were taken by Miss B. Mauritz in cooperation with the author.

With one exception (pl. 30, fig. 4) the specimens were whitened with ammonium chloride.

The photographs are not retouched.

The light comes from the upper left corner, except where the position of the fossil in the rock prevented this, or where certain features were brought out better with light from some other angle.

PLATE 9

Olenus alpha n. sp. — p. 100.

2aα (I), Mælum, Ringsaker, Norway. Coll.: W. C. Brögger.

- Fig. 1. × 5. Cranidium (P. M. O. no. 66756). *Holotype*.
 » 2. × 5. Cranidium (P. M. O. no. 66759), associated with cephalon of *Agnostus pisiiformis*.
 » 3. × 5. Cranidium (P. M. O. no. 30189).
 » 4. × 5. Free cheek (P. M. O. no. 66768).
 » 5. × 5. Cranidium (P. M. O. no. 66766a).
 » 6. × 5. Pygidium (P. M. O. no. 66757).

Olenus gibbosus (Wahlenberg 1821) — p. 105.

- Fig. 7. × 5. Cranidium (P. M. O. no. 30075). 2aβ (II) *gibb.*, Viul, Ringerike, Norway. Coll.: O. Holtedahl, 1908. Figured by Holtedahl, 1910, pl. II, fig. 11 as *Olenus truncatus*.

Parabolina? quadrisulcata n. sp. — p. 128.

- Fig. 8. × 5. Cranidium (RM. no. Ar. 149). *Holotype*. III, Funäs, Myssjö Parish, Jämtland, Sweden. Coll.: C. Wiman, 1891. Figured by Westergård, 1922, pl. VI, fig. 25 as *Olenus*(?) sp.

Parabolina lobata lobata (Brögger 1882) — p. 122.

- Fig. 9. × 5. Cranidium (P. M. O. no. 66790) with short and oblique eye ridges. 2:δ (Vc) *lob.*, Kårtveitbekken, Eiker, Norway. Coll.: H. Neumann and T. Strand, 1945.
 » 10. × 5. Cranidium (P. M. O. no. 19937). *Holotype*. 2dδ (Vc) *lob.*, Vestfossen, Eiker, Norway. Coll.: W. C. Brögger, 1879. Figured by Brögger, 1882, pl. XII, fig. 11 as *Ctenopyge*(?) *lobata*.
 » 11. × 1.35. Dorsal shield (P. I. U. no. V. ar. 4284) of form with short and oblique eye ridges. Vc *lob.*, Råbäck alum shale quarry, Kinnekulle, Västergötland, Sweden. Coll.: Exc., 1941.

Parabolina kinnekullensis n. sp. — p. 121.

- Fig. 12. × 1.05. Dorsal shield (RM. no. Ar. 38115). *Holotype*. Vc *lob.*, Trollmen, Kinnekulle, Västergötland, Sweden.

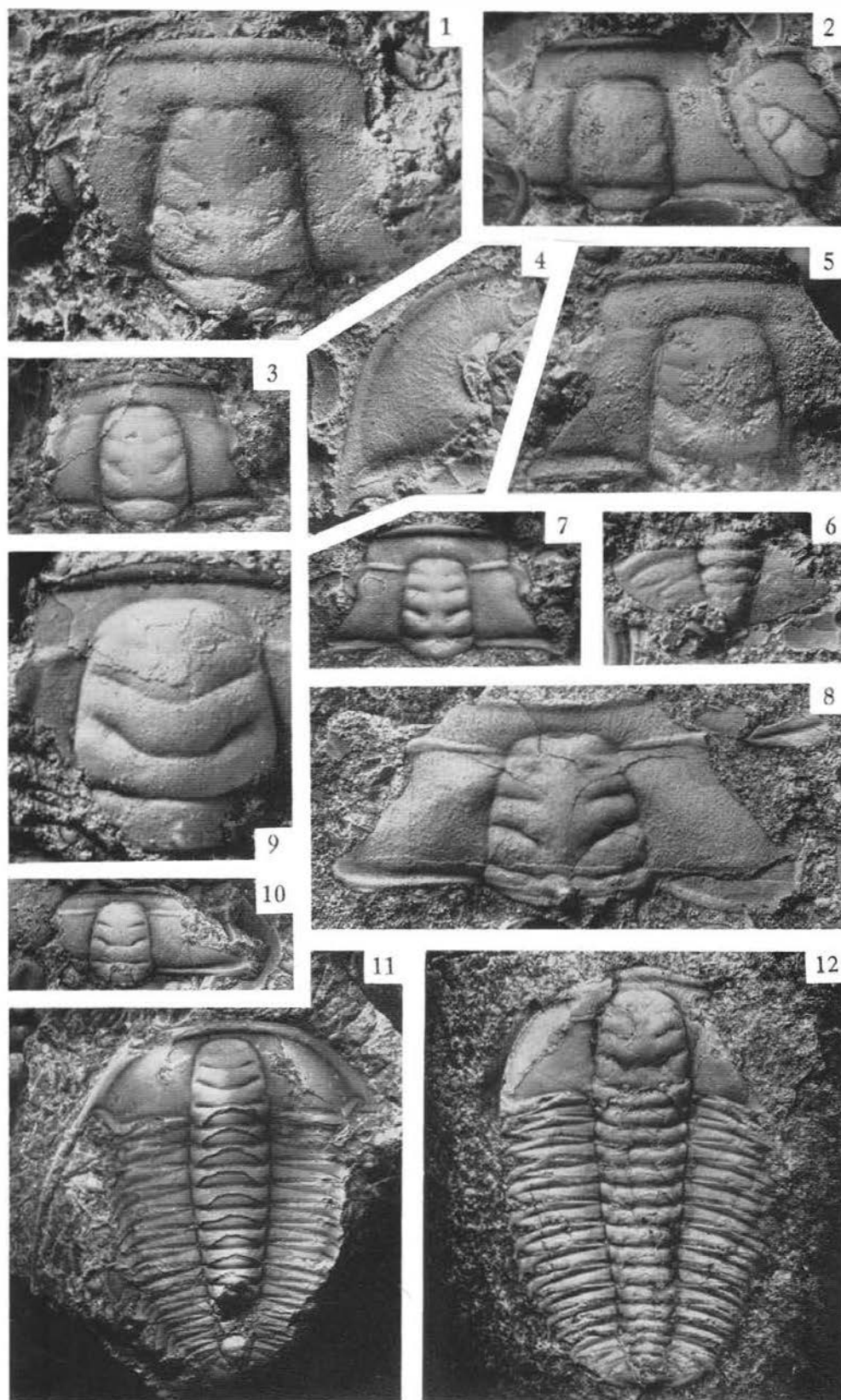


PLATE 10

Parabolina acanthura (Angelin 1854) — — p. 116.

- Fig. 1. $\times 5$. Free cheek (P. M. O. no. 66794). 2de (VI) *acan.*, beach at Nærsnes gård in Røyken, Norway. Coll.: G. Henningsmoen, 1951.
- » 2. $\times 5$. Cranidium (P. M. O. no. 66805). Hor. & loc. as fig. 1. Coll.: N. Spjeldnæs, F., Nikolaisen, & G. Henningsmoen, 1954.
- » 3. $\times 5$. Free cheek (P. M. O. no. 66814). 2ea *hirs.*, beach at Nærsnes gård in Røyken, Norway. Coll.: G. Henningsmoen, 1951.
- » 4. $\times 5$. Free cheek (P. M. O. no. 66816). Other data as for fig. 3.
- » 5. $\times 5$. Cranidium (P. M. O. no. 66815). Other data as for fig. 3.
- » 6. $\times 2.1$. Dorsal shield (P. M. O. no. 66817). 2de (VI) *ecorne*, beach at Nærsnes gård in Røyken, Norway. Coll.: G. Henningsmoen, 1951.

Bienzillia? wimani (Westergård 1917) — — p. 146.

- Fig. 7. $\times 5$. Fragmentary cranidium (P. M. O. no. S 904). 2e β (L. Trem.), Jaren in Hadeland, Norway. Coll.: L. Stormer, 1919.
- » 8. $\times 5$. Free cheek (P. M. O. no. S 947). Other data as for fig. 7.
- » 9. $\times 5$. Anterior part of cranidium (P. M. O. no. S 959). Other data as for fig. 7.

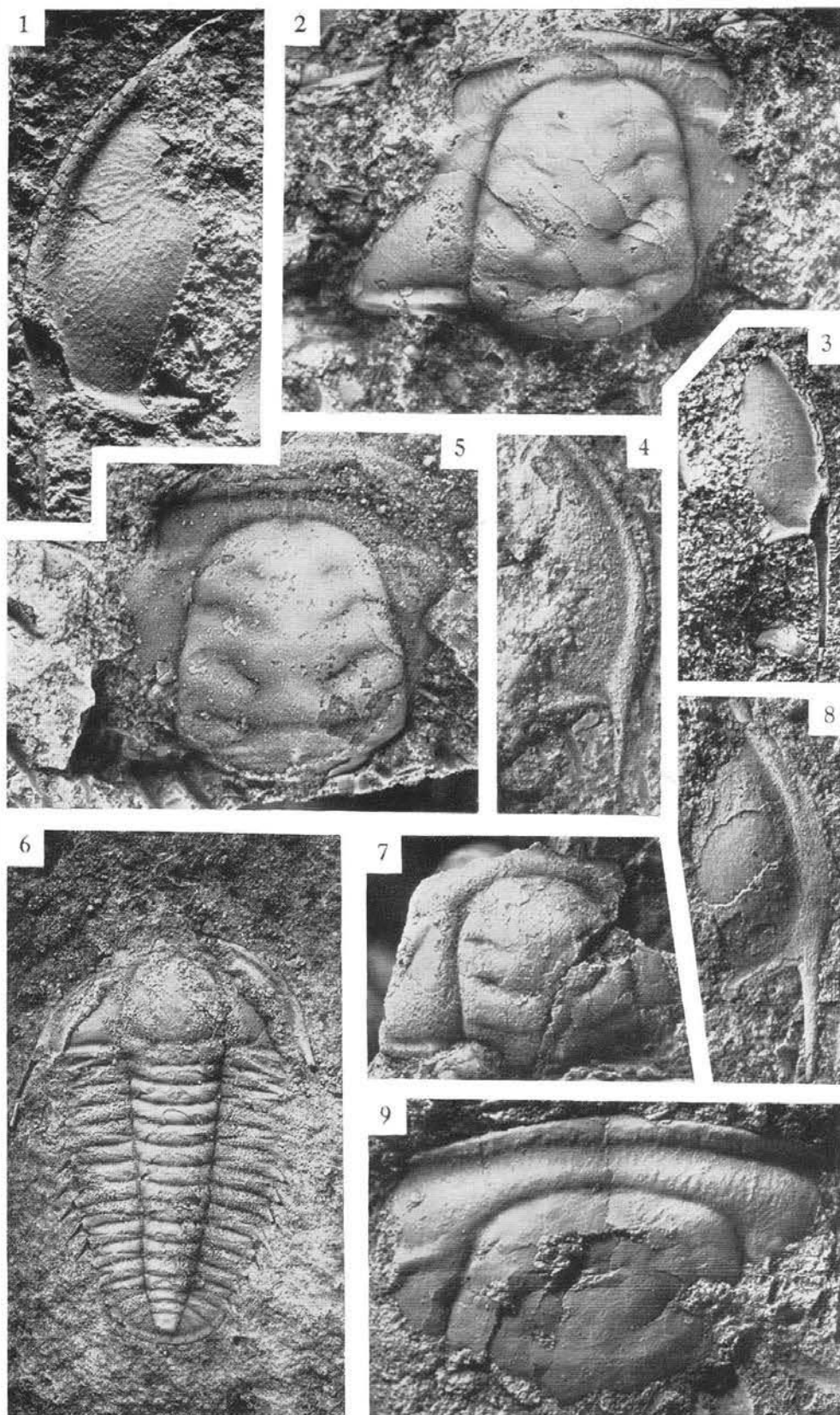


PLATE 11

Bienwillia tetragonalis broeggeri n. subsp. — — p. 145.

3aa (U. Trem.), Vekkero, Oslo, Norway. Coll.: L. Stormer, 1918—19.

Fig. 1. $\times 5$. Plasteline cast of impression of cranium (P. M. O. no. 482).

» 2. $\times 5$. Cranium (P. M. O. no. 488). *Holotype*.

» 3. $\times 3$. Free cheek (P. M. O. no. 66827). Figured by Stormer, 1920, pl. I, fig. 7 as *Parabolinella limitis*.

» 4. $\times 5$. Cranium (P. M. O. no. 66828). Figured by Stormer, 1920, pl. I, fig. 7 as *Parabolinella limitis*.

» 5. $\times 5$. Pygidium (P. M. O. no. 484). Figured by Stormer, 1920, pl. I, fig. 8 as *Parabolinella limitis*.

» 6. $\times 5$. Pygidium (P. M. O. no. 66829).

» 7. $\times 5$. Hypostoma (P. M. O. no. 439). Figured by Stormer, 1920, pl. II, fig. 7 as *Parabolinella?*

Triarthrus angelini angelini Linnarsson 1869 — — p. 148.

Fig. 8. $\times 5$. Pygidium (P. M. O. no. 66830). Base of 3aγ (U. Trem.), Skara, Vestfossen, Eiker, Norway. Coll.: Gunnar Henningsmoen 1954.

» 9. $\times 5$. Unusually large cranium (P. M. O. no. S 1136). Base of 3aγ (U. Trem.), Bygdøy Sjøbad, Oslo, Norway. Coll.: L. Stormer, 1918.

» 10. $\times 5$. Cranium (P. M. O. no. 66831) showing tuberculation. Other data as for fig. 8.

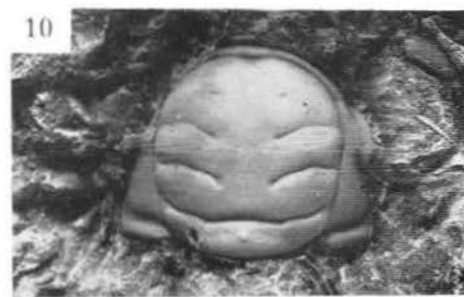
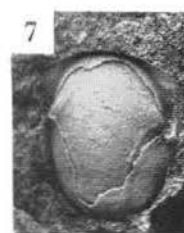


PLATE 12

Parabolinella limitis Brögger 1882 — — p. 135.

- Fig. 1. $\times 4.1$. Cranidium (P. M. O. no. 20032a). $3a\beta$ (U. Trem.), Stensberggt., Oslo, Norway. Coll.: J. Kiær, 1911.
- » 2. $\times 4.1$. Cranidium (P. M. O. no. 693). Other data as for fig. 1.
- » 3. $\times 2.5$. Cranidium (P. M. O. no. 20034). *Lectotype*. $3a\beta$ (U. Trem.), St. Olavsgt. Oslo, Norway. Coll.: Th. Münster. Figured by Brögger, 1882, pl. III, fig. 2.
- » 4. $\times 4.1$. Free cheek (P. M. O. no. 691e). Other data as for fig. 1.
- » 5. $\times 5$. Hypostoma (P. M. O. no. S 984). $3a\beta$ (U. Trem.), Vekkerø, Oslo, Norway. Coll.: L. Stormer, 1919.

Parabolinella triarthra (Callaway 1877) — — p. 138.

- Fig. 6. $\times 5$. Cranidium (P. M. O. no. A 17390). Shineton Shales, Shineton, Shropshire, England. Coll.: J. Kiær, 1904.
- » 7. $\times 5$. Cranidium (P. M. O. no. A 17389). Other data as for fig. 6.

Parabolinella lata n. sp. — — p. 135.

- Fig. 8. $\times 5$. Cranidium (P. M. O. no. 1287a). *Holotype*. $3a\gamma$ (U. Trem.), S. Bjerkåsholme, Royken, Norway. Coll.: ?, 1915.

Parabolinella rugosa Brögger 1882 — — p. 137.

- Fig. 9. $\times 5$. Cranidium (P. M. O. no. 1267a). $3a\gamma$ (U. Trem.), S. Bjerkåsholme, Royken, Norway. Coll.: ?, 1915.

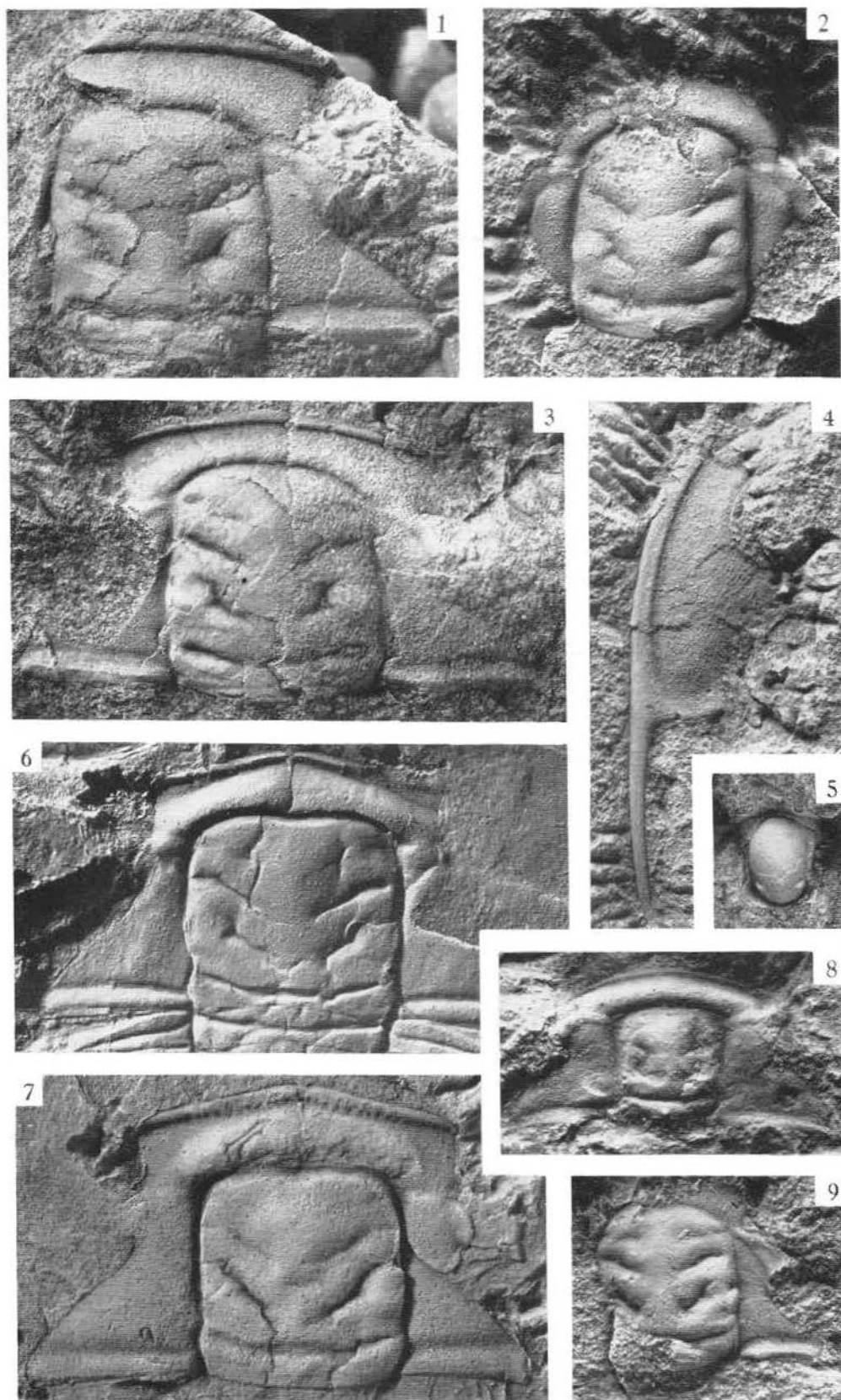


PLATE 13

All $\times 5$.

Leptoplastus raphidophorus Angelin 1854 — — p. 175.

- Fig. 1. Free cheek (P. M. O. no. 29155a). 2c (IV) *raph.*, Slemmestad, Røyken, Norway. Coll.: O. Holtedahl, 1908.
- » 2. Cranidium (P. M. O. no. 30318). 2c (IV) *raph.*, loose block, Stange, Hamar area, Norway. Coll.: W. C. Brögger, 1881. Figured by Holtedahl, 1910, pl. I, fig. 4 as *Leptoplastus ovatus*.
 - » 3. Free cheek (P. M. O. no. 30320). Other data as for fig. 2.
 - » 4. Free cheek (P. M. O. no. 29155c). Other data as for fig. 1.
 - » 5. Cranidium (P. M. O. no. 29155d). Other data as for fig. 1.
 - » 6. Cranidium (P. M. O. no. 29155b). Other data as for fig. 1.
 - » 7. Axial shield (RM. no. Ar. 2114d). *Lectotype*. IV *raph.*, Andrarum, Scania, Sweden.

Leptoplastus ovatus Angelin 1854 — — p. 173.

- Fig. 8. Cranidium (P. M. O. no. 30338b). 2c (IV) *ovat.*, Jonsberg, Romedal, Hamar area. Old coll.
- » 9. Cranidium (P. M. O. no. 30339a). Other data as for fig. 8.
 - » 10. Free cheek (P. M. O. no. 30338c). Other data as for fig. 8. Figured by Holtedahl, 1910, pl. I, fig. 11 as *Leptoplastus ovatus* var. *explanata*.

Leptoplastus claudicans (Moberg & Möller 1898) — — p. 165.

- Fig. 11. Small, but relatively well-preserved cranidium (P. I. L. no. LO 1377). Loose block, Andrarum, Scania, Sweden. Coll.: Tullberg.
- » 12. Free cheek (P. I. L. no. LO 1380). Hor., loc., & coll. as fig. 11. Figured by Moberg, 1898, pl. 16, fig. 4, as *Acerocare claudicans*.
 - » 13. Large, but badly preserved cranidium and pygidium (lower right quadrangle) (P. I. L. no. 1379). Other data as for fig. 11.

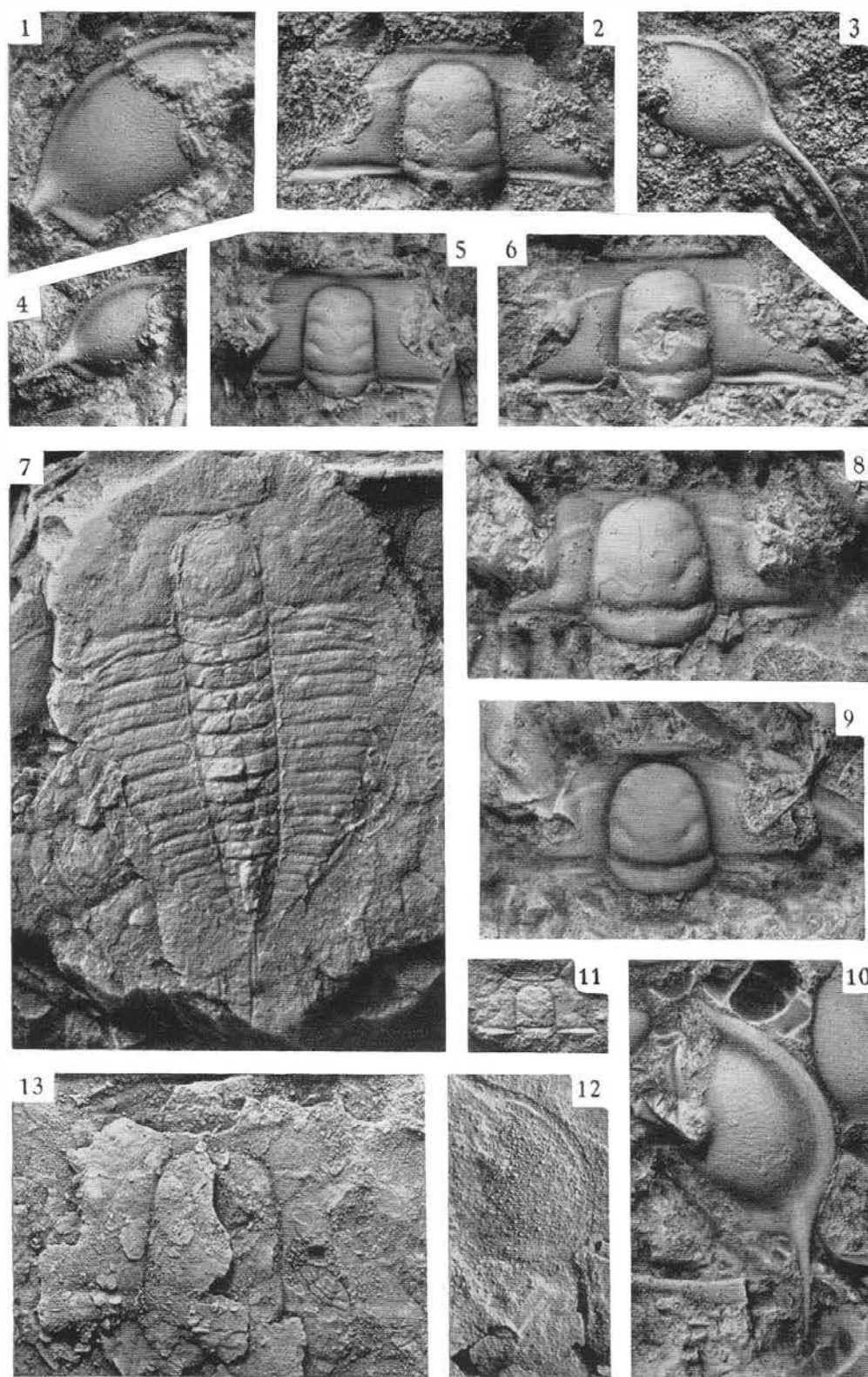


PLATE 14

All $\times 5$.

Leptoplastus crassicorne (Westergård 1944) — — p. 167.

- Fig. 1. Free cheek (P. M. O. no. 30350). 2c (IV) *crass.*, Evjevika, Ringsaker, Norway. Coll.: T. Strand, 1926.
- » 2. Free cheek (P. M. O. no. 28989). 2c (IV) *crass.*, Krekling, Eiker, Norway. Coll.: W. C. Brögger, 1879.
- » 3. Free cheek (P. M. O. no. S 392). 2c (IV) *crass.*, Ringsaker, Norway. Coll.: L. Størmer, 1919.
- » 4. Cranidium (P. M. O. no. 19916c). Other data as for fig. 2.
- » 5. Free cheek (P. M. O. no. 28988a). Other data as for fig. 2.
- » 6. Pygidium (P. M. O. no. 19916a). Other data as for fig. 2.
- » 7. Cranidium (P. M. O. no. S 409c). Other data as for fig. 3.
- » 8. Cranidium (P. M. O. no. 28998). Other data as for fig. 2.
- » 9. Free cheek (P. M. O. no. 30336). 2c (IV) *ovul.*, Jønsberg, Romedal, Hamar area. Old coll.
- » 10. Cranidium (P. M. O. no. 30338d). Other data as for fig. 9.
- » 11. Cranidium (P. M. O. no. 30338e). Other data as for fig. 9.
- » 12. Pygidium (P. M. O. no. 30336c) and counterpart of cranidium. Other data as for fig. 9.
- » 13. Spines of free cheeks (P. M. O. no. 30336b). Other data as for fig. 9.

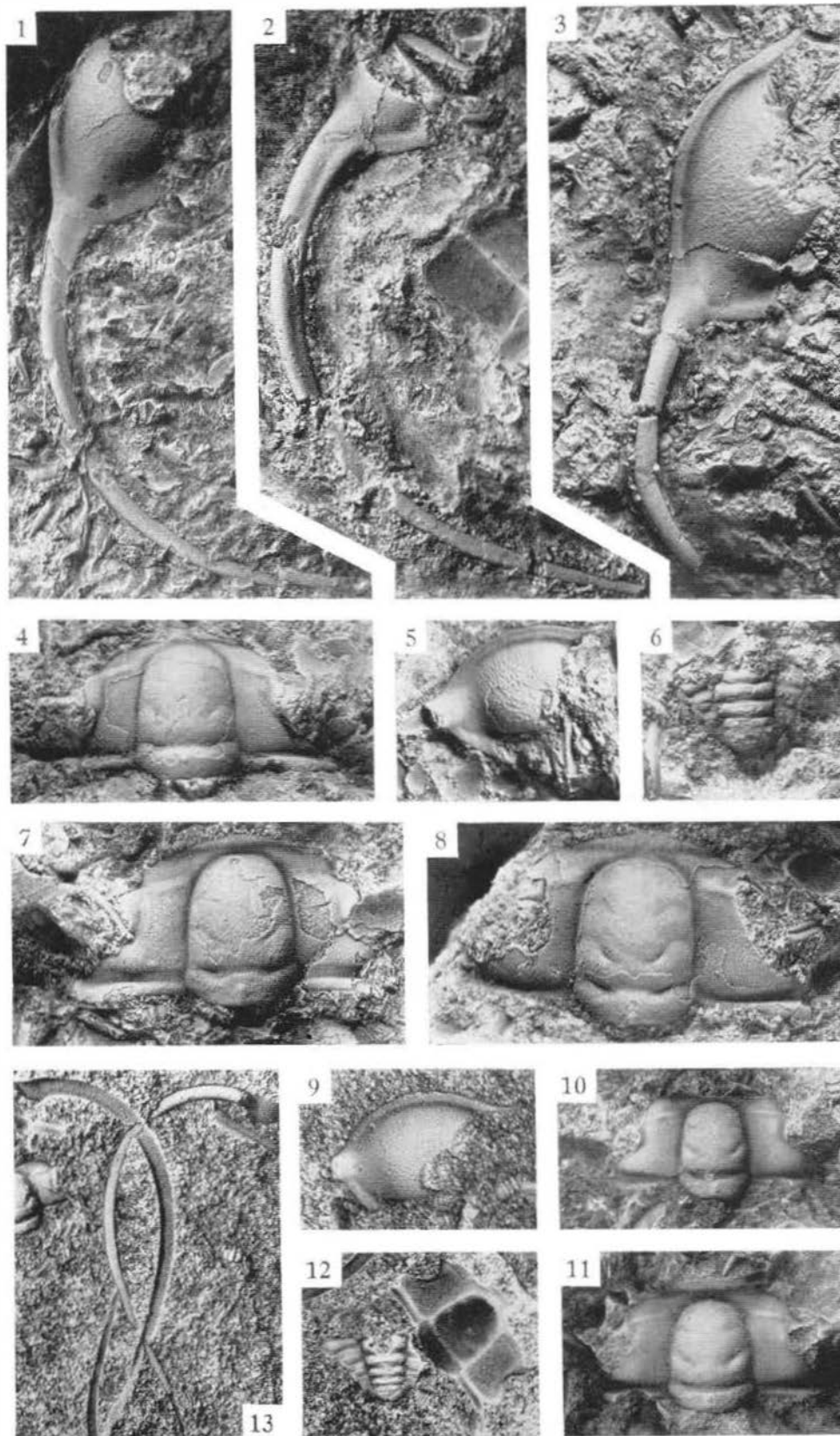


PLATE 15

Leptoplastus norvegicus (Holtedahl 1910) — — p. 170.

- Fig. 1. $\times 5$. Cranidium (P. M. O. no. 30334d). Other data as for fig. 7.
- » 2. $\times 5$. Free cheek (P. M. O. no. 28996). 2c (IV) *crass.*, Krekling, Eiker, Norway. Coll.: W. C. Brögger, 1897. Figured by Holtedahl, 1910, pl. III, fig. 13 as *Leptoplastus longispinus*.
- » 3. $\times 5$. Thoracic segment (P. M. O. no. S 407). 2c (IV) *crass.*, Ringsaker, Norway. Coll.: L. Størmer, 1919.
- » 4. $\times 5$. Free cheek (P. M. O. no. S 409a) with rather great genal angle. Other data as for fig. 3.
- » 5. $\times 5$. Pygidium (P. M. O. no. 28997). Other data as for fig. 2.
- » 6. $\times 5$. Free cheek (P. M. O. no. S 391). Other data as for fig. 3.
- » 7. $\times 3.5$. Axial shield (P. M. O. no. 30334a). *Lectotype*. 2c (IV) *crass.*, Hamar area. Acquired for the Museum by W. C. Brögger, 1898.
- » 8. $\times 3.5$. Counterpiece (P. M. O. no. 30334b) of the cranidium of the lectotype (fig. 7). Other data as for fig. 7.
- » 9. $\times 5$. Cranidium (P. M. O. no. 28988b). Other data as for fig. 2.
- » 10. $\times 5$. Cranidium (P. M. O. no. 30334c). Other data as for fig. 7.

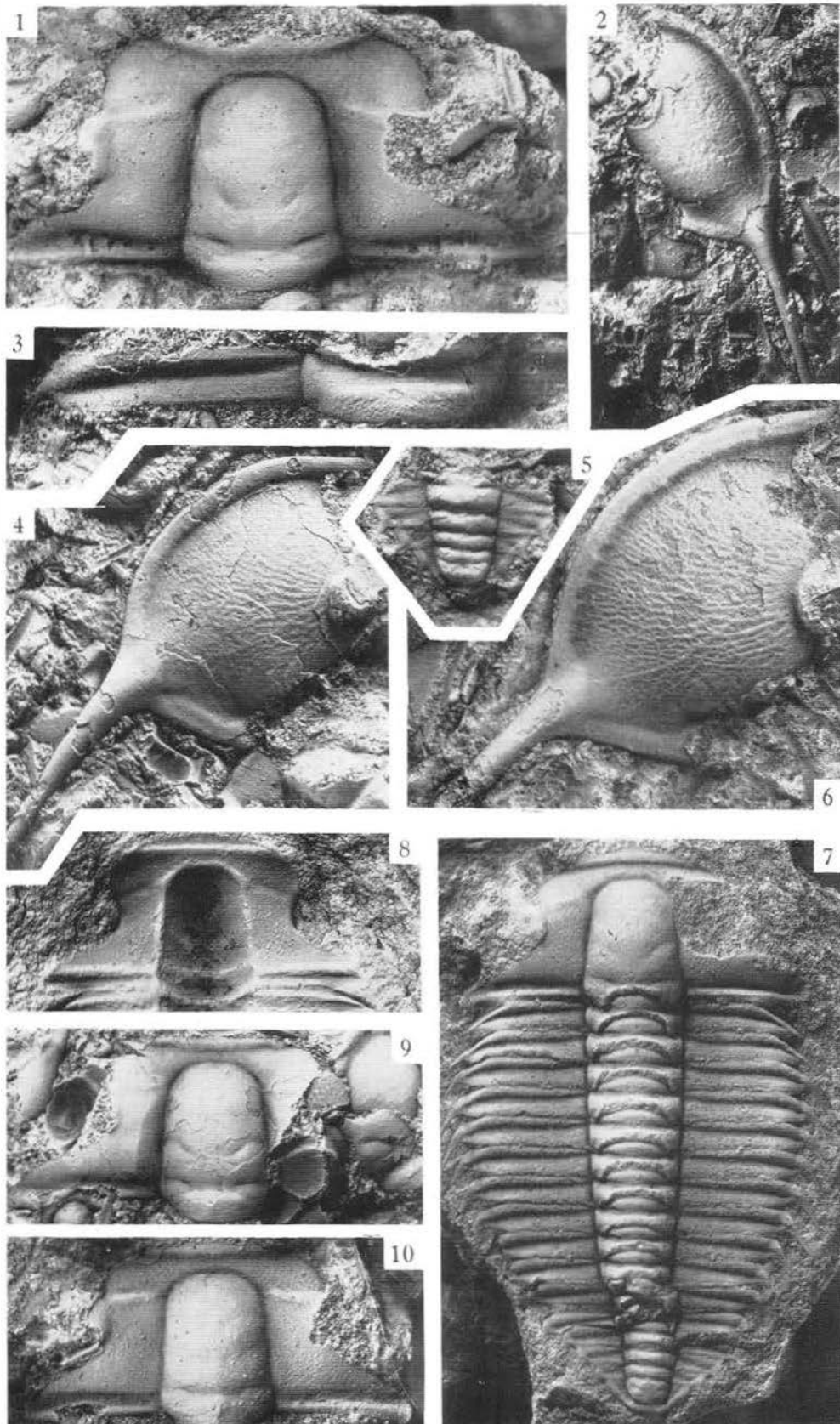


PLATE 16

Leptoplastus norvegicus (Holtedahl 1910) — — p. 170.

- Fig. 1. $\times 5$. Cranidium (P. M. O. no. S 406). 2c (IV) *crass.*, Ringsaker, Norway.
Coll.: L. Stormer, 1919.
» 2. $\times 5$. Pygidium (P. M. O. no. S 409b). Field data, cf. fig. 1.

Eurycare explanatum (Holtedahl 1910) — — p. 179.

- Fig. 3. $\times 5$. Cranidium (P. M. O. no. 30337a). *Lectotype*. 2c (IV) *ovul.*, Jonsberg, Romedal, Hamar area, Norway. Coll.: ?
» 4. $\times 5$. Counterpiece of pygidium (P. M. O. no. 30337b). Field data, cf. fig. 3.
» 5. $\times 5$. Cranidium (P. M. O. no. 30338a). Field data, cf. fig. 3.

Eurycare latum (Boeck 1838) — — p. 181.

- Fig. 6. $\times 3.7$. Cranidium (P. M. O. no. 66927). 2c (IV), Toyen, Oslo, Norway. Coll.: Th. Münster.
» 7. $\times 5$. Small cranidium (P. M. O. no. 66833). 2c (IV), Gamlebyen, Oslo, Norway, Coll.: Corneliusen.
» 8. $\times 5$. Small cranidium (P. M. O. no. 66834). Field data, cf. fig. 7.
» 9. $\times 5$. Small cranidium (P. M. O. no. 56383a). Hor. & loc. as for fig. 7. Coll.: C. Boeck. *Lectotype*.

Leptoplastus angustatus (Angelin 1854) — — p. 164.

- Fig. 10. $\times 5$. Free cheek (P. M. O. no. 19975). 2c (IV) *ang.*, Slemmestad, Royken, Norway, Coll.: O. Holtedahl, 1908.
» 11. $\times 5$. Axial shield (P. M. O. no. 30651). 2c (IV) *ang.*, Herredsvang, Romedal, Hamar area, Norway. Coll.: L. Gaustad.
» 12. $\times 5$. Axial shield (P. M. O. no. 66840). 2c (IV) *ang.*, Løyten, Hamar area, Norway. Coll.: ?
» 13. $\times 5$. Free cheek (P. M. O. no. 30325). 2c (IV) *ang.*, Evjevika, Ringsaker, Norway. Coll.: T. Strand, 1927.

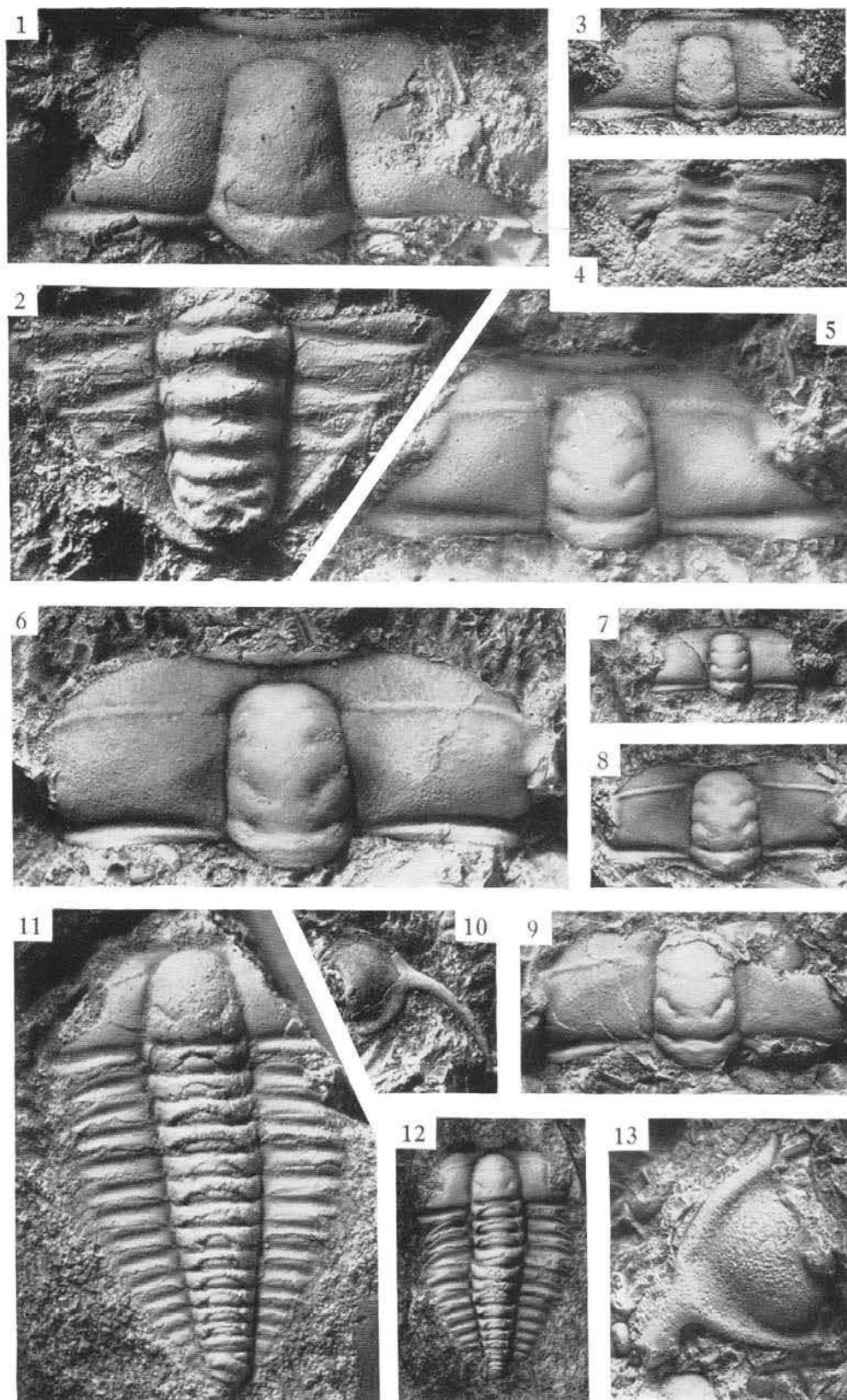


PLATE 17

All $\times 6.1$.

Leptoplastus neglectus (Westergård 1922) — — p. 168.

- Fig. 1. Dorsal shield (RM. no. Ar. 1725). Andrarum in Scania?, Sweden. Coll.: ?
Figured by Westergård, 1922, pl. X, fig. 2 as *Leptoplastus raphidophorus*.
- » 2. Free cheek (P. M. O. no. 19978a). 2d α (Va) *negl.*, Slemmestad, Royken, Norway. Coll.: O. Holtedahl, 1908.
 - » 3. Cranidium (P. M. O. no. 29162). 2d α (Va) *negl.*, Slemmestad, Royken, Norway. Coll.: T. Kjerulf excursion.
 - » 4. Cranidium (S. G. U.). *Lectotype*. Va *negl.*, Andrarum, Scania, Sweden. Coll.: A. H. Westergård, 1913. Figured by Westergård, 1922, pl. X, fig. 11, as *Ctenopyge neglecta*.
 - » 5. Cranidium (RM. no. Ar. 1725). Associated with the dorsal shield in fig. 1.
 - » 6. Cranidium (P. M. O. no. 19978d). Other data as for fig. 2.
 - » 7. Cranidium (P. M. O. no. 19978c). Other data as for fig. 2.

Ctenopyge (*Eoctenopyge*) *postcurrens* Westergård 1944 — — p. 193.

The illustrated specimens belong to a form close to *Leptoplastus neglectus*.

- Fig. 8. Free cheek (P. M. O. no. H 2716d). 2d α (Va) *postc.*, Nærsnes, Royken, Norway. Coll.: W. C. Brögger, 1880.
- » 9. Cranidium (P. M. O. no. H 2716f). Other data as for fig. 8.
 - » 10. Free cheek (P. M. O. no. H 2716e). Other data as for fig. 8.

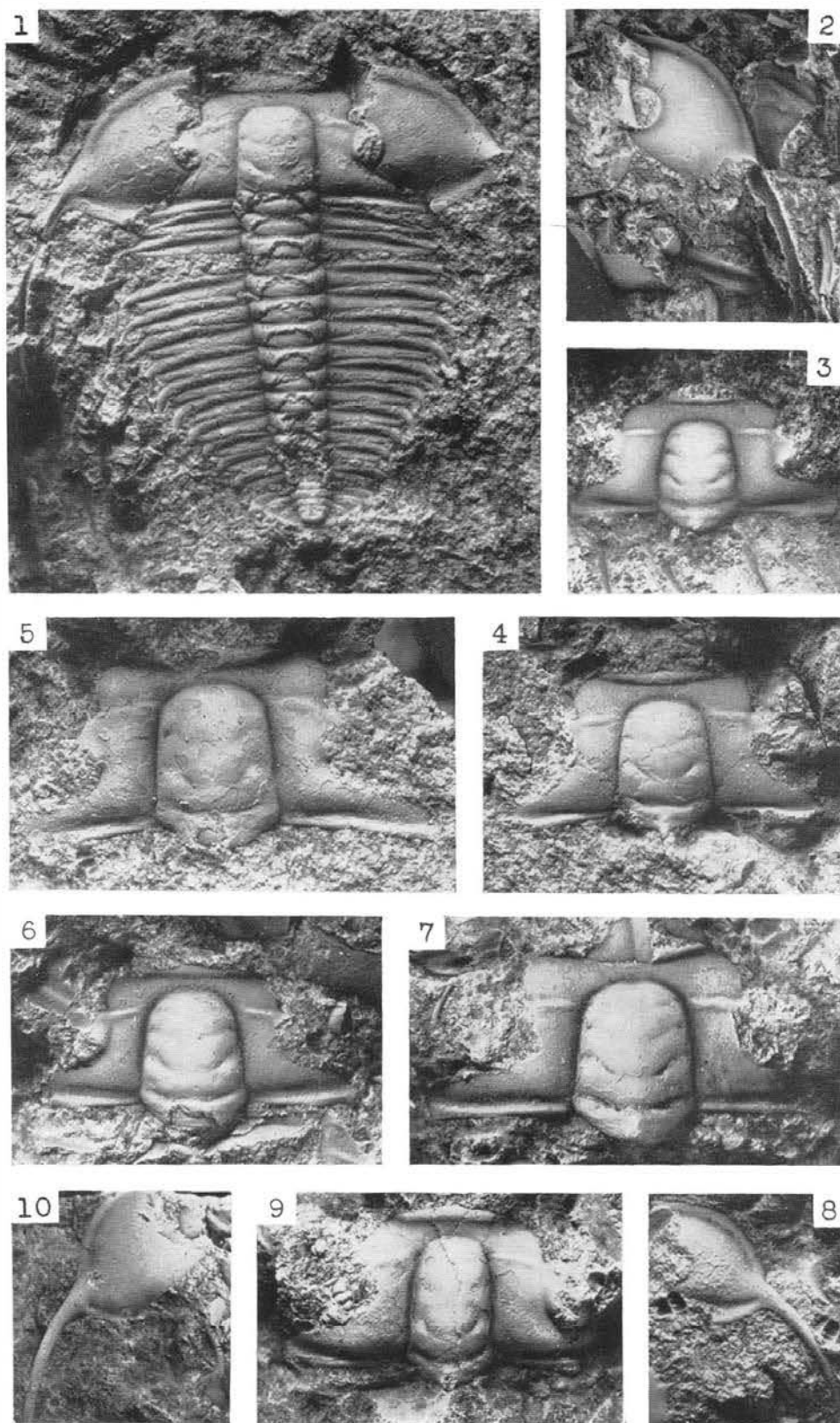


PLATE 18

Ctenopyge (Eoctenopyge) flagellifera (Angelin 1854) — p. 189.

- Fig. 1. $\times 6.3$. Axial shield without pygidium (P. M. O. no. 66841). 2d α (Va) *flag.*, Nærsnes, Røyken, Norway. Coll.: N. Spjeldnæs, 1954.
- » 2. $\times 6$. Free cheek (S. G. U.). Associated with the lectotype. Va, *flag.*, Andrarum, Scania, Sweden. Coll.: A. H. Westergård, 1913.
- » 3. $\times 6$. Free cheek (P. M. O. no. 19985d). 2d α (Va) *flag.*, Gamlebyen, Oslo, Norway. Coll.: Corneliussen.
- » 4. $\times 6.3$. Free cheek (G. S. M. no. Pe 2607K). Va *flag.*, Block C (?), Dryton Brook, Shropshire, England. Coll.: E. S. Cobbold.

Ctenopyge (Eoctenopyge) drytonensis Cobbold 1934 — p. 188.

- Fig. 5. $\times 6.4$. Cranidium (G. S. M. no. 51778) of this species? Holotype of *Ctenopyge parabola*. Figured by Cobbold & Pocock, 1934, pl. 45, fig. 11 as *Sphaerophthalmus(?) parabola*. Block A, Dryton Brook, Shropshire, England. Coll.: E. S. Cobbold.
- » 6. $\times 6.4$. Cranidium (G. S. M. no. 51773 B). Figured by Cobbold & Pocock, 1934, pl. 45, fig. 19. Block A.
- » 7. $\times 6.4$. Cranidium (G. S. M. no. 51780 B). Figured by Cobbold & Pocock, 1934, pl. 45, fig. 13 as *Sphaerophthalmus(?) parabola*. Block A.
- » 8. $\times 6.5$. Cranidium (G. S. M. no. 51776). *Holotype*. Figured by Cobbold & Pocock, 1934, pl. 45, fig. 9. Block A.
- » 9. $\times 6.4$. Cranidium (G. S. M. no. 51775). Figured by Cobbold & Pocock, 1934, pl. 45, fig. 8 as *Eurycare angustatum*. Block A.
- » 10. $\times 6$. Plasteline cast of free cheek (P. M. O. no. 19985c). 2d α (Va) *flag.*, Gamlebyen, Oslo, Norway. Coll.: Corneliussen.
- » 11. $\times 6.4$. Free cheek (G. S. M. no. 51781 A). Figured by Cobbold & Pocock, 1934, pl. 45, fig. 14 as *Ctenopyge flagellifera angusta*. Block A.
- » 12. $\times 6.4$. Free cheek (G. S. M. no. 51770). Figured by Cobbold & Pocock, 1934, pl. 45, fig. 16 as *Ctenopyge flagellifera*. Block A.
- » 13. $\times 6.5$. Free cheek (G. S. M. no. 51774). Figured by Cobbold & Pocock, 1934, pl. 45, fig. 7 and doubtfully referred to *Eurycare angustatum*. Block A.
- » 14. $\times 6.6$. Free cheek (G. S. M. no. 51777b). Figured by Cobbold & Pocock, 1934, pl. 45, fig. 10 as *Sphaerophthalmus(?)* sp. indet. Block A.

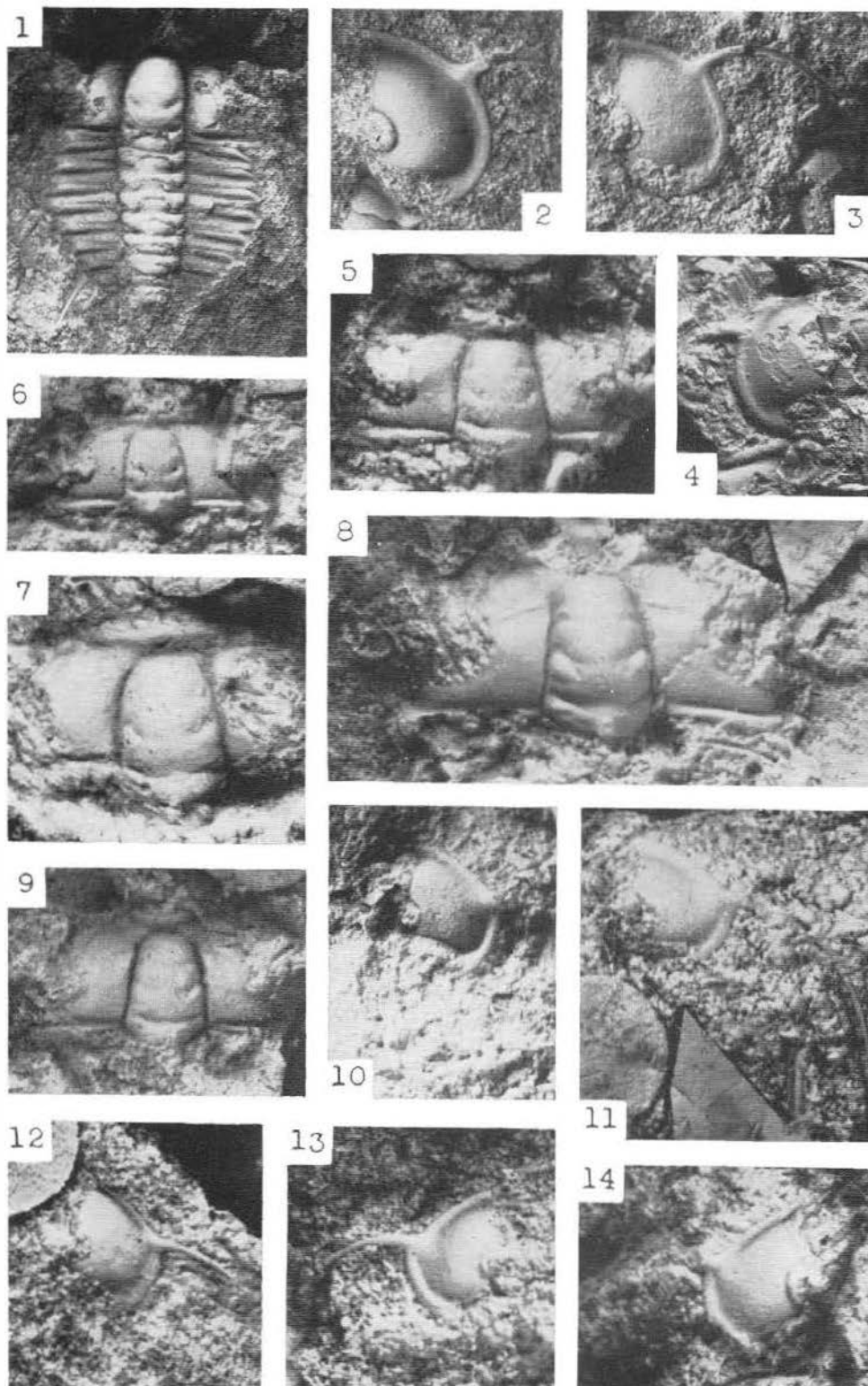


PLATE 19

All $\times 6.1$.

Ctenopyge (Eoctenopyge) modesta n. sp. — — p. 191.

- Fig. 1. Cranidium (P. M. O. no. 29191a). 2d β (Vb) *sim.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880.
- » 2. Free cheek (P. M. O. no. 29497a). *Holotype*. 2d β (Vb) *sim.*, Slemmestad, Røyken, Norway. Exc. 1880.
- » 3. Free cheek (P. M. O. no. 29191b). Tilted to show the curvature of the spine. The genal field is seen rather much from the side and thus appears too narrow. Other data as for fig. 1.
- » 4. Free cheek (P. M. O. no. 29349a). 2d β (Vb) *sim.*, Slemmestad, Røyken, Norway. Coll.: ?
- » 5. Axial shield without posterior part (P. M. O. no. 29497b). Other data as for fig. 2.
- » 6. Cephalon (P. M. O. no. H 2724). 2d β (Vb) *sim.*, Slemmestad, Røyken, Norway. Coll.: ? Figured by Brögger, 1882, pl. II, fig. 15 as *Ctenopyge flagellifera*.
- » 7. Hypostoma (P. M. O. no. 66842a). 2d β (Vb) *sim.*, Sars gt., Oslo, Norway. Coll.: F. Nikolaisen, 1954.
- » 8. Cranidium (P. M. O. no. 29349b). Other data as for fig. 4.
- » 9. Anterior part of axial shield (P. M. O. no. 66843). Other data as for fig. 7.
- » 10. Part of thorax (P. M. O. no. 66844). Other data as for fig. 7.

Ctenopyge (Eoctenopyge) angusta Westergård 1922 — — p. 187.

- Fig. 11. Free cheek (P. M. O. no. 26869a). 2d β (Vb) *spect.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880.
- » 12. Hypostoma (P. M. O. no. 19990b). Other data as for fig. 11.
- » 13. Cranidium (P. M. O. no. 26869b). Other data as for fig. 11.
- » 14. Free cheek (P. M. O. no. 19986b). Other data as for fig. 11.
- » 15. Free cheek (P. M. O. no. 29488a). 2d β (Vb), *spect.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1879.
- » 16. Free cheek (P. M. O. no. 19990c). Other data as for fig. 11.
- » 18. Cranidium (P. M. O. no. 26869c). Other data as for fig. 11.

Ctenopyge (Ctenopyge) affinis gracilis n. subsp. — — p. 201.

- Fig. 17. Axial spine (P. M. O. no. 19993a). 2d β (Vb) *aff.*, Slemmestad, Røyken, Norway. Coll. W. C. Brögger, 1880.
- » 19. Free cheek (P. M. O. no. 19993d). Other data as for fig. 17.
- » 20. Cranidium (P. M. O. no. 19993b). Other data as for fig. 17.
- » 21. Cranidium (P. M. O. no. 19993c). Other data as for fig. 17.

Ctenopyge (Ctenopyge) affinis affinis Westergård 1922 — — p. 200.

- » 22. Cranidium (P. M. O. no. 29388). 2d β (Vb) *aff.*, Nærsnes, Røyken, Norway. Coll.: W. C. Brögger & Krohn, 1880.

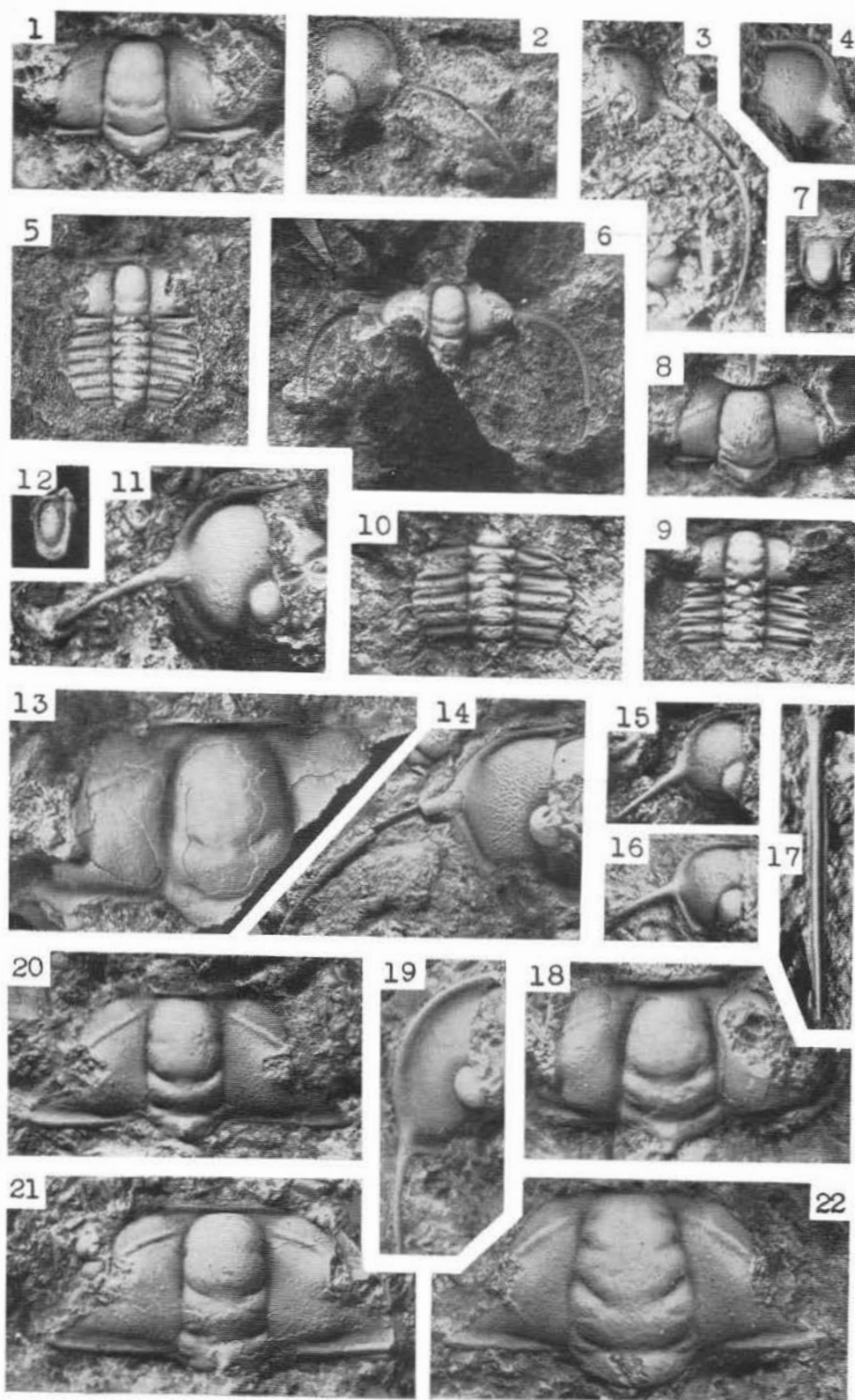


PLATE 20

All $\times 6.2$.

Ctenopyge (Mesoctenopyge) erecta Westergård 1922 — — p. 194.

- Fig. 1. Pygidium (P. M. O. no. 61465a) 2d β (Vb) *sim.*, Loose block, corner Drammensveien/Parkveien, Oslo, Norway. Coll.: ?, 1898.
- » 2. Free cheek (P. M. O. no. 66846). 2d β (Vb) *sim.*, Sars gt., Oslo, Norway. Coll.: F. Nikolaisen, 1954.
 - » 3. Hypostoma (P. M. O. no. 61465b). Other data as for fig. 1.
 - » 4. Free cheek (P. M. O. no. 66842b), tilted to show the curvature of the spine. Other data as for fig. 2.
 - » 5. Pygidium (P. M. O. no. 61465c). Other data as for fig. 1.
 - » 6. Cranidium (P. M. O. no. 61464a). Other data as for fig. 1.
 - » 7. Cranidium (P. M. O. no. 61464b). Other data as for fig. 1.
 - » 8. Counterpiece of large cranidium (P. M. O. no. 61465d). Other data as for fig. 1.
 - » 9. Cranidium (P. M. O. no. 61465e). Other data as for fig. 1.

Ctenopyge (Mesoctenopyge) similis n. sp. — — p. 195.

- Fig. 10. Cheek spine (P. M. O. no. S 486a). 2d β (Vb) *sim.*, Hadeland, Norway. Coll.: L. Stormer, 1919.
- » 11. Free cheek (P. M. O. no. S 486b). Other data as for fig. 10.
 - » 12. Cranidium (P. M. O. no. S 481). *Holotype*. Other data as for fig. 10.
 - » 13. Pleuron (P. M. O. no. S 487). Other data as for fig. 10.
 - » 14. Hypostoma (P. M. O. no. S 482b). Other data as for fig. 10.

Ctenopyge (Mesoctenopyge) tumidoides n. sp. — — p. 199.

- Fig. 15. Cranidium (P. M. O. no. 29488b). 2d β (Vb) *spect.*, Slemmestad, Royken, Norway. Coll.: W. C. Brögger, 1879.

Ctenopyge (Mesoctenopyge) tumida Westergård 1922 — — p. 198.

- Fig. 16. Cranidium (P. M. O. no. 66847). 2d β (Vb) *tum.*, Rosenkrantzgt. 8, Oslo, Norway. Coll.: O. Holtedahl, 1911.

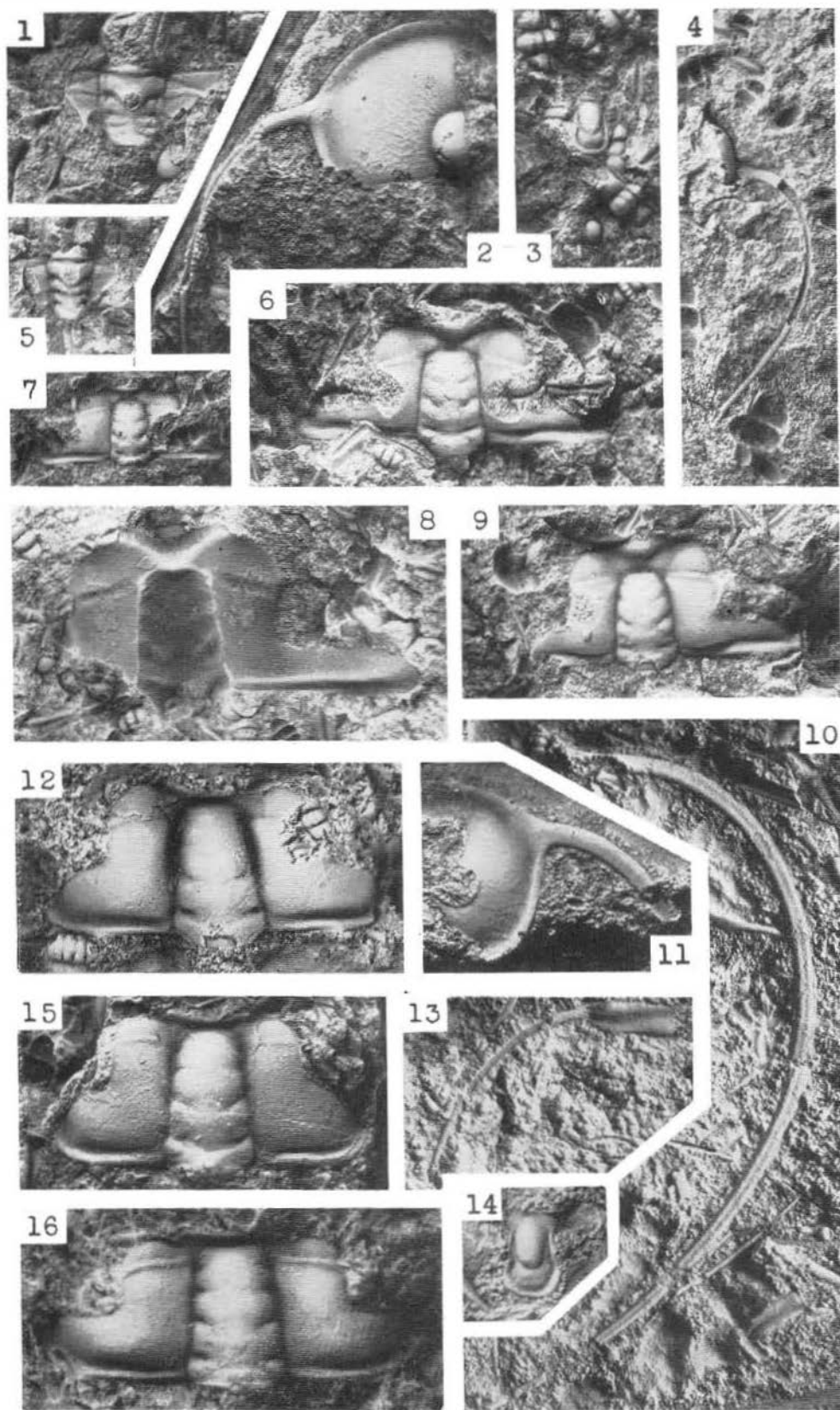


PLATE 21

Ctenopyge (Mesoctenopyge) spectabilis Brögger 1882 — — p. 197.

- Fig. 1. $\times 6.1$. Hypostoma (P. M. O. no. 29374). 2d β (Vb) *spect.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880. Figured by Brögger, 1882, pl. XII, fig. 12a.
- » 2. $\times 6.1$ Cranidium (P. M. O. no. 29816a). Hor. & loc. as for fig. 1. Coll.: Brögger, 1879.
- » 3. $\times 6.1$. Free cheek (P. M. O. no. 19991b). Other data as for fig. 1.
- » 4. $\times 6.1$. Cranidium (P. M. O. no. 29816b). Other data as for fig. 2.
- » 5. $\times 6.1$. Cranidium (P. O. M. no. 29816d). Other data as for fig. 2.
- » 6. $\times 5.0$. Free cheek (P. M. O. no. 29816c). Other data as for fig. 2.
- » 7. $\times 6.1$. Cranidium (P. M. O. no. 29816e). Other data as for fig. 2.

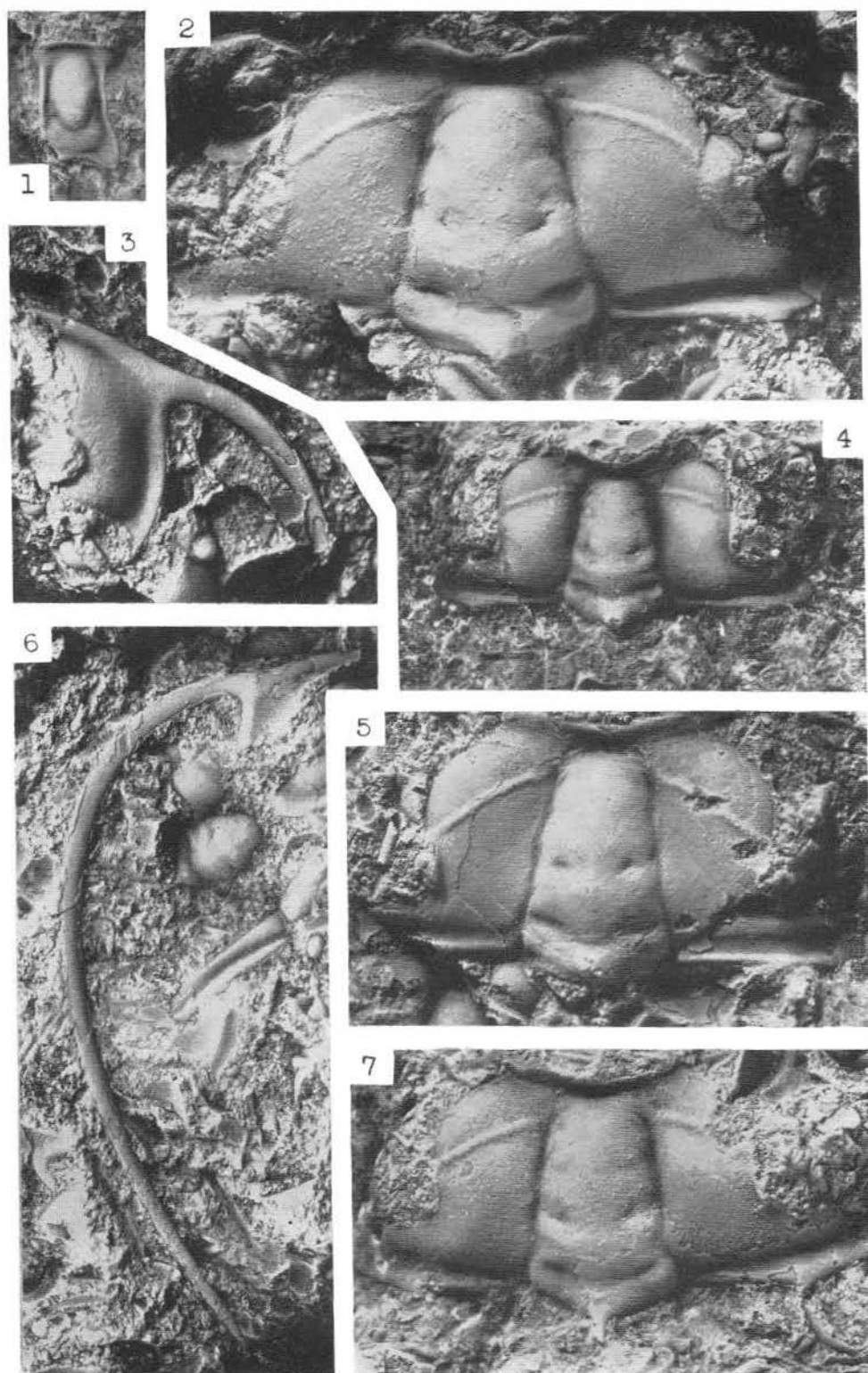


PLATE 22

All $\times 6.3$.

Ctenopyge (Ctenopyge) fletcheri (Matthew 1901) — — p. 205.

- Fig. 1. Free cheek (P. M. O. no. 30112c). 2d γ (Vc) *linn.*, Viul, Ringerike, Norway. Coll.: J. Schetelig, 1913.
- » 2. Cranidium (P. M. O. no. 30112d). Other data as for fig. 1.
 - » 3. Free cheek (P. M. O. no. 30112a). Other data as for fig. 1.
 - » 4. Free cheek (P. M. O. no. 30112e). Other data as for fig. 1.
 - » 5. Free cheek (P. M. O. no. 30112f). Other data as for fig. 1.
 - » 6. Free cheek (P. M. O. no. 30112g). Other data as for fig. 1.

Ctenopyge (Ctenopyge) linnarssonni Westergård 1922 — — p. 207.

- Fig. 8. Cranidium (P. M. O. no. 29502). 2d γ (Vc) *linn.*, Slemmestad, Røyken, Norway. Coll.: Exc. 1931.

Ctenopyge (Ctenopyge) pecten (Salter 1864) — — p. 208.

- Fig. 9. Cranidium (P. M. O. no. 30080a). 2d γ (Vc) *linn.*, Viul, Ringerike, Norway. Coll.: ?
- » 10. Counterpiece of pygidium (P. M. O. no. 30080b). Other data as for fig. 9.

Sphaerophthalmus humilis (Phillips 1848) — — p. 215.

- Fig. 7. Cranidium (P. M. O. no. 30112h). 2d γ (Vc) *linn.*, Viul, Ringerike, Norway. Coll.: J. Schetelig, 1913.
- » 11. Hypostoma (P. M. O. no. 30112i) (upper right corner) and cranidium (P. M. O. no. 30112j). Other data as for fig. 7.
 - » 12. Free cheek (P. M. O. no. 30112k). Other data as for fig. 7.
 - » 13. Pygidium (P. M. O. no. 29340d). 2d γ (Vc), Slemmestad, Røyken, Norway. Coll.: ?
 - » 14. Part of thorax (P. M. O. no. 30112m). Light from below. Other data as for fig. 7.
 - » 15. Cranidium (P. M. O. no. 30112n). Other data as for fig. 7.

Sphaerophthalmus majusculus Linnarsson 1880 — — p. 218.

- Fig. 16. Large cranidium (P. M. O. no. 19995). 2d γ (Vc), Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880.
- » 17. This species? Free cheek (P. M. O. no. 30112p). Other data as for fig. 7.

Sphaerophthalmus alatus (Boeck 1838) — — p. 212.

- » 18. Free cheek (P. M. O. no. 19993e). 2d β (Vb) *aff.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880.
- » 19. Free cheek (P. M. O. no. 19993f). Other data as for fig. 18.
- » 20. Axial shield without pygidium (P. M. O. no. 19994). 2d β (Vb) *tum.* or *aff.*, Vippetangen, Oslo, Norway. Coll.: K. O. Bjørlykke, 1892.
- » 21. Cranidium (P. M. O. no. 19993g). Other data as for fig. 18.
- » 22. Free cheek (P. M. O. no. 56371b). Associated with the lectotype (figs. 23—24).
- » 23—24. Front and dorsal view of cranidium (P. M. O. no. 56371). *Lectotype*. 2d β (Vb) *tum.* or *aff.* The alum shale quarry, Gamlebyen, Oslo, Norway. Old coll.
- » 25. Cranidium (P. M. O. no. H 2715b). 2d β (Vb) *tum.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880.
- » 26. Cranidium (P. M. O. no. H 2715c). Other data as for fig. 25.

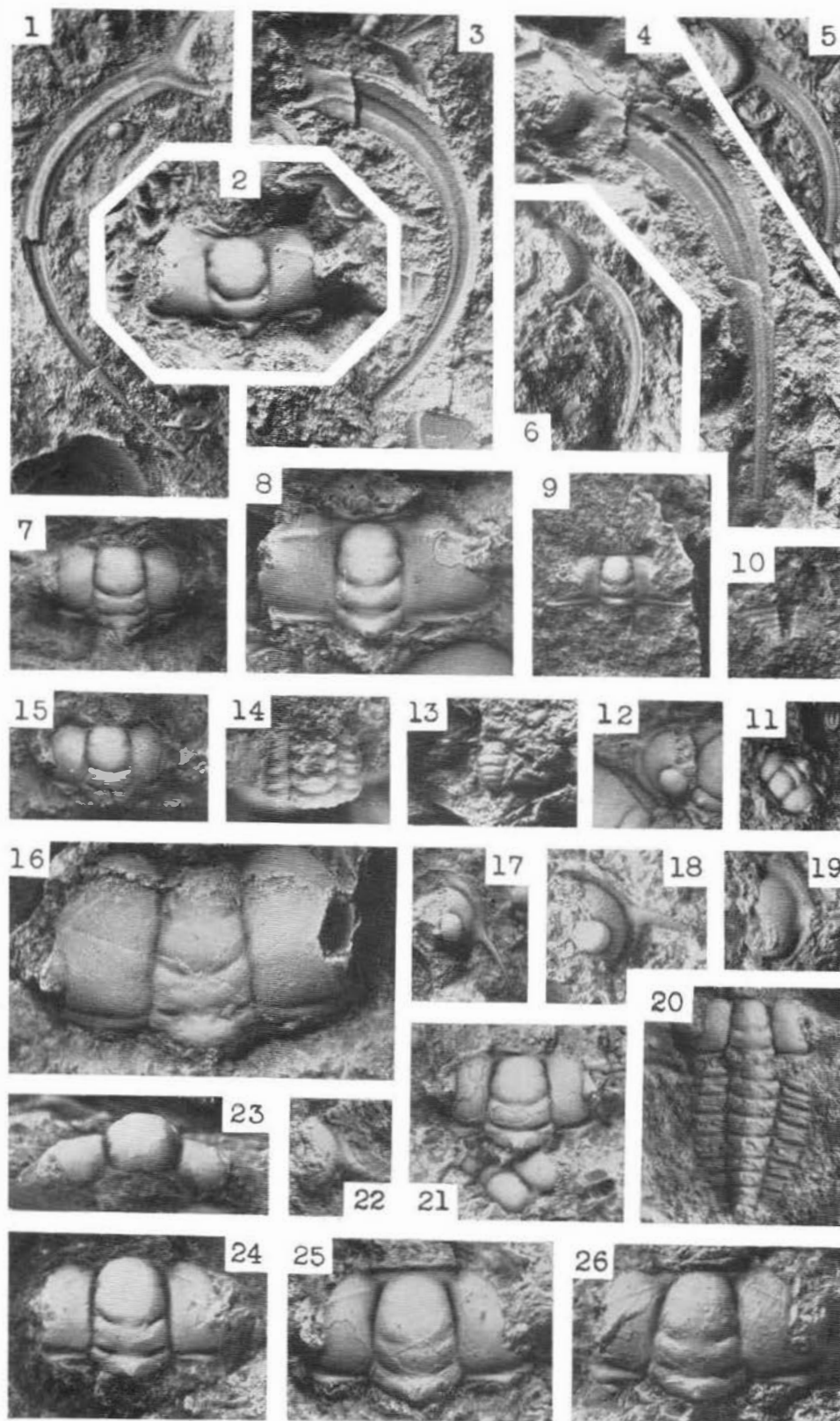


PLATE 23

All $\times 5$.

Protopeltura aciculata pusilla Westergård 1922 — p. 223.

- Fig. 1. Axial shield (P. M. O. no. H 2807). Pygidium somewhat displaced and overturned. 2b (III) *spin.*, riverside above Gjøgrefoss, Sandsvær, Norway. Coll.: A. Heintz, 1937.
- » 2. Small and somewhat disconnected dorsal shields (P. M. O. nos. 29023b-d). 2b (III) *spin.*, Gjøgrefoss, Sandsvær, Norway. Coll.: W. C. Brögger, 1879.
 - » 3. Hypostoma (P. M. O. no. H 2808). Other data as for fig. 1.
 - » 4. Free cheek (P. M. O. no. H 2809). Other data as for fig. 1.
 - » 5. Small axial shield (P. M. O. no. 19917). Other data as for fig. 2.
 - » 6. Cranidium (P. M. O. no. 29023a). Other data as for fig. 2.

Protopeltura broeggeri (Holtedahl 1910) — p. 225.

- Fig. 7. Cranidium (P. M. O. no. 29249). 2d α (Va) *brögg.*, Slemmestad, Røyken, Norway. Coll.: O. Holtedahl, 1908.
- » 8. Larval axial shield (P. M. O. no. 19979b). Other data as for fig. .
 - » 9. Cranidium (P. M. O. no. 19982). Other data as for fig. 7.
 - » 10. Incomplete dorsal shield with hypostoma (P. M. O. no. 66849a). 2d α (Va) *brögg.*, Slemmestad, Røyken, Norway. Coll.: A. W. Smith, 1951.
 - » 11. Free cheek (P. M. O. no. 19979a). Other data as for fig. 7.
 - » 12. Cranidium (P. M. O. no. 29831). Other data as for fig. 7.
 - » 13. Free cheek (P. M. O. no. 29178). Other data as for fig. 7.
 - » 14. Thorax (P. M. O. no. 19981). Other data as for fig. 7. Figured by Holtedahl, 1910, pl. III, fig. 5, as *Leptoplastus Bröggeri*.
 - » 15. Pygidium (P. M. O. no. 29174). *Lectotype*. Other data as for fig. 7. Figured by Holtedahl, 1910, pl. III, 6, as *Leptoplastus Bröggeri*.

Protopeltura holtedahli n. sp. — p. 227.

- Fig. 16. Free cheek (P. M. O. no. 66850). 2d α (Va) *holt.*, Slemmestad, Røyken, Norway. Coll.: O. Holtedahl, 1908.
- » 17. Cranidium (P. M. O. no. 29251). *Holotype*. Other data as for fig. 16.
 - » 18. Free cheek (P. M. O. no. 29253b). Other data as for fig. 16.
 - » 19. Cranidium (P. M. O. no. 29173). Other data as for fig. 16.
 - » 20. Cranidium (P. M. O. no. 29191). Other data as for fig. 16.
 - » 21. Hypostoma (P. M. O. no. 29232). Other data as for fig. 16.
 - » 22. Post-cephalic shield (P. M. O. no. 19974). Other data as for fig. 16. Figured by Holtedahl, 1910, pl. II, fig. 3, as *Peltura præcursor*.

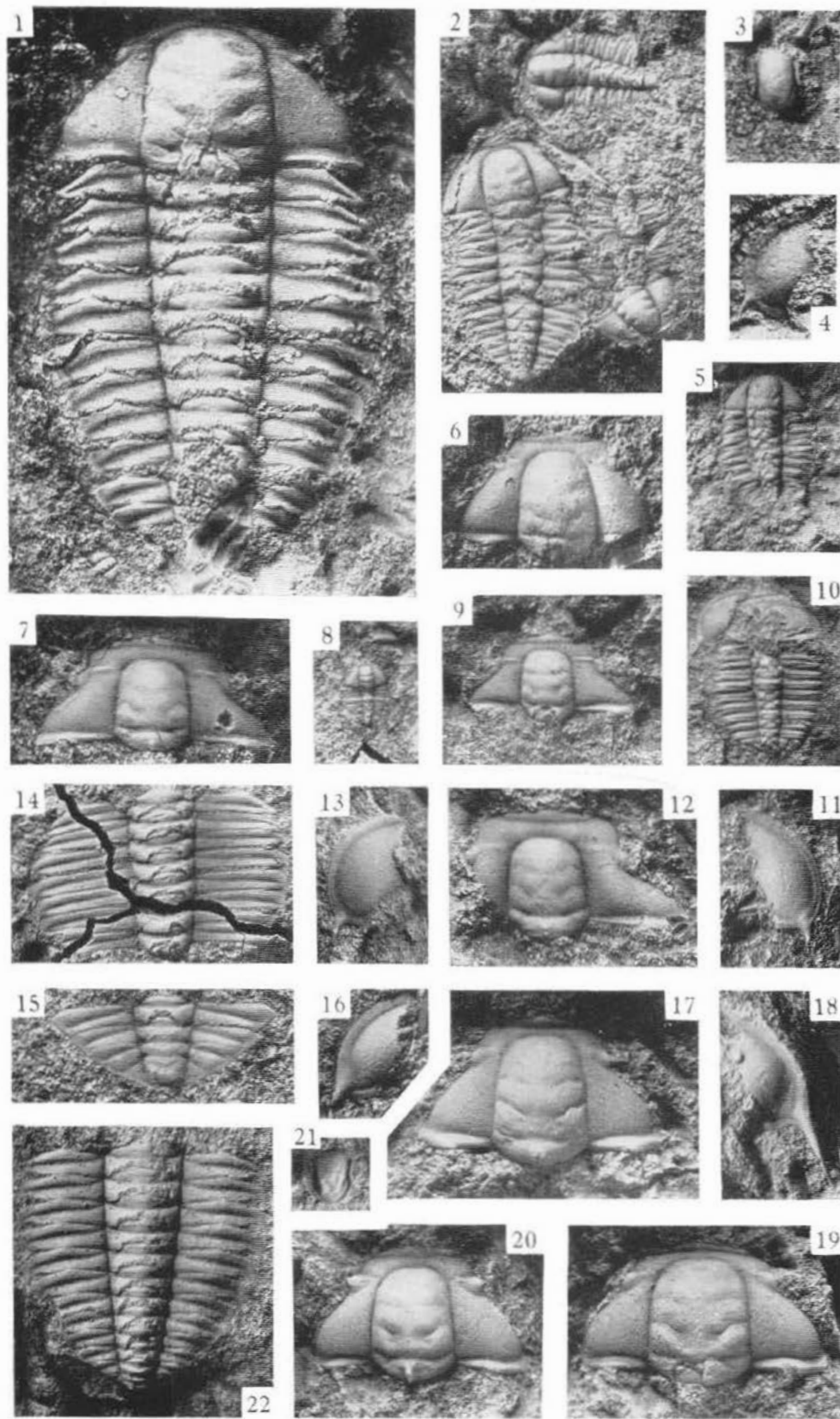


PLATE 24

Protopeltura praeursor Westergård 1922 — — p. 229.

- Fig. 1. $\times 27$. Axial shield (P. M. O. no. 66851). 2d α (Va) *flag.*, Nærnes, Røyken, Norway. Coll.: G. Henningsmoen, 1950.
- » 2. $\times 5$. Cranidium (P. M. O. no. H 2716a). 2d α (Va) *postc.*, Nærnes, Røyken, Norway. Coll.: W. C. Brögger, 1880.
- » 3. $\times 5$. Free cheek (P. M. O. no. H 2716c). Other data as for fig. 2. Figured by Brögger, 1882, pl. I, fig. 14b, as *Protopeltura acanthura*.
- » 4. $\times 5$. Hypostoma (P. M. O. no. 29188). Other data as for fig. 2. Figured by Brögger, 1882, pl. II, fig. 14a, as *Protopeltura acanthura*.
- » 5. $\times 5$. Pygidium (P. M. O. no. H 2716b). Other data as for fig. 2. Figured by Brögger, 1882, pl. I, fig. 14c, as *Protopeltura acanthura*.

Protopeltura bidentata (Brögger 1882) — — p. 224.

- Fig. 6. $\times 5$. Pygidium and three posterior segments (P. M. O. no. 29369). 2d β (Vb) *sim.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880. Figured by Brögger, 1882, pl. II, fig. 7a, as *Peltura bidentata*.
- » 7. $\times 5$. Free cheek (P. M. O. no. 52902). 2d β (Vb) *sim.*, Sarsgt., Oslo, Norway. Coll.: Exc., 1934.
- » 8. $\times 5$. Cranidium (P. M. O. no. 29790). 2d β (Vb) *sim.*, corner Kirkegt./Karl Johansgt., Oslo, Norway. Coll.: Sveen, 1923.
- » 9. $\times 5$. Axial shield (P. M. O. no. H 2721). *Lectotype*. 2d β (Vb) *sim.*, Slemmestad, Røyken, Norway. Coll.: J. Vogt, 1880.
- » 10. $\times 4.3$. Axial shield with displaced cranidium (P. M. O. no. 52901). Other data as for fig. 7.

Protopeltura planicauda (Brögger 1882) — — p. 228.

- Fig. 11. $\times 5$. Free cheek (P. M. O. no. H 2715d). Associated with the lectotype (fig. 13).
- » 12. $\times 5$. Pygidium (P. M. O. no. 20003). Light from the lower right. 2d β (Vb), *sim.*, Nedre Slottsgt., Oslo, Norway. Coll.: ?
- » 13. $\times 5$. Pygidium (P. M. O. no. H 2715a). *Lectotype*. 2d β (Vb) *tum.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880.

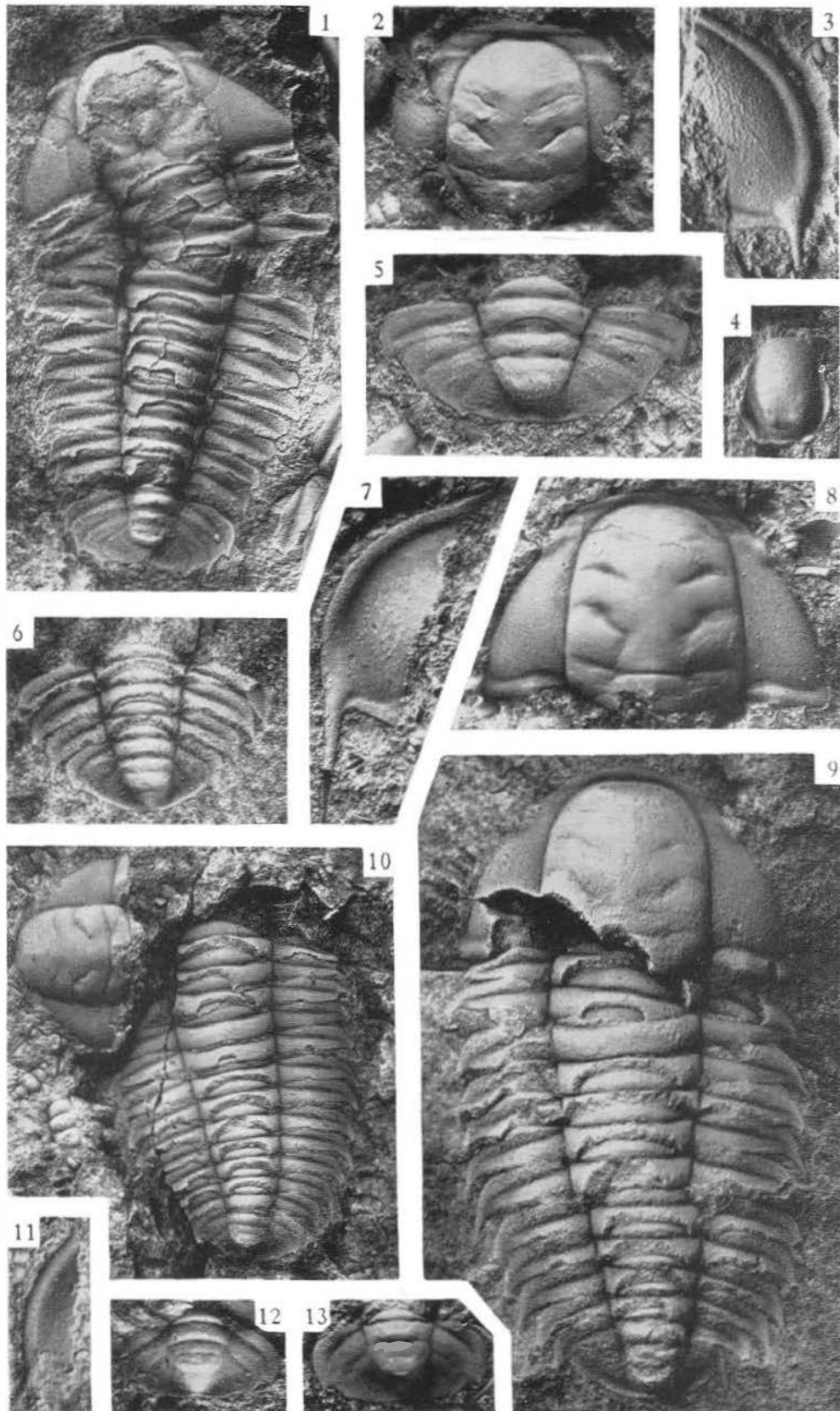


PLATE 25

All $\times 5$.

Peltura acutidens Brögger 1882 — — p. 233.

- Fig. 1. Cranidium (P. M. O. no. 29308d). 2d β (Vb) *tum.*, Slemmestad, Røyken, Norway. Coll.: O. Holtedahl, 1908.
- » 3. Hypostoma (P. M. O. no. 29308b). Other data as for fig. 1.
 - » 4. Cranidium (P. M. O. no. 29308a). Other data as for fig. 1.
 - » 7. Free cheek (P. M. O. no. 29308c). Other data as for fig. 1.
 - » 9. Pygidium (P. M. O. no. 19996). 2d β (Vb) *tum.*, Slemmestad, Røyken, Norway. Coll.: Exc., 1891.
 - » 11. Pygidium (P. M. O. no. H 2720). *Lectotype*. 2d β (Vb) *tum.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880. Figured by Brögger, 1882, pl. II, fig. 9.

Peltura minor (Brögger 1882) — — p. 235.

- Fig. 2. Hypostoma (P. M. O. no. 29461). 2d β (Vb) *tum.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1879.
- » 5. Pygidium (P. M. O. no. H 2713a). *Lectotype*. 2d β (Vb) *tum.*, Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880. Figured by Brögger, 1882, pl. II, fig. 10, as *Cyclognathus costatus* var. *minor*.

Peltura scarabacoides scarabacoides (Wahlenberg 1821) — — p. 237.

- Fig. 6. Large hypostoma (P. M. O. no. 29549). 2d γ (Vc), Slemmestad, Røyken, Norway. Coll.: T. Strand, 1928.
- » 13. Free cheek (P. M. O. no. H 2719b), 2d γ (Vc). Slemmestad, Røyken, Norway. Coll.: W. C. Brögger, 1880.
 - » 14. Pygidium (P. M. O. no. H 2719a). Other data as for fig. 13. Figured by Brögger, 1882, pl. II, fig. 12.

Peltura scarabacoides westergårdi n. subsp. — — p. 239.

- Fig. 8. Free cheek (P. M. O. no. 66854c). Other data as for fig. 10.
- » 10. Cranidium (P. M. O. no. 66853a). 2d γ (Vc) *lob.*, Slemmestad, Røyken, Norway. Coll.: G. Henningsmoen, 1941.
 - » 12. Free cheek (P. M. O. no. 66853b). Other data as for fig. 10.
 - » 15. Pygidium (P. M. O. no. 66854a). Other data as for fig. 10.
 - » 16. Hypostoma (P. M. O. no. 66854b). Other data as for fig. 10.
 - » 17. Pygidium (P. M. O. no. 29033). 2d δ (Vc) *lob.*, Vestfossen, Eiker, Norway. Coll.: W. C. Brögger, 1879.

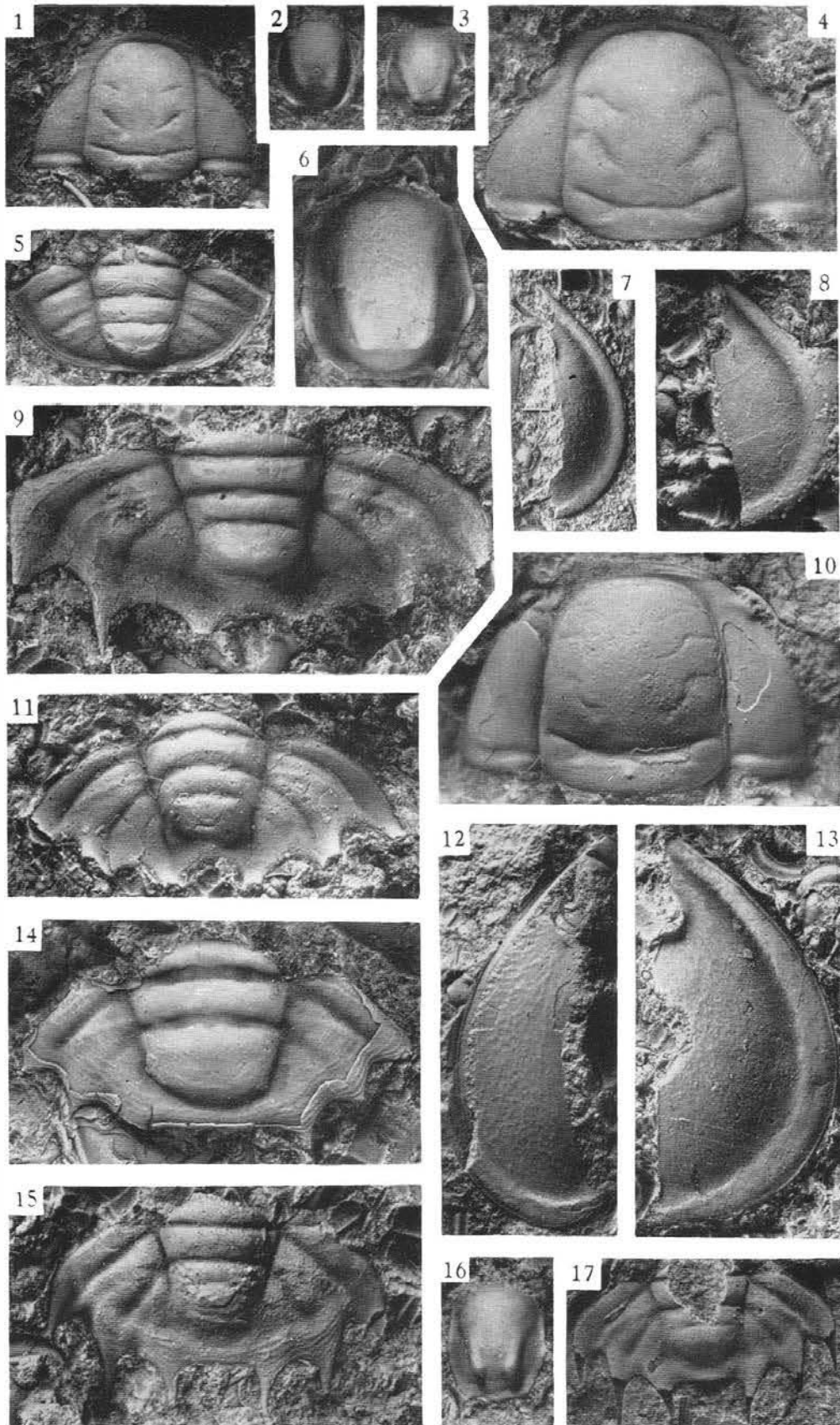


PLATE 26

Peltura scarabaeoides scarabaeoides (Wahlenberg 1821) — — p. 237.

- Fig. 1. $\times 3.8$. Somewhat disconnected dorsal shields (P. M. O. no. 66859). 2d γ (Vc) *linn.*, Slemmestad, Royken, Norway. Coll.: T. Strand, 1933.
- » 2. $\times 3.8$. Counterpiece of dorsal shield with hypostoma almost in situ (P.M.O. no. 66860). Other data as for fig. 1.

Peltura paradoxa (Moberg & Möller 1898) — — p. 236.

All $\times 5$.

- Fig. 3. Free cheek (P. M. O. no. 30793a). 2d δ (Vc) *par.*, Furetangen, Modum, Norway. Coll.: J. Kiær.
- » 4. Cranidium (P. M. O. no. 30795). Other data as for fig. 3.
- » 5. Pygidium (P. M. O. no. 30793b). Other data as for fig. 3.
- » 6. Pygidium (P. M. O. no. 30793c). Light from below. Other data as for fig. 3.

Peltura transiens (Brögger 1882) — — p. 240.

All $\times 5$.

- Fig. 7. Small cranidium (P. M. O. no. 66873). 2d ϵ (VI) *trans*, Vestfossen, Eiker, Norway. Coll.: G. Henningsmoen and P. Padget, 1950.
- » 8. Counterpiece of pygidium (P. M. O. no. 19947a). *Lectotype*. 2d ϵ (VI) *trans*., Vestfossen, Eiker, Norway. Coll.: W. C. Brögger, 1879.
- » 9. Free cheek (P. M. O. no. 66871). Other data as for fig. 7.
- » 10. Free cheek (P. M. O. no. 66872a). Other data as for fig. 7.
- » 11. Cranidium (P. M. O. no. 66870). Other data as for fig. 7.
- » 12. Hypostoma (P. M. O. no. 66872b). Other data as for fig. 7.
- » 13. Pygidium (P. M. O. no. 19947b). Other data as for fig. 8.

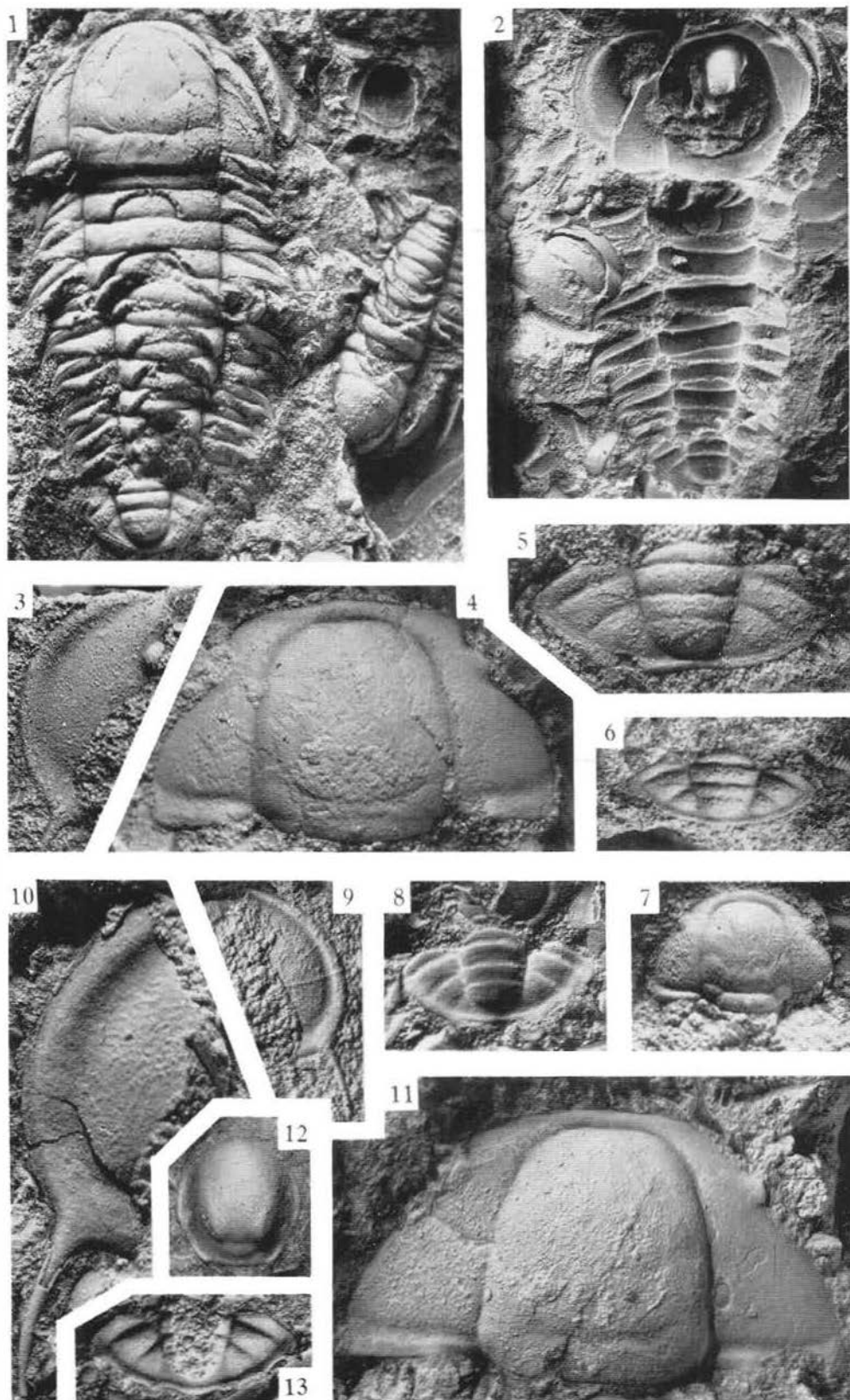


PLATE 27

All $\times 5$, except fig. 8 ($\times 3.8$).

Peltura costata (Brögger 1882) — — p. 234.

- Fig. 1. Cranidium (P. M. O. no. 29010a). 2d ϵ (VI) *cost.*, railway section near Lunje, Vestfossen, Eiker, Norway. Coll.: W. C. Brögger, 1879.
- » 2. Free cheek (P. M. O. no. 29010b). Other data as for fig. 1.
 - » 3. Small cranidium (P. M. O. no. 29010c). Other data as for fig. 1.
 - » 4. Part of thoracic segment (P. M. O. no. 29010d). Other data as for fig. 1.
 - » 5. Free cheek (P. M. O. no. 29010e). Other data as for fig. 1.
 - » 7. Free cheek (P. M. O. no. 29010f). Other data as for fig. 1.
 - » 9. Pygidium (P. M. O. no. 29017). *Lectotype*. 2d ϵ (VI) *cost.*, Henstad, Vestfossen, Eiker, Norway. Coll.: W. C. Brögger, 1879. Figured by Brögger, 1882, pl. I, figs. 5c-d.

Peltocare norvegicum (Moberg & Möller 1898) — — p. 247.

- Fig. 6. Hypostoma (P. M. O. no. 491). 3a α (U. Trem.), Vekkerø, Oslo, Norway. Coll.: L. Stormer, 1918—1919.
- » 8. $\times 3.8$. Counterpiece of axial shield with hypostoma in situ (P. M. O. no. 66881). Other data as for fig. 6. Figured by Stormer, 1920, pl. I, fig. 5, as *Acerocare norvegicum*.
 - » 10. Free cheek (P. M. O. no. 460). Other data as for fig. 6.
 - » 11. Pygidium (P. M. O. no. 66882). 3a α (U. Trem.), corner Sarsgt./Helgesensgt., Oslo, Norway. Coll.: N. Spjeldnæs and G. Henningsmoen, 1950.
 - » 12. Cranidium (P. M. O. no. 66883). Other data as for fig. 11.
 - » 13. Hypostoma (P. M. O. no. 437). Other data as for fig. 6. Figured by Stormer, 1920, pl. II, fig. 9, as hypostoma of *Acerocare*?
 - » 14. Pygidium (P. M. O. no. 66884). Other data as for fig. 11.

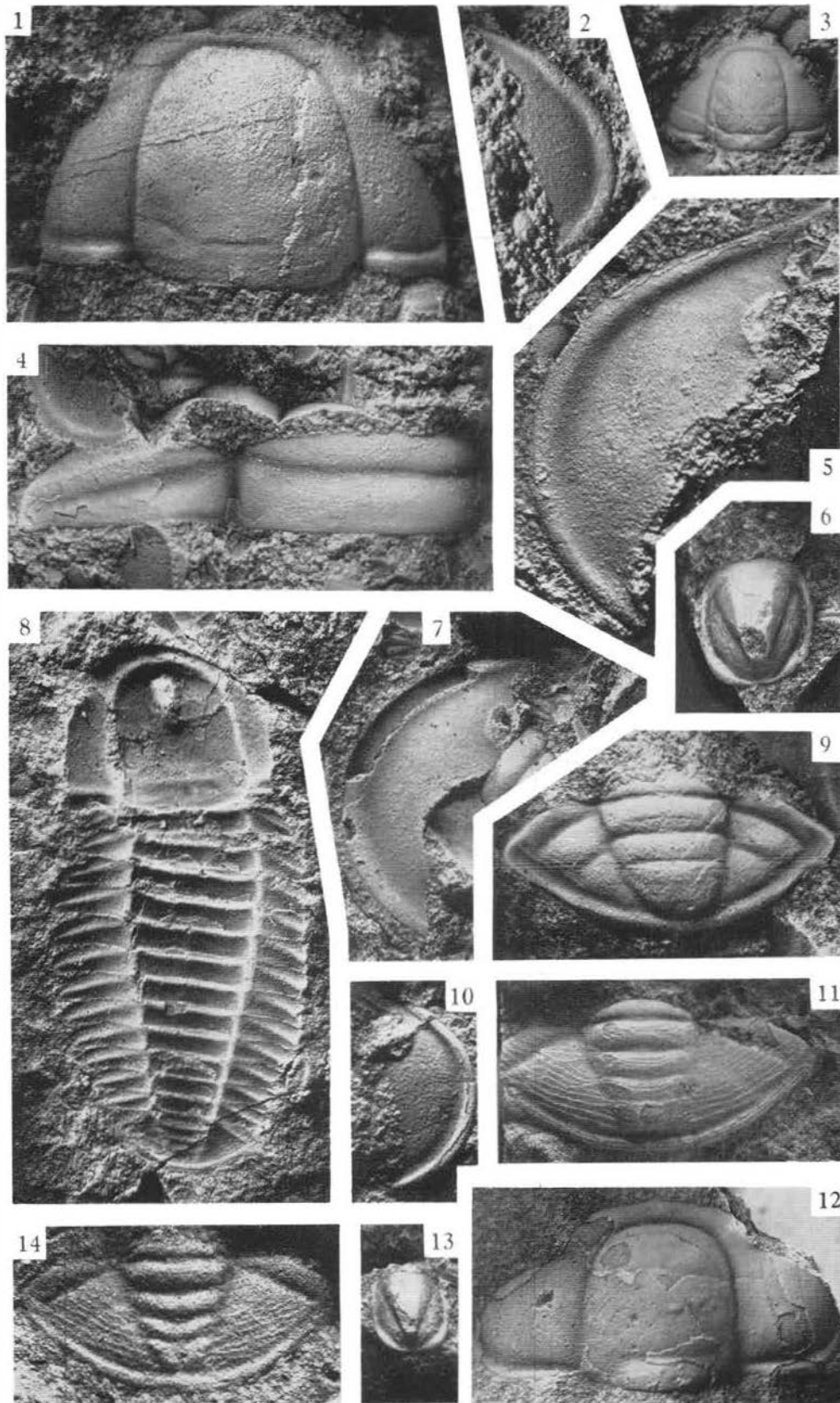


PLATE 28

All $\times 6.2$.

Pelturina punctifera n. gen. & n. sp. — — p. 250.

- Fig. 1. Large cranidium (P. M. O. no. 66795). 2d ϵ (VI) *ecorne*, beach at Nærnes gård, Røyken, Norway. Coll.: G. Henningsmoen, 1951.
- » 2. Pygidium (P. M. O. no. 30305). 2d ϵ (VI) *West.*, Brumunddalen, Ringsaker, Norway. Coll.: Exc., 1931.
- » 3. Cranidium (P. M. O. no. 66806). *Holotype*. 2d ϵ (VI) *ecorne*, beach at Nærnes gård, Røyken, Norway. Coll.: N. Spjeldnæs, F. Nikolaisen, and G. Henningsmoen, 1954.
- » 4. Cephalic axis (P. M. O. no. 66887). 2d ϵ (VI) *West.*, Nærnes, Røyken, Norway. Coll.: H. Neumann and T. Strand, 1945.

Acerocarina micropyga (Linnarsson 1875) — — p. 252.

- Fig. 5. Cranidium (P. M. O. no. 29798). 2d ϵ (VI) (*cost.?*), Gamlebyen, Oslo, Norway. Coll.: Corneliussen.

Westergårdia scanica (Westergård 1909) — — p. 257.

- Fig. 6. Cranidium (P. M. O. no. 66885a). 2d (VI) *West.*, Nærnes, Røyken, Norway. Coll.: H. Neumann and T. Strand, 1945.

Westergårdia lata (Matthew 1892) — — p. 254.

- Fig. 7. Cranidium (P. M. O. no. 66885b). Other data as for fig. 6.
- » 8. Plaster cast of one of the cranidia (R. O. M. P. no. 333) on which Matthew based his description. The original is from the *Acerocare* zone (previously included in the *Peltura* zone) at Saint John, New Brunswick, Canada.
- » 9. Free cheek (P. M. O. no. 66886). Other data as for fig. 6.
- » 10. Plaster cast of one of the thoracic shields (R. O. M. P. no. 333) on which Matthew based his description. Same locality as fig. 8.

Jujuyaspis angusta n. sp. — — p. 261.

- Fig. 11. Free cheek (P. M. O. no. 35675a). 2e β (L. Trem.), Steinsodden, Ringsaker, Norway. Coll.: O. E. Schiotz, 1904.
- » 12. Cranidium (P. M. O. no. 35675b). Other data as for fig. 11.
- » 13. Cranidium (P. M. O. no. 35674). *Holotype*. Other data as for fig. 11.
- » 14. Part of pleuron (P. M. O. no. 35675c). Other data as for fig. 11.
- » 15. Pygidium (P. M. O. no. 35675d). Other data as for fig. 11.

Jujuyaspis keideli norvegica n. subsp. — — p. 263.

- Fig. 16. Cranidium (plasteline cast) (P. M. O. no. 35878a). 2e α (L. Trem.), Stein, Ringsaker, Norway. Coll.: T. Strand, 1925.
- » 17. Pygidium (P. M. O. no. 35878b). Other data as for fig. 16.
- » 18. Thoracic segments (P. M. O. no. 66774). 2e α (L. Trem.), Nærnes, Røyken, Norway. Coll.: G. Henningsmoen, 1951.
- » 19. Pygidium (P. M. O. no. 35880). Other data as for fig. 16.
- » 20. Cranidium (P. M. O. no. 35881). Other data as for fig. 16.
- » 21. Cranidium (P. M. O. no. 35878c). *Holotype*. Other data as for fig. 16.

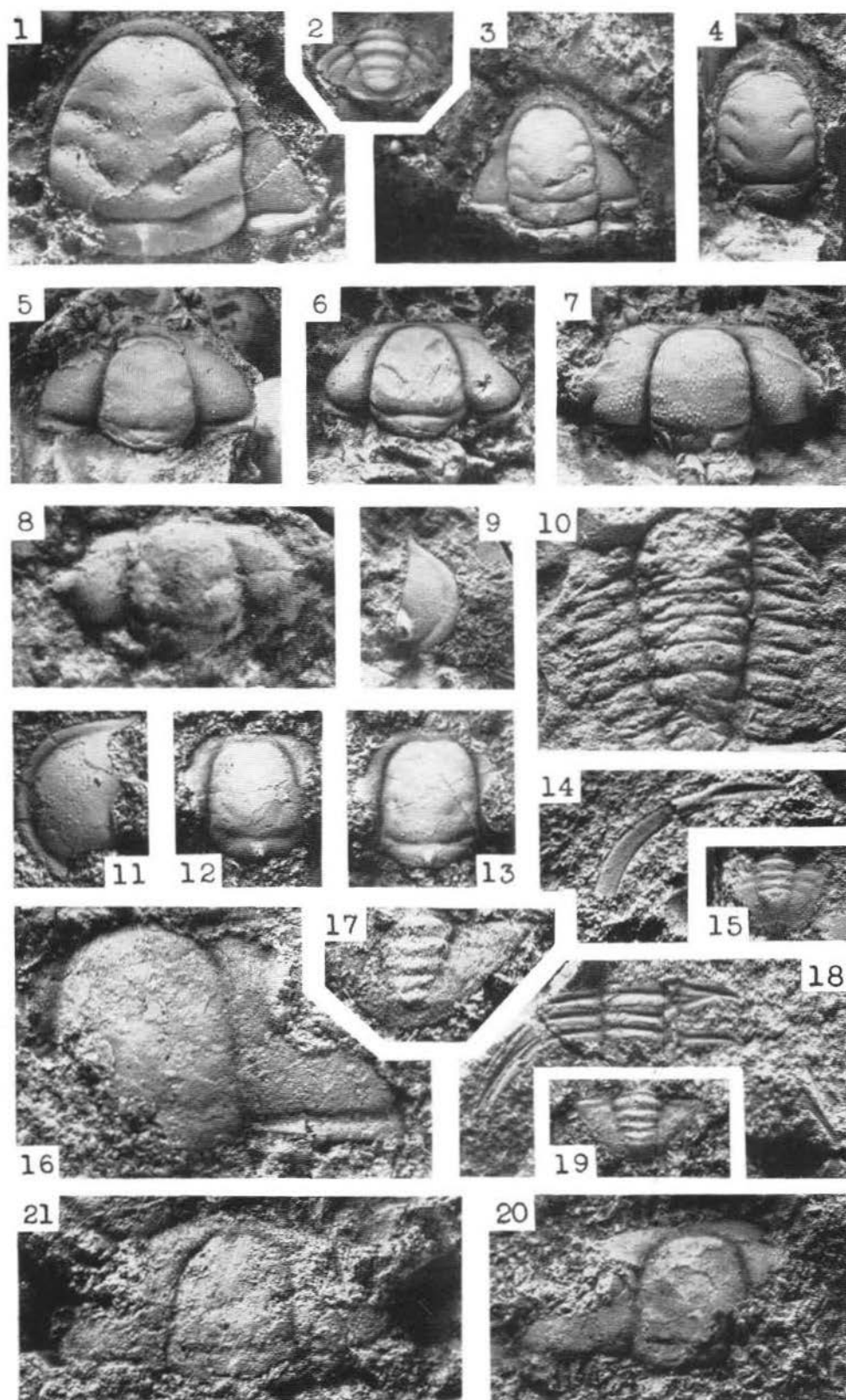


PLATE 29

All $\times 6.1$.

Boeckaspis hirsuta (Brögger 1882) — — p. 258.

- Fig. 1. Cranidium (P. M. O. no. 29525). 2e α (L. Trem.), Nærsnes, Røyken, Norway. Coll.: W. C. Brögger, 1880.
- » 2. Pygidium (P. M. O. no. H 2712). *Lectotype*. Other data as for fig. 1.
 - » 3. Pygidium (P. M. O. no. 66898). 2e α (L. Trem.), Nærsnes, Røyken, Norway. Coll.: G. Henningsmoen, 1949.
 - » 4. Thorax (P. M. O. no. 66899). 2e α (L. Trem.), beach at Nærsnes gård, Røyken, Norway. Coll.: N. Spjeldnæs, 1953.
 - » 5. Cranidium (P. M. O. no. 66901a) showing tubercles in front of eye ridges. 2e α (L. Trem.), beach at Nærsnes gård, Røyken, Norway. Coll.: G. Henningsmoen, 1951.
 - » 6. Free cheek (P. M. O. no. 66901b). Other data as for fig. 5.
 - » 7. Free cheek (P. M. O. no. 66902a). Other data as for fig. 5.
 - » 8. Hypostoma (P. M. O. no. 66902b). Other data as for fig. 5.

Boeckaspis mobergi (Wiman 1905) — — p. 259.

- Fig. 9. Free cheek (P. M. O. no. S 706). 2e β (L. Trem.), Jaren, Hadeland. Coll.: L. Stormer, 1919. Figured by Stormer, 1922a, pl. I, fig. 3.
- » 10. Cranidium (P. M. O. no. S 799). Other data as for fig. 9.
 - » 11. Cranidium (P. M. O. no. 66906), showing well the tubercle on the left eye ridge. 2e β (L. Trem.), Mælum, Ringsaker, Norway. Coll.: G. Henningsmoen, 1951.
 - » 12. Pygidium and thoracic segments (P. M. O. no. S 802). Other data as for fig. 9.

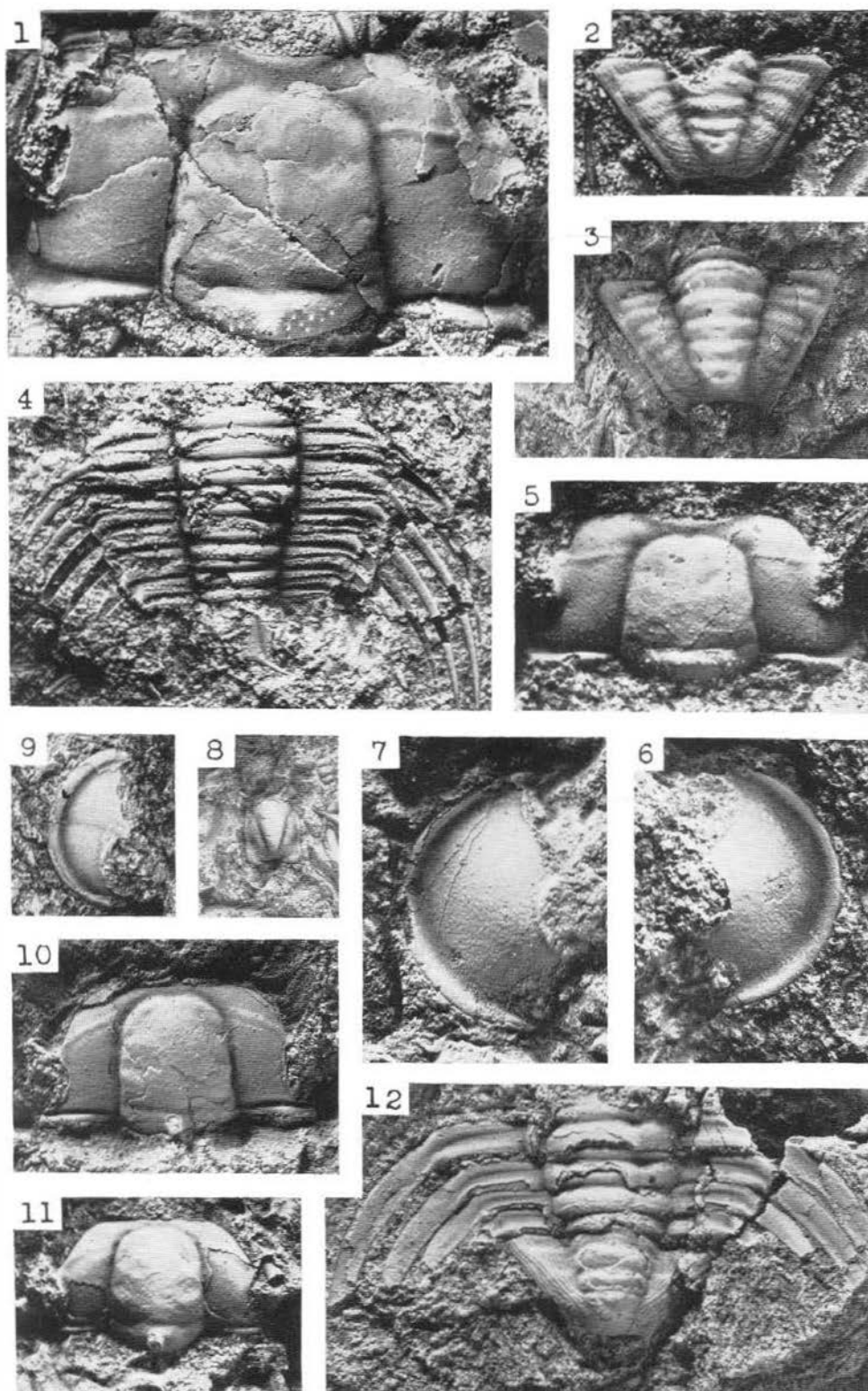


PLATE 30

All $\times 5$.

Acerocare ecorne Angelin 1854 — — p. 243.

- Fig. 1. Larval cranium (P. M. O. no. 66912a) with cranial spines. 2d ϵ (VI) *ecorne*, beach at Nærsnes gård, Røyken, Norway. Coll.: G. Henningsmoen and N. Spjeldnæs, 1950.
- » 2. Cranium (P. M. O. no. 66920). Hor. & loc. as for fig. 1. Coll.: G. Henningsmoen, 1951.
 - » 3. Free cheek (P. M. O. no. 66923). Hor. & loc. as for fig. 1. Coll.: G. Henningsmoen, 1954.
 - » 4. Internal surface of cranium (R. M. no. Ar. 9808e), showing muscle marks. Not whitened. Loose block, Blockhusudden, Uppland, Sweden.
 - » 5. Axial shield with hypostoma in situ (P. M. O. no. 66818a) and cranium possibly of the same individual. Detail of plate 31. Hor. & loc. as for fig. 1. Coll.: G. Henningsmoen, 1951.
 - » 6. Dorsal shield (P. M. O. no. 66818b). Detail of plate 31.
 - » 7. Pygidium (P. M. O. no. 66911). Other data as for fig. 1.
 - » 8. Pygidium (P. M. O. no. 669112b). Other data as for fig. 1.

Acerocare tullbergi (Moberg & Möller 1898) — — p. 243.

- Fig. 9. Thorax and pygidium (S. G. U.). Loose stinkstone concretion, Andrarum, Scania, Sweden.
- » 10. Free cheek (S. G. U.). From the same concretion as fig. 9. Figured by Moberg & Möller, 1898, pl. 14, fig. 7, and by Westergård, 1922, pl. XVI, fig. 16.
 - » 11. Small cranium (S. G. U.). *Lectotype*. From the same concretion as fig. 9. Figured by Moberg & Möller, 1898, pl. 14, fig. 6, and by Westergård, 1922, pl. XVI, fig. 15.

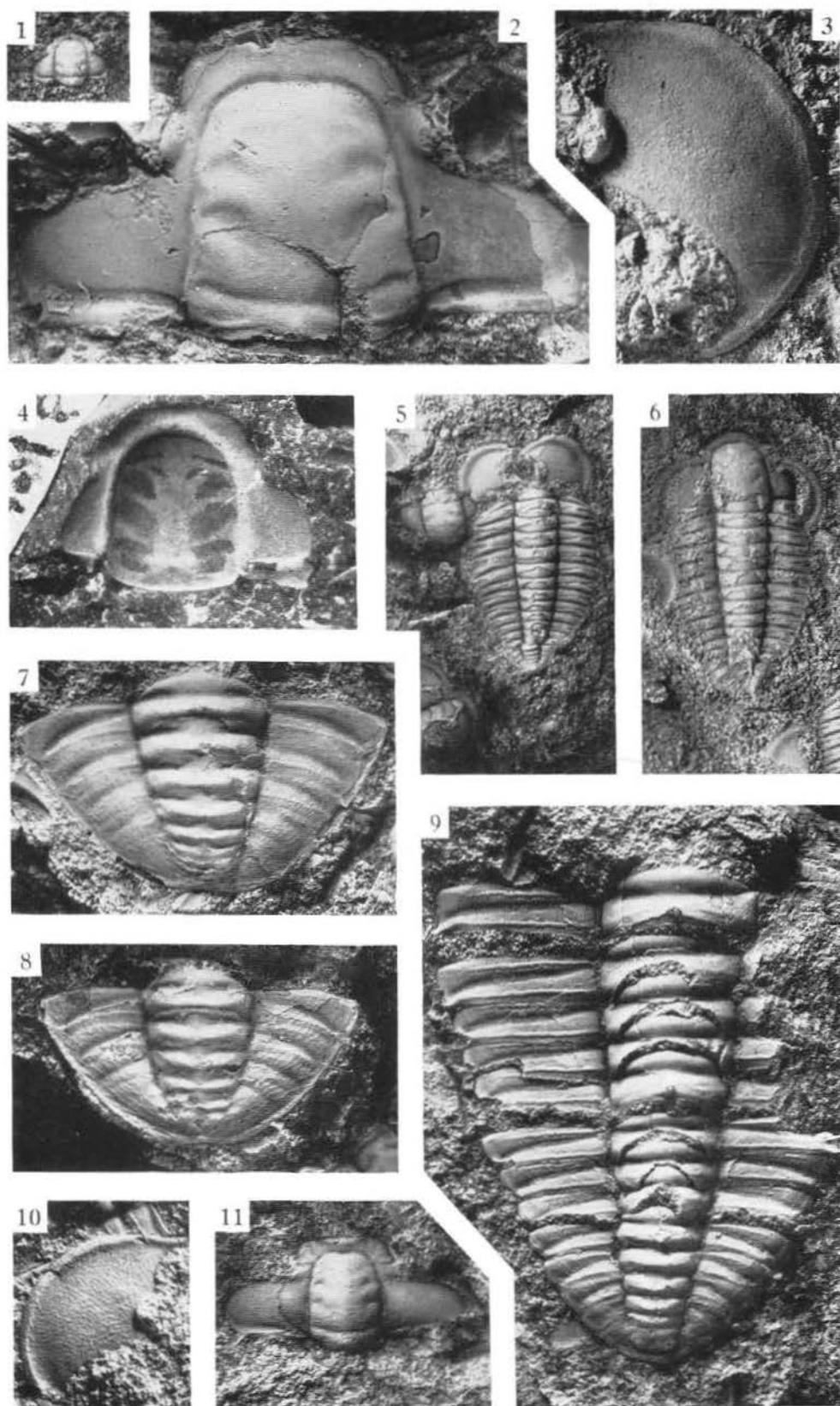


PLATE 31

Acerocare ecorne Angelin 1854 — — p. 71.

Bedding surface of stinkstone lens with numerous more or less entire dorsal shields, at least some apparently in moulting position. $\times 2.5$. 2♂ (VI) *ecorne*, beach at Nærsnes gård, Røyken, Norway. Coll.: G. Henningsmoen, 1951. (P. M. O. no. 66818.)

