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Contents

Abstract

Twenty-four new species and subspecies of olenid trilobites are described from the Valhallfonna Formation, north Ny Friesland, Spitsbergen. Twenty-three of these are of Arenig age; one is of probable Llanvirn age. The fauna is the product of a hitherto unknown post-Tremadoc diversification of the Olenidae, due to the persistence into the Arenig of the peculiar environmental conditions to which the family was adapted in the Upper Cambrian and Tremadoc, represented by bituminous black limestone and black shale lithologies. Graptolites are preserved in the same rocks, enabling correlation with the north American graptolitic zonal sequence.

All the species, and five of the ten genera present, are new. The greatest diversity of species belong to a new subfamily, the Balnibarbiinae, with two genera, *Balnibarbi* n. gen. (seven species and subspecies) and *Cloacaspis* n. gen. (three species). The subfamily Hypermecaspidinae is represented by three species of *Hypermecaspis* and one of *Tropidopyge*, Triarthrinae by one species of *Bienvillia* and three of *Triarthrus*, Plicatolininae by a species of *Plicatolina*. There are three new genera of Pelturinae: *Psilocara* n. gen. (two species), *Svalbardites* n. gen. (two species), and *Anaximander* n. gen. (one species).

The species of the subfamily Balnibarbiinae have an exceptionally complete record in the Spitsbergen succession, and from bed by bed collections a phylogeny for the group has been established. Three evolutionary lineages are recognised, involving modifications of almost every feature of the exoskeleton. From a discussion of the mode of evolution it is concluded that the period of derivation of a new species from its ancestor is short compared with its subsequent duration, and that this speciation pattern is consistent with the allopatric model.

The range of morphology displayed by the Arenig olenids is compared with that of previously known faunas. Suggestions are made relating the main morphological types to the constraints of the olenid environment.

Genal caeca of some Spitsbergen olenids show that more than one system of internal organs is represented by the caecal network. The distinctive structure of the anterior border of the Balnibarbiinae is described, and the importance of the sutural ridge in the ontogeny of olenids and as a feature persisting in the adult is shown.

New information is given on the ontogeny of species of the Balnibarbiinae, Hypermecaspidinae, Pelturinae and Triarthrinae.

I. Introduction

This is the first of a series of papers describing the trilobites of the Ordovician rocks of northern Ny Friesland, Spitsbergen, based on material collected in 1967 by a Cambridge University expedition, and in 1971 by an expedition organised from the Paleontologisk Museum, Oslo, and operated in conjunction with the Norsk Polarinstitutt. Previously, only one species of Ordovician trilobite from Spitsbergen has been described in detail (GOBBETT 1960). The trilobite fauna is now known to be one of the most diverse in the world, and the large numbers of species involved necessitates the publication of the descriptive palaeontology in several parts. The succession in north Ny Friesland has been described recently by FORTEY and BRUTON (1973), and the stratigraphic terminology and locality information given there will be followed in the present work. The Ordovician is here understood to include rocks of Canadian age, partly equivalent to the Tremadocian of Britain, following the usage of most north American workers.

Trilobites of the family Olenidae are confined to the upper of the two Ordovician Formations, the Valhallfonna Formation, and, with the exception of one species, are limited further to the lower Member of the Formation, the Olenidsletta Member of Arenig age. But although largely confined to 145 m out of almost 750 m of Ordovician strata the olenids found in that part of the section display an astonishing diversity, are common in most beds, and found in an excellent state of preservation. The presence of five new olenid genera testifies to the vigour with which the olenids continued to evolve after the Tremadocian. This variety of Arenigian olenids is at the present time unique to Spitsbergen, and they seemed, therefore, an appropriate group to describe first.

Acknowledgements

Professor GUNNAR HENNINGSMOEN of the University of Oslo not only organised the 1971 expedition to Spitsbergen, but also helped the author greatly with his broad knowledge of the olenids. I am very much indebted to Dr. DAVID L. BRUTON of the Paleontologisk Museum, Oslo, who had the exhausting task of registering the material, and was an absolutely invaluable companion in the field. Without the enthusiastic support of Dr. TORE GJELSVIK, director of the Norsk Polarinstitutt, it would not have been possible to collect at all from the remote area in Ny Friesland. Finally I would like to thank Professor H. B. WHITTINGTON and Mr. W. B. HARLAND of Cambridge University for allowing me to work on the material collected by Cambridge expeditions, and particularly Professor WHITTINGTON for his constant encouragement and wise advice, and for constructively criticising earlier drafts of the work.

II. Occurrence and age of the olenid trilobites

The stratigraphic distribution of the Olenidae found in the Valhallfonna Formation is shown in Fig. 1. It will be seen that the Olenidae are found in greatest diversity in two parts of the Olenidsletta Member: between 4 m and 75 m from the base of the member, and again between 102 m and 145 m. The dominant lithologies of these parts of the section are finely crystalline black limestones and shales, the former often with perfectly regular fine laminations, having a conchoidal fracture and, when broken, emitting a strong, bituminous or sulphureous odour. The appearance of olenids near the base of the Valhallfonna Formation is very striking, associated with the rapid change in lithology from the white limestones of the underlying Kirtonryggen Formation. In these "transition beds" certain olenids (such as *Tropidopyge alveus* n. sp.) may also be found in some abundance in lighter coloured, more coarsely crystalline limestones. Between 75 m and 102 m the only olenid to occur commonly throughout is *Bienvillia stikta* n. sp. In this part of the section grey, crystalline limestones with irregular, streaky laminations alternate with even bedded black flags, and the trilobite fauna is dominated by species of the families Asaphidae, Nileidae and Raphiophoridae. Again, in the Profilbekken Member, the finely crystalline black limestones and shales are absent, and with them the diverse olenid fauna, the only species being *Triarthrus parapunctatus* n. sp., and that very rare. There is no doubt of the close association in the Spitsbergen Ordovician of dark limestones and shales with the abundant and fully developed olenid fauna, and that the conditions under which these rock types were deposited as sediments were also the conditions which favoured numbers and variety of Olenidae. The more widely distributed *Triarthrus* may have been more tolerant of other environmental conditions.

The black limestones are closely similar to the black, bituminous limestones ("stinkkalk") of the Upper Cambrian and Tremadocian of Scandinavia, which are likewise associated with a particular abundance of olenid trilobites. The conditions of deposition of the black limestone and associated sediments have been discussed at length by HENNINGSMOEN (1957, pp. 61–70), who concluded that they were generally formed in stagnant (oxygen depleted) conditions, conditions in which the Olenidae, but few other trilobites, were particularly adapted to survive. The continued proliferation and evolution of the Olenidae in the Arenigian of Spitsbergen may be attributed to the persistence there of the same type of environment in which the family flourished in the Upper Cambrian and Tremadocian. The quietness of the bottom waters is attested to by the preservation of such large, extremely thin-shelled species as *Hypermecaspis venulosa* n. sp., and the common occurrence of free cheeks connected by the narrow ventral doublure. Such remains could surely not have endured much transport. The occurrence of a few olenid exoskeletons interpreted as moults points to the same conclusions (Pl. 12, Fig. 1).

The quiet, stagnant bottom conditions to which the Olenidae were adapted were also favourable for the preservation of graptolites. This fortunate concomitance enables a good stratigraphic control on the occurrence of the olenids in terms of the north American graptolite succession using BERRY's (1960) zones. The lowest beds of the Olenidsletta Member belong to the upper part of the *fruticosus* zone, low in the Arenig (FORTEY and BRUTON 1973, p. 2233) and probably equivalent to the *deflexus* zone of Britain, while the top 45 m of the Member contain graptolites indicative of the *Isograptus* zone of north America, and probably correlate with the zone of *Didymograptus hirundo* of Britain (FORTEY 1971, p. 198). Only *Triarthrus parapunctatus* n. sp. occurs with the typical Whiterock assemblage of the Profilbekken Member and may be early Llanvirnian in age. Between the rich *fruticosus* and *Isograptus* assemblages the diagnostic graptolites of the *protobifidus* and *bifidus* zones also occur, although the faunas are generally poorer in species, and inter-zonal boundaries hard to define precisely. These graptolite occurrences enable the stratigraphic ranges of the olenids to be calibrated against the graptolite zonal scheme as indicated in Fig. 1.

Individual stratigraphic ranges may be generalised into four broad successive groups of species which may prove to be of stratigraphic use elsewhere. These are, in ascending order:

Group 1: *Balnibarbi ceryx* n. gen., n. sp., *B. sombrero* n. gen., n. sp., *B. scimitar* n. gen., n. sp., *Hypermecaspis venulosa* n. sp., *Tropidopyge alveus* n. sp., *Psilocara patagiatum* n. gen., n. sp. The first two named occur immediately above the last four, and as a whole the group corresponds to the *fruticosus* zone. *Svalbardites hamus* n. gen., n. sp. also occurs.

Group 2: *Balnibarbi erugata* n. gen., n. sp., *B. pulvurea* n. gen., n. sp., *Cloacaspis dejecta* n. gen., n. sp., *Anaximander clavatus* n. gen., n. sp. (approximates to the *protobifidus* and part of the *bifidus* zones). *Bienvillia stikta* n. sp. and *Svalbardites hamus* n. gen., n. sp. also occur.

Group 3: *Balnibarbi tholia* n. gen., n. sp., *B. erugata* n. gen., n. sp., *Bienvillia stikta* n. sp. (approximates to the upper part of the *bifidus* zone and perhaps earliest *Isograptus* zone).

Group 4: *Cloacaspis ekphymosa* n. gen., n. sp., *C. senilis* n. gen., n. sp., *Hypermecaspis latigena* n. sp., *H. brevifrons* n. sp., *Triarthrus papulosus* n. sp., *T. thor* n. sp., *Svalbardites hebaxis* n. gen., n. sp. (*Isograptus* zone).

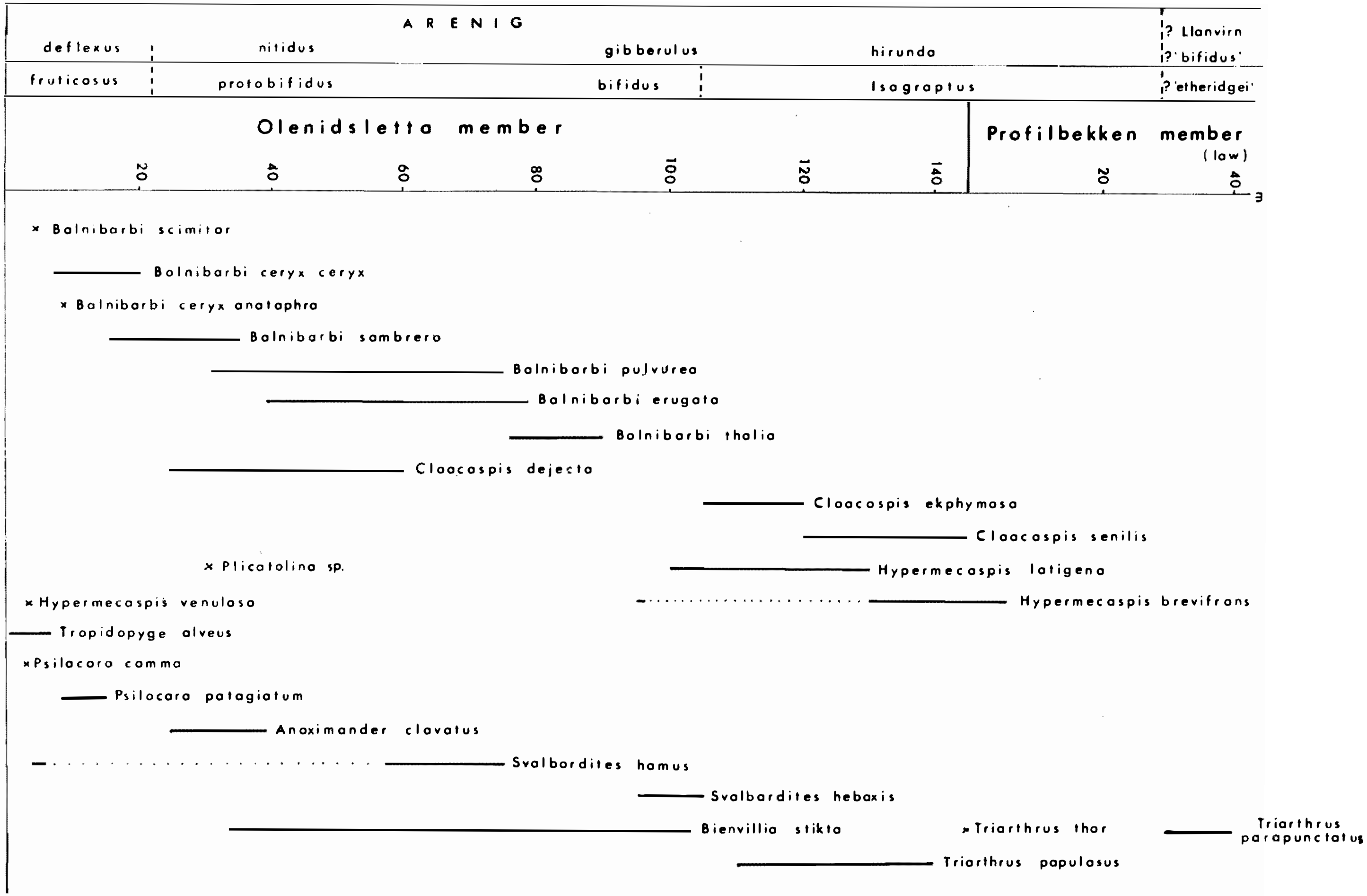


Fig. 1. Stratigraphic ranges of the olenid species through the Valhallfonna Formation, with approximate correlations with British and north American (Berry, 1960, on right) graptolite zones.

III. Relationship to other olenid faunas

A. Genera present

Of the ten genera of olenid trilobites from the Arenigian of Spitsbergen five are new, indicating that evolution of the family continued actively after Tremadocian times. On the other hand subfamilies which are present in Tremadocian rocks, with an almost worldwide distribution, continue into the Spitsbergen succession, these being the subfamilies Triarthrinae, Hypermecaspidinae, Pelturinae and Plicatolininae. The most abundant species in the new fauna are assigned to a new subfamily, the Balnibarbiinae, and the presence of nine species of this subfamily in the Arenigian shows the rapid diversification of which the family was still capable later in its history. Within this new subfamily some species are of a "conservative" type (such as *Cloacaspis senilis* n. gen., n. sp.), strongly recalling *Parabolinella*, but the phylogenetic and stratigraphic information from Spitsbergen demonstrates that these species are secondarily derived from more "specialised" ancestors (see p. 19).

Of the genera known to occur in other localities, *Triarthrus* and *Bienvillia* are the most geographically widespread and have the longest stratigraphic range. The Spitsbergen species *Bienvillia stikta* n. sp. is strikingly similar to triarthrines described by HARRINGTON and LEANZA (1957) from Argentina. *Tropidopyge* has hitherto been recorded from Norway, Sweden, and South America (Colombia) in Tremadocian rocks, and probably also occurs in Wales. *Hypermecaspis* occurs in South America, China, Nevada, and Newfoundland in rocks ranging in age from Tremadocian to Llanvirnian. *Plicatolina* is known from Argentina, Norway, Nevada, and Vermont, and a closely related genus from Mexico, all in the early Tremadocian. The scattered localities for these genera, and their occurrence together in Spitsbergen, seem to bear little relation to the faunal provinces suggested on the basis of trilobite distributions for the early Ordovician, most recently and in greatest detail by WHITTINGTON and HUGHES (1972, p. 242).

B. Morphological features and remarks on their possible functional significance

The Arenigian olenids described below display some morphological features which are rare among Tremadocian and earlier species, and may perhaps be regarded as general evolutionary trends within the family. Species of *Balnibarbi* n. gen., *Cloacaspis* n. gen., *Tropidopyge*, *Hypermecaspis* and *Bienvillia* (*B. stikta* n. sp.) all show divergent anterior branches of the facial sutures. In some species this divergence approaches ninety degrees to the sagittal line. Divergent anterior branches of the facial suture are rare among Tremadocian olenids and when they occur the divergence is small (see for example, *Parabolinella argentinensis* KOBAYASHI 1936, figured by HARRINGTON and LEANZA 1957, Fig. 37). Divergent sutures may be connected with the presence of large palpebral lobes with the anterior limits close to the glabella, a feature which the above named also possess. If the anterior branch of the suture is supposed to cut the anterior border at a relatively constant position, then when the anterior limit of the palpebral lobe is at a certain distance from the glabella the suture runs forward to the anterior border more or less parallel to the sagittal line: when it is closer the anterior branch becomes divergent, when further away convergent. Some support for this hypothesis may be found also among the Leptoplastinae: *Eurycare latum* (BOECK 1838), which has the eyes very far from the glabella, has the anterior branches of the facial suture strongly convergent; *E. explanatum* (HOLTEDAHL 1910) has less convergent anterior sutures, and the eyes are closer to the glabella; in *Leptoplastus norvegicus* (HOLTEDAHL 1910) the palpebral lobes are closer still, and the sutures converge but slightly anteriorly; all three species have an anterior border of similar width (trans.) relative to that of the glabella (see HENNINGSMOEN 1957, Pls. 15, 16). On the other hand this explanation can hardly account for the variation in the degree of divergence of the anterior branch of the suture in *Balnibarbi* n. gen. and *Cloacaspis* n. gen. species, which have the palpebral lobes in similar positions close to the glabella.

Cranidia of a number of the species from Spitsbergen have an anterior border furrow with minute pits. This again seems to be a feature more common among the Arenigian olenids than earlier assemblages, although some Tremadocian species such as *Parabolinella argentinensis* KOBAYASHI 1936, *P. triarthra* (CALLAWAY 1877) and *Angelina hyeronimi* (KAYSER 1876) possess such punctation. The pits are not continued laterally in the border furrow of the free cheek. They may have developed from the small depressions that commonly occur on the anterior border furrow of olenids, between neighbouring caeca as they run in to the anterior border. In *Balnibarbi* n. gen. the pits correspond ventrally with nodes developed on the dorsal surface of the cephalic doublure (see Pl. 5, Fig. 10), a complex structure surely with functional significance. Divergent anterior branches of the facial suture also serve to extend the length of the cranidial border, and hence the extent of the pitted "fringe". Further discussion of these pits is given after the description of *Balnibarbi pulvurea* n. gen., n. sp. below.

All the Hypermecaspidinae from Spitsbergen, and several species of *Balnibarbi* n. gen., have large pygidia compared with most Upper Cambrian and Tremadocian olenids, but these species occur along with others with relatively smaller pygidia. The pygidial doublure of the species with large pygidia is invariably broad, and closely reflexed against the dorsal surface. The functional significance of increased pygidial size is not clear: possibly, as suggested by HENNINGSMOEN (1957, p. 77), a large pygidium functioned as a "counterbalance" during swimming for the large cephalon, in conjunction with long genal spines in such species as *Balnibarbi pulvurea* n. gen., n. sp., or it seems equally possible that a large pygidium may also have enabled more secure enrollment, particularly adpressed against the broad cephalic border of most Balnibarbiinae and Hypermecaspidinae.

Among the later species of the subfamily Pelturinae there is a tendency for the facial sutures to become proparian, this tendency reaching its greatest expression known hitherto in the genus *Saltaspis*, which appears in the Tremadoc and continues into the early Arenig Rocks of Sweden (TJERNVIK 1956). The new pelturinid genera from Spitsbergen, *Anaximander* n. gen. and *Svalbardites* n. gen., carry this evolutionary trend still further, although in gross morphology resembling Upper Cambrian *Peltura* species more closely than *Saltaspis*.

Overall morphology of the Spitsbergen olenids varies between two extreme types. In one the convexity is very low, a broad or extremely broad preglabellar field stretches outwards almost horizontally in front of the glabella, and the pygidium is large, in the other the exoskeleton is narrower, more convex (sag., trans.), with a narrow, downsloping preglabellar field. The latter type of morphology corresponds to what HENNINGSMOEN (1957, p. 78) termed the *Peltura* type and includes the new species of *Bienvillia*, *Cloacaspis* n. gen., *Psilocara* n. gen., *Svalbardites* n. gen., *Balnibarbi tholia* n. gen., n. sp. and *Hypermecaspis brevifrons* n. sp. All except the last named have relatively small pygidia. The former type of morphology is probably closest to the *Olenus* type of HENNINGSMOEN, although some Spitsbergen species exceed in wideness and flatness any pre-Arenig species. The best examples are *Hypermecaspis venulosa* n. sp., *Tropidopyge alveus* n. sp., *Balnibarbi sombrero* n. gen., n. sp., and *B. erugata* n. gen., n. sp.

A functional explanation for these morphological types may be suggested if they are assumed to be the product of a response to the constraints of the "Olenid sea" environment. Below the sediment surface it is possible that strongly reducing conditions pertained, toxic to animal life. This possibility is consistent with the perfectly laminated olenid bearing limestones, which lack bioturbation and any other evidence of infauna. To the trilobite feeding on the top of the sediment surface it was important not to disturb it sufficiently to penetrate the "poisonous" lower layers, or to escape rapidly if conditions became dangerous. The convex morphological type had more room for muscles which assisted in rapid and vigorous swimming (RICHTER 1919, p. 229, HENNINGSMOEN 1957, p. 78) enabling rapid escape from unfavourable conditions. The generally long thorax and small pygidium no doubt lent the trilobite great flexibility. The greatly flattened morphological type could scarcely have been a vigorous swimmer. The effect of the broad preglabellar field and large pygidium and the wide doublure doubled back beneath the free cheeks and the pygidium is to extend the area covered by the carapace peripherally, while the central body area remains quite narrow. The low axis probably indicates relatively weak musculature. These features suggest that the flattened morphological type was adapted to resting on the sediment surface, disturbing it as little as possible by spreading its weight over an increased area. In the case of *Hypermecaspis venulosa* n. sp. additional "upthrust" may have been obtained from the displacement of the sediment/water layer by the concave preglabellar field. The extreme thinness of the exoskeleton of this and other flat species no doubt also was important in preventing sinking.

C. Remarks on caeca

A number of the Spitsbergen olenids have well preserved genal caeca. Öpik (1961) has described examples of such caeca in a number of trilobites and accepts that they are the impressions of lateral ramifications of the alimentary canal. The free cheek of *Tropidopyge alveus* n. sp. has the doublure of the free cheek closely reflexed against the dorsal exoskeleton, such that the ventral surfaces of the caeca are impressed upon the dorsal surface of the doublure (Pl. 16, Fig. 2). From this it is clear that the caeca are irregularly anastomosing tubes with a subcircular cross section in this species, and that they terminate quite close to the lateral margin of the cephalon after passing between the dorsal exoskeleton and the doublure. However, in *Hypermecaspis brevifrons* n. sp. (Pl. 14, Fig. 2) there is a second type of genal ridge. This ridge passes from the mid point of the eye backwards across the cheek to the genal angle, in the process cutting across a number of genal caeca which are arranged in a more or less radial fashion. The caeca apparently pass over the ridge, which has a diameter twice that of the caeca near to the eye. The ridge is independent therefore of the caecal system, and probably represents the impression of a different kind of internal organ lying ventrally below the caeca. Closely comparable ridges are present also on the free cheeks of some species of *Balnibarbi* n. gen. (Pl. 7, Fig. 2), where the ridges run into the marginal rim in front of the genal angle. This structure is what Öpik (1967, p. 172, Figs. 33, 75) has termed the principal genal or caecal vein.

Impressions of the ventral surfaces of the caeca are also present on the dorsal surface of the doublure underlying the cranidial border in species of *Balnibarbi* n. gen. (Pl. 5, Fig. 10, Pl. 3, Fig. 2). In this case the caeca do not terminate, but pass anteriorly into the marginal cephalic rim — essentially a tube running around the front margin of the cephalon. The cephalic rim presumably served for the enclosure and protection of circum-cephalic organs. It is of interest to note in this connection that *Limulus* has a marginal artery running around the prosoma (Fage in Grassé 1949, p. 234). Possibly the marginal rim included a similar vessel in *Balnibarbi*, which supplied the sensory apparatus represented by the border furrow pits and nodes on the doublure. Whether the caeca terminated within the marginal rim or whether their passage into it is of greater functional significance is not certain.

The occurrence of two distinct types of ridge on the free cheek of *Hypermecaspis* and *Balnibarbi* species (i.e. grooves on the internal surface of the exoskeleton) indicates that not all cephalic canals may be interpreted as alimentary glands and that some other internal organs, such as of circulation, may rarely be impressed upon the exoskeleton.

IV. Systematic descriptions

Terminology

The terminology used largely follows that of the *Treatise* (HARRINGTON, MOORE, and STUBBLEFIELD in MOORE 1959, p. 0–117). Terms for particular structures present on certain of the olenids described below are:

Post-palpebral furrow. — On *Cloacaspis* n. gen. a furrow running from the posterior end of the palpebral lobe and crossing the fixed cheek to meet the posterior border furrow inside the posterolateral angle of the cranidium (see Pl. 11, Fig. 16).

Sutural ridge. — On small olenid growth stages and some adults (WHITTINGTON 1965, p. 333), a ridge on the edge of the postocular fixed cheek following the line of the suture and defined by a distinct furrow.

Pleural nodes. — Inflated triangular areas on the adaxial parts of the thoracic pleurae of species of the new olenid subfamily Balnibarbiinae.

Terms applied to the description of *surface sculpture* are used in the following sense:

Punctae. — Fine scale, closely-spaced pitting in the dorsal surface of the exoskeleton.

Pits. — Coarser than punctae, often arranged in lines (pits in the anterior border furrows of olenids) or associated with apodemes on the internal surface of the exoskeleton.

Terrace lines. — Step-like changes in the relief of the surface of the exoskeleton, usually on a fine scale.

Ridges. — Raised lines on the dorsal surface of the exoskeleton.

Granules. — Small scale protuberance from the exoskeleton, not reflected on internal moulds.

Family OLENIDAE BURMEISTER 1843

Diagnosis. — Facial sutures opisthoparian, rarely proparian, meeting in front medially. Free cheeks of most species united by narrow (sag., exsag.) doublure. Hypostoma not attached at suture to doublure, but to ventral membrane of cephalon. Thorax with 9–19 segments, pleurae with simple diagonal pleural furrows. Exoskeleton usually very thin.

Remarks. — The difficulty of diagnosing this family has been commented upon by several authors (RASETTI 1951, p. 202, HENNINGSMOEN 1957, p. 95). The diagnosis given above is an attempt to give a short list of characters by which an olenid may be distinguished from other trilobites. In all other characters of the dorsal exoskeleton the Olenidae exhibit such a range of variation (particularly incorporating the new genera described below into the family) that a full diagnosis summarising the form of the facial sutures, size and position of the eyes, number and type of glabellar furrows, and size and segmentation of the pygidium would be so generalised as to have little or no diagnostic value. The rather simple glabella of olenids, tapering forwards, or with parallel or slightly convex sides, or expanding very slightly in width anteriorly distinguishes these trilobites from *Richardsonella* and allied genera with apparently similar cephalic doublure (see PALMER 1968, Pl. 14, Fig. 8).

Well preserved specimens showing the fused nature of the free cheeks have been found among the hypermecaspidinids (Pl. 24, Fig. 9), triarthrinids (Pl. 22, Fig. 6) and the Balnibarbiinae, n. subfam. (Pl. 3, Fig. 1). This characteristic seems to be typical of many Olenidae, although PALMER (1962, Fig. 35) indicates that a rostral plate was present on *Olenus gibbosus* WAHLENBERG. The doublure connecting the free cheeks is narrow (sag., exsag.), and it is most improbable that the hypostoma was attached to the doublure in species with a broad preglabellar field (see discussion of *Balnibarbi pulvurea* n. gen., n. sp. below).

Subfamily BALNIBARBIINAE n. subfam.

Diagnosis. — Heteropygous to subisopygous olenid trilobites, having subquadrate glabella with four pairs of glabellar furrows, the two anterior pairs short (trans.) pits, the two posterior arcuate or flexed, occupying over one third glabellar width. The anterior pair of furrows are reduced to smooth areas on the dorsal surface of the exoskeleton in some species. Eyes large, close to the glabella. Preglabellar field narrow to extremely broad. Facial sutures moderately to strongly divergent in front of and behind palpebral lobes. Free cheeks with long genal spines. Anterior border furrow may be pitted, with corresponding nodes on the inner surface of the ventral doublure. Thorax (where known) of fourteen segments, the penultimate of which bears a long axial spine. Pleural furrows branch near the axis outlining a triangular node adjacent to the axial furrow, referred to as the "pleural node". A similar node (or nodes) is developed adaxially on the anterior of the pygidial pleural field. Pygidial axis with from two to four rings, nearly reaching the posterior border, which is indented and arched up on the mid line. Exoskeleton very thin, with surface sculpture of lines, pustules, a combination of both, or smooth.

The subfamily is described so far only from Spitsbergen, although I have collected a species certainly related to *Cloacaspis* n. gen. in Nevada (Ikes Canyon, Monitor Range), and the subfamily may also occur at other localities in the Western United States (R. J. Ross, personal communication 1972). The cranidium figured by Ross (1965, Pl. 8, Fig. 4) from the Seward Peninsula, Alaska, as *Triarthrus* sp. is more similar to *Cloacaspis* n. gen. than any other olenid. These occurrences suggest that the subfamily may in the future prove to be widespread.

Discussion. — The trilobites described below belonging to this subfamily are the product of a remarkable burst of evolutionary activity in the early Ordovician of a hitherto undescribed group of olenids. The pleural nodes on thorax and pygidium at once distinguished members of this subfamily from other olenids; other important characters are the divergent preocular sutures and large pygidia of some species, and the very large eyes placed close to the glabella. The glabella itself is of rather conservative olenid type, resembling closely that of some *Parabolinella* species (e.g. *P. triarthroides* HARRINGTON) and some species of *Triarthrus*. The hypostoma is also of a type similar to that of known olenids (especially triarthrinids). There is, therefore, no reason to doubt that the Balnibarbiinae should be included within the Olenidae. The general resemblance of *Balnibarbi* n. gen. to the Hypermecaspidinae is due to homeomorphy rather than any phylogenetic relationship, since the hypermecaspidinids differ in most details, particularly in their complex glabellar segmentation and simple pleurae lacking nodes. Morphologically convergent forms in families other than the Olenidae, differing from *Balnibarbi* n. gen. mainly in the character of the glabella and cephalic doublure, include *Pseudokainella* (Kainellidae) and *Loganellus* (Loganellidae.) The lithologies associated with the occurrence of *Balnibarbi* n. gen. and the hypermecaspidinids (*Hypermecaspis* n. sp.) are known to have been similar in the Spitsbergen Ordovician (black, bituminous limestones and shales) and from the descriptions of the enclosing rocks containing *Pseudokainella* (HARRINGTON and LEANZA 1957) and *Loganellus* (RASETTI 1944) it seems possible that these genera also were adapted to a black limestone/shale environment, in which case their morphological similarity may be the result of adaptation to a similar environment.

PHYLOGENY OF THE BALNIBARBIINAE (Fig. 2)

The continuity of the record of trilobites of this subfamily in the Olenidsletta Member, and their abundance as fossils, has enabled a detailed study to be made of the stratigraphic and morphological relationships of the ten species and subspecies which are described below. The evidence indicates that the species form phyletically linked series evolving through the Arenig. From the subtle intergradations that occur between species and their nearly continuous stratigraphic record it seems very probable that the evolutionary record is exceptionally complete.

Three evolutionary lineages are recognised:

1. involving the three *Cloacaspis* species
2. involving the *Balnibarbi* species *B. pulvurea* and *B. tholia*
3. involving the *Balnibarbi* species *B. sombrero* and *B. erugata*

Balnibarbi ceryx and *B. scimitar* lie at the origin of these lineages. During the course of the evolution of the group changes occur in almost every feature of the exoskeleton. The *Balnibarbi pulvurea/tholia* and *Cloacaspis* evolutionary lineages have as their common point of origin the early species *Balnibarbi ceryx*. That this species itself was probably derived from *B. scimitar* is discussed below. The characters of *Balnibarbi ceryx* which undergo subsequent modification may be briefly listed: (a) preglabellar field of moderate width, (b) anterior branches of facial sutures diverge at 55–60 degrees to the sagittal line, (c) palpebral lobes narrow (trans.), arcuate, with posterior limits just anterior to where the occipital furrow meets the axial furrows, (d) postocular cheeks triangular in outline, (e) four pairs of glabellar furrows visible on well pre-

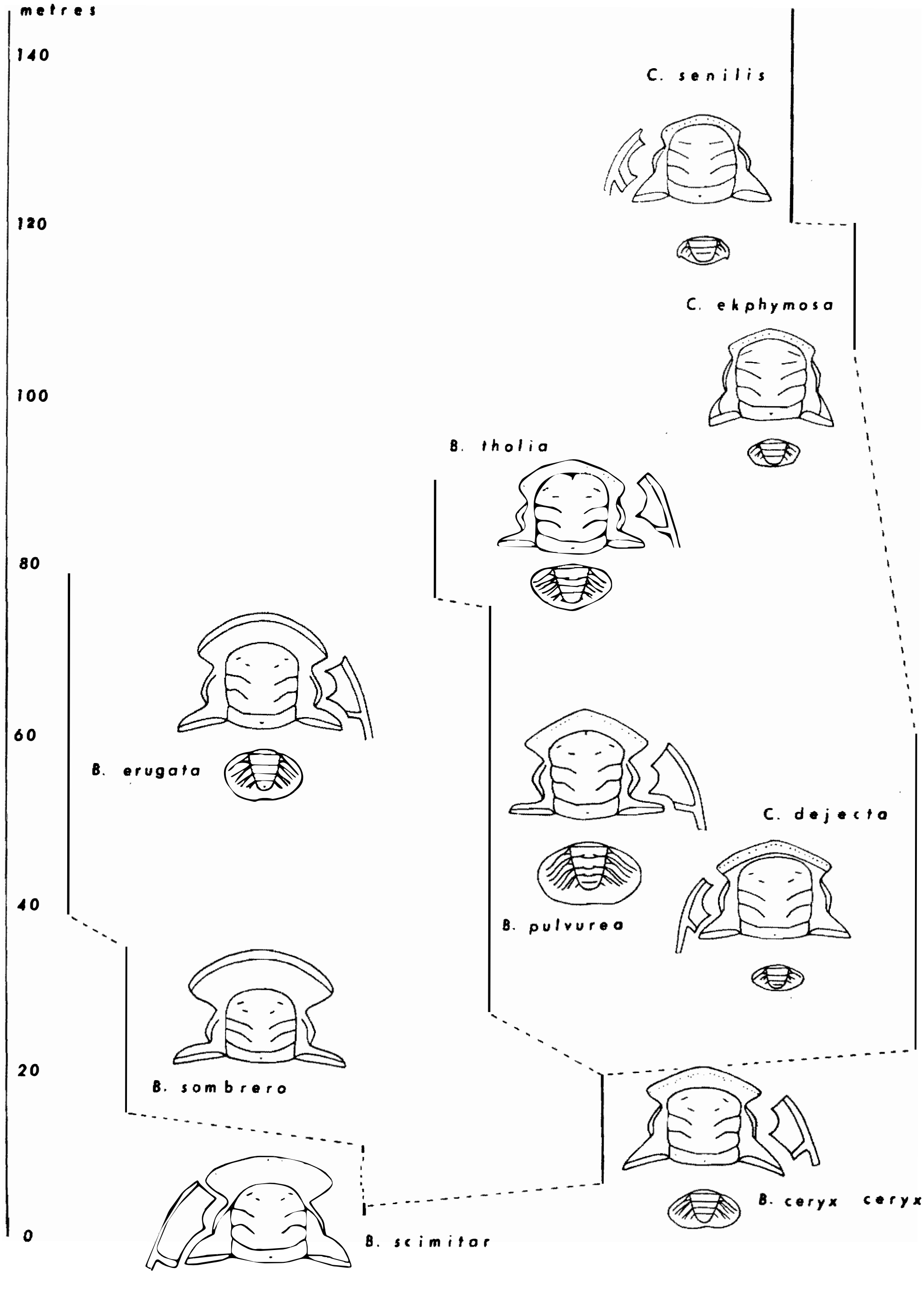


Fig. 2. Phylogeny of the Balnibarbiinae (*Balnibarbi* n. gen. and *Cloacaspis* n. gen. spp.) in the Olenidsletta Member of the Valhallfonna Formation. Dashed lines show the proposed phyletic links between species, and indicate the thickness of strata over which the changes take place.

served specimens, (f) glabella parallel sided, (g) posterior border of the fairly wide free cheek curves forwards towards genal spine, (h) pygidium of fairly small size with three axial rings. The evolutionary line leading to *B. pulvurea* and *B. tholia* is characterised by an expansion of the preglabellar field, often accompanied by an increase in the amount of divergence of the preocular sutures, while the postocular fixed cheeks become long, narrow strips defined anteriorly by a backward migration of the palpebral lobe, which becomes broad and geniculate; the pygidium increases greatly in relative size, and there is a fourth axial ring. The *Cloacaspis* line involves a progressive reduction in the width of the preglabellar field accompanied by decrease in the divergence of the preocular sutures, while the post-ocular fixed cheeks become progressively less wide (tr.) and strap-like, more triangular; the anterior glabellar furrow becomes reduced to a smooth area externally but is still visible on internal moulds; the pygidium is relatively smaller with only two axial rings and, ultimately, a spinose border. The posterior border of the free cheek curves forward to the genal spine.

B. ceryx lies at the origin of these two lines and possesses an intermediate set of characters. Its assignment to *Balnibarbi* rather than *Cloacaspis* was thus rather an arbitrary decision, based on its greater resemblence to later *Balnibarbi* species such as *B. tholia* than to later *Cloacaspis* species.

1. *Cloacaspis lineage*

The oldest species of *Cloacaspis*, *C. dejecta* n. sp., occurs a few metres above *B. ceryx*, and shows the reduction in the preglabellar field typical of the genus. The preocular divergence of the facial sutures is about 40 degrees, the postocular fixed cheek more triangular than that of *B. ceryx*; the glabellar furrow 4P is in some examples not visible on the external surface of the exoskeleton. The pygidium is small and with the third axial ring only faintly indicated by a short pit separating it from the posterior part of the axis. The pygidial margin is entire. The later species of *Cloacaspis*, *C. ekphymosa* and *C. senilis*, are characterised by an even more reduced preglabellar field, divergence of preocular sutures not exceeding 20 degrees to the sagittal line, postocular fixed cheeks rather narrowly (tr.) triangular. Lateral glabellar furrow 4P is present as a smooth area on the external surface of the exoskeleton, but is visible on internal moulds and on flattened specimens. The anterior border is rounded. The pygidium has only two axial rings, and its posterior margin is at first angulate (*C. ekphymosa*) then equipped with short spines (*C. senilis*). These species of *Cloacaspis*, like *C. dejecta* and *Balnibarbi ceryx* have the posterior margin of the free cheek curving forward to the genal spine. There can be little doubt that *C. ekphymosa* was the direct ancestor of *C. senilis*, and the details of this transition are discussed below (p. 41).

While these *Cloacaspis* species form a continually evolving gradation from *B. ceryx* in the characters of the preglabellar field, sutures, pygidium, etc., they are each uniquely characterised by particular patterns of surface sculpture which are described in the systematic part, and each of which may be derived from that of the preceeding species (this has been shown in the transition *C. ekphymosa* — *C. senilis* to be due to a peculiar form of recapitulation). The reduction in width of the preglabellar field in this lineage is shown quantitatively in Fig. 3.

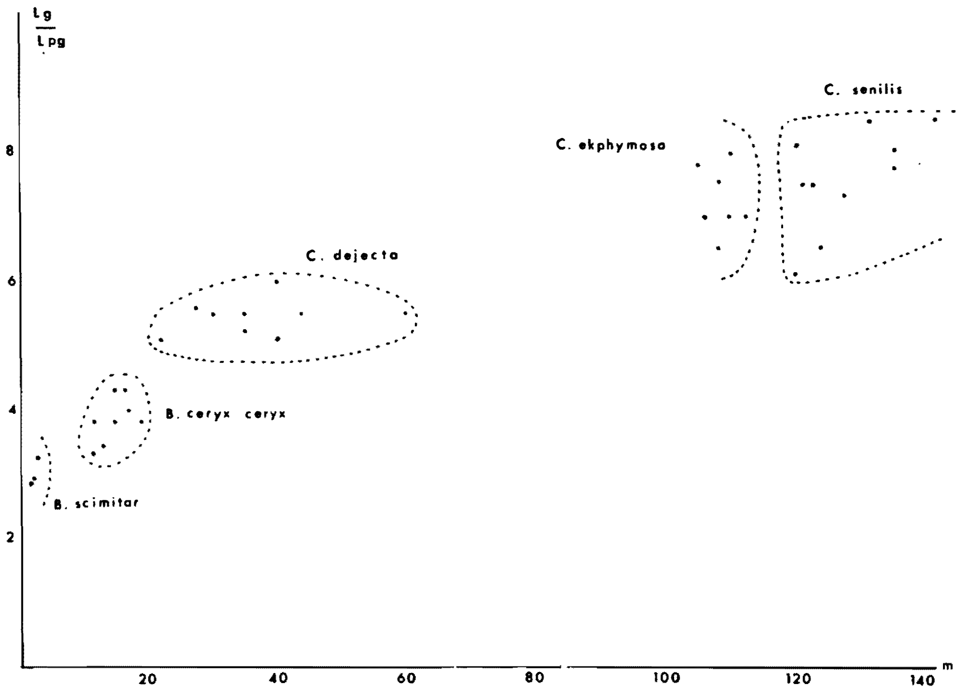


Fig. 3. Graph to show the decrease in width of the preglabellar field in the series *Balnibarbi scimitar* – *B. ceryx ceryx* – *Cloacaspis dejecta* – *C. ekphymosa* – *C. senilis*. The sagittal length of the glabella (Lg) divided by the width of the preglabellar field + anterior border (Lpg) (measured with the preglabellar field horizontal) is plotted against stratigraphic occurrence in m. Both flattened and unflattened material is included.

2. *pulvurea-tholia lineage*

The species of *Balnibarbi* succeeding *B. ceryx*, *B. pulvurea*, shows the opposite tendencies to those outlined in the *Cloacaspis* series. The preglabellar field is broader, especially anterolaterally where the sutures are strongly divergent, the post-ocular fixed cheeks are narrower (exsag.) and strap-like, the eye further back, while the posterior border of the free cheek no longer curves forward to the genal spine. The pygidium is relatively larger than that of *B. ceryx*, with *four* axial rings, and in the pleural fields *two* pairs of pleural nodes are visible, suggesting that perhaps an extra segment has been retained in the pygidium. The dorsal surface of *B. pulvurea* is uniformly granulate. As in all *Balnibarbi* species the four glabellar furrows are all well defined. *B. tholia*, which succeeds *B. pulvurea* is very similar, but with the preglabellar field more convex, and with a different sort of surface sculpture, with complex arrangements of raised lines as well as granules.

3. *sombrero-erugata lineage*

The *sombrero-erugata* lineage differs from that of *B. ceryx* and its derivatives in lacking distinct pits in the anterior furrow of the cranidium. The front margin of the cranidium is evenly rounded towards the mid line, and the overall convexity of the cranidium is low. Both species are without surface sculpture. There is no doubt that the earlier *B. sombrero* gave rise to *B. erugata*, the resemblance between cranidia of the two species being complete except for the greatly expanded preglabellar field of the former. The transition between the two species occurs at 35m from the base of the Olenidsletta Member in the type section, where a single transitional specimen has been discovered. *B. sombrero* itself occurs in the same beds as *B. ceryx*, low in the Olenidsletta Member.

The discovery in 1971 of a *Balnibarbi* species, *B. scimitar*, antedating these early species, indicates that they themselves had a common ancestor within the Valhallfonna Formation. Larger specimens of *B. scimitar* have a broad preglabellar field, evenly rounded anterior border (and glabella), highly divergent preocular sutures, and lack sculpture, and in general appearance are similar to *B. sombrero*. On the other hand the anterior border furrow is pitted, the posterior limit of the palpebral lobe is anterior to the occipital furrow where it meets the axial furrow, and the posterior border of the free cheek curves forwards to the genal spine, being similar in these features to *B. ceryx*. This resemblance is more apparent on small cranidia of *B. scimitar*, which not only have a shorter preglabellar field, but also have a pointed anterior border (Pl. 7, Fig. 9). In short, *B. scimitar* lies morphologically between and stratigraphically immediately below *B. ceryx* and *B. sombrero*, and is considered to be their common ancestor. It therefore lies at the root of the whole of the Spitsbergen balnibarbiinid radiation.

MODE OF EVOLUTION

It is of interest to note that the *Cloacaspis* species, which are of a rather conservative olenid type, comparing in gross morphology with such genera as *Parabolinella*, *Protopeltura* and *Triarthrus*, have evolved from the early *Balnibarbi* species which are less similar in gross morphology to previously known olenids. I have remarked above on the similarity of the smaller cranidia of *B. scimitar* to those of *B. ceryx*. Small cranidia of *B. ceryx* themselves have a shorter preglabellar field giving them a closer resemblance to *Cloacaspis* species (Pl. 9, Fig. 4). In the lineage *scimitar-ceryx-Cloacaspis*, therefore, the smaller individuals of the ancestral species resemble the larger cranidia of the derived species, that is, evolution proceeds neotenously. Conversely, in the series *ceryx-pulvurea-tholia* new specific characters are modifications of features which are most completely expressed in the adult of the ancestral species, for example increase in divergence of sutures, or increased convexity of the preglabellar field. The selection pressures which operated to produce such changes are obscure, but from the fact that species with similar morphology, particularly with regard to the preglabellar field, are present also among the Hypermecaspidinae it is evident that their operation was of general importance.

From the distribution of the Balnibarbiinae in the Spitsbergen sections the period of duration of the species is believed to have been relatively long compared with the period of derivation from the ancestral species, that is, once their morphology was established, and this was a rapid process, the species remained stable for a long time. It might be argued that the *appearance* of rapid speciation might be given by non-sequences in the succession at the points of origin of the new species. The strength of this hypothesis may be diminished on two counts: (a) there is no lithological indication of non-sequence or a reduced rate of sedimentation at the parts of the section where new species originate, (b) as Fig. 2 shows the times of origin of new species do not correspond in the different lineages. If there were hiatuses within the section it might be expected that new stocks would appear simultaneously thereafter. I had also at one time considered the possibility that what appeared to be "lineages" were, in fact, different sexual dimorphic pairs occurring together in the same beds. Again the non-synchronous way in which the species change, and also the presence of *three* species groups, discourages such an explanation.

If the duration of species with little morphological change is relatively long compared with that of their derivation from their ancestors, this implies that evolution in this case defines discrete morphological groups with a particular stratigraphic range — that is, that palaeontological species seem to have real meaning among these olenids rather than being arbitrary points on a continuous morphological spectrum changing with time.

On the basis of present material there is no evidence to suggest the presence of repeated evolutionary trends within successive species such as KAUFMANN (1933) has shown in species of *Olenus* from the Upper Cambrian of Scania, Sweden. However, in the probable phyletic series *Olenus transversus-truncatus-wahlenbergi* there is a progressive decrease in the width of the preglabellar field, and an increase in the degree of curvature of the posterior border of the free cheek to the genal spine, changes analogous to those occurring in the series *B. ceryx* — *Cloacaspis* in Spitsbergen. The Scania succession is extremely thin and condensed, the thickness of strata through which the six successive *Olenus* species studied by KAUFMANN occur being only 2.5 metres; this might well represent the equivalent sediment in time terms to the 175 m of the Olenidsletta Member. An unfossiliferous gap of half a metre such as occurs between the *Olenus wahlenbergi* and *Olenus attenuatus* zones in Scania (KAUFMANN 1933, Fig. 2) probably represents a considerable time gap in that section. The succession in Spitsbergen may be considered to be relatively complete.

In a recent discussion of the allopatric model of speciation ELDREDGE (1971) has indicated that discontinuous species-lineages might prove to be the rule among Palaeozoic invertebrates. New species and subspecies originating within marginal populations which have become isolated may spread and replace the ancestral species with a suitable change in conditions. The evolutionary record of the Balnibarbiinae in Spitsbergen is remarkably complete.

The relatively sudden appearance of the new species compared with their subsequent duration seems to accord well with the allopatric model, although there is no evidence to suggest that drastic changes occurred in the olenid environment such as may happen in epieric habitats. Possibly the replacement of one species by another may have been due to subtle changes in the degree of oxygenation or in the organic constituents of the sediment which are not readily reflected in obvious lithological change.

The surface sculpture of the Balnibarbiinae is unlikely to have served as a means of strengthening the exoskeleton, as it is always on the finest scale and never reflected on the internal moulds, that is, it is a purely surface feature. Yet the radical changes which occur in the sculpture in the history of the subfamily indicate that it must have had some adaptive significance. It is suggested that sculptural patterns may have been of importance in the recognition of members of the same species (balnibarbiinids all had large eyes) when closely related species existed in the same environment.

ORIGIN OF THE BALNIBARBIINAE

The resemblance of balnibarbiinids to certain triarthrinids has already been commented upon, and there can be little doubt that the nearest relatives of the new subfamily are to be found among that group of the Olenidae. By far the most similar species to the early *Balnibarbi* species are to be found in the genus *Agalatus* LISOGOR (LISOGOR 1961) from the Tremadocian of Kazakhstan. The cranidium of this genus is very similar in form to that of the balnibarbiinids, with large eyes close to the glabella, divergent preocular sutures, and glabellar furrows of balnibarbiinid type. The minute pygidium, however, show no sign of the diagnostic pleural node of the balnibarbiinids, and for this reason *Agalatus* is probably best excluded from the Balnibarbiinae.

Genus *Balnibarbi* n. gen.

Type species. — *Balnibarbi pulvurea* n. gen., n. sp.

Diagnosis. — Balnibarbiinid trilobites with broad preglabellar field, facial sutures highly divergent in front of eyes. Four pairs of glabellar furrows. Postocular fixed cheeks narrow, strap-like. Pygidium of medium to large size, with three or four axial rings.

Balnibarbi pulvurea n. gen., n. sp.

(Pls. 1, 2, 3; Fig. 4)

Stratigraphic range. — Middle part of the Olenidsletta Member, 28–75 m from base (corresponds approximately to *bifidus* and *protobifidus* zones).

Material. — Holotype, cranidium PMO NF 732. Abundant other material includes cranidia: PMO NF 579, 598, 618, 628, 712, 714, 718, 722, 764, 1845, 2068, 3017, 3025, 3028, SMA 84013–4, 84016, 84018, 84020; pygidia: PMO NF 616, 753, 765, 3021–3, SMA 84015, 84019; free cheeks: PMO NF 3018–9, 3024, SMA 84017; hypostomata: PMO NF 723, 730, SMA 84021–2; thorax: PMO NF 3027, 3020.

Diagnosis. — A *Balnibarbi* species having a broad preglabellar field, facial sutures highly divergent in front of eyes. Anterior border comes bluntly to a point medially. Anterior border furrow with about 40 distinct pits. Eye far back, delimiting a narrow (exsag.), strip-like postocular cheek. Pygidium very large, convex, with four axial rings; pleural nodes visible opposite first two axial rings. External surface covered with minute granules, except on anterior border, which bears strong striae, and in furrows.

Description. — Glabella parallel sided or expanding very slightly anteriorly, transverse width almost equal to length, moderately convex (trans.), sloping downwards anteriorly, gently rounded in front. Four pairs of glabella furrows are well impressed, 1P and 2P equally spaced from the occipital furrow at their outer ends, 3P and 4P close together on anterior part of glabella, consisting of short, elongate pits. 1P and 2P extend to 0.4 glabella width. The inner end of 1P slopes backwards at 70 degrees to sagittal line; at a point half way along its length it bends sharply abaxially to run towards the axial furrow at right angles to the sagittal line, this part of the furrow being shallower. Just before reaching the axial furrow it is deflected anteriorly. 2P is of similar length, running inwards and gently backwards with only the slightest suggestion of a backward bend towards its inner end. 3P is a short pit the long axis of which is directed very gently backwards, almost in line with the inner end of 2P but not reaching as far across the glabella. 4P is of similar form to 3P, but is directed in the opposite direction and is placed more laterally on the frontal lobe of the glabella, opposite its anterolateral corner. On the mid line the front of the glabella is minutely indented, and running backwards from this indentation on to the frontal lobe there is a short, shallow furrow. Occipital furrow curves backwards for its lateral one third, this part of the furrow being sinuous, while the middle part is horizontal, broader and shallower. There are indications of this horizontal part continuing laterally on to the occipital ring as a faint furrow. Occipital ring widest laterally, with a faint median node. The glabellar lobes are not inflated; due to the opposing curves of the occipital furrow and glabellar furrow 1P, glabellar lobe 1P is wider (exsag.) than 2P. Axial and preglabellar furrows deep, the former deepened and widened at the anterolateral corners of the glabella to produce a pair of apodemes.

Fixed cheeks slope downwards and outwards both in front of, and behind the eyes, the preocular part being continuous with the preglabellar field. Posterior limit of palpebral lobe opposite a point behind the lateral part of the occipital furrow, anterior limit opposite glabellar furrow 2P. The palpebral lobe is geniculate, the anterior end closer to the glabella, which it almost touches, with a broad rim, at its mid point of almost the same width (trans.)

as the adjacent part of the fixed cheek. The palpebral furrow is well defined, shallower medially, its posterior one third subparallel to the sagittal line, the anterior part deflected adaxially at a low angle, corresponding with the inward bend of the palpebral lobe. Postocular fixed cheek narrow (exsag.) strip-like, of width (trans.) 0.7 that of occipital ring. Posterior border furrow shallower than axial furrows, straight, except adaxially where it curves posteriorly to meet axial furrow at the posterior margin. Posterior border flat, and broad. Preglabellar field widest (exsag.) laterally; it is wider also on the mid line than in front of the lateral part of the glabella. It slopes steeply downwards to the anterior border, and is inflated slightly in front of the preglabellar furrow. This inflated part is bounded anteriorly by a shallow furrow which runs parallel to the anterior border. In front of this furrow the preglabellar field slopes more gently. The anterior border is of about one quarter the width of the preglabellar field, its inner half horizonal, the outer half downsloping, bowed upwards on mid line. The shallow anterior border furrow has 35–40 fairly evenly spaced pits along its length. Similar pits are visible in some specimens in the preglabellar furrow. The external surface of the cranidium, and the rest of the surface of the dorsal exoskeleton, is covered with minute granules. Caeca are prominent on the preglabellar field, especially anterior to the shallow mid-preglabellar furrow; they run forward between the anterior pits, dying out on the anterior border. Facial sutures marginal, or nearly so, in front of the anterior border, highly divergent (60–80 degrees) to the sagittal line in front of the palpebral lobes, curving adaxially near the anterior border. Behind the palpebral lobes the sutures swing out almost at right angles to the sagittal line, running backwards at a low angle until curving sharply posteriorly at their distal ends to cut the posterior border at a high angle.

Free cheeks broad, united as a single piece by narrow ventral doublure. Posterior border does not curve forward to the genal angle. Lateral border continuous with the anterior border and of similar form, continued into a long, outward-curved blade-like genal spine. Genal caeca are prominent. One caecum, which is more prominent than those arranged more or less radially to the eye, runs transversely across the cheek from the centre of the eye to meet the marginal rim between the lateral border of the cheek and the doublure well in front of the genal angle. Eye lenses not preserved. The ventral doublure curves upwards beneath the anterior border, where it flattens out and bears a row of small nodes which are believed to have connected ventro-dorsally with the pits in the anterior border. Such a structure is characteristic of the balnibarbiinids as a whole. A reconstruction of this border is given in Fig. 4C. It resembles a very narrow trinucleid fringe. The tips of the ventral nodes have minute perforations.

Hypostoma with very large middle body surrounded by narrow lateral and posterior borders. The middle body is elliptical in outline, inflated, especially towards its anterior margin. Deep, short middle furrows commence at 0.4 hypostomal length and run backwards on to the middle body almost parallel with sagittal line, cutting off a short ridge from the middle body between the middle furrows and lateral border furrows. Lateral borders steep, converging

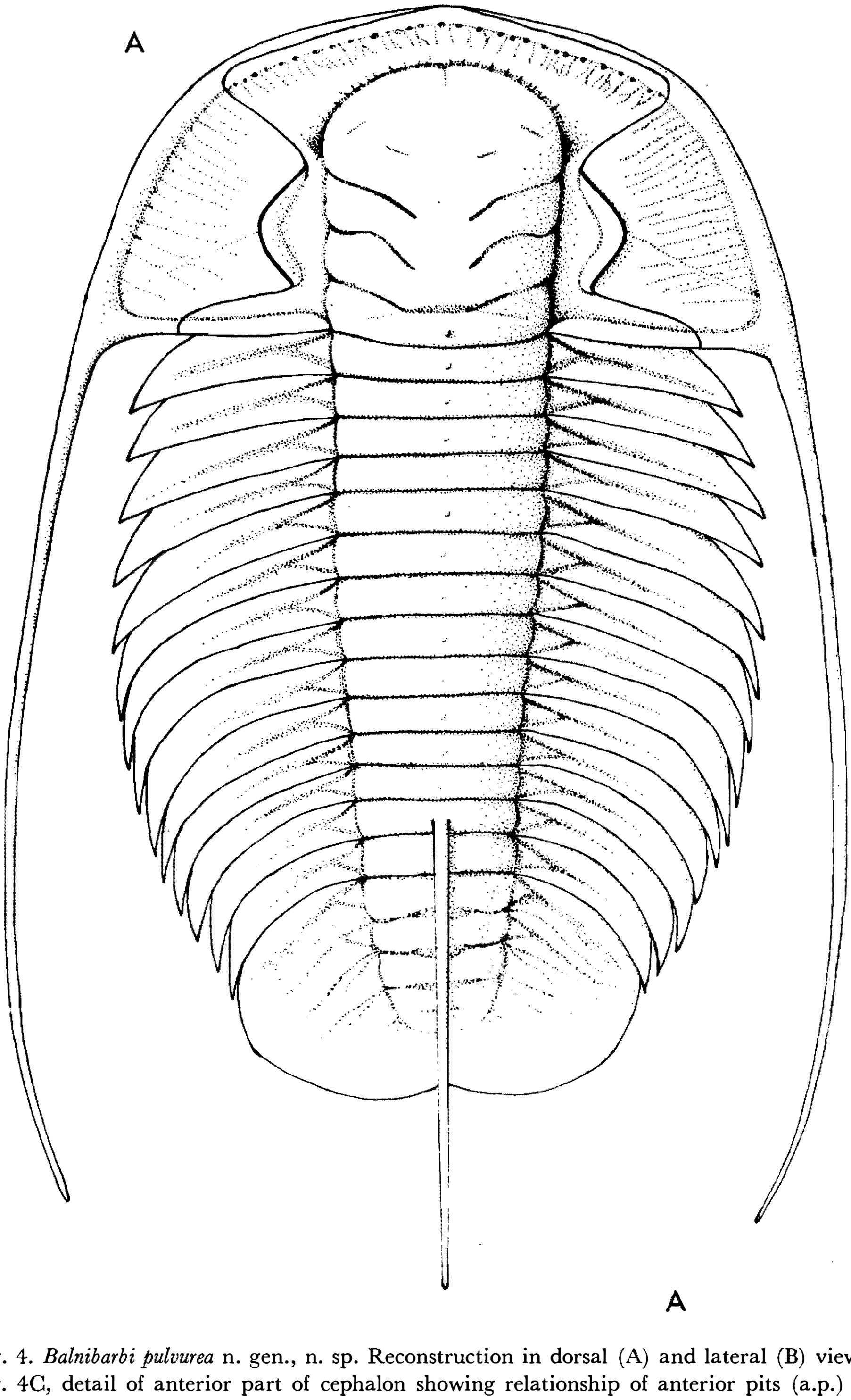
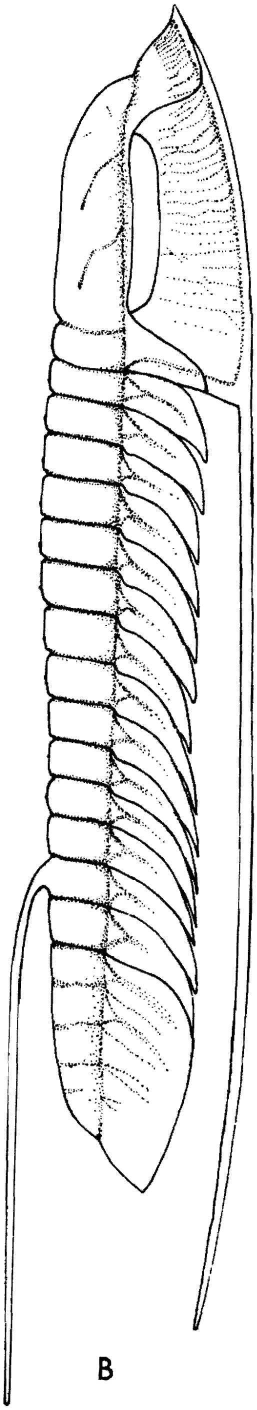


Fig. 4. *Balnibarbi pulvurea* n. gen., n. sp. Reconstruction in dorsal (A) and lateral (B) views. Fig. 4C, detail of anterior part of cephalon showing relationship of anterior pits (a.p.) in preglabellar furrow to nodes (v.n.) on doublure. Fig. 4D, Hypothetical reconstruction of partly enrolled *B. pulvurea* showing disposition of genal and thoracic spines.



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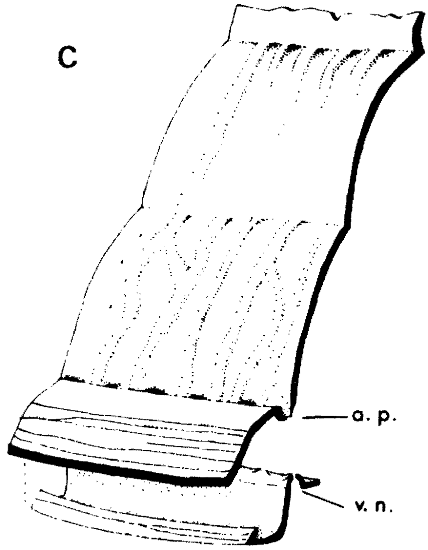

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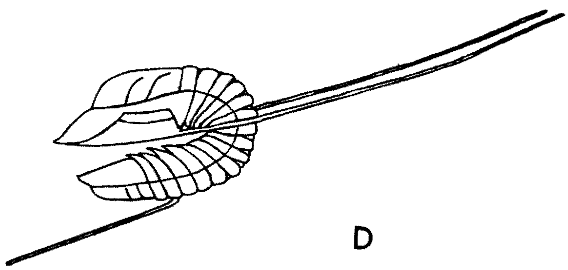


D

backwards, coming to a point posteriorly. Low, narrow posterior border wider on mid line. The pointed tips of the lateral borders and a median expansion of the posterior border give the posterior outline of the hypostoma a three pointed appearance. Anterior margin bowed forwards on mid line. Anterior wings broad, steeply sloping. Large elliptical (long axis sag.) maculae are present on the sides (on internal moulds) of the middle body (Pl. 1, Fig. 7), the surfaces of which are covered with closely spaced pits.

Thorax of 14 segments, of subequal width anteriorly, the last four segments tapering slightly to the pygidium. Axis moderately convex, occupying more than one third the width of the thorax, tapering slightly posteriorly, outlined by deep axial furrows. Inter-ring furrows deep and straight. Each axial ring bears a small median tubercle except the penultimate one which has a long blade-like median spine which extends well beyond the back margin of the pygidium. Each axial ring has a crescentic articulating half ring half the width (sag.) of the axial ring. Thoracic pleurae pointed, their anterolateral margins directed backwards, particularly on more posterior segments. Pleural furrows directed obliquely backwards from ring furrow almost to tips of pleurae, where they are faint. Near the axial end of each pleural furrow there is a conspicuous branch furrow, inward-posteriorly directed, which meets the axial furrow opposite the mid point of the axial ring. This furrow, together with the proximal part of the pleural furrow and the axial furrow, outlines a prominent triangular, adaxial *pleural node*, which is moderately inflated, in shape an isosceles triangle with a laterally pointing acute angle of 30 degrees. This pleural node is a diagnostic feature of the Balnibarbiinae and has been observed on all thoracic segments associated with both *Balnibarbi* and *Cloacaspis* species. The articulation is close to the axis and consists of elevated bosses on the anterior margin of each pleura, with corresponding sockets in the posterior margin of the preceeding thoracic segment, or most anteriorly, the posterior border of the cephalon.

Pygidium broadly oval in outline twice as wide (trans.) as long, with convex axis and downward sloping pleural fields. Axis occupies 0.35 pygidial width at anterior margin, tapering very gently posteriorly at 25 degrees, occupying 0.8 the length of the pygidium. Axial rings four, of decreasing width (sag.) posteriorly, with rounded terminal piece one sixth the length of the axis. Ring furrows deeper laterally, their median one third being much wider and shallower. The axial rings are narrower (sag.) adjacent to this median part of the ring furrows. Axial furrows well defined anteriorly, less so posteriorly. Pleural fields almost horizontal adaxially, sloping downwards laterally, with 3 distinct pairs of pleural and inter-pleural furrows not reaching posterior border, and slightly inflated pleural bands, which slope backwards at a low angle. The pleural furrows are broad, interpleural furrows shallower. Adjacent to the first two axial rings there are triangular pleural nodes indentical to those developed on the thorax. The posterior border is slightly concave, narrower on the mid line, where it is upward-arched. Anterior border rounded, sloping backwards at 60 degrees to sagittal line, with broad, triangular down-sloping articulating facet anteriorly. Arcuate articulating half ring of half the width of the first axial ring (sag.) Doublure broad, fully half the width of the pleural fields, closely reclined beneath the dorsal surface, narrowing behind the axis. The doublure has a surface sculpture of very closely set terrace lines which are subparallel to the posterior border.

Very small cranidia (Pl. 1, Fig. 8) strongly resemble those of *Cloacaspis senilis* n. sp. the ontogeny of which is fully described below.

Discussion. — *Balnibarbi pulvurea* n. gen., n. sp. is characterised especially by its pointed anterior border, posteriorly positioned eyes (with broad, geniculate palpebral rims) and narrow (exsag.) fixed cheeks, and very large pygidium with two pairs of adaxial pleural nodes. The granulate surface sculpture is also characteristic; it was probably derived from that of *B. ceryx* by spreading over the whole surface of the exoskeleton. On the front part of the glabella the granules show a tendency to amalgamate to form low transverse ridges. This tendency is carried further in the closely related succeeding species, *B. tholia* n. gen., n. sp. on which such ridges are extremely prominent, both on the front of the glabella and the preglabellar field. *Balnibarbi ceryx — pulvurea — tholia* thus form a sculptural series consistent with their phylogenetic relationships deduced from gross morphological criteria. There is evidence also from the *Cloacaspis* species described below that sculptural details may be of considerable importance in deducing phyletic relationships.

The anterior pits in this species, and in the other Balnibarbiinae, do not continue into the anterolateral border furrow of the free cheek. It seems reasonable to conclude from this that their function is related particularly to their position in the anterior border of the cranidium. It is in this region that the narrow ventral doublure is developed, and also the preglabellar part of the sutures at, or immediately above the anterior margin, that is, it represents a point of weakness in the exoskeleton. The nodes developed on the upper surface of the ventral doublure seen in *B. pulvurea* n. gen., n. sp., *B. erugata* n. gen., n. sp., and *Cloacaspis dejecta* n. gen., n. sp. are extremely likely to connect ventrodorsally with the pits in the anterior border furrow. It seems therefore that the primary function of the pits is simply that of strengthening the anterior border region of the cephalon by a series of rod-like struts through the anterior border.

No enrolled specimens of this or other Balnibarbiinid species have been found, but with their well developed articulation and articulating half rings it is extremely probable that they were able to do so. A hypothetical reconstruction of the partially enrolled exoskeleton (Fig. 4d) enables some light to be thrown on the function of the axial thoracic spine and genal spines. During enrollment the axial spine would become directed at an angle from the sphere of enrollment, with the extremely long genal spines at a different angle. Such an attitude of spines renders the effective diameter of the enrolled trilobite much larger than if no spines were developed. This may well have acted as a protection against relatively small potential predators. (The modern Puffer Fish ingests water when threatened to inflate to several times its normal size, the inflation causing protective spines to stick out at a steep angle.) The thoracic spine may also have functioned as a "turning over" device like the telsonic spine of the recent *Limulus.*

Among the many specimens of *Balnibarbi* and *Cloacaspis* species no evidence of a rostral plate has been found, and it is overwhelmingly probable that it was not developed among these olenids. A similar conclusion has been reached for other members of the family (HENNINGSMOEN 1957). Among *Balnibarbi* species the hypostoma, if ventrally below the glabella as in many other known trilobites, could not possibly have articulated with the ventral doublure connecting the free cheeks as the preglabellar width is far too great. It is certain therefore that it was separated from the anterior doublure, and supported partially at least by the ventral membrane. The anterolateral deepening of the axial furrow corresponds with an apodeme on the internal surface. These structures were probably attached to the anterior wings of the hypostoma, which would then be brought beneath the glabella into the "normal" position, though it is not possible to deduce its attitude relative to the glabella. The antero-median furrow of the glabella (cf. *B. pulvurea* n. gen., n. sp. and *B. tholia* n. gen., n. sp.) or the corresponding median indentation on other balnibarbiinids (or median smooth line on *Cloacaspis senilis* n. gen., n. sp.) may have been connected with musculature for the support of the anterior edge of the hypostoma.

Balnibarbi ceryx ceryx n. gen., n. sp., n. subsp.

(Pl. 8, Figs. 1—6; Pl. 9, Figs. 1, 3, 4.)

Stratigraphic range. — Olenidsletta Member, lower part 7–20 m from base (zone of *T. fruticosus* 3-branch).

Material. — Holotype, cranidium, SMA 84034. Other material includes cranidia: SMA 84037–40, PMO NF 558, 549, 567, 2074, 3033; free cheeks: SMA 84035; pygidium: SMA 84036; incomplete dorsal exoskeleton: PMO NF 2067, 1875, 551, SMA 84033.

Diagnosis. — A *Balnibarbi* species with pygidium of moderate size with three axial rings. Preglabellar field of less width (sag., exsag.) than other species of the genus; anterior border comes to a point on mid line. Posterior border curves forward to long genal spine. Surface sculpture of scattered granules on anterior part of preglabellar field.

Description. — Cephalon semicircular, sloping away anteriorly and laterally from gently convex glabella. Glabella subrectangular, almost parallel sided, expanding very slightly in front of the occipital ring in some specimens, gently rounded anteriorly, with a minute anterior median indentation in its outline. Four glabellar furrows, of which 1P and 2P are well defined, 3P and 4P shallow elongate pits which may not be visible on badly crushed specimens. 1P and 2P are defined for over one third the glabellar width and for the inner half of their course they are deepened and slope posteriorly at an angle of 60–70 degrees to the sagittal line, 1P the more noticeably backward directed. Abaxially, they curve to become almost transverse and are much shallower. Just before meeting the axial furrow they are deflected sharply anteriorly and considerably deepened. On crushed specimens some of these details may be obscured: 1P retains a conspicuous median kink while 2P may appear almost straight. 3P is a short elongate pit in line with the inner ends of 1P and 2P; 4P is similar in size and shape to 3P, placed in a more lateral position on the frontal lobe of the glabella, and sloping in the opposite direction to 3P. Occipital furrow sloping gently backwards laterally, horizontal, and slightly wider, towards midline. Occipital ring widest near axial furrow, with an elongate (sag.) median node. Glabellar lobe 1P longer (exsag.) than 2P due to the fact that furrow 1P and the lateral part of the occipital furrow curve in opposite directions. Axial and preglabellar furrows well defined, deepened at the anterolateral corners of the glabella.

Fixed cheeks sloping gently downwards except inside palpebral lobes. Palpebral lobe large, posterior limit close to the glabella opposite a point half way between furrow 1P and the occipital furrow, and curving inwards and forwards to anterior end which almost, but not quite, touches the glabella, half way between furrow 2P and the front of the glabella. The palpebral rims are broad, outlined by a distinct furrow, which is parallel to the axis posteriorly, bent inwards at about 20 degrees anteriorly. Postocular fixed cheeks fairly narrow (exsag.), triangular, bounded by a deep posterior border furrow which is parallel to the posterior border except adaxially where it curves backwards to meet the axial furrow near its posterior extremity. Posterior border elevated to form an articulating socket close to the occipital ring. Preglabellar field widest medially and anterolaterally, inflated slightly in front of glabella, then sloping down rather steeply to a broad depression parallel to the anterior border. Anterior border furrow not deeply impressed, containing 34–42 closely spaced distinct pits. These are not arranged strictly in one line; a few pits may form a second row posterior to the main one. Rather flat anterior border (about one third the width of the preglabellar field exsag.) comes to a point on mid line. Surface sculpture on anterior border of parallel terrace lines. On the anterior, depressed part of the preglabellar field there are scattered, minute granules.

Facial sutures strongly divergent both behind and in front of the eyes: in front of the eyes they diverge at 55–60 degrees to the sagittal line in dorsal view curving round at their anterior extremities to meet marginally (or just supramarginally) on mid line. They cut the posterior border at an acute angle.

The free cheeks are broad, sloping downwards from the eye. Eye lenses not preserved, eye presumably crescentic. Posterior and anterolateral borders continuous with those on the cranidium, very gently convex. Posterior border curves forward to obtuse genal angle, which is produced into a very long bladelike genal spine which exceeds the length of the rest of the dorsal exoskeleton, and which is continuous with the lateral border, curving outward in a gentle arc anteriorly, curving adaxially beyond the pygidium. The pits of the anterior border furrow are not continued on the free cheek. Faint genal caeca are developed which radiate from the eye region. Free cheeks united as a single piece by narrow ventral doublure, a fuller description of which is given for another species (p. 23).

Pygidium twice as wide as long, with three axial rings, pleural areas wider than anterior part of the axis (trans.). Axis fairly convex, tapering at about 30 degrees to almost reach the posterior border, rounded posteriorly. Ring furrows well defined, their median one-third slightly broader. Axial rings decrease in width (sag.) posteriorly. Terminal piece convex, small, rounded posteriorly. Pleural fields slope down from the axis; adjacent to the first axial ring a pleural node is developed, comparable to, although smaller than, those on the thoracic pleurae. A very faint second node can be seen in some examples opposite the second axial ring. Both pleural and inter-pleural furrows are well defined, curving gently backwards and dying out just before reaching the posterior border. From the third (posterior) ring furrow only the inter-pleural furrow continues on to the pleural field. The posterior border is arched up on the mid line, so that the pygidium narrows postaxially. The anterior margin of the pygidium is bounded by a downsloping, broad (trans.) articulating facet. There are faint indications of caeca near the posterior border of some specimens.

Discussion. — This species, the second earliest balnibarbiinid, is abundant in the lower part of the Valhallfonna Formation, a stratigraphic position which supports the evolutionary conclusions outlined above. It is distinguished from *B. erugata* n. gen., n. sp. by its relatively narrower pre-glabellar field, its narrower pointed anterior border with conspicuous pits in the anterior border furrow, its more anteriorly placed eyes and hence wider (exsag.) postocular cheeks, and by its surface sculpture. It is distinguished from *B. pulvurea* n. gen., n. sp. principally by its narrower preglabellar field, more anteriorly positioned eyes, different surface sculpture, and by its smaller pygidium with only three axial rings. A particular form of *B. ceryx*, distinguished here as a subspecies *B. ceryx anataphra*, is discussed below.

Balnibarbi ceryx anataphra n. gen., n. sp., n. subsp.

(Pl. 9, Figs. 5—7)

Stratigraphic range. — This subspecies has been identified at only one horizon, in a bed of black stinkstone 8–8.2 m from the base of the Valhallfonna Formation at the type section.

Material. — Holotype: cranidium PMO NF 651; cranidia: PMO NF 638, 641, 643; free cheek, PMO NF 642.

Diagnosis. — A subspecies of *Balnibarbi ceryx* with pits not developed in the anterior border furrow, external surface smooth, and preglabellar field slightly narrower than that of *B. ceryx ceryx*.

Discussion. — The specimens included in this subspecies are so closely similar to those of *B. ceryx ceryx* that the erection of a separate species for their inclusion does not seem to be justified. They have been found only in one bed, but within that bed all specimens have the characters of *B. ceryx anataphra*, none those of *B. ceryx ceryx*. The smooth anterior border furrow and lack of sculpture is similar to *B. sombrero* and *B. erugata*, although in most other features *B. ceryx anataphra* is easily distinguished from these species. It is possible that effacement of pits may have been a phenotypic variation induced by some short-lived environmental change affecting a whole population of *B. ceryx ceryx*. The discreteness of the population, however, probably justifies its taxonomic recognition. The sagittal width of the preglabellar field (plus anterior border) is less than 0.2 the length of the glabella in this subspecies, compared with a ratio of 0.25–0.3 in *B. ceryx ceryx*. The width of the preglabellar field is similar to that of the earliest species of *Cloacaspis* n. gen. to occur in the Valhallfonna Formation, *C. dejecta* n. gen., n. sp.

Balnibarbi erugata n. gen., n. sp.

(Pl. 5, Figs. 1—10)

Stratigraphic range. — Olenidsletta Member 39m to 79m from base.

Material. — Holotype, cranidium, PMO NF 3016. Among abundant other material are cranidia: PMO NF 679, 695, 733, 772, 817, 1697, 1688, 2072, 2873, SMA 84042–5, 84048; free cheeks: PMO NF 843, 866, 683, SMA 84046–7; pygidia: PMO NF 715, 848, SMA 84049; hypostoma: PMO NF 2874.

Diagnosis. — A *Balnibarbi* species with a moderately large pygidium with 4 axial rings. Glabella rounded anteriorly. Preglabellar field broad, anterior border furrow lacking distinct pits. Wide anterior border rounded on mid line. Palpebral lobes commence at a point just posterior to occipital furrow, limiting a very narrow postocular fixed cheek. External surface smooth.

Description. — Cephalon semicircular, of low convexity. Glabella subparallel sided, broadly rounded anteriorly, with a distinct anteromedian indentation in its outline. Glabellar furrows of the same general form as *B. ceryx* n. sp. 2P curves posteriorly at its inner end to a lesser degree than 1P. 3P is an elongate pit parallel to the inner end of 2P; 4P is fainter, placed laterally to 3P and sloping in the opposite direction, the single subtended between these two furrows being about 30 degrees. At the anterolateral corner of the glabella the axial furrow is deepened into a pit. The posterior limit of the palpebral lobe is behind the point where the occipital furrow meets the axial furrow; its anterior limit just behind the pit at the corner of the glabella. Palpebral lobe gently curved, rather than geniculate as in *B. pulvurea*, outlined by a well-defined arcuate palpebral furrow. An eye ridge may be present as an obscure bulge passing from the anterior limit of the palpebral lobe to the axial furrow. Postocular fixed cheeks narrow (sag.), strip-like. Facial sutures diverge in front of eyes at an angle of about 80 degrees, behind the eyes initially at nearly 90 degrees to sagittal line, curving backwards towards their distal ends to cut the posterior border at a high acute angle. Preglabellar field widest anterolaterally, of almost uniform width (sag., exsag.) in front of the glabella. Anterior border furrow shallow with only faint indications of pits on the external surface, appearing as faint indentations in the anterior border. Anterior border flat, slightly wider on the mid line. Caeca can be seen as corrugations in the external surface, especially in front of the preglabellar furrow and in the anterior border furrow. External surface smooth, except on the anterior border, which bears a parallel series of terrace lines.

Free cheeks with long genal spines, similar to those of *B. ceryx*, except that the posterior border does not curve forward to the genal spine. The narrow (trans.) ventral doublure connecting the free cheeks bears about 30 distinct nodes, which are thought to connect dorsoventrally with the rather faint depressions in the anterior border furrow. The tip of each node is perforated (Pl. 5, Fig. 10). Between the nodes caeca are visible as irregular depressions, which in conjunction with the convex caecae visible on the dorsal surface formed a narrow tube passing between the nodes on the doublure into the anterior border region. The structures are reminiscent of a harpid or trinucleid fringe on a small scale.

Pygidium with a fourth axial ring defined posteriorly by a short furrow, relatively larger and longer than that of *B. ceryx*, but otherwise similar. The posterior margin is less markedly indented on the mid line.

Thoracic segments associated on the same bedding planes as cranidia and pygidia and free cheeks of this species are of typical balnibarbiinid type. One thoracic segment has the long, blade-like axial spine comparable to that on the penultimate segment of *B. ceryx*.

Discussion. — This species is easily distinguished from *Balnibarbi pulvurea* by the rounded anterior margin of the cranidium and glabella without distinct pits in the border furrow, by its gently curved palpebral lobes, and lack of surface sculpture. The difference from *B. sombrero*, the only *Balnibarbi* species which resembles it, are discussed below.

Balnibarbi sombrero n. gen., n. sp.

(Pl. 6, Figs. 1—4)

Stratigraphic range. — Olenidsletta Member, 15m to 35m from base.

Material. — Holotype, cranidium, PMO NF 835. Other material consists of cranidia: PMO 2054, 2383, SMA 84041, 84354.

Diagnosis. — A *Balnibarbi* species with the preglabellar field greatly developed. Anterior margin of glabella and anterior border rounded medially.

Facial sutures diverge at an extremely high angle to the sagittal line in front of the eyes (up to 80 degrees). External surface smooth.

Description. — Cranidia only can be assigned to this species. Glabella similar in form to that of *B. erugata.* Occipital furrow curving backwards laterally, where it is slightly sinuous, horizontal medially, where the occipital ring is narrowest. Preglabellar field very wide (sag., trans.), greatly expanded laterally, of relatively even width in front of glabella. Anterior border furrow without distinct pits. Anterior border flat, very slightly wider on mid line, rounded medially. Postocular fixed cheeks narrow (exsag.), long and strap-like, similar to those of *B. erugata.* External surface smooth, except for parallel terrace lines on the anterior border.

Discussion. — This species occurs as a rare associate of *B. ceryx* and only the cranidia have been certainly identified. It is clearly very close to *B. erugata* with which it shares most distinctive features, including the rounded anterior border and glabella, lack of distinct pits in the anterior border furrow and smooth exoskeleton. However the great development of the preglabellar field serves to distinguish this species from specimens of *B. erugata* in which the glabellar size is similar. *Balnibarbi scimitar* has a similar rounded glabella and anterior border, and similarly highly divergent preocular branches of the facial suture, but is immediately distinguished by its strongly caecate preglabellar field and pitted anterior border furrow and wider (exsag.) postocular cheeks.
Stratigraphic occurrence and morphology of this species suggests that it is the intermediate species on the evolutionary series *scimitar* — *sombrero* — *erugata*, as has been discussed above.

Balnibarbi scimitar n. gen., n. sp.

(Pl. 6, Fig. 5; Pl. 7, Figs. 1—10; Pl. 9, Fig. 2)

Stratigraphic range. — This species has only been found in the lowest part of the Olenidsletta Member, in one bed not more than 6m from the base of the Valhallfonna Formation in melt stream D on Olenidsletta.

Material. — Holotype, cranidium PMO NF 17. Other material: cranidia, PMO NF 21, 2071, 2768, 2785, 2999; free cheeks, PMO NF 13, 14, 2779; 2 pygidia: PMO NF 3032, 3045; hypostoma PMO NF 3044; thorax PMO NF 3031.

Diagnosis. — A *Balnibarbi* species with broad, strongly caecate preglabellar field, rounded towards mid line, steeply sloping posteriorly but flat anteriorly. Border furrow minutely pitted. Palpebral lobes narrow, gently curved, posterior limits anterior to occipital furrow. Glabella with broadly rounded anterior margin. Posterior border of free cheek curves forwards to genal angle. Pygidium probably relatively small. Dorsal surface of exoskeleton lacking surface sculpture.

Description. — The glabella of this species is parallel sided, with an almost semicircular anterior outline resembling that of *B. erugata* most closely, but transversely more convex. Glabella furrows similar to those of *B. erugata*, 3P and 4P very short. The posterior half of the preglabellar field slopes downwards to a lesser degree than the frontal lobe of the glabella, but anteriorly sharply flattens out to become horizontal or almost so, the distinct line along which this change of slope takes place being subparallel to the front margin of the glabella. The preglabellar field has a width of about 0.3 that of the length of the glabella on the sagittal line (measured on uncrushed specimens in dorsal view), and widens quite rapidly exsagittally. It is strongly caecate. Within the shallow anterior border furrow there are small pits, on some specimens less distinct than those of *B. ceryx* or *B. pulvurea*, and numbering 30–35 on available material. Anterior border narrow and flat. Anterior margin of cranidium evenly rounded about the mid line, although smaller specimens (glabellar length 0.5 cm or less) may have an almost pointed anterior margin more like that of larger specimens of *B. ceryx*. Palpebral lobes narrow, with a gently curved outline, and posterior limits in front of the occipital furrow where it meets the axial furrows. Facial sutures diverge at 80–90 degrees in front of the palpebral lobes, anteriorly curving gently and quite uniformly adaxially to pass in front of the anterior border. Behind the palpebral lobes the sutures diverge at a similar high angle, but this angle decreases posteriorly, the sutures cutting the posterior margin to form an acute angle of about 60 degrees, and outlining triangular posterior cheeks.

Free cheeks narrower (trans.) than other *Balnibarbi* species, and strongly caecate. Posterior border curves very gently forwards to the genal angle to subtend an angle of almost 90 degrees with the genal spine. Note particularly the strongly developed genal vein (Pl. 7, Fig. 2), which crosses the cheek almost transversely at a quite different angle from the forward-running, finer genal caeca.

An incomplete thorax in full relief shows twelve thoracic segments of typical balnibarbiinid form. It is quite convex, the height approaching half the transverse width. Each axial ring bears a small median tubercle.

Pygidium was probably of similar relative size of that of *B. erugata*. Certainly there are no specimens to suggest the pygidium was as large as that of *B. pulvurea*. It is convex, with an axis with three axial rings and a terminal piece. Four pairs of pleural furrows, well defined, and three pairs of less distinctly defined interpleural furrows. A single pair of pleural nodes is present adjacent to the anterior axial ring. The depressed border is distinctly narrower and upward arched on the mid line. All parts of the dorsal exoskeleton lack surface sculpture.

Discussion. — This species is quite distinctive, perhaps being closest to *B. erugata* and *B. sombrero* in the shape of the glabella, anterior outline and form of the palpebral lobes. From both it is distinguished by its greater convexity, strongly caecate preglabellar field with pitted anterior border furrow, curved anterior branch of the facial suture, and by its more anteriorly situated palpebral lobes with correspondingly wider (exsag.) postocular cheeks. It has been pointed out above that there is a resemblance to *B. ceryx ceryx* in the position of the palpebral lobes, the form of the pygidium, and in the posterior border of the free cheek curving forward to the genal spine. *B. ceryx ceryx* is easily distinguished by its subrectangular glabella, straight anterior branches of the facial sutures, and in lacking the broad, flat anterior part of the preglabellar field characteristic of *B. scimitar*. The minute apodemal pits in the axial furrows opposite glabellar furrows 4P in *B. scimitar* are markedly less well developed than the corresponding features in *B. pulvurea*.

Balnibarbi tholia n. gen., n. sp.

(Pl. 4, Figs. 1—9)

Stratigraphic range. — Middle part of the Olenidsletta Member 76m to 90m from the base.

Material. — Holotype, cranidium, SMA 84024. Other material includes cranidia: SMA 84025, 84026, PMO NF 2818, 2825, 2828; pygidium SMA 84027; free cheek SMA 84028.

Diagnosis. — A *Balnibarbi* species with broad, convex preglabellar field, facial sutures moderately divergent in front of eyes, which are smaller than those of other *Balnibarbi* species. Surface sculpture with anastomosing ridges on anterior part of glabella and posterior part of preglabellar field, granulate elsewhere.

Discussion. — This species most closely resembles *B. pulvurea*, from which it differs in several details. The preglabellar field slopes down much more steeply compared with that species, and bulges out markedly in front of the glabella. The inner end of glabellar furrow 2P is directed backwards more strongly, so that it parallels the inner end of 1P closely. 3P, by contrast, is not backwards sloping, and is at right angles to sagittal line. The palpebral lobe is shorter than in other *Balnibarbi* species, its posterior limit opposite but not behind, the lateral end of the occipital furrow, the anterior limit opposite the outer end of glabellar furrow 2P. The preocular divergence of the facial sutures does not exceed 60 degrees. The surface sculpture is complex. Towards the front of the glabella there are fine, anastomosing raised lines, though the extreme anterior of the glabella is granulate. The anterior part of the preglabellar field, in front of the shallow median transverse furrow, is covered with a rather open network of raised lines; the anterior part is minutely granulate. The anterior border bears strong, subparallel striae. Other parts of the exoskeleton are granulate like *B. pulvurea*. Pygidium similar to that of *B. pulvurea*, but more convex.

Genus *Cloacaspis* n. gen.

Type species. — *Cloacaspis senilis* n. gen. n. sp.

Diagnosis. — Balnibarbiinid trilobites with facial sutures moderately divergent in front of eyes. Preglabellar field short. Glabella with four pairs of glabellar furrows of typical balnibarbiinid type; 3P and 4P tend to be longer than in *Balnibarbi* species, and 4P may not be visible on dorsal surface. Postocular fixed cheeks triangular. Posterior border of free cheek curves forward to long genal spine. Pygidium small, with two (or traces of a third) axial rings. Posterior border of pygidium may bear short spines.

Included species: *C. senilis* n. gen., n. sp., *C. dejecta* n. gen., n. sp., *C. ekphymosa* n. gen., n. sp.

Cloacaspis senilis n. gen. n. sp.

(Pl. 10, Figs 1—16; Pl. 11, Figs. 1—11, 13; Pl. 12, Fig. 7; Fig. 5)

Stratigraphic range. — Upper part of the Olenisletta Member, 120 to 145m (*Isograptus* Zone).

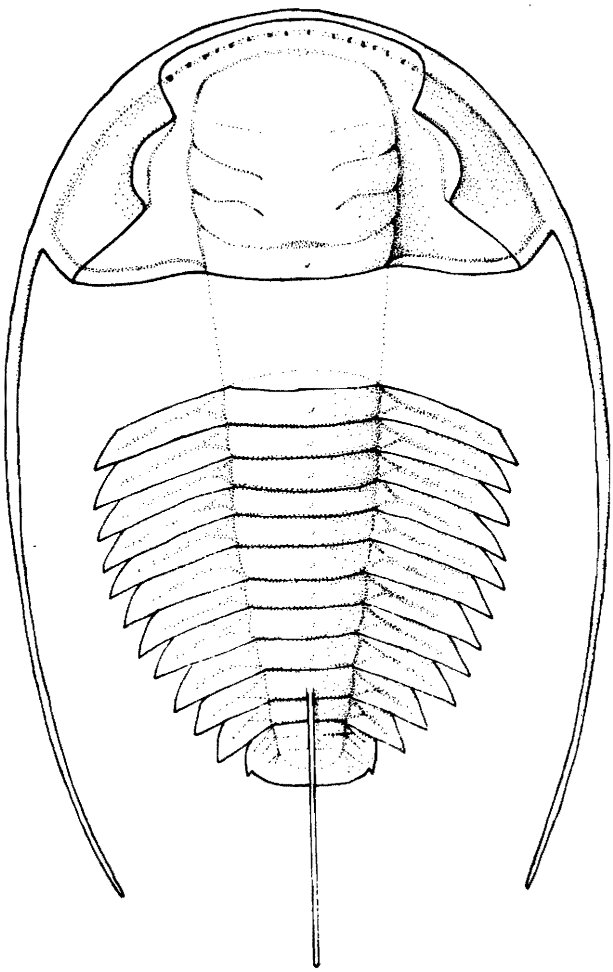
Material. — Holotype, cranidium, SMA 84050. Abundant further material includes cranidia: SMA 84051, 84053, 84056, 84058—63, PMO NF 1638–9, 1641, 1839, 1872, 2221, 2961, 2976; free cheeks: SMA 84055, PMO NF 1736, 1765; pygidia: SMA 84052, 84054; hypostoma: SMA 84064; incomplete thorax and pygidium: SMA 84057.

Diagnosis. — A *Cloacaspis* species having a short preglabellar field with about 20 pits in the anterior border furrow. Facial sutures diverge at about 20 degrees to the sagittal line in front of the eyes. Glabella with three pairs of glabellar furrows, the fourth pair visible as smooth patches on the dorsal surface and shallow pits on the internal mould. Surface sculpture of raised ridges on the preglabellar field, and in front of 2P on the glabella. Pygidium with two axial rings, and a pair of short spines on the posterior border.

Description. — Glabella barrel shaped, rather longer than wide, moderately convex (tr.) sloping down to preglabellar field in front of glabellar furrow 3P. Maximum width at a point opposite furrow 1P, anteriorly rounded.

Glabellar furrows extend to well over one third glabellar width. 1P and 2P are of typical balnibarbiinid form (similar to those of *Balnibarbi pulvurea*). 3P is an elongate pit, over half the length of 2P, sloping backwards at a low angle. 4P is apparent on the dorsal surface as a smooth area in the surface sculpture, on internal moulds as a faintly impressed furrow sloping in the opposite direction to 3P (angle between 3P and 4P about 15 degrees). A smooth median line runs backwards on to the frontal lobe of the glabella in the same position as the median furrow of *Balnibarbi pulvurea* and *B. tholia*. Occipital furrow is directed backwards laterally, horizontal and slightly wider for its

Fig. 5. Reconstruction of *Cloacaspis senilis* n. gen., n. sp. (× 3).



median one third. Occipital ring slightly wider towards the axial furrow, with an elongate (sag.) median tubercle near its posterior margin. Axial and preglabellar furrows well defined, deepened slightly at anterolateral corners of glabella. Preglabellar furrow indents the frontal lobe of the glabella on mid line. Postocular fixed cheeks form an acute triangle with lateral angle of about 30 degrees, steeply downsloping. Palpebral lobes large and close to the glabella, on mature individuals the posterior limit opposite a point just behind where the occipital furrow meets the axial furrow, sloping inwards anteriorly to almost touch the glabella to a point almost opposite glabellar furrow 3P. The distinct palpebral furrow is parallel to the axis for the posterior one third of its course, its anterior part deflected inwards at 20 degrees to the axial line. Narrow preglabellar field of almost uniform width except on mid line, where it is slightly wider due to the anteromedian indentation of the glabella. Shallow anterior border furrow with about 20 pits, which are irregularly distributed. Narrow, slightly convex anterior border of uniform width. Surface sculpture of anastomosing raised lines on the anterior border, preglabellar field, and the front of the glabella anterior to glabellar furrow 2P. Facial sutures diverge at about 80 degrees behind the palpebral lobes, cutting the posterior border at an acute angle, and diverge at 15–20 degrees in front of the palpebral lobes, anteriorly curving adaxially to run supramarginally along the front of the anterior border to meet at mid line.

Narrow free cheeks united as a single piece by narrow ventral doublure and very narrow (sag.) supramarginal band. The free cheek carries a raised ridge which follows the outline of the eye, especially prominent anteriorly. Posterior border curves forward to the genal angle making an acute angle of about 50 degrees with the genal spine. Posterior and lateral border furrows deep, meeting at an obtuse angle. Lateral border continuous with long, blade-like genal spines, which curve outwards anteriorly, adaxially distally.

No complete specimen is known. On an articulated thorax and pygidium (Pl. 10, Fig. 14) there are 11 segments but this specimen is small, and possibly incomplete. Each thoracic segment bears the pleural node typical of the subfamily. The pleurae of the first three segments known are narrow (trans.) and pointed. Articulating boss close to the axis, on a line with the acute angle of the pleural node. The axis tapers gently throughout its length. Each axial ring bears a median node similar to that on the occipital ring, except the penultimate axial ring which has a long median axial spine projecting far beyond the pygidial margin.

Pygidium twice as wide as long, with a convex axis standing above down-sloping pleural fields. Axis occupying half pygidial width, tapering posteriorly at a low angle and rounded posteriorly where it slopes down steeply to the posterior border. There are two axial rings and a rounded terminal piece (which is about one third axial length). The anterior ring furrow is complete, slightly wider and shallower medially on larger pygidia, the second an elongate pit dying out laterally. Pleural fields with two pairs of pleural furrows, which do not reach the posterior border, and one pair of interpleural furrows between them, sloping gently backwards. Adjacent to the first axial ring there is a small but distinct pleural node. The arcuate (trans.) posterior border is arched up considerably on the mid line, and bears a pair of short spines laterally, with an angulation adaxially on larger specimens. Surface sculpture of fine parallel lines on the pleural fields similar to that developed on the frontal lobe of the glabella.

Hypostoma is extremely like that of *Balnibarbi pulvurea* (p. 23), having the "three pointed" posterior margin and steep lateral borders of that species.

Flattening of cranidia of this species increases the slope of the inner parts of the glabellar furrows 1P and 2P, while the anterior glabellar furrows may either be obliterated or exaggerated. The fixed cheeks open outwards. The degree of flattening may also vary, but the characteristic surface sculpture is preserved on all but the most distorted specimens.

Ontogeny (Pl. 11, Figs. 1–11, Fig. 6): Small cranidia (about 2.4 mm long) retain a general similarity to those of the adult, but differ in most details. The glabellar furrows are deeper and narrower and furrow 4P becomes clearly visible. The palpebral lobes are relatively further forward, and the fixed cheeks relatively longer (exsag.) and narrow (trans.) so that the facial suture is almost straight, inwardly directed from posterior and anterior border. The occipital tubercle is more prominent. Remarkably, the surface sculpture is granulate (like *C. ekphymosa*). The smooth exoskeleton with ridges of the adult has not been seen on cranidia smaller than 3.5 mm long.

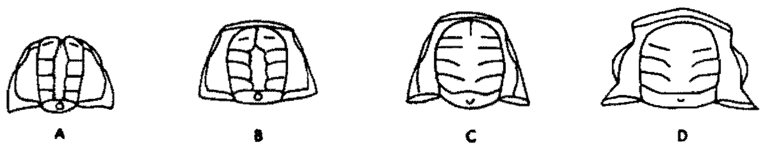


Fig. 6. Outline drawings of cranidia of *Cloacaspis senilis* n. gen., n. sp. showing ontogeny. A. Early meraspis (× 20). B. Very small cranidium (× 10) with inner ends of glabellar furrows, joined by subsidiary furrows. C. Small cranidium (× 8); remnant of sutural ridge present as a post-palpebral furrow. D. Small cranidium with adult proportions (× 4).

Smaller cranidia (1.6 mm long) show an increase in the length of the glabella relative to its width. The four glabellar furrows are regularly distributed along its length and differ considerably from those of the adult. 1P, 2P and 3P are of the same length, 1P and 2P parallel and directed backwards at an angle of about 25 degrees, 3P at right angles to sag. line. 4P remains as a distinct, elongate pit. A median furrow runs back from the front of the glabella as far as glabellar furrow 3P. The median smooth line of the adult cranidia is probably homologous to this furrow, which is also developed on the frontal lobes of *Balnibarbi pulvurea* and *B. tholia*. A sutural ridge is developed parallel to the postocular suture.

The overall convexity of the smallest cranidium (0.7 mm) is greater, and the maximum width is not at the posterior border but opposite glabellar lobe 2P. The glabella is forward expanding, almost twice as long and wide, and steeply downturned anteriorly, so that in dorsal view 4P is not visible. The glabellar lobes are inflated and joined at their inner ends by shallow furrows. Because of the anterior expansion of the glabella the first three furrows increase in length (trans.) anteriorly. The glabellar furrow 4P is an elongate pit, not as deep or distinct as the other three furrows, on the steeply sloping part of the frontal lobe. The glabellar lobes are progressively more inflated anteriorly. The mid line of the glabella is inflated slightly opposite glabellar lobes 1P and 2P, anterior to this it forms a median depression between the glabellar lobes and bisects the downturned frontal lobe as a V-shaped notch. The occipital ring is narrow (sag., trans.), convex. There is a narrow preglabellar field. Fixed cheeks horizontal near the axis, downsloping steeply laterally and anteriorly to a sharp break in slope at the posterior border and sutural ridge.

The posterior border and sutural ridge merge without a break, at the obtuse posterolateral angle there is a small fixigenal spine. The sutural ridge is bowed slightly outward near to the posterior border, subparallel to the sagittal line anteriorly. At a point opposite glabellar furrow 2P it is set off by a short furrow from the palpebral lobe, which continues in line with the sutural ridge, curving inwards to a point close to the outer end of glabellar furrow 3P. The palpebral furrow continues inwards to meet the axial furrow adjacent to glabellar lobe 4P.

The ontogenetic changes may be summarised as follows: (I) with increasing cranidial size a decrease in convexity; (II) a relative posterior migration of the glabellar furrows; (III) decrease in the prominence of glabellar furrows 3P and 4P. 3P especially is as well developed as 1P and 2P on small cranidia, becoming reduced to a pit late in ontogeny. 4P remains as a pit through all known early stages, on larger cranidia only visible as a smooth area on the frontal lobe; (IV) glabellar lobes lose their inflation, and the mid-glabellar depression is lost. The furrow bisecting the frontal lobe of small cranidia becomes reduced to a median smooth line on larger individuals; (V) backward migration of the eye relative to the glabellar furrows, corresponding with a lateral expansion of the postocular fixed cheeks. Palpebral lobe becomes more geniculate.

Discussion. — The changes in the relative position of the palpebral lobe during ontogeny and the development of the postocular fixed cheeks is comparable to that described by WHITWORTH (1970) for *Leptoplastus crassicornis*. The forward expanding meraspide glabella is not found in this latter species, nor in *Peltura scarabaeoides* (cf. WHITTINGTON 1958), but is characteristic of *Triarthrus* (cf. WHITTINGTON 1957, 1965, see also *T. papulosus* n. sp.). The median glabellar depression of the meraspid cranidium and lobal inflation is not known from other olenids, perhaps resembling *Paradoxides* in this respect (WESTERGÅRD 1931). In the very early cranidia of the above species, and also in *Hypermecaspis latigena* n. sp., *Olenus gibbosus* (cf. STRAND 1927), and *Balnibarbi pulvurea* n. gen., n. sp. (Pl. 1, Fig. 8) there are evidently three principal glabellar furrows. What is striking, however, are the morphological differences between early ontogenetic stages even within the single family Olenidae. This suggests that ontogenies are useful only in confirming relationships between closely related genera, for example within a single subfamily. The similarity of the earliest cranidia of *Cloacaspis senilis* n. gen., n. sp. and *Balnibarbi pulvurea* n. gen., n. sp. confirms their close relationship deduced from stratigraphic and morphological criteria. The Olenidae are a family with a long time range and wide distribution, and the differences between included genera (compare *Sphaerophthalmus*, *Hypermecaspis*, *Leiobienvillia*, *Balnibarbi*) are so marked that, were they not connected by well documented intermediates, they might well have been referred to different families. It seems unlikely that ontogenies separated in time, on separate evolutionary lines would be identical, indeed, they may be a valuable aid in unravelling the complex ways in which the different subfamilies were derived. It remains debatable whether the family Olenidae is "equivalent" to other trilobite families, or whether the existing subfamilies should be afforded familial status.

Relation between C. senilis *n. gen., n. sp. and* C. ekphymosa *n. gen., n. sp. and the sutural ridge of olenids.*

These two species range through the upper part of the Olenidsletta Member, *C. senilis* immediately following *C. ekphymosa* and their ranges not overlapping. Mature cranidia of *C. ekphymosa* are granulate (as well as having ridges on the frontal lobes of the glabella), and possess a well developed post-palpebral furrow (see diagnosis of *C. ekphymosa*) which crosses the postocular fixed cheek. Otherwise the cranidium is identical to that of larger *C. senilis*. As stated above (p. 39) immature cranidia of *C. senilis* are granulate, and furthermore have a post-palpebral furrow (Pl. 11, Fig. 8) which joins the posterior border furrow well inside the posterolateral angle. Thus the small cranidia of the later species have the diagnostic features of the species immediately preceeding it. There can be no doubt from this close morphological interrelationship and their stratigraphic occurrence that *C. ekphymosa* gave rise to *C. senilis*, the latter showing this partial 'recapitulation' in its ontogeny. Such 'recapitulation' is not perfect, however, for the postpalpebral furrow of *C. ekphymosa* is more geniculate than that of immature *C. senilis*. The pygidium of *C. ekphymosa* has a pair of posterior angulations which in *C. senilis* are further developed into short spines.

The post-palpebral furrows in *C. ekphymosa* and immature *C. senilis* are a later development of the furrow which outlines the sutural ridge on smaller cranidia, migration of this furrow inwards across the cheek occurring through ontogeny (Pl. 11, Figs. 5, 6). This provides another example of the persistence of this feature, which has already been remarked on *Triarthrus fischeri* (WHITTINGTON 1965) and also occurs on *T. papulosus* n. sp. (p. 70). It is probable that the "lateral borders" of *Porterfieldia* COOPER 1953 and *Triarthrus caecigenus* WHITTARD 1961 are other examples of the retention and modification of the sutural ridge. The presence of such a ridge at some early stage in the ontogeny is characteristic of all olenids the ontogeny of which is known to the author. WHITTINGTON (1957a) has apparently not drawn in the ridges on *Triarthrus eatoni* (ibid. Fig. 10c) although they are visible on his photographs of the same ontogenetic series (WHITTINGTON 1957b, Pl. 116, Fig. 4). It may be apparent as more ontogenies are known that the sutural ridge is of particular value as one of the defining characters of the Olenidae as a whole.

Cloacaspis ekphymosa n. gen., n. sp.

(Pl. 11, Figs. 12, 14—18)

Stratigraphic range. — Upper part of the Olenidsletta Member, 105m to 120m.

Material. — Holotype, cranidium, SMA 84075. Other material includes cranidia: SMA 84076 — 7, 84355 — 7; pygidium: SMA 84078.

Diagnosis. — A *Cloacaspis* species with short preglabellar field, pitted anterior border furrow; preocular sutures diverge at a fairly low angle (20 degrees).

Surface sculpture granulate, with ridges in addition on the frontal lobe of the glabella. Behind the palpebral lobe there is a furrow which crosses the postocular fixed cheeks from the palpebral lobe, joining the posterior border furrow inside the posterolateral angle of the cranidium (*post palpebral furrow*). Pygidium small, with two axial rings; posterior border lacking spines.

Discussion. — The relation of this species to *C. senilis* has already been discussed in the preceeding paragraphs. It is distinguished from that species by the granulate surface sculpture on larger cranidia, in the possession of a post-palpebral furrow, and in having the posterior margin of the pygidium not produced into spines. The narrow palpebral lobes are further forward than in *C. senilis*, the posterior limit in front of the occipital furrow. The post-palpebral furrow passes posteriorly from the back part of the palpebral furrow sub-parallel to the sagittal line, flexed adaxially for the posterior half of its course to meet the posterior border furrow (at 90 degrees) inside its lateral limit.

Cloacaspis dejecta n.gen., n. sp.

(Pl. 12, Figs. 1—6)

Stratigraphic range. — Lower part of the Olenidsletta Member 24m to 60m from base.

Material. — Holotype, cranidium, PMO NF 2058. Other material includes cranidia: PMO NF 819, 820, 826, 1841, 2070, 2802, 2976, SMA 84029, 84031; pygidia: PMO NF 3046, SMA 84032; free cheek: SMA 84030; dorsal exoskeleton lacking cranidium: PMO NF 1868 — 9; thorax : PMO NF 2069.

Diagnosis. — A *Cloacaspis* species with a preglabellar field of greater sagittal width than *C. senilis* or *C. ekphymosa*, facial sutures diverge at 40 — 45 degrees to sagittal line in front of the eyes. Preglabellar field consists of a posterior inflated part, anteriorly a broad depressed area. Surface sculpture of granules in glabella, axial and border furrows only. Pygidium small, with two axial rings and a third outlined by an incomplete inter-ring furrow, margin without spines.

Description. — All specimens of this species are slightly crushed, and its convexity cannot therefore be compared directly with that of *C. senilis*. Slightly crushed individuals of that species compare closely with those of *C. dejecta*, and it is probable that their convexities were similar. Glabellar subquadrate, slightly longer than wide, rounded anteriorly. Occipital and glabellar furrows of very similar form to those of *C. senilis*, the inner end of 2P hardly deflexed posteriorly. 3P and 4P are short pits similar to those of *Balnibarbi ceryx*; 4P may not be visible on the dorsal surface. Palpebral lobes have their posterior limit opposite a point halfway between the occipital furrow and glabellar furrow 1P, anterior limit opposite 3P. They are narrow (trans.) and but slightly flexed adaxially anteriorly. Postocular fixed cheek triangular, about 0.6 width of the occipital ring, laterally defined by the postocular suture which cuts the posterior border at an acute angle. Preocular divergence of the facial sutures is 40 — 45 degrees. Preglabellar field moderately narrow (sag., exsag.) but relatively wider than that of *C. senilis* (and *C. ekphymosa*). Immediately in front of the glabella there is narrow (sag.) inflated area parallel to the anterior border. Betewen this inflated band and the anterior border there is a wider depressed area. Anterior border furrow shallow with about 40 distinct pits. Flat anterior border half to two thirds the width of the preglabellar field, coming to a point on the mid line. Free cheeks similar to those of *C. senilis*, but slightly wider (trans.) than that species. The narrow doublure connecting the free cheeks bears small nodes of similar spacing to the pits in the anterior border; the structure of the anterior border is similar to that described for species of *Balnibarbi*. Beneath the lateral borders the doublure is sharply reflexed. Surface sculpture of minute granules on the preglabellar depressed area, and in the axial and glabellar furrows.

Thorax of 14 segments, each of which is of typical balnibarbiinid form, as described for *B. pulvurea*. The edges of each pleura are bounded by extremely narrow, convex rims that coalesce to form a minute spine of the tip of the pointed pleura.

Pygidium small, transversely elliptical in outline. Axis occupying more than one third pygidial width anteriorly, almost reaches the posterior border, tapers gently posteriorly, with two well defined axial rings and on the rounded terminal piece a faint elongate transverse pit incompletely outlining the reduced third axial ring. Pleural fields downsloping except adaxially, with three deep pairs of pleural furrows which slope backwards (at about 60 degrees to the sagittal line) parallel to the anterior border and three, much fainter pairs of interpleural furrows. Both pleural and interpleural furrows die out before reaching the posterior border, which lacks spines and narrows on the mid line, where it is arched slightly upwards.

Discussion. — This species is the morphological and stratigraphic intermediate between *Balnibarbi ceryx* and the later *Cloacaspis* species (p. 17). The granulation *in* the glabellar and axial furrows is unusual among trilobites, generally the furrows are smooth when the rest of the exoskeleton is covered with granules or ridges, as in *Balnibarbi pulvurea*, *B. tholia* and *Cloacaspis senilis*.

Apart from the surface sculpture, the markedly depressed area on the anterior part of the preglabellar field is a particularly characteristic feature distinguishing this species from *C. senilis* and *C. ekphymosa*.

Subfamily HYPERMECASPIDINAE Harrington and Leanza 1957

Following Henningsmoen (1959, p. 161) this group of trilobites is here regarded as a subfamily of the Olenidae, rather than as a separate family as proposed by Harrington and Leanza (1957, p. 120). The inclusion of the species described below into the subfamily requires some modification of the diagnosis given in the *Treatise* (Harrington in Moore, 1959, pp. 269 — 270).

Diagnosis. — Subisopygous (rarely micropygous) Olenidae with elliptical dorsal exoskeleton. Cephalon semicircular to subelliptical in outline, with opisthoparian sutures. Glabella tapering forward, anterior margin truncate or rounded, with four or five pairs of lateral glabellar furrows, 1P short, transverse, shallowing rapidly away from the axial furrows, inner ends of furrows 2P strongly backwards-sloping, 3P less strongly so. On large cranidia of some species the outer ends of furrows 2P and 3P are very shallow, so that the deepened inner ends appear "isolated" within the glabella. Occipital ring subdivided by transverse furrows, the most prominent of which isolate triangular lateral lobes. Palpebral lobes large, close to the glabella. Preglabellar field short to extremely broad. Facial sutures convergent or divergent in front of the palpebral lobes, posterior branches highly divergent, outlining narrow (exsag.) postocular fixed cheeks. Thorax (where known) of 19 segments, pleurae spinose. Pygidium with elliptical or fan-shaped outline, axis with three to eight axial rings, tapering, and continued posteriorly as a narrow ridge. Pygidial margin without spines. Pygidial pleural furrows well defined, curving backwards, and shallowing before reaching the posterior margin. Pygidial doublure broad.

Genus *Hypermecaspis* Harrington and Leanza 1957

Type species. — *Hypermecaspis inermis* Harrington and Leanza 1957 (by original designation).

Discussion. — Three species assigned to this genus occur in the Spitsbergen Arenigian. One of these, *H. brevifrons* n. sp., is very close to the type species of the genus. The other species differ in some ways from those previously assigned to the genus, notably in having a wide preglabellar field and divergent preocular sutures. Since they are similar in most other respects to other species of the genus, particularly with regard to glabellar segmentation and the form of the pygidium, they are retained in *Hypermecaspis*. One minor difference of glabellar segmentation between the Spitsbergen species and those described by Harrington and Leanza (1957) is that the Argentine species are stated to have five pairs of glabellar furrows, whereas the new species described herein have four. It will be noted that the anterior fourth and fifth pairs of glabellar furrows on *H. inermis* (Harrington and Leanza 1957, Fig. 46, 2,3) and *H. armata* (*ibid*. Fig. 48, 4) correspond almost exactly in position with the inner and outer ends of the fourth pair of furrows on *H. venulosa* n. sp. and *H. brevifrons* n. sp. The appearance of two pairs of furrows in the Argentinian material may be in part due to flattening. Whittington (1965, p. 336) has made a similar suggestion concerning *Hypermecaspis* cf. *bulmani* which has an anterior pair of glabellar furrows much like the Spitsbergen species.

Hypermecaspis latigena n. sp.

(Pl. 13, Figs. 1—9; Pl. 14, Fig. 10)

Stratigraphic range. — Upper part of the Olenidsletta Member 100 — 130 metres, corresponding to the earlier part of the *Isograptus* zone.

Material. — Holotype, cranidium PMO NF 3002. Other material includes cranidia: PMO NF 3001, 3047, 1134, 1139, 1640, SMA 84070 — 1, 84074, 84080; pygidia: PMO NF 1154, 1633; free cheek: PMO NF 3003; hypostomata: SMA 84079, PMO NF 1327.

Diagnosis. — A *Hypermecaspis* species of moderate convexity, with fairly wide preglabellar field (about 0.3 length of glabellar on the sagittal line) which slopes gently downwards anteriorly. Free cheeks very wide (trans.) bearing short genal spines.

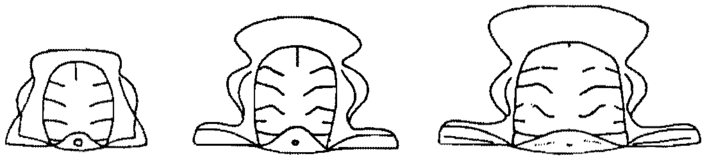
Description. — From the outline of the fused free cheeks, the cephalon of this species is three times as wide as long with a broadly arcuate anterior outline. The cranidium is moderately convex (sag., trans.), progressively less so on larger specimens. Glabella of width at the occipital ring about equal to its sagittal length; on small cranidia occipital width is less than glabellar length. Glabella is gently convex transversely, and its anterior one-third slopes downwards, with maximum width at the occipital ring, tapering evenly forwards so that its width across the anterolateral corners is 0.8 that at the occipital ring. The front margin of the glabella is gently rounded towards the mid line. Four pairs of glabellar furrows, 4P reaching the axial furrow almost at the anterolateral corner of the glabella. The distance between furrow 2P and 3P (exsag.) is greater than that between 1P and 2P and between 3P and 4P, while the distance between these pairs of furrows exceeds that between 1P and the occipital furrow. Thus adjacent to the axial furrow glabellar lobe 3P is the widest (exsag.), 1P is the shortest, while 4P and 2P are equal in width. Glabellar furrow 1P is the shortest (trans.), deep near the axial furrow and shallowing rapidly transversely, on no specimen reaching as far across the glabella as the other three furrows. These furrows are deflexed backwards and deepened at their inner ends, reaching across more than one third the width of the glabella, the backward deflection decreasing anteriorly, so that the inner half of 4P is hardly turned backwards, that of 2P strongly so, its mid part also being bowed forwards. On large cranidia, the outer part of glabellar furrows 2P to 4P are very faint so that the deepened, backward sloping inner ends appear to be almost isolated within the glabella. The outer end of the isolated part of furrow 2P also appears to bifurcate. There is evidently a line of "glabellar inflation" which effaces part of the glabellar furrows of larger cranidia and which runs parallel to the axial furrows. Such a condition pertains on the specimens of the type species and *H. inermis* (see Harrington and Leanza 1957, Fig. 48, 4). The narrow (sag., exsag.) frontal lobe of the glabella is bisected medially by a shallow furrow which runs backwards on the mid line as far as the inner ends of the glabellar furrows 4P; again on the large cranidia this furrow becomes faint. Lateral part of the occipital furrow shallow, curving gently backwards from the axial furrow. Median one half to one third of the occipital furrow transverse or curving gently forwards to the sagittal line. From this part of the occipital furrow a narrow furrow runs obliquely backwards and outwards across the occipital ring to meet the axial furrow at the posterior margin of the cranidium, outlining a slightly inflated lateral lobe on the occipital ring. On large cranidia two shallow furrows divide the mid part of the occipital ring transversely, the posterior of the two with the prominent occipital tubercle at its mid point. The occipital ring is slightly wider medially, of sagittal width about one fifth the length of the glabella. Axial and preglabellar furrows shallow, except for a slight deepening of the former at the anterolateral corners of the glabella to form a shallow pair of pits.

Preglabellar field and postocular cheeks downsloping, palpebral lobes horizontal. Postocular cheeks narrow (exsag.) and strap-like, of a transverse width slightly less than that of the occipital ring. Palpebral lobes of length half that of the glabella with a gently arcuate outline. The posterior limit of the palpebral lobe is close to the glabella opposite where the occipital furrow meets the axial furrow, anterior limit actually touches the glabella at the outer end of glabellar furrow 4P. The broad, crescentic palpebral rim is outlined by a shallow furrow. The preglabellar field continues the downward slope of the front of the glabella (at 20 — 30 degrees to the horizontal), extending to 0.3 glabellar length on the sagittal line, from which it widens abaxially. Caeca fairly prominent. Anterior border narrow, horizontal; shallow border furrow without pits. Front margin of cranidium gently rounded. A faintly impressed furrow which parallels the front margin of the glabella runs across the preglabellar field a short distance in front of the glabella; along the line of this furrow the caeca are generally more deeply impressed. Facial sutures diverge in front of the palpebral lobes; the degree of divergence is rather variable, measured examples falling in the range 30 — 50 degrees to the sagittal line.

The external surface of the cranidium is smooth, except for a few terrace lines on the anterior border parallel to the anterior margin of the cranidium. The exoskeleton is so thin that the differences between internal moulds and specimens retaining the exoskeleton are negligible.

Free cheeks very wide, gently sloping down from the eye region, on which the lenses are not preserved. Genal angles acute, and prolonged into short, pointed, slightly outward-directed genal spines. The lateral border of the cheek is wide, defined by a shallow furrow which is confluent with the posterior branch of the facial suture where it cuts the posterior margin, and runs inwards anteriorly parallel to the lateral margin of the cheek. This shallow furrow probably marks the extent of the ventral extension of the doublure, which is broad, and closely reflexed against the dorsal exoskeleton. The doublure carries fine terrace lines which are subparallel to the lateral margin of the cheek, sparely dichotomising, and like other species of the genus have the steep surface of the terrace facing posteriorly.

Hypostoma (Pl. 14, Fig. 10) generally similar to that of the balnibarbiinids, but more convex, with a large, greatly inflated oval middle body with only faint middle furrows. Surface sculpture of fine raised lines. The narrow (exsag., trans.) anterior wings have a pronounced downward slope. The middle body is irregularly corrugated posteriorly, where it slopes gently downwards to the three-lobed posterior border.



A B C

Fig. 7. Outline drawings of cranidia of *Hypermecaspis latigena* n. sp., showing ontogeny. A. Probable meraspis (× 10) at a stage before the appearance of the 1P glabellar furrow of the adult. B. Small cranidium (× 5). C. Mature cranidium, natural size.

Smallest cranidium (Pl. 13, Fig. 8) has the glabella longer than wide, broadly rounded anteriorly, with maximum transverse width at its mid-point. Three pairs of glabellar furrows which are shorter (trans.) than those of large cranidia, gently curved posteriorly. A prominent median furrow bisects the frontal lobe of the glabella. The occipital ring is conspicuously wider medially, and bears a prominent median tubercle. The occipital furrow curves forwards to the mid-line, but near where it meets the axial furrow there are indications of a short transverse furrow branching off the occipital furrow and outlining a small triangular area adjacent to the axial furrow. It is the adaxial migration of this furrow at later ontogenetic stages that produces the compound occipital ring of the adult (see Fig. 7). Fixed cheeks much narrower than on large cranidia, while the palpebral lobes are further forward. Behind the palpebral lobes there is a short sutural ridge. Note that the short glabellar furrow 1P of the adult is not present on this small cranidium. It is inserted between the occipital furrow and the first major posterior glabellar furrow at a later stage in the ontogeny.

Pygidium fan shaped in outline, transverse width exceeding sagittal length. Axis short, less than half the pygidial length, tapering at about 30 degrees and of decreasing convexity posteriorly. There are four axial rings and a short terminal piece, the axial rings of decreasing width (exsag.) posteriorly, and very gently convex. Ring furrows faint medially. Four pairs of relatively deep pleural furrows and three shallower pairs of interpleural furrows, which do not reach the posterior margin. Pleural furrows adaxially curve backwards at about 70 degrees to the sagittal line, more distally curving inwards to become subparallel to the sagittal line. Interpleural furrows do not curve backwards so strongly, or reach as far back. Anterior border of similar outline to first pleural furrow, gently convex, sloping downwards anteriorly into broad (trans.) ill-defined articulating facet. The postaxial ridge reaches the posterior margin of the pygidium, which has a broadly arcuate outline.

Discussion. — The broad, gently downsloping preglabellar field, very wide free cheek with its extremely wide, faintly defined lateral border, easily distinguish this species from all others of the genus.

Hypermecaspis brevifrons n. sp.

(Pl. 14, Figs. 1—9; Pl. 24, Fig. 9)

Stratigraphic range. — A single cranidium attributed to this species has been found at 95 m. All other material is from the top 15 m of the Olenidsletta member, and the lowest 6 m of the Profilbekken member.

Material. — Holotype, cranidium SMA 84072. Other material includes cranidia: SMA 84078, 84358, PMO NF 434; pygidia: SMA 84069, 84076, 84359; free cheeks: SMA 84077, 84073.

Diagnosis. — A *Hypermecaspis* species with a narrow preglabellar field steeply downturned in front of the glabella; anterior border also slopes downwards. Free cheeks broad, with genal spines. Pygidium convex, slightly wider than long, posterior margin very gently arcuate in outline.

Discussion. — This species agrees in most features with *H. latigena*, and a full description will not be given to avoid unnecessary repetition. *H. brevifrons* differs from *H. latigena* most obviously in having a short, steeply sloping preglabellar field. This slope is the downward continuation of that of the front part of the glabella, which is also steep in this species. All cranidial furrows are relatively deep compared with *H. latigena*, so that the glabella is distinctly defined, the glabellar furrows deep at their inner ends. The definition of the anterior border of the cranidium is, by contrast, indistinct, and in many specimens no border is visible, the slope of the preglabellar field continuing uniformly to the anterior margin of the cranidium. The stratigraphically earliest cranidium (Pl. 14, Fig. 9) assigned to *H. brevifrons* has a more distinct anterior border, gently convex, medially downwards-sloping, laterally almost horizontal. Possibly this represents an earlier stage in the evolution of the species. The free cheek is like that of *H. latigena* in outline with very prominent genal caecae radiating from the region of the eye, but dying out on a line delimiting the broad lateral border of the cheek. This border narrows anteriorly, and bears numerous very fine anastomosing terrace lines parallel to the edge of the cheek. A prominent ridge (Pl. 14, Fig. 2) runs from the mid point of the eye almost to the genal angle, cutting across the line of the genal caecae and running on to the border of the cheek. Similar ridges can be seen on the cheeks of some *Balnibarbi* species. The convex, fan shaped pygidium is only slightly wider than long (maximum width 1.2 times sag. length), narrower than those of the other species of *Hypermecaspis* in Spitsbergen. The doublure, as in other species, is very closely reflexed against the dorsal exoskeleton and covered with very fine and crowded terrace lines. The course of the interpleural furrows is marked on the doublure by narrow grooves. Posterior margin of the pygidium very gently curved.

In having a short preglabellar field this species resembles the type species *H. inermis* HARRINGTON and LEANZA 1957, *H. bulmani* HARRINGTON and LEANZA 1957 (described and figured by BULMAN, 1931, pp. 90 — 91, Pl. 11, 4,5), *H.* cf. *bulmani* WHITTINGTON 1965 (WHITTINGTON 1965, pp. 335 — 337, Pl. 18, 17 — 22) and *H. kolouros* ROSS (1970, p. 71, Pl. 10, 14 — 19). These species are distinguished from *H. brevifrons* by the following characters:

(a) *H. inermis* lacks genal spines, and has a transversely wider pygidium.
(b) *H.* cf. *bulmani* has a distinct, horizontal anterior border on the cranidium, and a transversely wider pygidium with a strongly curved outline to the posterior margin. Comparison with *H. bulmani* is more difficult due to the distortion of the type material; the species has a fifth axial ring in the pygidium and associated a sixth pair of pleural furrows.
(c) *H. kolouros* has a cranidial border like that of *H.* cf. *bulmani*, smaller palpebral lobes anteriorly situated, and a transversely wider pygidium with only three axial rings.

Hypermecaspis venulosa n. sp.

(Pl. 15, Figs. 1 — 9)

Stratigraphic range. — This species has only been recognised in the lowest part of the Olenidsletta member, not more than 6 m from the base of the Valhallfonna Formation in melt stream D on Olenidsletta. It is associated there with *Balnibarbi scimitar* n. gen., n. sp. and *Psilocara patagiatum* n. gen., n. sp.

Material. — Holotype, cranidium, PM NF 12. Other material: 5 cranidia: PMO NF 11, 18, 3039, 533, 2773; free cheeks: PMO NF 19, 2772; pygidia: PMO NF 16, 2783; hypostoma: PMO NF 3013.

Diagnosis. — A *Hypermecaspis* species of low convexity, and with an extremely broad, almost horizontal preglabellar field, on the sagittal line about 0.8 glabellar length. Preglabellar field and free cheeks strongly caecate. Facial sutures diverge at about 40 degrees in front of the eyes, curving gently adaxially near the anterior border. Front margin of cranidium, like that of glabella, gently rounded towards mid line. Free cheeks narrow (trans.), genal spines lacking. Pygidium fan shaped, similar to those of the other species described herein, but of length only two thirds its width, and of low convexity.

Description. — Cranidium of very low convexity, such that the preglabellar field extends in front of the glabella horizontally or with very gentle concavity. The glabella is subquadrate, occupying slightly more than half the cranidial length, with its maximum width at the occipital ring, this being slightly less than its sagittal length. In front of the occipital ring the glabella tapers forwards, very gradually, to its anterolateral corners. Front margin rounded towards mid line. Glabellar furrows are of similar form to those of other species of the genus, 4P very faint, and the frontal lobe of the glabella bisected by a distinct furrow (sag.) running backwards to almost meet the inner ends of glabellar furrows 4P.

The preglabellar field of this species is extraordinarily broad, exceeding in width that of any other olenid known to me, five sixths the length of the glabella on the sagittal line, broader still exsagittally. The preglabellar field is crossed by very conspicuous caeca, which run normal to the front margin of the glabella, consisting of sparsely dichotomising ridges, connected by frequent dissepiments. Over the anterior one third of the preglabellar field the caeca become fainter, and tend to become subparallel to the sagittal line, dying out altogether before reaching the anterior margin of the cranidium. The anterior border itself is very narrow (sag., exsag.), gently convex and curved about the midline almost parallel to the front of the glabella but with a lesser radius of curvature. It is worth noting also that the exoskeleton of this species is excessively thin (see Pl. 15, Fig. 2) forming a scarcely discernable skin over the surface. (If the thorax contained a large number of thoracic segments as in known complete hypermecaspidinids the complete exoskeleton would certainly exceed 6 cm in length — an appreciable size for such a delicate animal). The long, very broad sickle shaped palpebral lobes are close to the glabella as in other *Hypermecaspis* species, extending backwards as far as the outer end of the occipital furrow. No specimens are available showing the posterior fixed cheeks, but as outlined by the posterior branch of the facial suture on the free cheek they were long (trans.) and narrow (exsag.) as in the other species described herein. The anterior branch of the facial suture diverges at almost exactly 40 degrees to the sagittal line on available specimens, and for the posterior two thirds of its course maintains this direction, in front of this swinging adaxially, progressively strongly so anteriorly, in a uniform curve.

Free cheek of general outline resembling a quadrant of a circle with a slightly rounded genal angle of 90 degrees. Genal caeca are equally strong on the free cheek as on the preglabellar field, but die out on a line subparallel to the edge of the cheek. This lateral part of the cheek is flexed downwards, more steeply so towards the genal angle. It seems probable that the smooth area on the anterior part of the preglabellar field and the lateral part of the free cheek is the area covered ventrally by the doublure.

Pygidium fan shaped, with maximum width at the posterior margin, this being one and a half times the sagittal length. The axis has four distinctly defined axial rings, occupies just under half the sagittal length of the pygidium, and is continued posteriorly as an indistinct ridge. In most respects this pygidium may be likened to a short, wide, less convex version of that of *H. latigena* n. sp., with pleural and interpleural furrows of similar form, and a wide doublure (0.5 sag. length of pygidium medially), closely reflexed beneath the dorsal exoskeleton, and covered with very fine terrace lines.

Discussion. — The extraordinarily broad, strongly caecate preglabellar field of this species is so distinctive that there is no possibility of confusion with other species of *Hypermecaspis*. The pygidium is relatively wider than those of the other species of the genus described herein. It is of particular interest to notice the strong resemblance in gross morphology between this species and *Lauzonella planifrons* (BILLINGS) from the upper Cambrian of Quebec (RASETTI 1944, Pl. 37, Figs. 22 — 25). The glabellar segmentation of *H. venulosa* is, however, so typically hypermecaspidinid that its affinities are not in doubt, and the resemblance to *Lauzonella* is likely to be due to convergence. Other genera of the Loganellidae closely resemble the Balnibarbiinae, as discussed above (p. 15).

The fragmentary pygidium figured by ROSS (1965, Pl. 8, Fig. 30) from the Seward Peninsula, Alaska, is probably that of a hypermecaspidinid, and resembles that of *H. venulosa* most closely of the species described here.

Genus *Tropidopyge* HARRINGTON and KAY 1951

Type species. — *Dicellocephalus broeggeri* MOBERG and SEGERBERG 1906, designated HARRINGTON and KAY 1951.

Discussion. — The genus *Tropidopyge* was erected by HARRINGTON and KAY (1951) with *T. broeggeri* (MOBERG and SEGERBERG 1906) as type species. Of this species only the pygidium is known, although it is possible that the hypermecaspidinid described by BRØGGER (1882, p. 104) as *Parabolinella rugosa* is the associated cranidium (HARRINGTON in MOORE 1959, p. 0—270), in which case the latter name will have priority over *T. broeggeri*. The association is not finally proved, however; attempts to find a cranidium of "*P.*" *rugosa* associated with numerous pygidia of the type species in the collections of Lund University met with no success. The holotype pygidium of the type species is figured on Pl. 16, Fig. 6. The new species described below is placed in *Tropidopyge* because of the very close resemblance of its pygidium to that of the type species. The *Tropidopyge* pygidium differs from that of *Hypermecaspis* principally in its elliptical, as opposed to fan shaped outline, having weak or absent interpleural furrows, and a broad, ill defined depressed pygidial border. The cranidium associated with the Spitsbergen species differs from that of *Hypermecaspis* species in having the eyes further from the glabella, which has an almost semicircular anterior outline, and much narrower (trans.) free cheeks. In other respects *Tropidopyge* resembles *Hypermecaspis*. The difference between the species described below and *Hypermecaspis* species are considered sufficient to warrant their generic separation, although the concept of *Tropidopyge* will be clarified considerably when complete material of the type species is certainly identified.

Tropidopyge alveus n. sp.

Stratigraphic range. — Confined to the lower 6 metres of the Olenidsletta Member in the type section.

Material. — Holotype, cranidium, PMO NF 487. Other material includes cranidia: PMO NF 3008, 639, 470, 473, 482, 486, 488, 493, 1761; pygidia: PMO NF 3007, 490, 485, 469, 481, 472; free cheeks: PMO NF 477, 479.

Diagnosis. — A *Tropidopyge* species of low convexity, with a broad preglabellar field, 0.5 glabellar length on the sagittal line. Facial sutures diverge at about 20 degrees in front of the palpebral lobes, cutting the anterior margin sharply at a right angle. Palpebral lobes are more strongly curved and further away from the glabella than in *Hypermecaspis* species. Genal spines lacking. Pygidium two thirds as long as wide with a broadly elliptical outline, surface sculpture of closely spaced rather irregular terrace lines.

Description. — Cranidium of low convexity, with the preglabellar field sloping downwards very gently in front of the glabella, and the postocular fixed cheeks more steeply so laterally. Glabella with an outline like an inverted U, with maximum width at the occipital ring, this being equal to its sagittal length. In front of the occipital ring the glabella tapers uniformly forwards to its broadly rounded front margin. Glabellar furrows are similarly placed to those of species of *Hypermecaspis* described above, but on larger cranidia 2P, 3P and 4P not reaching the axial furrows. Furrow 2P is directed backwards at an angle of about 45 degrees to the sagittal line, 3P slopes backwards more gently, while 4P is directed almost transversely. There is a tendency towards bifurcation of the outer end of 2P in a comparable position to that occurring on species of *Hypermecaspis*. The occipital furrow likewise dies out before reaching the axial furrows, and is shallowest over the mid-part of the glabella. Occipital ring occupies 0.2 sagittal length of the glabella, of similar compound type to other hypermecaspidinids, and with a small occipital tubercle. Preglabellar and axial furrows hardly impressed, defined more by an abrupt change in slope around the glabella.

Preglabellar field of width on the sagittal line 0.5 glabellar length, widening uniformly exsagitally. Front margin of cranidium rounded, very gently so, consisting of narrow, upturned rim. Subparallel to the anterior margin, and running in an even curve across the midline of the preglabellar field there is a shallow furrow which defines a change in slope of the preglabellar field, which is less in front of the furrow than behind. The preglabellar field is crossed by fine caeca, much less coarse than in *H. venulosa*. The palpebral lobes of this species are relatively further away from the glabella than other species described herein, so that its anterior limit opposite glabellar furrow 4P does not closely approach the glabella, and its posterior limit opposite furrow 1P almost twice as far from the glabella. In outline the lobe is strongly curved, and the palpebral rim is ill defined. The postocular fixed cheek is narrow (exsag.), of transverse width almost that of the occipital ring, with the flat, abaxially widening posterior border seen also on *H. latigena* n. sp. Facial sutures diverge within one or two degrees of twenty degrees in front of the palpebral lobes on all examined specimens, run forwards in a straight course to cut the anterior border quite sharply at an approximate right angle.

Free cheek transversely narrower than those of the other species described here, without a genal spine, and sloping downwards from the region of the eye to the lateral margin, this slope being greater posteriorly. The doublure is broad, closely reflexed beneath the dorsal surface with its inner margin subparallel to the margin of the cheek. The doublure is covered with fine anastomosing grooves on its dorsal surface, which run slightly oblique. Anteriorly the doublure narrows greatly, more or less along the line of the anterior branch of the facial suture, so that over the midline it is narrow like that of other olenids. A shallow, oblique groove near the posterior margin may represent a vincular notch. The cheek is finely caecate like the preglabellar field. The caeca are marked by shallow grooves on the dorsal surface of the doublure; they therefore formed delicate tubes passing between the ventral surface of the dorsal exoskeleton and the closely adpressed doublure.

The pygidium is transversely elliptical in outline, length two thirds its maximum width, which lies posterior to its mid length. Axis tapers at 30 — 40 degrees, of decreasing convexity posteriorly, not exceeding half the length of the pygidium. Four axial rings of decreasing width (sag., exsag.) posteriorly, and an indistinctly defined terminal piece. The anterior three axial rings retain distinct "ghost" articulating half rings, shown up as narrow transverse furrows running across the mid part of each ring. The terminal piece of the axis is continued posteriorly as a rather irregular post-axial ridge which almost reaches the posterior margin. This ridge is reflected ventrally by a groove in the doublure. Pleural fields gently downsloping laterally and postaxially, nearly horizontal adjacent to the axis. Four pairs of quite shallow pleural furrows curve backwards parallel to the anterior margin of the pygidium, dying out before reaching the posterior margin. Only the most anterior pair of interpleural furrows is visible. The dorsal surface of the pleural fields of the pygidium is covered with very fine and numerous undulating terrace lines. Similar but rather stronger terrace lines are present on the dorsal surface of the pygidial doublure, which as with other species of the Hypermecaspidinae is broad, reaching to just behind the tip of the axis, closely reflexed against the dorsal exoskeleton.

Discussion. — The pygidium of this species is closely similar to that of the type species, *T. broeggeri* (Pl. 16, Fig. 6), which has, however, a distinct and steeply downturned articulating facet, and about half the number of terrace lines on the dorsal surface as *T. alveus* n. sp., and about one third the number on the pygidial doublure.

Subfamily PELTURINAE Hawle and Corda 1847

Genus *Psilocara* n. gen.

Type species. — *Psilocara comma* n. gen., n. sp.

Diagnosis. — Pelturinae with very narrow fixed cheeks, of transverse width less than one third that of the occipital ring, and large palpebral lobes, which extend further backwards than in any other pelturinid. Glabella subsquare in outline, not tapering; 2 pairs of lateral glabella furrows faint or absent on dorsal surface. Distinct horizontal anterior border to the cranidium. Narrow free cheeks with or without genal spines. Small, wide pygidium with two axial rings, and one pair of short pleural furrows, margin entire. Surface sculpture of fine raised lines.

Discussion. — This genus is erected to include two distinctive species from the early Arenig of the Olenidsletta Member, *Psilocara comma* and *P. patagiatum*. In general appearance these species are most similar to species of *Peltura* (especially *P. scarabaeoides* (WAHLENBERG 1821)) and *Peltocare*, but the large palpebral lobes extending far backwards on the cranidium are an exceptional feature among pelturinids, and all *Peltura* and *Peltocare* species have small, anteriorly positioned palpebral lobes. The non-tapering glabella of the new species, their very narrow fixed cheeks and the presence of a distinct anterior border on the cranidium also sets them apart from *Peltura* and *Peltocare* species. Indeed the *Psilocara* cranidium by itself in some ways resembles large-eyed *Triarthrus* species such as *T. parchaensis* HARRINGTON and LEANZA 1957 as much as any pelturinid. However the resemblance of the free cheek and pygidium to those of other pelturinids is such that its assignment to this subfamily is not in doubt.

The "smoothed out" species *Psilocara patagiatum* is the latest of a number of superficially similar but independently derived olenids. The genus *Leiobienvillia* RASETTI has small palpebral lobes, wide fixed cheeks and no anterior border, although its general furrow effacement gives it some similarity to *Psilocara* n. gen. *Leiobienvillia* was probably derived from the triarthrinid *Bienvillia*. Similarly *Leurostega* ROBISON and PANTOJA-ALOR 1968 is generally similar to *Psilocara patagiatum*, but has smaller palpebral lobes, lacks an anterior border on large cranidia, and has a narrower glabella with a longer (sag.) preglabellar field. *Leurostega* may possibly have been derived from *Protopeltura* (ROBISON and PANTOJA-ALOR 1968, p. 792). Both *Leiobienvillia* and *Leurostega* occur in Tremadocian rocks. No doubt the effacement of dorsal furrows was of functional significance in *Psilocara* n. gen., *Leurostega* and *Leiobienvillia*. It seems to be associated with rather high convexity, narrow preglabellar areas and small pygidia, that is with the *Peltura* morphological type (see p. 11).

It is considered that the ancestor for the *Psilocara* species may be discovered among late Tremadocian or early Arenigian *Peltocare* species. In *Peltocare norvegicum* (MOBERG and MÖLLER) the glabella of larger specimens shows a tendency to become subsquare in outline (see HENNINGSMOEN 1957, Pl. 27, Fig. 12; ROBISON and PANTOJA-ALOR 1968, Pl. 103, Fig. 17), glabellar furrows are effaced, while the pygidium is generally similar in form and sculpture to that of *Psilocara*. It may be noted here that the genus *Alimbetaspis* BALASHOVA (1961, p. 121) is extremely similar to *Peltocare*, so much so that the separation of the type species, *A. kelleri* BALASHOVA 1961, from *Peltocare* may prove to be of little value.

Psilocara comma n. gen., n. sp.

(Pl. 17, Figs. 1 — 8; Pl. 19, Figs. 11, 13 — 15, 18; Fig. 8)

Stratigraphic range. — This species has been identified only from black limestones in melt stream C on Olenidsletta at an horizon about 3m above the base of the Olenidsletta Member, which is well exposed there. (Early Arenig:— *fruticosus* (3 branch) zone.)

Material. — Holotype: cranidium, PMO NF 2540; cranidia: PMO NF 2544, 3034, 2539, 2545 — 6, 3042 — 3, 2542; 2 free cheeks: PMO NF 2543, 2538; pygidium, PMO NF 2541; possible hypostoma: PMO NF 3035.

Diagnosis. — A *Psilocara* species with distinct axial and preglabellar furrows, lateral glabellar furrows faint. Palpebral lobes with curved outline. Free cheeks with slender genal spines.

Description. — Cranidium convex, with the line of maximum convexity on the midline of the glabella, sloping downwards laterally on to the postocular fixed cheeks, and forwards on to the preglabellar field. The sagittal length of the glabella of larger individuals scarcely exceeds the maximum transverse width, on smaller specimens (sag. length 2 mm or less) the glabella is relatively longer, the width/length ratio being about 0.8. The glabella expands in width very slightly forwards, the front margin being broadly rounded medially. The occipital furrow is well defined, laterally sloping gently backwards, horizontal or slightly bowed forwards for its median one-third. Glabellar furrows by contrast very faint on the dorsal surface, rather more clearly visible on internal moulds. The furrows extend across more than one third of the transverse width of the glabella and have a gently arcuate outline, deeper, and directed backwards to a greater degree at their inner ends, 1P opposite the posterior parts of the palpebral lobes, 2P opposite the anterior parts. Axial and preglabellar furrows deep.

Fixed cheeks with very narrow (trans.) triangular outline, and decreasing in width anteriorly. Long, narrow palpebral lobes with a gently curved outline, posterior limits opposite the outer ends of the occipital furrow, while a transverse line joining the anterior limits is at three-quarters (sag.) glabellar length. The length of the lobes on available material varies between 0.42 and 0.46

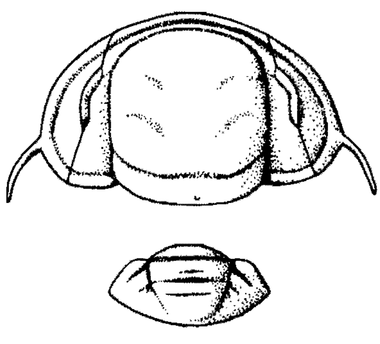


Fig. 8. Cephalon and pygidium of *Psilocara comma* n. gen., n. sp. About twice natural size.

sagittal length of glabella. Palpebral furrows deep, bowed outwards medially. Preglabellar field narrow, forming an almost vertical slope around the front of the cranidium. Its posterior one third is inflated, forming a ridge around the front of the glabella, the anterior part of the preglabellar field is depressed, slightly concave. Border furrow deep. The narrow, gently convex anterior border is horizontal, and arched gently upwards towards the sagittal line. The broad, deep posterior border furrow outlines a rather narrow (exsag. about half width of occipital ring) posterior border, which decreases in width abaxially. Posterior branch of the facial suture cuts the posterior border at a high acute angle (74 — 84 degrees as measured from photographs of specimens in dorsal view) running inwards anteriorly at an angle of less than 20 degrees to the sagittal line to the palpebral lobes. Anterior branches subparallel.

Free cheek with typical pelturinid outline but for the large "eye area", which shows no trace of lenses. The posterior border curves forwards to the genal spine, which is quite short (equal to, or slightly exceeding the length of the eye), slender, gently curved and outwardly directed, such as to make a right angle with the posterior border. Border furrow shallow. The lateral border of the cheek is flat and downsloping. The dorsal surface of the free cheek, and the preglabellar field and fixed cheek areas of the cranidium carry a surface sculpture of fine, anastomosing raised lines — these lines are subparallel on the lateral border of the free cheek and continue on to the genal spine. The surface of the glabella is minutely granulate on the holotype, and the same sculpture has been seen on two other well preserved specimens.

A hypostoma occurring in association with cranidia of *P. comma* (Pl. 19, Figs. 14, 18) may possibly belong to this species. It is very convex with a steeply sloping border posteriorly. The oval middle body, three quarters as wide as long, slopes downwards almost vertically posteriorly, where there is a faint indication of bilobation. A convex, narrow rim surrounds the border posteriorly, anterolaterally approaching the glabella closely, and steeper. The surface of the hypostoma is covered with fine anastomosing ridges like those on the cephalon.

Pygidium twice as wide as long, transversely convex. Axis of transverse width anteriorly half maximum width of pygidium, tapering gently (30 degrees) posteriorly, with a broadly rounded terminal piece. Two axial rings, the anterior one slightly wider (sag.) than the posterior one, defined by ring furrows which are deeper medially. There is a short, transverse furrow in the middle of the anterior ring. Axial furrows deep anteriorly, shallowing posteriorly, and not defined around the tip of the axis. Pleural fields with triangular outline, sloping downwards steeply posteriorly, and particularly postaxially. Only the anterior pygidial pleural furrows are distinctly defined — these are short, extending just over halfway across the pleural fields, quite deep and directed backwards at about 45 degrees to the sagittal line. There is a faint impression of a second pair of pleural furrows. Fulcra prominent, close to the axis. Steeply downturned triangular articulating facets which are directed backwards parallel to the pleural furrows, and meet the posterior margin at an obtuse angle. Posterior margin with a gently curved outline, without spines and without a distinct border, upward arched about midline. Dorsal surface of pygidium with fine raised lines which are subparallel to the posterior margin.

A number of thoracic segments are associated with the other parts of this species, and there is no reason to doubt that they belong here. The transverse width of the pleura is less than that of the axis, and it is bluntly pointed. A deep pleural furrow extends almost to the tip of the pleura. Fulcra close to the axis. Strongly developed triangular articulating facet occupies the major part of the width (exsag.) of the pleura laterally.

Discussion. — A discussion of the morphological distinctions between *Psilocara comma* and *P. patagiatum* is given in the following paragraphs. The relative stratigraphic ranges of *P. comma* and *P. patagiatum* are not certainly established as they have not been found in the same section. *P. patagiatum* does not occur lower than 8m from the base of the Olenidsletta Member in the type section: it occurs at a similar horizon in stream D. The ranges of the two species thus approach to within two metres, *P. comma* only having been found in the one locality on stream C 6m from the base of the Member. It is considered probable that further collecting will show that the ranges of the species may overlap.

Psilocara patagiatum n. gen., n. sp.

(Pl. 18, Figs. 1 — 12; Pl. 19, Figs. 12, 16, 17)

Stratigraphic range. — Type section: 6 — 14m from the base of the Olenidsletta Member. Stream D on Olenidsletta, not more than 9m from the base of the Olenidsletta Member there (Early Arenig).

Material. — Holotype, cranidium, PMO NF 2781, stream D locality. Cranidia: PMO NF 3011 — 2, 559, 562, 565, 570, 574, 646, 652 — 3; SMA 84086 — 9; free cheek: PMO NF 3010; thorax: PMO NF 2784.

Diagnosis. — A *Psilocara* species with axial and preglabellar furrows very shallow or almost effaced on dorsal surface. Palpebral lobes long, straight. Free cheeks lacking genal spine.

Discussion. — This species is best discussed in relation to *P. comma*, which it resembles in most general features. The most obvious difference between the two species is the smoothness of *P. patagiatum*, with the glabella scarcely defined from the cheeks, so that to the naked eye cranidia of the species appear to be quite featureless. This difference is maintained even in early ontogenetic stages — cranidia of *P. patagiatum* as small as 1.3mm long still have the glabella scarcely visible, while on comparably sized cranidia of *P. comma* it is clearly visible, transversely convex. On flattened cranidia axial and preglabellar furrows are generally more clearly visible, and the fixed cheeks and preglabellar area "spread out" around the glabella. Lateral glabellar furrows are not visible on the dorsal surface of the glabella, but are visible on well preserved internal moulds, having the same disposition and form as those of *P. comma*; there is an indication of a faint pair of pits far forward on the glabella representing the traces of short 3P furrows on one specimen (Pl. 18, Figs. 8, 9). The palpebral lobes of *P. patagiatum* are relatively straight, rather than bowed outwards as in *P. comma*, and their length compared to that of the glabella varies between 0.45 and 0.53, that is some specimens are distinctly longer-eyed than *P. comma* although there is some overlap between the two species. The palpebral furrows also run inwards-forwards in a straight course. The free cheek is narrower (trans.) than that of *P. comma*, and lacks the genal spine of that species. Except for the extraordinarily large visual area the cheek of *P. patagiatum* is similar to those of *Peltura* species. The front of the glabella, preglabellar field and the free cheek carries a sculpture of fine, irregularly anastomosing raised lines. No pygidium has been identified for this species.

The smooth, convex and narrow cephalon of this species exemplifies the *Peltura* type of morphology (Henningsmoen 1957, p. 78) particularly well. The species of *Peltura* and morphologically similar species of *Triarthrus* all seem to have small eyes, relatively far forward compared with *Psilocara patagiatum*, a placement which Henningsmoen (1957, p. 78) considered to be connected with an actively swimming mode of life. By contrast *P. patagiatum* has the largest eyes of any olenid known to me and they extend far back. Other Valhallfonna olenids, such as the Balnibarbiinae, Hypermecaspidinae and *Bienvillia stikta* n. sp. are also large-eyed compared with most Cambrian forms. The question arises if there was some condition in the environment in which the Valhallfonna rocks accumulated which particularly favoured large eyed trilobites, such as illumination of very low intensity necessitating highly developed eyes for good vision. Or the explanation may be found by considering changes in the structure of the marine biota as a whole since Cambrian times. The beds immediately underlying these from which *Psilocara* species were obtained are crammed with nautiloids — the upper Canadian was the early peak of nautiloid evolution. It is impossible not to be struck by the close proximity of what were probably the first major predators and these large eyed *Psilocara* species and perhaps it may be suggested that these active trilobites developed large eyes as additional protection from cephalopod predators.

Genus *Anaximander* n. gen.

Type species. — *Anaximander clavatus* n. gen., n. sp.

Diagnosis. — Small proparian olenid trilobites having gently convex cranidium and subcircular cranidial outline. Glabella subsquare in outline, not greatly elevated above cheeks, occupying more than half the cranidial width, its front margin deeply cleft by the preglabellar furrow. Two pairs of gently arcuate glabellar furrows. Palpebral lobes of moderate size opposite, and symmetrically disposed to, the anterior pair of glabellar furrows. Fixed cheeks gently convex, downsloping. Posterior border curves forward without a break into lateral border, which almost reaches the palpebral lobe. Preglabellar field fairly wide, gently inflated. Anterior border narrow, bowed upwards towards the sagittal line. External surface granulate. Thorax of at least twelve segments. Pygidium resembling that of *Svalbardites* n. gen.

Anaximander clavatus n. gen., n. sp.

(Pl. 21, Figs. 1 — 7; Fig. 9)

Stratigraphic range. — Olenidsletta Member 24 — 39m from base.

Material. — Holotype, cranidium with exoskeleton PMO NF 815. Other cranidia: PMO NF 838, 840, 1852, 1288, SMA 84122 — 4. Flattened dorsal exoskeleton: PMO NF 1873; external mould of free cheek: PMO NF 1878.

Diagnosis. — As *Anaximander clavatus* n. sp. is the only species yet known of the genus, the diagnosis follows that of the genus given above.

Description. — Cranidium small, not exceeding 3.5mm in length, gently convex (sag., trans.), outline subcircular. Glabella occupying about 0.6 cranidial width, sloping gently downwards anteriorly, low and flat, scarcely elevated above the cheeks (Pl. 21, Figs. 4 — 7). It tapers slightly forwards from its maximum width a little in front of the occipital ring, the maximum width being equal to the sagittal length. Two pairs of fairly deep, very gently arcuate

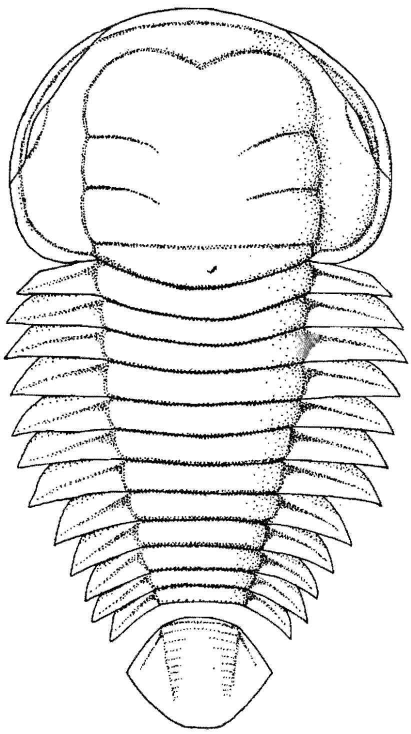


Fig. 9. Reconstruction of dorsal exoskeleton of *Anaximander clavatus* n. gen., n. sp. Exact number of thoracic segments uncertain. About × 12.

lateral glabellar furrows extend more than one third of the way across the glabella, their inner ends pointing slightly backwards. The distance between the outer ends of these furrows (exsag.) is similar to that between 1P and the occipital furrow, but less than that between 2P and the front of the glabella. There are a pair of shallow pits on the frontal lobe of the glabella in line with the inner ends of 2P, possibly corresponding with a third pair of furrows. Occipital furrow deepest medially, straight. Occipital ring convex, widening medially, where it stands above the glabella, with median tubercle. Axial furrows shallow, curving adaxially around the rounded anterolateral corners of the glabella into the broadly V-shaped preglabellar furrow, which notches deep into the frontal lobe of the glabella. Fixed cheeks gently convex, sloping downwards rather steeply. Palpebral lobes fusiform, of length about 0.3 that of glabella (sag.), far out and low down on cheek opposite and symmetrically disposed to glabellar furrow 2P. Each palpebral lobe is defined by a distinct furrow, and stands out almost horizontally against the slope of the cheek. Gently convex posterior border widening slightly abaxially, curving without a break into the lateral border, so that the posterolateral edge of cheek is broadly rounded. Lateral border closely approaches the palpebral lobe. Border furrow deep. Preglabellar field widest medially, continuing downward slope of the front of the glabella, slightly inflated. Anterior border furrow deep, outlining a narrow, horizontal anterior border, arched broadly upwards medially. Surface sculpture, except in furrows and on the borders, of fine granules. Free cheek very small, anterolaterally positioned and consisting largely of a convex border. The facial suture is correspondingly short, cutting the lateral border just behind the palpebral lobe, and running inwards and forwards to cut the anterior border at an obtuse angle.

One specimen (Pl. 21, Fig. 1) shows twelve thoracic segments. Since the pygidium is also present, although displaced, it is possible that this represents the complete thorax. Preservation is poor, however, and the possibility of there being several more segments cannot be eliminated. The thorax expands in width to about the fifth segment, tapering posteriorly. Axial rings narrow (sag., exsag.) and band-like, of transverse width about seven times their length (sag.), separated by deep inter-ring furrows. Mid part of the thoracic axis not well preserved and may possibly have carried median nodes like that on the occipital ring, although there is no evidence for them on the exfoliated mid-part of the thoracic axis (for this reason they are not shown on the reconstruction of the dorsal exoskeleton, Fig. 9). Pleurae transversly narrower than thoracic axis, bluntly pointed, with deep pleural furrows reaching to their tips.

The pygidium is only known from one specimen associated with the incomplete dorsal exoskeleton. It is completely flattened and evidently had an excessively thin cuticle. In general form it is similar to that of *Svalbardites* species, described below from better preserved material. In outline it is lozenge-shaped, with a broad axis anteriorly half as wide as the maximum width of the pygidium tapering very gently posteriorly and apparently reaching the posterior margin of the pygidium. Four very narrow (sag., exsag.) axial rings are present on the anterior part of the axis, outlined by shallow furrows which pass transversely across the mid part of the axis. Posteriorly three or four more rings are faintly indicated by furrows on those parts of the axis adjacent to the axial furrows.

Discussion. — The deeply cleft front margin of the glabella and the distinctive forward-curving border of the fixed cheek serve to distinguish *Anaximander* from all other olenid genera. It is certainly related to *Svalbardites* n. gen., described below, the cheeks of which are almost identical, but which has a distinctively different glabella warranting its generic separation from *Anaximander*. *Svalbardites* and *Anaximander* together constitute a new group of pelturines, and I know of no species in the literature which might be a candidate for their possible ancestor.

The broad identation of the front of the glabella of *A. clavatus* is an exaggerated development of a small median notch which is not uncommon among olenids (see for example *Acerocare ecorne* as figured by WESTERGÅRD 1922 Pl. 16, Figs. 6, 12, and *Balnibarbi tholia* (Pl. 4, Fig. 2) and *Bienvillia stikta* (Pl. 22, Fig. 3) herein).

Genus *Svalbardites* n. gen.

Type species. — *Svalbardites hamus* n. gen., n. sp.

Diagnosis. — Small proparian trilobites with furrows largely effaced on dorsal surface of exoskeleton. Cranidium subcircular, glabella occupying over half the cranidial width, subsquare in outline. Two pairs of glabellar furrows visible on internal moulds which extend more than one third across the glabella, gently bowed forwards at mid length, inner ends curving sharply backwards, hook-like. Palpebral lobes far forward, almost at edge of cheeks, fairly small. Posterior border curves evenly into lateral border, which closely approaches the palpebral lobe. Free cheeks minute. Pygidium lozenge shaped. Pygidial axis broad, gently tapering, ill defined posteriorly, with about 8 axial rings of which only the first two or three are defined across the mid line of the axis. Pleural fields smooth except for one pair of pleural furrows.

Included species: *S. hamus* n. gen., n. sp., *S. hebaxis* n. gen., n. sp.

Svalbardites hamus n. gen., n. sp.

(Pl. 20, Figs. 1 — 12, Fig. 10)

Stratigraphic range. — Olenidsletta Member, in the lowest 3 — 5 metres of the Member in beds of transitional character with the Kirtonryggen Formation. Particularly abundant in the interval from 57 — 75 m from the base of the Member (*fruticosus* to *bifidus* Zones).

Material. — An abundant species almost throughout its range, several hundred cranidia being present in the collections. Holotype, partly exfoliated cranidium, PMO NF 3014. Registered material includes cranidia: PMO NF

3000, 749, 1516, 1757, 708, 726, 860, 869, 873, 884, 1754 — 5, SMA 84125 — 6, 84130, 84132 — 3; pygidia: SMA 84127 — 8, PMO 3015; free cheek: SMA 84131.

Diagnosis. — As for genus.

Description. — Small trilobites, sagittal length of cranidium not exceeding 3 mm. Cranidium subcircular in outline, gently convex (sag., trans.), with maximum width at about one quarter sagittal length from posterior margin. Glabella occupying 0.6 maximum width of cranidium, hardly elevated above cheeks, defined by very shallow axial and preglabellar furrows, subsquare in outline, sagittal length slightly exceeding maximum width, tapering very gently anteriorly. Axial furrows are slightly deeper adjacent to occipital ring. Occipital and glabellar furrows not visible on dorsal surface, faintly visible on internal moulds. Two pairs of glabellar furrows extending more than one third across the glabella, the distance between their outer ends about equal to the distance between 1P and the occipital furrow and between 2P and the front of the glabella. Outer two thirds of glabellar furrows curve gently forwards (1P at a slightly higher angle), inner ends curve sharply posteriorly, initially subparallel with the sagittal line, their distal ends curving outwards abaxially, so that the outline of the furrows resembles a hook. Outer part of the occipital furrow curves backwards, inner part horizontal, with hook-like extremities in line with inner ends of glabellar furrows. Occipital furrow not visible over median one quarter of glabella. Occipital ring about one fifth glabellar length, widening adaxially, posterior margin gently arcuate, its mid part projecting further backwards than fixed cheeks. Minute occipital tubercle. Fixed cheeks narrow, gently convex, laterally steeply downsloping. Palpebral lobes far forwards, opposite glabellar furrow 2P, narrow and spindle shaped, about one fifth the length of the cranidium, sloping inwards at 30 — 35 degrees

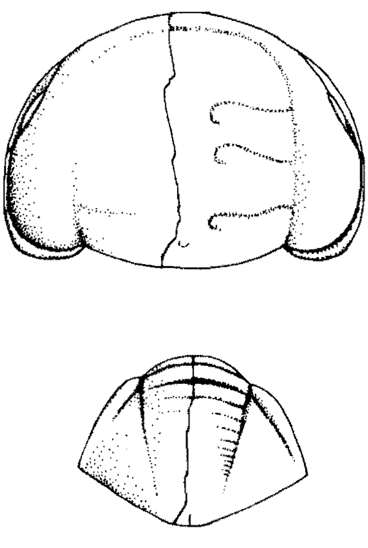


Fig. 10. Cephalon and pygidium of *Svalbardites hamus* n. gen., n. sp. Exoskeleton removed on right-hand side to show furrows of glabella and pygidial axis which are only visible on internal moulds. About × 12.

to the sagittal line. Preglabellar field of less width (sag., exsag.) than occipital ring, continuing gentle downward slope of frontal lobe of glabella, slightly wider medially. Posterior border furrow deep especially on the internal moulds. Posterior and lateral borders continuous, with subcircular outline around posterior part of cheeks, widest posterolaterally, narrowing towards the axial furrows and the palpebral lobes. Cross section of borders semicircular. Lateral border runs forwards and slightly inwards almost to palpebral lobe. Anterior border apparently lacking. Surface sculpture on cranidium of minute granules.

Facial sutures proparian, short, close to the edge of the cephalon, cutting lateral border just behind palpebral lobes at a low acute angle and running in an almost straight line inwards at about 30 degrees to the sagittal line to cross the anterior margin a short distance in front of the palpebral lobes. The free cheek so defined is extremely small, narrow (trans.) crescentic, with lateral border of similar form to that of fixed cheek occupying the major part of its width. Eye surface not preserved.

Pygidium gently convex (sag., trans.), lozenge shaped, of length about three quarters maximum width, which is at approximately two thirds sagittal length posteriorly. Axis broad, at first axial ring almost exactly half maximum pygidial width, of low convexity (trans.). Axial furrows progressively fainter posteriorly and not defining tip of axis, converging backwards at about 20 degrees. On internal moulds 7 to 9 very narrow (sag., exsag.) axial rings are visible, of which only the first two are clearly defined by deep ring furrows across the middle of the axis, where they curve gently forwards. Posteriorly the ring furrows are narrow and shallow, confined to lateral one third of axis. Where the exoskeleton is preserved only the anterior axial ring is defined clearly, while the second is very faintly visible. Dorsal surface of exoskeleton covered by very fine and crowded raised lines. Articulating half ring crescentic, about equal in width (sag.) to first axial ring. Pleural fields downsloping, very gently convex adaxially, smooth except for anterior pair of pleural furrows which slope backwards at 45 degrees to sagittal line, and become fainter abaxially, to die out at about half way across pleural fields. Anterolateral borders adaxially slope backwards parallel with pleural furrows, laterally curving slightly posteriorly to meet posterior margins at an obtuse angle (about 110 degrees). Posterior margins convergent backwards, laterally at 125 — 130 degrees, transverse postaxially, slightly upward arched on mid line. A minute furrow can be seen on one specimen running from what was probably the tip of the axis on the sagittal line to the posterior margin (Pl. 20, Fig. 11).

Small cranidia are more convex (sag., trans.) with a broader (sag.) occipital ring curving more noticeably posteriorly.

Discussion. — This peculiar trilobite could not, considered by itself, be assigned readily to the Olenidae. It is placed here in the systematic descriptions because of its resemblance and probable close relationship to *Anaximander clavatus* n. gen., n. sp. described above, which is far more olenid-like. The "hooked" glabellar furrows and lozenge shaped pygidium with many axial rings and smooth pleural fields set this species apart from the olenids as a whole. The pygidium is remarkably similar to those of species of the homalonotid genus *Plaesiacomia* HAWLE and CORDA (see DEAN 1966, Pl. 1, 3), which are of similar shape, and have smooth pleural fields with only one pair of pleural furrows, but apparently not more than two rings visible on the anterior part of the axis and with prominent vincular furrows. The type species, *P. rara* HAWLE and CORDA (DEAN 1966, Pl. 1, Figs. 1, 2, 7) has the eyes far forward, but the strongly tapering glabella is quite different from that of *Svalbardites* n. gen. *Plaesiacomia* is generally younger, not occurring before the Llanvirn, and a direct relationship with *Svalbardites* n. gen. seems unlikely, although the degree of convergence is remarkable. The possibility of a connection between the homalonotids and the olenids is intriguing, and may be relevant to suggestions (e. g. DEAN 1966a, p. 298) that the superfamily Calymenacea is polyphyletic.

Svalbardites hebaxis n. gen., n. sp.

(Pl. 19, Figs. 1 — 10)

Stratigraphic range. — Olenidsletta Member, occurring between 95 and 105 m. (occurring just below earliest *Isograptus* zone graptolites)

Material. — Holotype, cranidium, PMO NF 3009. Other material includes cranidia: PMO NF 3006, 731, 1462, 1549, 3037 — 8; pygidia: PMO NF 3004 — 5, 1441, SMA 84134. SMA 84135 — 6.

Discussion. — This species differs from the type species in a number of details. The fixed cheeks are narrower, and there is a more distinct genal angle between the posterior and lateral borders of the cranidium. No indications of glabellar furrows have been seen on specimens of sagittal length greater than 1 mm. The pygidium is shorter and wider, and on the internal mould (Pl. 19, Figs. 7, 8) the gently tapering axis is seen to be bluntly rounded posteriorly, the first four axial rings pass across the middle of the axis and are distinctly forward-arched medially.

Very small cranidia of this species, of sagittal length 0.6 mm (Pl. 19, Fig. 9) are more convex than those of the adult, but the characteristic forward curving posterior border is present even at this small size. The glabella, and particularly the occipital ring, are more distinctly defined and narrower (trans.) than on the large cranidia. The front margin of the glabella is broadly rounded. There are two pairs of shallow, short (trans.) gently arcuate glabellar furrows which curve backwards at their inner ends, although there is no sign of the "hook" typical of *S. hamus*.

This species occurs stratigraphically above the type species, and is particularly abundant in black, conchoidally fracturing limestones 103 m from the base of the Olenidsletta Member, where it is associated with *Micragnostus*.

Subfamily TRIARTHRINAE ULRICH, 1930

The subfamilial diagnosis of POULSEN (in MOORE, 1959, p. 0 — 267) is followed here.

Genus *Bienvillia* CLARK, 1924

Type species. — *Dikelocephalus? corax* BILLINGS, 1865 by original designation.

Remarks. — Some problems attend the definition of the characters by which *Bienvillia* may be distinguished from *Triarthrus*. According to HENNINGSMOEN (1957, p. 142) *Bienvillia* species differ from those of *Triarthrus* in having wider postocular cheeks and a relatively broad preglabellar field. Both these features vary greatly from species to species. For example, a new *Triarthrus* species described below, *T. papulosus* n. sp., has postocular fixed cheeks of a transverse width almost equal to that of the type species of *Bienvillia*, *B. corax* (BILLINGS), as figured by RASETTI (1954, Pl. 61, Fig. 15), but *T. papulosus* lacks the preglabellar field typical of *Bienvillia* species. The new species of *Bienvillia*, *B. stikta*, described below, is similar to *B. corax* in the proportions of its fixed cheeks, but has a relatively narrow preglabellar field. Flattened specimens of *B. stikta* have a preglabellar field of comparable width to similarly preserved specimens of *B. tetragonalis broeggeri* (HENNINGSMOEN 1957, Pl. 11, Fig. 4). Conversely *Triarthrus angelini* LINNARSSON 1869 (HENNINGSMOEN 1957, Pl. 11, Figs. 9, 10) possesses a preglabellar field of comparable width to that of *Bienvillia stikta* n. sp., but distinctively narrow (trans.) fixed cheeks.

It is clear that there is a general evolutionary trend from Tremadocian *Bienvillia*-type morphology, with broad fixed cheeks and preglabellar field (represented by such species as *B. shinetonensis* (RAW), *B. corax* (BILLINGS), *B. tetragonalis* (HARRINGTON), *B. micula* (RAYMOND), and *B. grandis* ROBISON and PANTOJA-ALOR), to *Triarthrus*-type morphology with narrow cheeks and lacking preglabellar field in the Llanvirn-Caradoc (with such species as *T. beckii* GREEN, *T. canadensis* SMITH, *T. glaber* BILLINGS, *T. fischeri* BILLINGS, *T. spinosus* BILLINGS, *T. humilis* HADDING, *T. eatoni* (HALL), *T. linnarssoni* THORSLUND, *T. skutensis* THORSLUND, *T. sinensis* CHANG and FAN, '*T.*' *convergens* WHITTARD, *T. thor* n. sp. and *T. parapunctatus* n. sp.). In rocks of latest Tremadocian and Arenig age it is not surprising that species with transitional combinations of characters occur, and their generic assignment is inevitably more arbitrary. As indicated above the transverse width of the fixed cheeks appears to be a particularly variable character, and it may prove to be preferable to regard the presence of a preglabellar field as the diagnostic character for assignment of a given species to *Bienvillia*. However, adoption of this criterion would result in the transfer to *Bienvillia* of some species which have been regarded as typical of *Triarthrus*, viz. *Triarthrus angelini* LINNARSSON 1869 and *T. parchaensis* HARRINGTON and LEANZA 1957. I prefer to leave the question of the affinities of such species open pending a revision of this group of olenids as a whole. However, I regard the assignment of the new species described below to *Bienvillia* as well established on the basis of its close resemblance to the Tremadocian species *B. grandis* ROBISON and PANTOJA-ALOR 1968.

Bienvillia stikta n. sp.

(Pl. 22, Figs. 1 — 15; Pl. 24, Figs. 5 — 7)

Stratigraphic range. — Olenidsletta Member 33 m to 103 m from the base.

Material. — Holotype, cranidium, PMO NF 584. This species is abundantly represented in collections throughout its range. Material includes cranidia: PMO NF 761, 754, 1588, 581 — 2, 609, 619, 735, 740, 754, 761, 870, 852, 1458, 1514 — 5, 1536, 1681, SMA 84090, 84094, 84095, 84098 — 9, 84119 — 20; pygidium: SMA 84093; free cheeks: SMA 84091, 84096; cranidia with thorax: SMA 84092, PMO NF 2623; thorax and pygidium PMO NF 2628.

Diagnosis. — A *Bienvillia* species of moderate convexity with a pitted anterior border furrow, short preglabellar field with a distinct median inflation. Glabella subquadrate, with two pairs of deep, gently curving furrows. Moderately large eyes (about 0.25 glabellar length) opposite, and symmetrically disposed to, the anterior glabellar furrows. Free cheek with long genal spine, posterior border not curving forward to the genal angle. Small pygidium with two axial rings.

Description. — Cranidium almost semicircular, moderately convex (sag., trans.). Glabella occupying half the width of the cranidium and 0.9 its length, gently rounded anteriorly, in small specimens almost parallel sided, in larger cranidia expanding slightly at glabellar lobe 1P. Two glabellar furrows, the distance between the outer ends of 1P and 2P equal to that between 1P and the occipital furrow, and equal to the width of the occipital ring (sag.). The furrows are well impressed, and occupy slightly more than one third the glabellar width, gently arcuate backwards, their inner ends (particularly of 1P) deflected more strongly backwards. On one specimen there is a faint indication of a third pair of furrows represented by shallow pits far forwards on the frontal lobe of the glabella. Occipital furrow deep, laterally sloping backwards for one quarter of its course, medially flexed slightly forwards. Occipital ring widest on mid line, bearing a median node which is prominent on small cranidia, less so on larger (1 cm long) cranidia. A faint furrow continuing outwards and backwards from the median part of the occipital furrow across the occipital ring to meet the axial furrow at the posterior margin may give some indication of the occipital ring being composite, as in *Balnibarbi pulvurea* n. gen., n. sp. and the hypermecaspidinids. Frontal lobe about one third glabellar length, sloping gently downwards, this slope being continued in the preglabellar field. Axial and preglabellar furrows well defined.

Triangular postocular fixed cheeks of length (exsag.) 0.4 that of the cranidium, nearly horizontal adjacent to the glabella, laterally sloping downwards and outwards. Preocular cheek narrow (exsag., trans.), sloping downwards and forwards as the lateral continuation of the preglabellar field. The short, steeply sloping preglabellar field is of about uniform width (exsag.) except medially, where it is slightly wider due to a characteristic median inflation. The moderately deep anterior border furrow marks an abrupt change in slope from the preglabellar field on to the horizontal anterior border. It bears 15 — 20 distinct pits. Anterior border of less than half the width of the preglabellar field, forming a horizontal rim rounded on the mid line, where it is arched slightly upwards. Palpebral lobe about four times as long as wide, outlined by a distinct palpebral furrow, opposite glabellar furrow 2P and symmetrically disposed to it, of length about equal to the distance between glabellar furrows 1P and 2P (about 0.25 glabellar length). It is inclined inwards anteriorly at about 20 degrees to the sagittal line, its anterior end close to the glabella. An indistinct eye ridge is visible on some specimens, continuing as a faint bulge from the anterior end of the palpebral lobe to meet the axial furrow immediately posterior to the anterolateral corner of the glabella. Posterior border furrow deep and straight, outlining the narrow, convex posterior border, which tapers slightly away from the axial furrow. Facial suture running forwards from the posterior border almost parallel to sagittal line, curving slightly adaxially behind palpebral lobes, in front of the eyes divergent at a low angle (about 20 degrees), curving adaxially anteriorly to pass in front of the anterior border. Surface sculpture of fine raised lines on the frontal lobe of the glabella, preglabellar field and the preocular fixed cheek.

Flattening (Pl. 22, Figs. 9, 11) markedly alters the appearance of cranidia of this species. The cranidium opens up along the mid line of maximum convexity, resulting in an apparent increase in the width of the fixed cheeks. The preglabellar field becomes pushed forwards horizontally and appears wider in dorsal view, while flattening out of the arched anterior border results in an apparently pointed anterior border to the cranidium. The characteristic median inflation is effaced, although the greater median preglabellar width is preserved. Flattening of the glabella exaggerates the relatively gently sinuosities of the glabellar and occipital furrows. Such differences make the comparison of material in different preservation states extremely difficult, and changes in almost all measurable characters render an evaluation of the effects of flattening essential before statistical methods may be used effectively for the characterisation of this species. The shape and position of the palpebral lobe remains constant, while the divergence of the preocular suture becomes, if anything, exaggerated. The close association of flattened and unflattened specimens places the conspecificity of the two preservation states beyond question in the collection under study.

Free cheeks nearly three times as long as wide, gently convex, sloping down to shallow posterior and lateral border furrows. Lateral border convex, and produced into a slender, hollow circular genal spine of a length equal to that of the free cheek. Posterior border convex, narrower than lateral border; genal angle 90 degrees. The eye is not preserved.

The free cheeks are united as a single piece with no sign of a connective or median suture on the narrow ventral doublure. The doublure bears parallel raised lines, and its width is similar to, or slightly greater than the width of the anterior border of the cranidium. The facial suture was presumably marginal, or very nearly so, anteriorly, so that the anterior margin of the cephalon had a "doubled back" structure similar to that described for the Balnibarbiinae (Fig. 4c). On the mid line the doublure was also arched up with the anterior border, so that on flattened specimens it apparently comes to a point medially (Pl. 22, Fig. 6).

Thorax of at least 10 segments, reaching maximum width at the fifth segment, the first two being rather narrow (trans.). Axis gently tapering throughout its length, about equal in width to the pleurae at the fifth segment, of relatively greater width anteriorly. Each axial ring bears a small median node. Axial furrows well defined. Pleurae pointed, sloping gently backwards anteriorly, more markedly so posteriorly. Pleural furrows straight and deep running out to the pointed tips of the pleurae. Articulating fulcra near the axis.

Pygidium very small, convex (about half as high as wide). Axis occupying half the pygidial width at the anterior margin of the pygidium tapering at a low angle posteriorly, with two axial rings and a broadly rounded terminal piece rather less than half the length of the axis, which slopes down steeply to posterior margin. Inter-ring furrows shallower medially. Prominent crescentic articulating half ring. Pleural fields steeply sloping downwards and backwards. Two pairs of pleural furrows which are deep (particularly the anterior part) and do not reach the posterior margin. One pair of much fainter interpleural furrows between the pleural furrows. Convex anterior border makes an angle of about 80 degrees with the posterior border, which is gently rounded towards the mid line, where it merges with the terminal piece of the axis.

Discussion. — This species is closely similar to *Bienvillia grandis* ROBISON and PANTOJA-ALOR 1968 (see particularly ROBISON and PANTOJA-ALOR 1968, Pl. 100, Fig. 16, where an uncrushed cranidium is figured) with regard to overall convexity, the width of the preglabellar field, proportions of the fixed cheeks and form of the glabellar furrows. The anterior border furrows of most specimens of *B. grandis* are apparently without pits although "they become well developed in some large holaspides" (ROBISON and PANTOJA-ALOR 1968, p. 788). *B. stikta* n. sp. and *B. grandis* are consistently distinguished on two features: the palpebral lobe on *B. grandis* is further back than that of *B. stikta*, its anterior limit opposite glabellar furrow 2P, whereas that of *B. stikta* is symmetrically disposed about 2P; the posterior branch of the facial suture of *B. grandis* cuts the posterior border at an acute angle, whereas that of *B. stikta* cuts the posterior border at a right angle. It may also be of specific importance that *B. grandis* reaches more than twice the maximum size of *B. stikta*. As described by HARRINGTON and LEANZA (1957) *B. tetragonalis* (HARRINGTON) lacks pits in the anterior border furrow, the facial suture cuts the posterior border at an acute angle, and the preocular sutures are convergent in front of the palpebral lobes. The same features also distinguish *B. shinetonensis* (RAW) (LAKE 1913, p. 70) and *B. micula* (RAYMOND) (RAYMOND 1937, Pl. 11, Fig. 19) from *B. stikta*. The type species, *B. corax* (BILLINGS), differs also from *B. stikta* in its broader preglabellar field, shorter palpebral lobes, and longer, straighter glabellar furrows (RASETTI 1954, Pl. 61, Fig. 15).

It is appropriate also to consider for comparison those species of *Triarthrus* which possess a preglabellar field, which, as indicated above, are probably closely related to Tremadocian *Bienvillia* species and to *B. stikta*. *T. parchaensis* HARRINGTON and LEANZA (1957) is similar to *Bienvillia stikta* in the width of the preglabellar field, the form of the glabellar furrows, and has a similar pygidium, but has much larger palpebral lobes which extend further backwards and therefore delimit narrow (exsag.) fixed cheeks. *T. rectifrons* (HARRINGTON) (HARRINGTON and LEANZA 1957, p. 115) from the Upper Tremadoc of Argentina is also closely similar to *B. stikta* in cranidial features, differing only in having a transversely truncate anterior margin to the cranidium; the free cheeks of *T. rectifrons* lack genal spines, however, and the pygidium is transversely much wider than that of *Bienvillia stikta*. These two differences apply also to *Triarthrus angelini* LINNARSSON (HENNINGSMOEN 1957, Pl. 11, Figs. 8 — 10), which in addition has narrower fixed cheeks than *Bienvillia stikta*, and on the glabella consistently has an anterior pair of pits representing the 3P glabellar furrows. *Triarthrus jemtlandicus* LINNARSSON 1875 (see ASKLUND 1936, Pl. 1, Figs. 6 — 8) has larger palpebral lobes than *Bienvillia stikta*, more posteriorly positioned, and is generally much less convex.

B. stikta is the most variable of the Spitsbergen olenids. Within a single population 75m from the base of the Valhallfonna Formation there are specimens which exhibit a wide range of convexity. The axis of maximum convexity lies along the sagittal line of the cranidium. The more convex specimens (Pl. 22, Fig. 5) have an anterior border which is more strongly arched upwards on the midline; the same arching about the sagittal line affects the glabella. In dorsal view this gives both the anterior outline of the cranidium and that of the glabella a more pointed appearance. The outer part of glabellar furrow 2P is more transverse on the more convex cranidia and its inner end curves correspondingly more sharply backwards. Flattening probably obscures such differences. Throughout its rather long stratigraphic range *Bienvillia stikta* shows no apparent trends of morphological change, cranidia at the top of its stratigraphic range having similar proportions to those near its first appearance (Pl. 24, Figs. 6, 7). However, specimens in the top 2m of the range of the species show one consistent difference from those stratigraphically below: the surface of the cranidium is more densely covered with very fine raised lines which are present on the occipital ring and on the posterior mid part of the glabella (Pl. 24, Fig. 5) as well as the front part of the cranidium and preglabellar field. In view of their similarity otherwise to earlier cranidia of *B. stikta* this difference is not considered sufficient by itself to formally name a second species of *Bienvillia* in Spitsbergen, although the sculptural change may prove to be stratigraphically consistent.

Genus *Triarthrus* GREEN, 1832

Type species. — *Triarthrus Beckii* GREEN, 1832 (by monotypy).

Remarks. — The genus *Triarthrus* is a large one, and many of the species are unfortunately in need of redescription or are inadequately illustrated. The three new species described below are known from well preserved, relief material, which can be compared only with difficulty with flattened material from shales, a common mode of preservation of *Triarthrus* species. As stated above it is likely that the stratigraphically early species assigned to *Triarthrus* are more closely related to *Bienvillia* than to later Ordovician *Triarthrus* species.

To the list of *Triarthrus* species given by HENNINGSMOEN (1957, p. 151), with which the species from Spitsbergen have been compared, may be added *T. convergens* WHITTARD 1961, *T. sinensis* CHANG and FAN 1965, and *T. turkestanicus* VEBER 1948.

Triarthrus papulosus n. sp.

(Pl. 23, Figs. 1 — 11)

Stratigraphic range. — Upper part of the Olenidsletta Member 110m to 140m (*Isograptus* Zone).

Material. — Holotype, cranidium, SMA 84100. Other material includes cranidia: SMA 84101 — 3, 84108, PMO NF 1643, 1645 (blocks with several examples), 1811; pygidium: SMA 84104; free cheeks: SMA 84105; incomplete exoskeleton: SMA 84107.

Diagnosis. — A *Triarthrus* species of low convexity with transversely wide fixed cheeks, glabella very gently rounded anteriorly, and expanding in width slightly forwards. Two arcuate glabellar furrows, 2P shallowing towards the axial furrow. Fairly small palpebral lobes (about 0.15 glabellar length) positioned anterior to glabellar furrow 2P, broad, outlined by a furrow which becomes faint anteriorly. Preglabellar field extremely short, absent medially. Surface of the exoskeleton covered with small granules except on anterior border and mid part of glabella. Pygidium small, with two axial rings.

Description. — Cranidium semicircular, of low convexity (sag., trans.). Glabella subrectangular, about 1.25 as long as wide, not elevated greatly above the fixed cheeks, expanding slightly forward to reach its maximum width at its anterolateral corners, very gently rounded anteriorly. Two pairs of rather broad (exsag.) glabellar furrows extending slightly more than one third of the way across the glabella, gently arcuate backwards, the outer end of 2P a little more than half way between the occipital furrow and the front of the glabella, 1P half way between 2P and the occipital furrow. 1P almost reaches the axial furrow, where it becomes fainter, 2P shallows on most specimens further away from the axial furrow. On smaller (2mm long) specimens it is similar to 1P. Well defined occipital furrow curves forward in the mid half of the glabella, laterally sloping concavely backwards. Occipital ring about one sixth glabellar length on mid line, widening sagittally, with median node. Axial furrows deep, preglabellar furrow shallowing towards the mid line, effaced medially.

Fixed cheeks slightly inflated near the axial furrows, laterally sloping gently downwards to the edge of the cranidium. Palpebral lobe fairly small (about 0.15 glabellar length), about three times as long as wide, outlined by a palpebral furrow which is distinct posteriorly, becoming much fainter anteriorly. Posterior limit of palpebral lobe is just posterior to the outer end of glabellar furrow 2P, running inwards at an angle of about 30 degrees to the sagittal line, its anterior end close to the glabella opposite the frontal lobe of the glabella. The form of the palpebral lobe does not change in small cranidia. Preglabellar field very narrow laterally, absent on mid line. Prominent anterior border, rounded medially and widest on the mid line, where it attains a width about equal to that of the palpebral lobe. Anterior border furrow fairly deep, on some specimens with up to 10 obscure pits.

On the holotype a faint furrow can be seen running backwards from the posterior end of the furrow outlining the palpebral lobe parallel to the postero-lateral edge of the fixed cheek (Pl. 23, Fig. 1). This furrow joins the posterior border furrow just inside its outer limit. The posterior border furrow is much deeper than this furrow, separating a prominent fairly narrow posterior border from the fixed cheek. Facial sutures subparallel to very slightly divergent in front of the eyes, behind the palpebral lobes running outwards and backwards at a low angle, near the posterior border curving adaxially to cut the border at 90 degrees. External surface of the cranidium covered with small granules, except on the anterior border and in furrows, and on the posterior mid part of the glabella.

Free cheeks united as a single piece by a narrow ventral doublure, with convex posterior and lateral borders. The posterior border curves forward to a long blade-like genal spine, which is directed outwards initially at an angle of 30 degrees to the sagittal line, curving adaxially at its distal end.

Pygidium small, axis occupying over half the pygidial width anteriorly decreasing in convexity posteriorly, barely tapering. Two axial rings; of the two ring furrows the first is complete, the second fainter near the axial furrow. Terminal piece of the axis occupies more than one third the length of the axis, bluntly rounded, sloping down steeply to the posterior border. Pleural fields slope down steeply, with two pleural furrows which do not reach the posterior border, and one faint interpleural furrow. There is a prominent crescentic articulating half ring. Posterior border entire.

Discussion. — This distinctive species resembles no other *Triarthrus* species closely. *T. spinosus* BILLINGS and *T. beckii* GREEN (redescribed by RUEDEMANN 1926) and *T. humilis* HADDING (NIKOLAISEN 1965, Pl. 1, Figs. 1 — 5), are covered with granules like the present species but differ in most other details of glabellar shape and furrows, width of fixed cheeks, and shape and size of palpebral lobes. The greatest cranidial similarity is probably to *T. punctatus* (CROSFIELD and SKEAT 1896), although comparison is difficult due to the distortion and partial flattening of the type and topotype material of this species. *T. papulosus* and *T. punctatus* are similar in the shape of the glabella and the width of the fixed cheek, although the species are distinguished in that *T. punctatus* lacks genal spines (LAKE 1919; Pl. XII, Fig. 3) and has well developed furrows outlining the sutural ridges on the fixed cheeks of large cranidia as well as small. *T. pacificus* (KOBYASHI 1955) from the McKay Group, British Columbia is also similar to *T. papulosus* in general cranidial proportions but with slightly narrower fixed cheeks; examination of the type material of this species indicates that the glabellar furrows of *T. pacificus* slope backwards more markedly, and are more deeply incised than those of *T. papulosus*, although further comparison is difficult due to the poor preservation of the McKay species.

The posterolateral furrow running backwards from the palpebral lobe is comparable to that outlining the sutural ridge in *T. fischeri* (WHITTINGTON 1965, p. 333) which otherwise is quite different from *T. papulosus* in having narrow fixed cheeks and deep glabellar furrows. WHITTARD (1961, p. 189) has redescribed *Triarthrus* (sensu lato) *caecigenus* from the Athens shale Virginia, and named and described *T.* (sensu lato) *convergens* from the Hope Shales, Shropshire, neither of which resemble *T. papulosus* n. sp. closely, but possess a lateral furrow on the fixed cheek like that on *T. fisheri* and *T. papulosus* n. sp. WHITTARD interpreted this structure as a lateral border furrow, the free cheeks being correspondingly reduced and the facial suture being considered proparian. It seems equally probable that this furrow outlines a sutural ridge as in the species under discussion, i.e. the free cheek and suture may be of more normal *Triarthrus* type. On small cranidia this sutural ridge furrow is more prominent, and in addition the glabella is more inflated than in larger specimens, relatively longer (sag.), and expands more noticeably forward. The frontal lobe of the glabella is longer and the eyes placed relatively further forward. These observations are in accordance with those made on *T. thor* n. sp. below, *T. eatoni* (HALL) (see WHITTINGTON 1957b) and *T. fischeri* BILLINGS (see WHITTINGTON 1965).

Triarthrus thor n. sp.

(Pl. 23, Figs. 12 — 23)

Stratigraphic range. — Uppermost part of the Olenidsletta Member, in one bed believed to be 145m from the base of the Valhallfonna Formation, on Profilbekken.

Material. — Holotype: partly exfoliated cranidium SMA 84109. Cranidia: SMA 84110 — 2, 84114; pygidium: SMA 84113; hypostoma; SMA 84115; protaspis: SMA 84116; free cheek: SMA 84359.

Diagnosis. — A *Triarthrus* species of low convexity, glabella subrectangular, not inflated towards mid line. Fixed cheeks very narrow. Two narrow (trans.)

well defined pairs glabellar furrows, which may be slightly sinuous. Preglabellar field lacking. Very small arched palpebral lobes far forward opposite frontal lobe of glabella. Free cheeks fairly broad with posterior border curving forward to genal spine. Pygidium small, with three axial rings.

Discussion. — This species differs from *T. papulosus* in the following features: the glabella does not expand forward to its anterolateral corners, even on smaller specimens (glabella length 1.5mm). The fixed cheeks are very narrow (trans.), especially on larger specimens, and are horizontal near the axial furrows, turning rather sharply downwards laterally. The palpebral lobes are

Fig. 11. Outline drawings of cranidia of *Triarthrus thor* n. sp., showing ontogeny. A. Protaspis (× 12). B. Very small cranidium (× 12). C. Small cranidium retaining sutural ridges (× 10). D. Mature cranidium (× 2).

small, arched, and far forward opposite the frontal lobe of the glabella. The glabellar furrows are narrow (exsag.) and do not shallow towards the axial furrow. On larger specimens they are gently undulating. The posterior part of the postocular facial suture is parallel to the axis for almost half the distance from the posterior border to the palpebral lobe on larger specimens. The external surface is apparently smooth. *T. thor* differs from *T. parapunctatus* n. sp. in having distinct glabellar furrows, and lacking punctate surface sculpture.

The low convexity, relatively shallow glabellar furrows and truncate anterior outline of the glabella serve to distinguish this species from *T. fischeri* BILLINGS (WHITTINGTON 1965, p. 331), *T. humilis* HADDING (NIKOLAISEN 1965, p. 232), *T. skutensis* THORSLUND and *T. linnarssoni* THORSLUND (THORSLUND 1940, Pl. 12). *T. thor* has been found only in one bed (not with *T. papulosus*), and a fairly complete size range of cranidia has been obtained (Pl. 23, Figs. 14, 17, 20; Fig. 11). The changes recurring in ontogeny are similar to those described by WHITTINGTON (1957, 1965) for other *Triarthrus* species. Small cranidia have a narrower, forward expanding glabella, and the sutural ridge is prominent on the fixed cheeks. Glabellar furrows are further back, and on the expanding frontal lobe of the glabella, a third pair of furrows are visible as shallow pits. The protaspis (Pl. 23, Fig. 23) has a long, very narrow glabella, which expands forwards, short (trans.) glabellar furrows, the third pair rather shallow pits far forward on the frontal lobe of the glabella. Proto-pygidium less than half the length of the glabella, with two axial rings and one pair of strongly grooved pleurae. The differences between the width of the fixed cheeks of *T. thor* and *T. papulosus* are quite marked in larger cranidia (Fig. 12), but in cranidia of glabellar length about 1.6 mm or less, the two species are not distinguishable on this basis. Indeed, all small *Triarthrus*

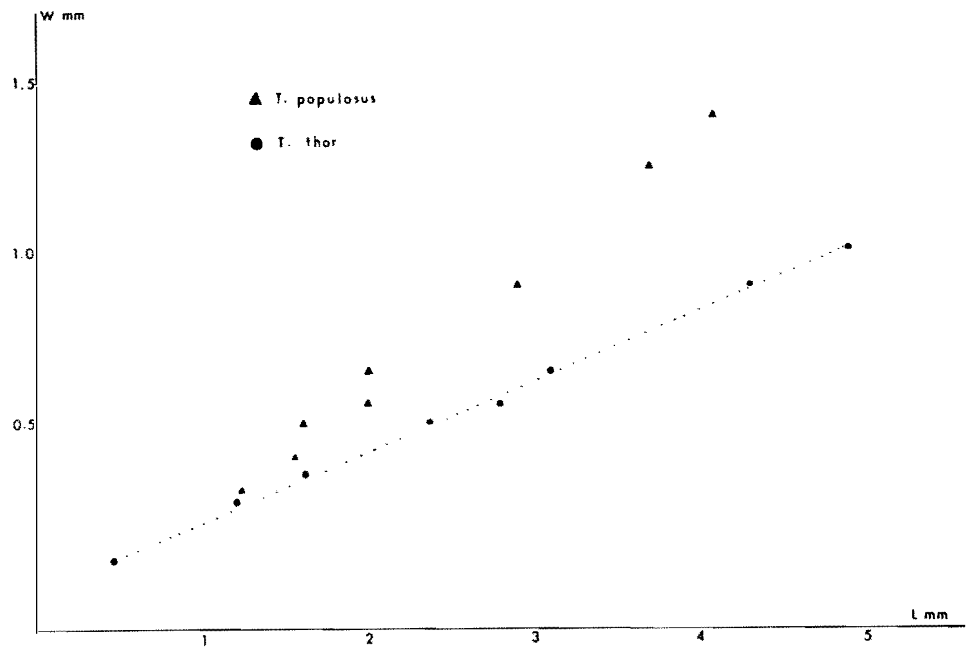


Fig. 12. Graph showing the relation of width of fixed cheek (W) to length of glabella (L) for *Triarthrus papulosus* n. sp. and *Triarthrus thor* n. sp. These species cannot readily be distinguished on any other measurable character.

cranidia in the present collections are extremely similar, and are probably not distinguishable into species on morphological grounds. In Fig. 12 measurements were made from single beds in which one species only of the adult cranidia was found, and the accompanying small cranidia were assumed to belong to that species.

T. turkestanicus Veber 1948 and *T. sinensis* Chang and Fan 1965 may be related to this species; they are insufficiently known for a meaningful comparison.

Triarthrus parapunctatus n. sp.

(Pl. 24, Figs. 1 – 4)

Stratigraphic range. — A rare trilobite of the Profilbekken Member, and the only olenid found in that part of the Valhallfonna Formation, specimens occurring between 20 and 40 m from the base of the Member (Whiterock stage — probably early Llanvirn).

Material. — Four cranidia, of which the holotype, SMA 84117 retains the exoskeleton. Other cranidia: SMA 84118, 84360, PMO NF 1386.

Diagnosis. — Cranidium only known. Punctate surface sculpture. Glabellar furrows very shallow both on external surface and on internal moulds, gently arcuate. Fixed cheeks narrow. Palpebral lobes small, far forward.

Discussion. — This species is the only known olenid with a strong punctate surface sculpture. In other respects it is closest to *Triarthrus thor* n. sp., from which it is distinguished in possessing very shallow, broad (exsag.), gently arcuate glabellar furrows, which are equally faint on internal moulds. Preglabellar field lacking, and there are apparently no pits in the anterior border furrow of this species. Anterior border narrow, gently convex.

It is of interest to note that within the species of Triarthrinae described here most types of surface sculpture are developed: ridges on *Bienvillia stikta*, granules on *Triarthrus papulosus*, and, most surprisingly, punctae on *T. parapunctatus.* The value such sculpture as an unequivocal specific character is obvious, as even small fragments of the exoskeleton can be identified, and sculpture may survive flattening or distortion.

Subfamily PLICATOLININAE ROBISON and PANTOJA-ALORS 1968

This subfamily was proposed by ROBISON and PANTOJA-ALORS (1968, p. 793) to include the genera *Plicatolina* SHAW 1951 and *Plicatolinella* ROBISON and PANTOJA-ALORS 1968. The subfamily has been reported from Argentina, Mexico, Norway, and the Eastern United States (Vermont) in rocks of Tremadocian age and in the Western United States in the upper Cambrian (TAYLOR 1971). The occurrence of *Plicatolina* in Spitsbergen is of particular interest, extending the stratigraphic range of the subfamily into the Arenigian, and the geographic range considerably northwards.

Genus *Plicatolina* SHAW 1951

Type species. — By original designation *Plicatolina kindlei* SHAW 1951

Plicatolina sp.

(Pl. 24, Fig. 8)

Stratigraphic range. — Olenidsletta, about 30 m from the base of the Olenidsletta Member.

Material. — A single cranidium PMO NF 2064.

Description. — The cranidium is flattened, and so the original convexity cannot be determined. The maximum width of the cranidium at the posterior margin is 1.6 times the sagittal length, cranidial outline trapezoidal. Glabella of tranverse width at the occipital ring equal to the sagittal length of the cranidium, maximum width just in front of the occipital ring, anteriorly tapering to its anterolateral corners, front margin truncate. Four pairs of deep, gently backward-inclined lateral glabellar furrows, extending far across the glabella to isolate a narrow median lobe, which narrows forwards as far as furrows 3P. The distance (exsag.) between successive pairs of glabellar furrows decreases anteriorly, while furrows 4P are far forward, almost at the anterolateral corners of the glabella, delimiting a narrow (exsag.) frontal lobe to the glabella. A depression running backwards on the midline bisecting the frontal lobe may represent a median furrow as in *Plicatolina kindlei* (SHAW 1951, Pl. 22, Fig. 13), although it may also be a product of crushing. Occipital furrow backward sloping for its lateral one third, medially transverse. Occipital ring of width (sag.) 0.2 sagittal length of glabella with a prominent median tubercle.

Palpebral lobes far forward, anterior limits opposite and close to the corners of the glabella, short and crescentic in outline, posteriorly outlined by shallow palpebral furrow. Preglabellar field narrow (less than 0.05 sag. length of glabella) of uniform width (sag., exsag.), anteriorly bounded by a deep narrow anterior border furrow and an extremely narrow (sag.) rim-like anterior border, gently curved towards the mid line. The relatively narrow (trans.) triangular postocular fixed cheeks carry a surface sculpture of scattered tubercles. Posterior border ill-defined, less than half the width (exsag.) of the occipital ring. Facial sutures cut the posterior border at 90 degrees, anteriorly converging forwards.

Discussion. — The relatively small, anteriorly positioned palpebral lobes close to the glabella indicate that this species should be assigned to *Plicatolina* rather than to *Plicatolinella.* In size and position of the palpebral lobes and in the form of the glabellar furrows this species compares closely with both *Plicatolina kindlei* SHAW (1951, p. 103, Pl. 22, Figs. 11 — 17) and *P. scalpta* HARRINGTON and LEANZA (1957, p. 111, Figs. 40, 41). From both it is distinguished by its narrow preglabellar field, and transversely narrower postocular cheeks which are only about one third the width of the glabella across the occipital ring, compared with two thirds the glabellar width in *P. kindlei* and *P. scalpta.* Although clearly a distinct species, I do not feel justified in naming it formally as such on the basis of the single cranidium known at present.

Glossary of new names, derivation of names

alveus (Latin) — a beehive, referring to the glabellar outline of *Tropidopyge alveus* n. sp.

anataphra (Greek) — without pitting

Anaximander (Greek) — Greek philosopher, and early recorder of geological observations (Masculine)

Balnibarbi — Mythical country visited by Lemuel Gulliver in SWIFT's *Gulliver's Travels*, populated by eccentric natural philosophers (Feminine)

brevifrons (Latin) — short front

ceryx (Greek) — a herald

clavatus (Latin) — cleft, referring to bisected front margin of glabella of *Anaximander clavatus* n. gen., n. sp.

comma — punctuation mark with similar appearance to palpebral lobe of *Psilocara comma* n. gen., n. sp.

Cloacaspis (Latin) — a sewer, referring to the stinkstones in which these trilobites are particularly common (+ — *aspis*) (Feminine)
dejecta (Latin) — downcast
ekphymosa (Greek) — an eructation of pimples
erugata (Latin) — smooth
hamus (Latin) — a hook, referring to the shape of the glabellar furrows of *Svalbardites hamus* n. gen., n. sp.
hebaxis (Latin) — blunt (+ — *axis*)
latigena (Latin) — wide cheeks
papulosus (Latin) — granulate
patagiatum (Latin) — with a border
Psilocara (Greek) — smooth-head
pulvurea (Latin) — covered with fine dust
scimitar — referring to the Persian weapon of the same name, the outline of which resembles the preglabellar field of *Balnibarbi scimitar* n. sp.
senilis (Latin) — like an old man
sombrero — Mexican hat with a broad brim
stikta (Latin) — pricked by a pin
Svalbardites — Svalbard is the group name for the islands including Spitsbergen (+ - *ites*) (Masculine)
tholia (Greek) — comical hat in Greek drama
thor — thunder god of Norse mythology, who carried a hammer resembling the glabella of *Triarthrus thor* n. sp.
venulosa (Latin) — veined

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Plates 1—24

Specimens blackened with photographic opaque and whitened with ammonium chloride before photography. Specimens preserved in relief are orientated such that the plane running through the posterior margin of the occipital or axial ring is vertical. For specimens with large palpebral lobes the dorsal view used here is closely similar to the "palpebral view", i.e. the orientation with the palpebral lobes horizontal.

Figured material is in the collections of the Paleontologisk Museum, Oslo (PMO NF) or the Sedgwick Museum, Cambridge (SMA).

PLATE 1

Fig. 1–8. *Balnibarbi pulvurea* n. gen., n. sp. .... (p. 21)

Fig. 1–4. Holotype, PMO NF 732, cranidium retaining exoskeleton. Fig. 1–3 × 4, dorsal, lateral and anterior views. Fig. 4 × 25, detail of the right anterior part of the cranidium showing granulate surface sculpture on the glabella and preglabellar field, caeca on the preglabellar field and pits in the anterior border furrow. Profilstranda, 75m from base of Olenidsletta Member.

Fig. 5, 6. Hypostoma, PMO NF 730, × 9, in ventral and lateral views. Same bed as holotype.

Fig. 7. Detail of macula of hypostoma, SMA 84021, × 15, showing minute pits impressed upon the internal mould of the exoskeleton. Same bed as holotype.

Fig. 8. Very small cranidium, × 12, SMA 84018, from the same hed as as the other material on Plate 1.

PLATE 1

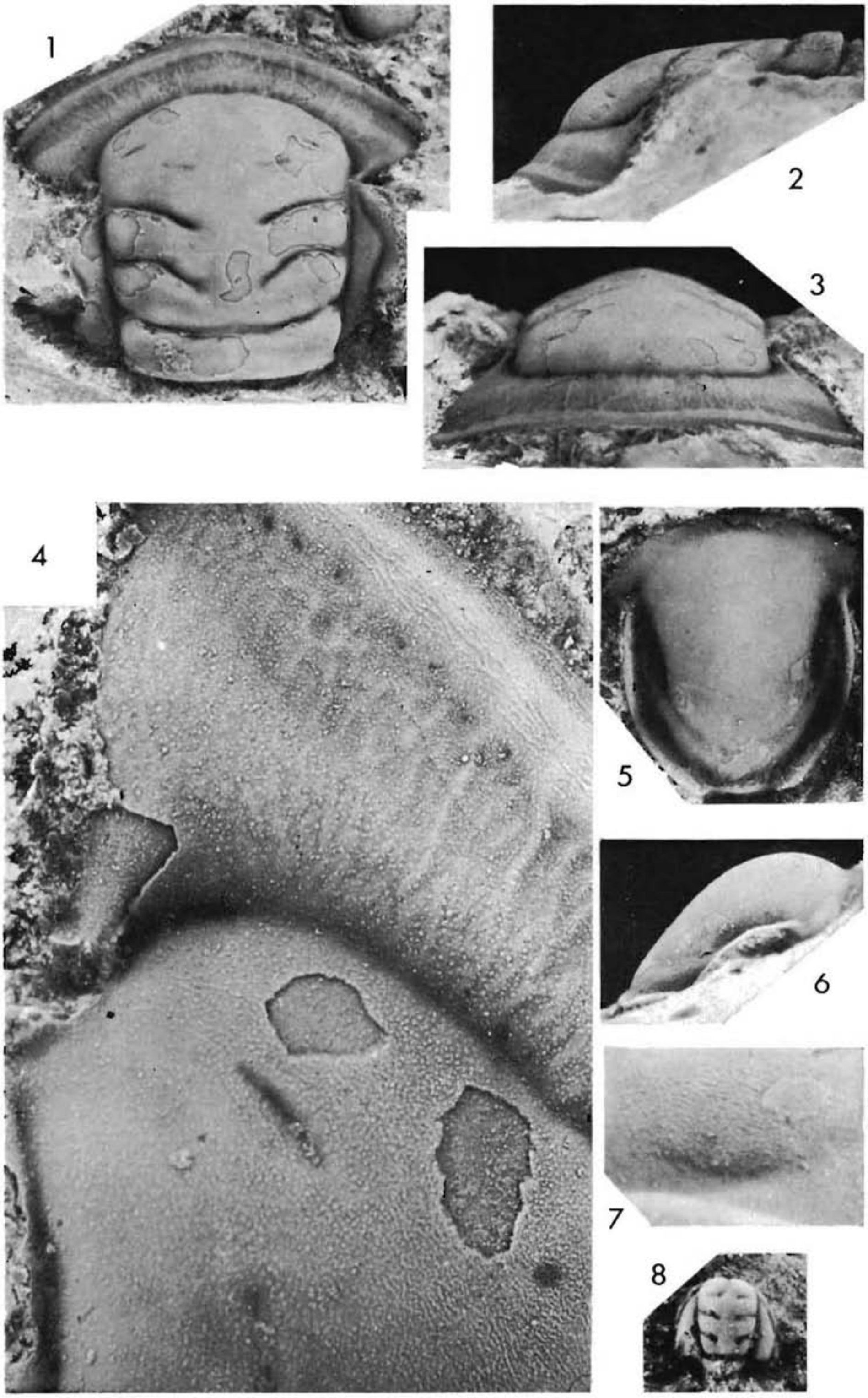


PLATE 2

Fig. 1–5. *Balnibarbi pulvurea* n. gen., n. sp. .... (p. 21)

Fig. 1. Flattened cranidium, PMO NF 3017, × 1.5. Shore section along Olenidsletta about 60m from base of Olenidsletta Member.

Fig. 2. Free cheek, PMO NF 3019, × 1.5, from the same bed as the cranidium of Fig. 1. Note genal caeca and backward directed principal genal vein.

Fig. 3. Thorax and pygidium, PMO NF 3027, × 1.5. Same bed as the other parts of the dorsal exoskeleton in Fig. 1 and Fig. 2. Incomplete on left side.

Fig. 4. Stratigraphically earliest cranidium, PMO NF 2068, × 2. 28m from base of Olenidsletta Member in shore section at Olenidsletta.

Fig. 5. Pygidium, SMA 84015, × 3. Dorsal surface removed to show doublure and terrace lines. 75m from base of Olenidsletta Member on Profilstranda.

PLATE 2

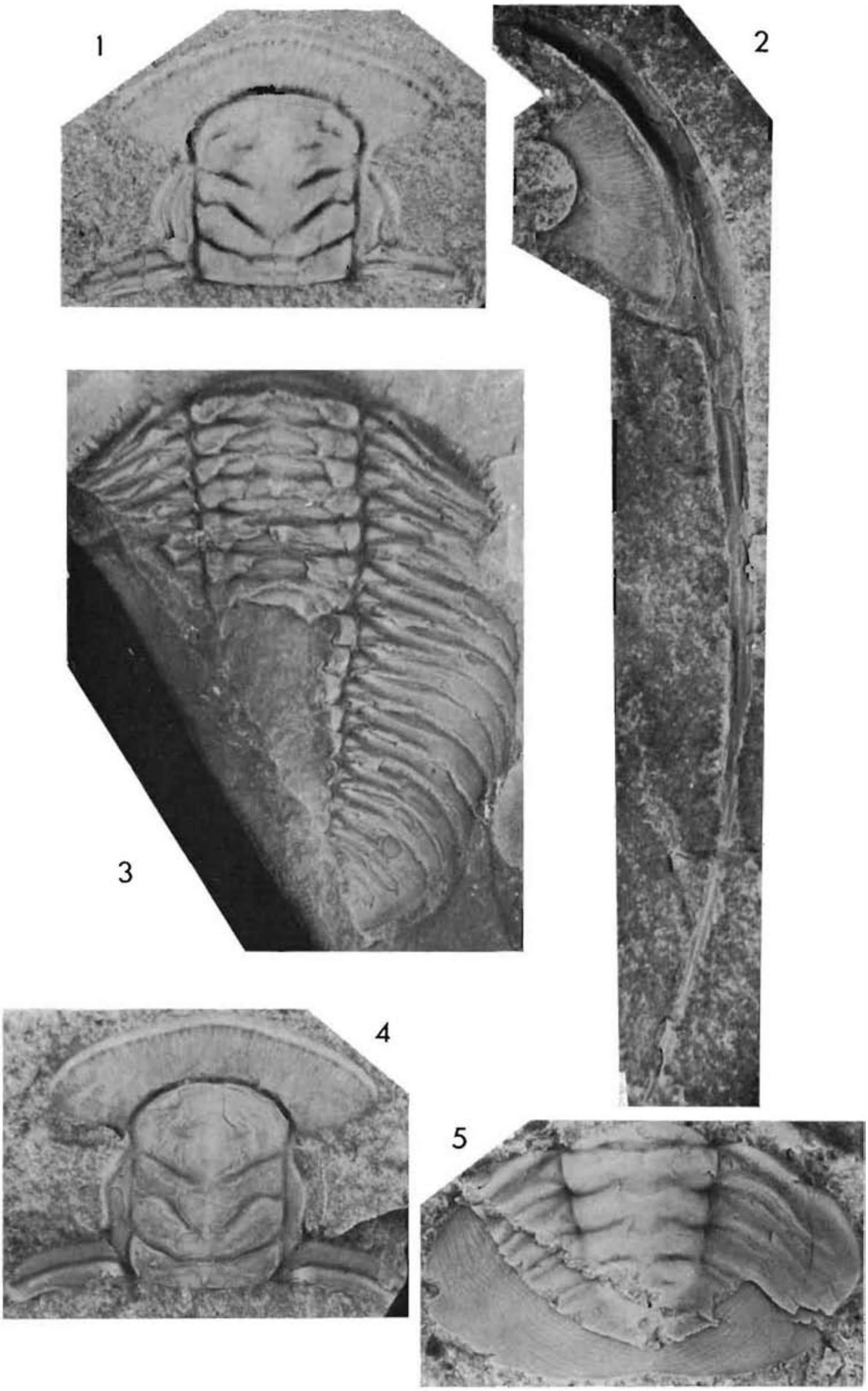


PLATE 3

Fig. 1. *Balnibarbi pulvurea* n. gen., n. sp. .... (p. 21)

Fig. 1. Free cheeks, PMO NF 3018, × 1.5. This specimen shows the fused nature of the free cheeks, which are connected by a relatively narrow strip of ventral doublure. Along shore at Olenidsletta 60m from base of Olenidsletta Member, from the same horizon as the specimens figured on Plate 2, Figs. 1–3.

Fig. 2. Detail of the mid part of the doublure of the previous specimen, × 10, showing perforated nodes on the doublure.

Fig. 3, 5, 7. Pygidium, PMO NF 765, × 6, in dorsal, posterior and lateral views, from the same bed as the holotype, Plate 1, Fig. 1–4. Note presence of triangular pleural nodes adjacent to first two axial rings.

Fig. 4, 6. Small cranidium, PMO NF 714, × 4, dorsal and lateral views. Same horizon as holotype, Plate 1, Figs. 1–4.

Fig. 8. Flattened pygidium, PMO NF 3021, × 2. Same bed as the free cheeks in Fig. 1.

PLATE 3

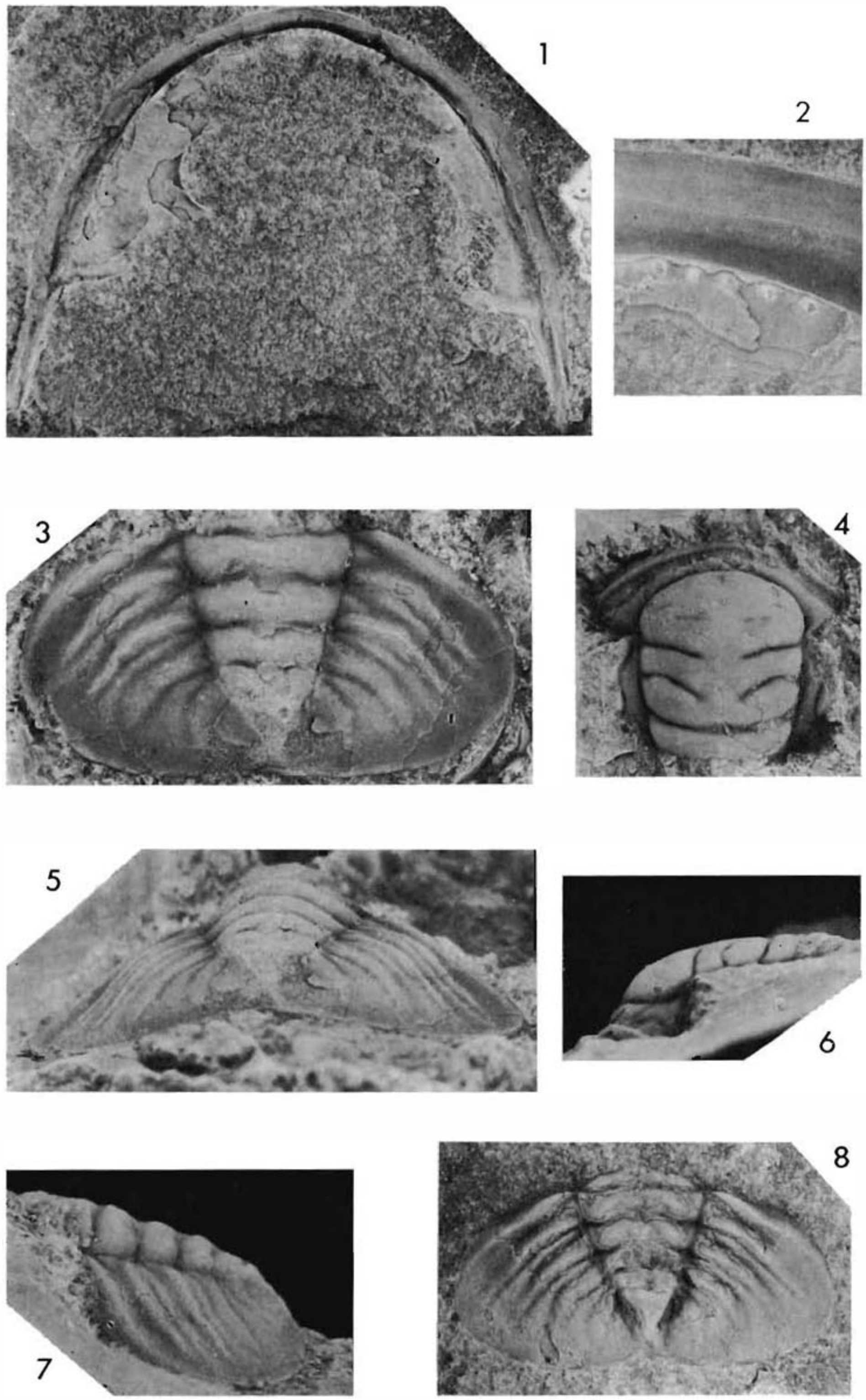


PLATE 4

Fig. 1–9. *Balnibarbi tholia* n. sp. .... (p. 35)

Fig. 1. × 15, Detail of anterior part of glabella and preglabellar field of an incomplete cranidium, SMA 84025, showing surface sculpture. Same bed as holotype, Figs. 2–4.

Fig. 2–4. Holotype, cranidium, SMA 84024, × 3, in dorsal, lateral and anterior views. Cranidium partly exfoliated, and incomplete of right side. Profilstranda, in a bed of grey, crystalline limestone 76m from base of the Olenidsletta Member.

Fig. 5, 6. Incomplete cranidium, PMO NF 400, × 3. Stratigraphically highest specimen, and the youngest *Balnibarbi* in Spitsbergen. Profilstranda, 90m from base of Olenidsletta Member.

Fig. 7. Exfoliated cranidium, SMA 84026, × 3. From the same bed as holotype, Figs. 2–4.

Fig. 8, 9. Incomplete exfoliated pygidium, SMA 84027, × 2, in dorsal and lateral views. From the same bed as the holotype, Figs. 2–4.

PLATE 4

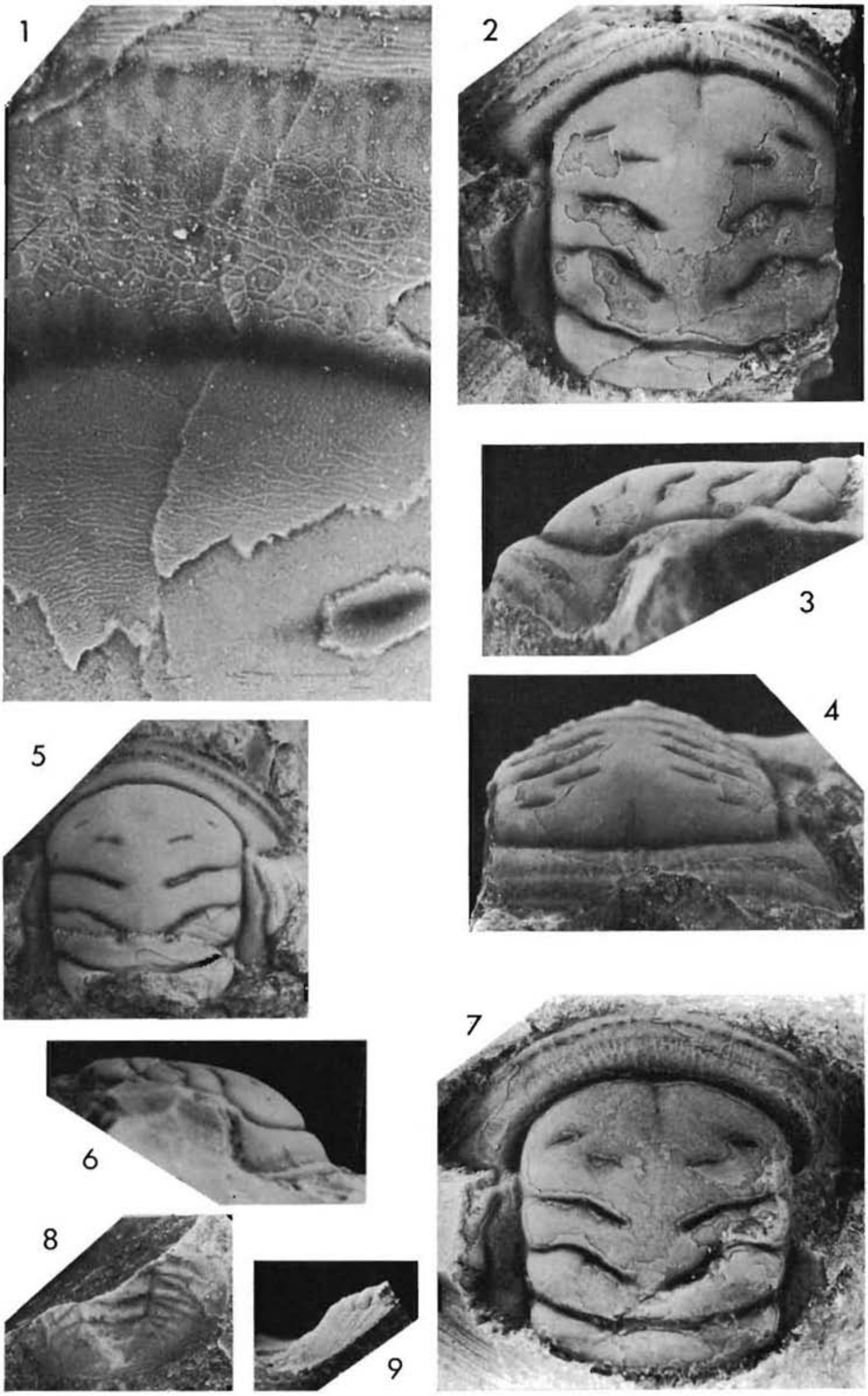


PLATE 5

Fig. 1–10. *Balnibarbi erugata* n. gen., n. sp. .... (p. 31)

Fig. 1–3. Holotype. cranidium, PM● NF 3016, × 3, in dorsal, lateral and anterior views. Cranidium in full relief, largely exfoliated, with left postocular fixed cheek preserved. Profilstranda, 65m from base of ●lenidsletta Member.

Fig. 4. Small cranidium, PM● NF 3030, × 10. Note relatively shorter preglabellar field. Profilstranda, 75m from base of ●lenidsletta Member.

Fig. 5. Latex cast of a pair of fused free cheeks, PM● NF 843, × 3. Note narrow strip of ventral doublure connecting the cheeks. Small pygidium in the centre belongs to *Opipeuter inconnivus* Fortey. Profilstranda, 60m from base of ●lenidsletta Member.

Fig. 6–8. Pygidium, PM● NF 715, × 6.5, in lateral, dorsal and posterior views. Profilstranda, 75m from base of ●lenidsletta Member.

Fig. 9. Latex cast of well-preserved flattened cranidium, SMA 84042, × 2. Profilstranda, about 60m from base of ●lenidsletta Member.

Fig. 10. Detail of doublure connecting free cheeks, SMA 84046, × 15, showing impressions of caeca running between nodes on posterior part of the doublure.

PLATE 5

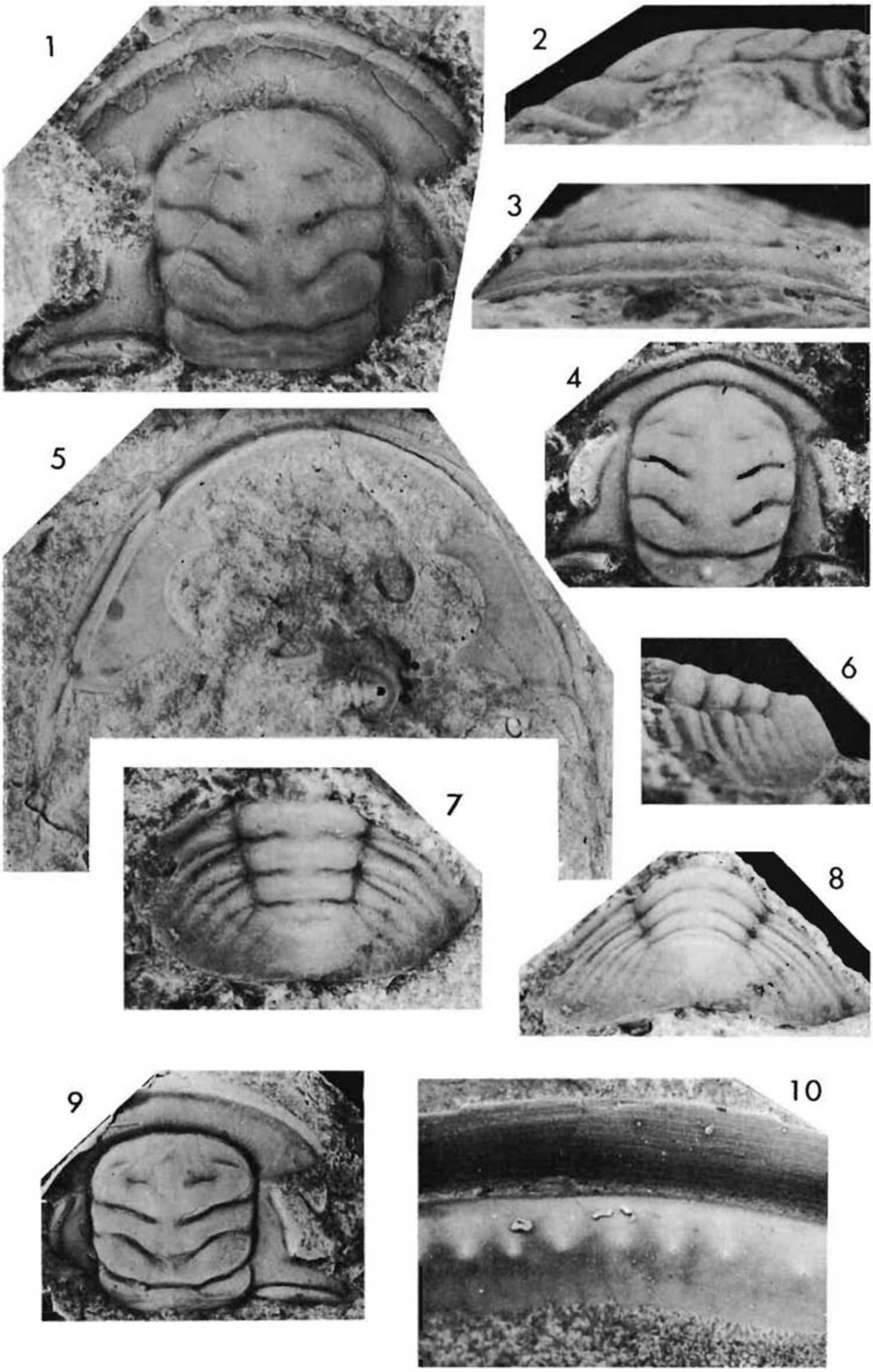


PLATE 6

Fig. 1–4. *Balnibarbi sombrero* n. gen., n. sp. .... (p. 32)

Fig. 1, 2. Holotype. cranidium, PMO NF 835, × 3. Fig. 2 shows detail of preglabellar field (× 5), showing lack of pits and sculpture. Profilstranda, 35m from base of Olenidsletta Member.

Fig. 3. Incomplete cranidium, SMA 84041, × 2. Profilstranda, about 24m from base of Olenidsletta Member.

Fig. 4. Small cranidium PMO NF 2054, × 3. Badly crushed. Shore section at Olenidsletta, 17m from base of Olenidsletta Member.

Fig. 5. *Balnibarbi scimitar* n. gen., n. sp. .... (p. 33)

Fig. 5. Flattened cranidium, PMO NF 2071, × 4. Cranidium with pits in border furrow like *B. scimitar*, and comparable postocular facial sutures, occurring just below first *B. sombrero*. Shore section along Olenidsletta, about 10m from base of Olenidsletta Member.

PLATE 6

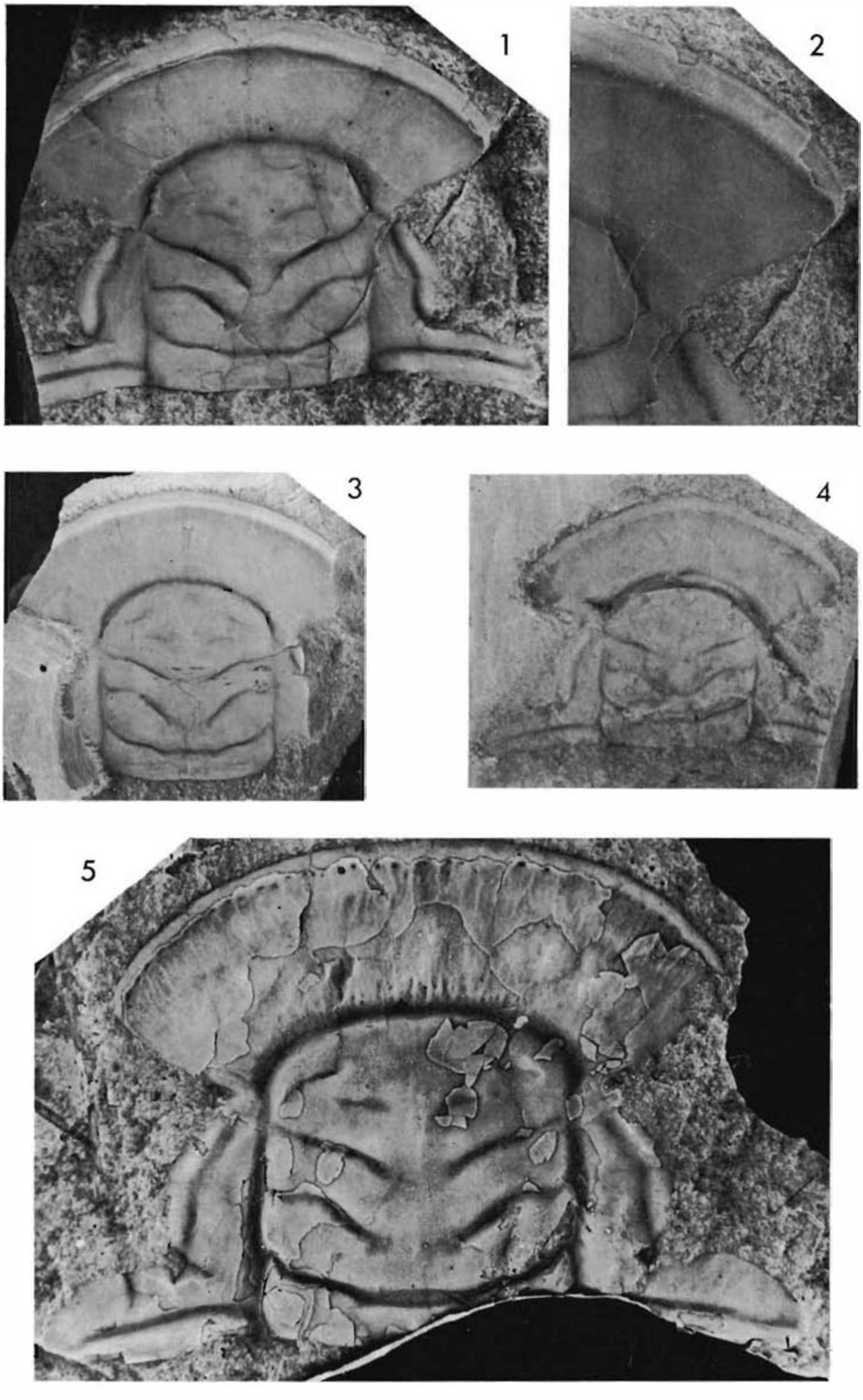


PLATE 7

Figs. 1–10. *Balnibarbi scimitar* n. gen., n. sp. .... (p. 33)

Fig. 1, 3, 8. Holotype, cranidium, PMO NF 2785, × 6, in dorsal, oblique and lateral views. Bed not more than 6m from base of Olenidsletta Member, on melt stream D on Olenidsletta.

Fig. 2. Free cheek, PMO NF 14, × 9. Note strong principal genal vein transversely directed and passing into marginal rim. Same horizon as holotype.

Fig. 4. Fused free cheeks, PMO NF.

Fig. 5, 7. Incomplete thorax of twelve segments, PMO NF 3031, × 4, in lateral and dorsal views. Same horizon as holotype.

Fig. 6. Pygidium, PMO NF 3045, × 5. Same horizon as holotype.

Fig. 9. 10. Small cranidium, PMO NF 2768, × 6, in dorsal and lateral views. Same horizon as holotype.

PLATE 7

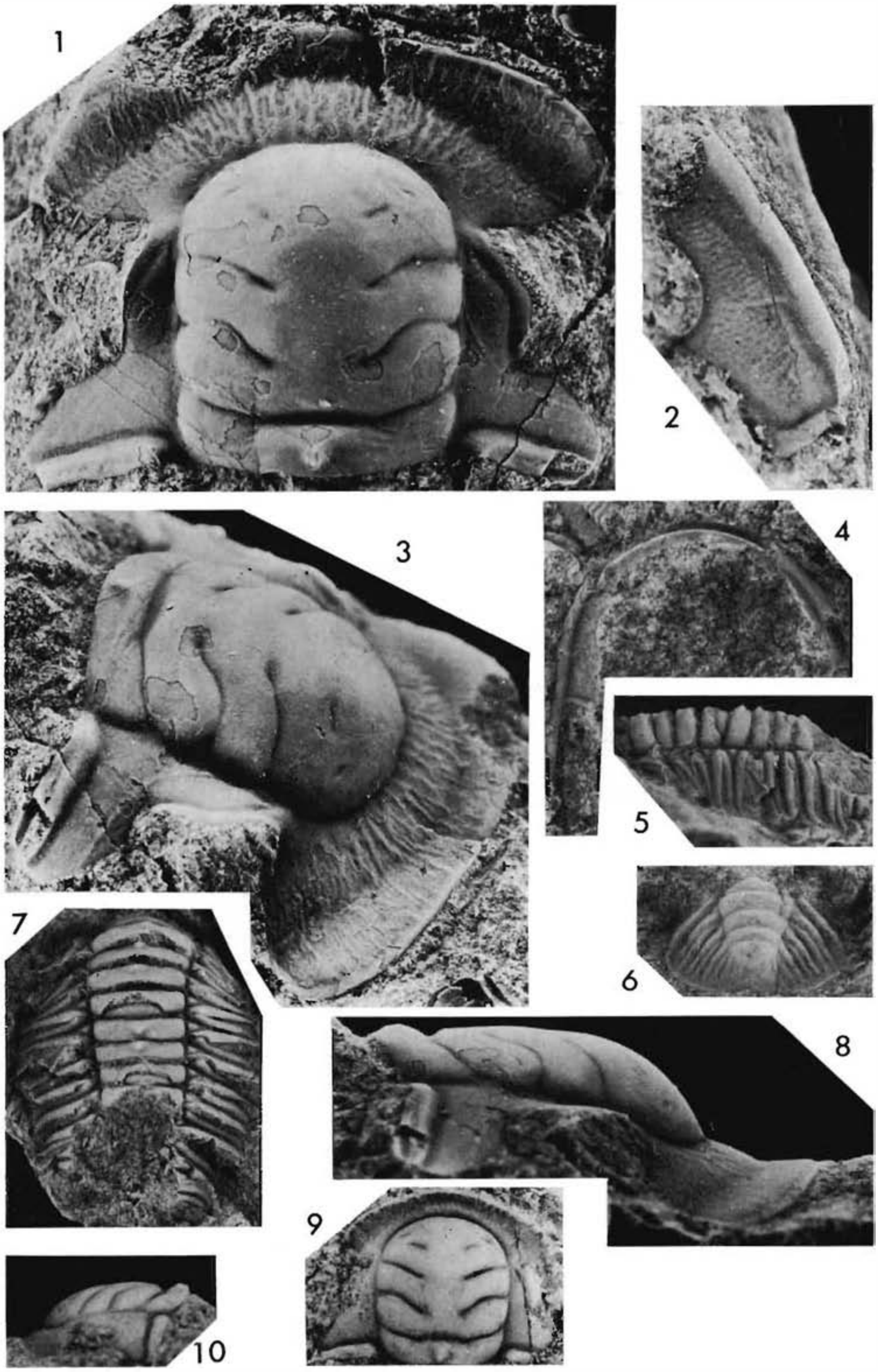


PLATE 8

Fig. 1–6. *Balnibarbi ceryx ceryx*, n. gen., n. sp., n. subsp. .... (p. 28)

Fig. 1. Holotype, cranidium, SMA 84034, × 4. The cranidium is flattened. Profilstranda, 10m from base of Olenidsletta Member.

Fig. 2. Pygidium, SMA 84036, × 5. View of slightly crushed specimen. Note strong anterior pair of pleural nodes, faint suggestion of second pair. Same horizon as holotype.

Fig. 3. Large cranidium, SMA 84039, × 3, from the same horizon as the holotype, Fig. 1.

Fig. 4. Detail of preglabellar field of cranidium, SMA 84040, × 30. Note granulation of anterior part of preglabellar field, pits in border furrow and caeca passing between the pits. Specimen from the same horizon as the holotype, Fig. 1.

Fig. 5. Stratigraphically high cranidium, PMO NF 2074, × 4. Incomplete on left side. Shore section of Olenidsletta, 20m from base of Olenidsletta Member.

Fig. 6. Free cheeks, SMA 84035, × 2. Note forward curve of posterior border to genal spine. Same horizon as holotype, Fig. 1.

PLATE 8

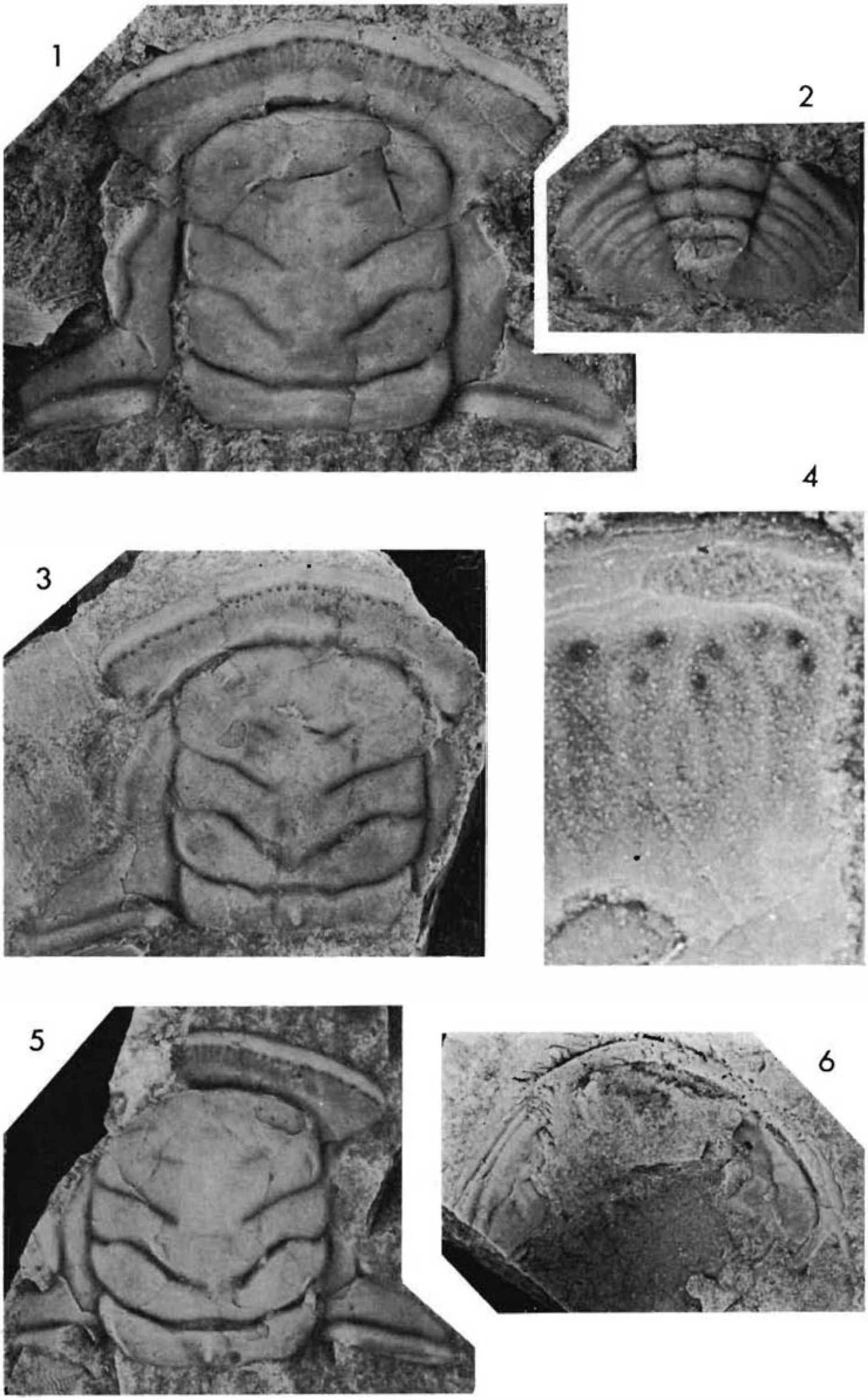


PLATE 9

Fig. 1, 3, 4. *Balnibarbi ceryx ceryx* n. gen., n. sp., n. subsp. .... (p. 28)

Fig. 1, 3. Cranidium, PMO NF 3033, × 4. Dorsal and lateral views of a specimen preserved in full relief. Melt stream C on Olenidsletta, about 7m from base of Olenidsletta Member.

Fig. 4. Small cranidium, SMA 84037, × 5. Compare with cranidium of *B. ceryx anataphra*, Fig. 7. Profilstranda, 10m from base of Olenidsletta Member.

Fig. 2. *Balnibarbi scimitar* n. sp. .... (p. 33)

Fig. 2. Cranidium, PMO NF 17, × 4. From the same bed as the holotype, Plate 7, Fig. 1.

Fig. 5–7. *Balnibari ceryx anataphra* n. gen., n. sp., n. subsp. .... (p. 30)

Fig. 5. Small cranidium, PMO NF 643, × 10. Profilstranda, 8m from base of Olenidsletta Member.

Fig. 6. Free cheek PMO NF 642, × 5. Same bed as previous specimen.

Fig. 7. Holotype, cranidium, PMO NF 651, × 10. Partly flattened. Profilstranda, 8m from base of Olenidsletta Member, in same bed as material figured on Figs. 5, 6.

PLATE 9

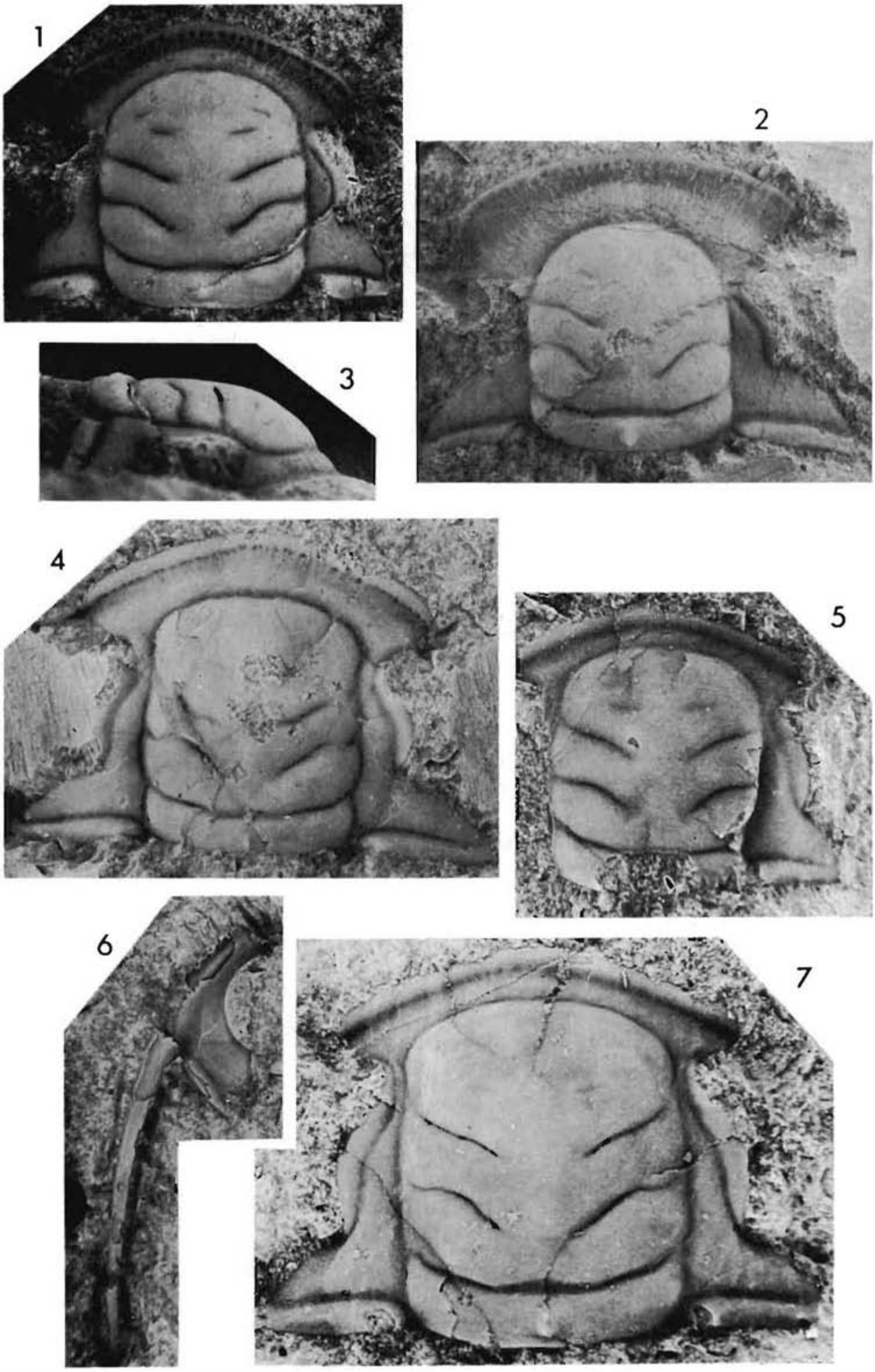


PLATE 10

Fig. 1–16. *Cloacaspis senilis* n. gen., n. sp. .... (p. 36)

Fig. 1–3. Holotype, SMA 84050, × 4. Partly exfoliated cranidium in dorsal, anterior and lateral views. Profilstranda, 130m from base of Olenidsletta Member.

Fig. 4, 5. Cranidium, SMA 84051, × 4, in dorsal, lateral views. Profilstranda, 140m from base of Olenidsletta Member.

Fig. 6. Cranidium, SMA 84053, × 3. Stratigraphically low specimen close to *C. ekphymosa* n. sp. Profilstranda 121m from base of Olenidsletta Member.

Fig. 7–9. Pygidium, SMA 84052, × 7, in dorsal, posterior and lateral views. Same bed as cranidium of Figs. 4, 5. Note minute pleural nodes adjacent to the anterior axial ring.

Fig. 10, 11. Pygidium, SMA 84054, × 5. Slightly damaged on left side. Same bed as cranidium of Figs. 4, 5.

Fig. 12, 15. Fused free cheeks, SMA 84055, × 2, in plan and lateral views. Exact horizon not known, specimen obtained from isolated limestone exposure of Profilstranda about 130m from base of Olenidsletta Member.

Fig. 13. Large cranidium, SMA 84056, × 1.4. Profilstranda, about 140 m from base of Olenidsletta Member.

Fig. 14. Small, probably incomplete thorax, SMA 84057, × 4. Note relatively small pygidium detached on right side, penultimate segment with long axial spine. About 140m from the base of the Olenidsletta Member.

Fig. 16. Detail of the anterior part of the holotype cranidium, Figs. 1–3, × 8. Note surface sculpture of ridges, large pits in border furrow, and smooth line on glabella representing the anterior glabellar furrow.

PLATE 10

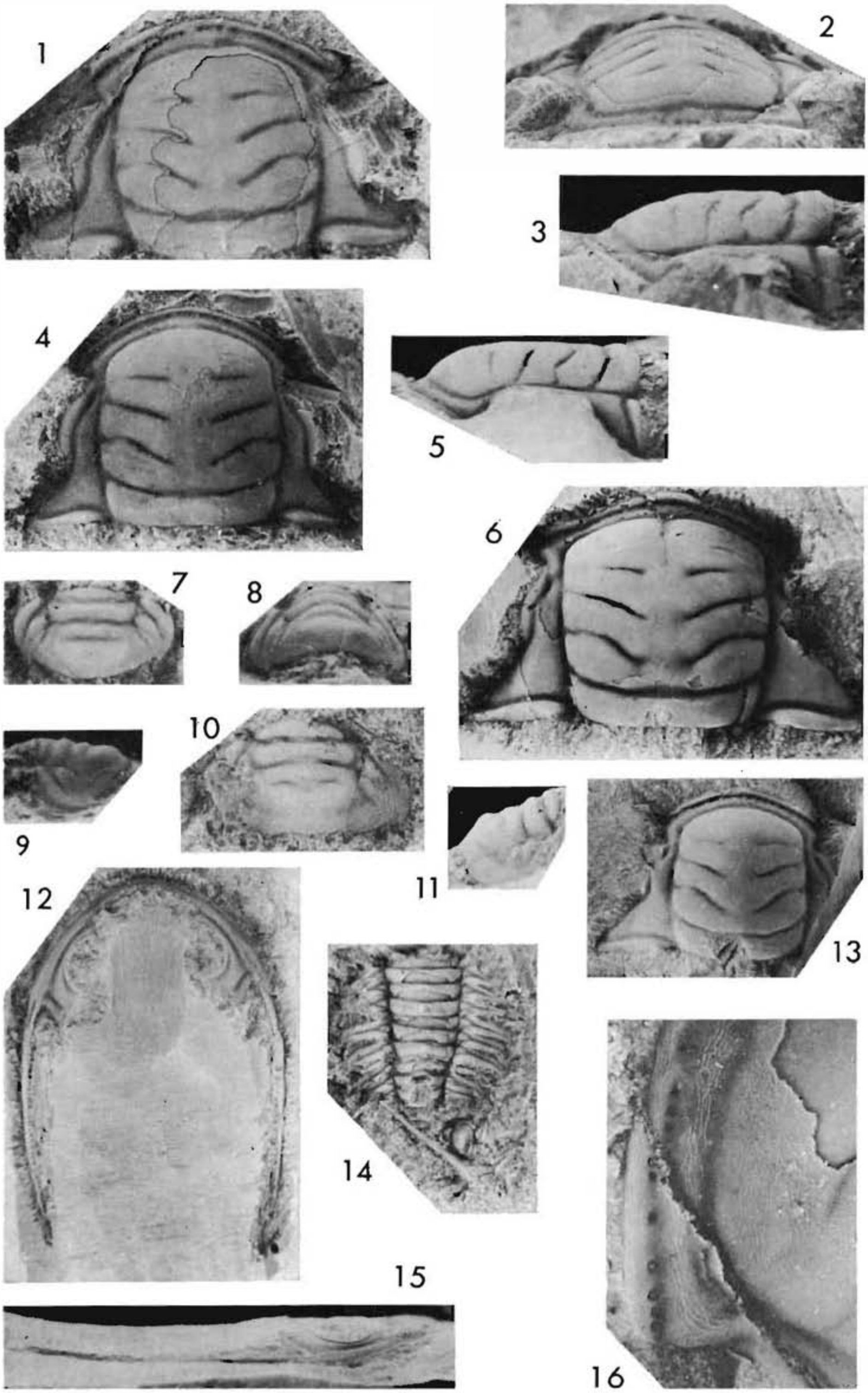


PLATE 11

Fig. 1–11, 13. *Cloacaspis senilis* n. gen., n. sp. .... (p. 36)

Fig. 1. Small cranidium, SMA 84058, × 4. Same bed as large cranidium on Plate 10, Figs. 4, 5.

Fig. 2. Small cranidium, SMA 84059, × 4, from same bed as the holotype, Plate 10, Figs. 1–3.

Fig. 3, 4, 8. Very small cranidium, SMA 84060, × 12, in dorsal and lateral views. Fig. 8, oblique view, × 40, showing granulation, well impressed glabellar furrows, and post-palpebral furrow on right of cheek. Profilstranda, 140m from base of Olenidsletta Member.

Fig. 5, 6. Possible meraspis cranidium, SMA 84061, × 8, in dorsal and lateral views. From the same bed as the cranidium in Fig. 1.

Fig. 7. Merapsis cranidium, SMA 84062, × 8. Note inflated glabellar lobes. Same bed as cranidium in Fig. 1.

Fig. 9–11. Smallest cranidium, SMA 84063, × 20, in dorsal lateral and anterior view. Profilstranda, about 130m from base of Olenidsletta Member.

Fig. 13. Hypostoma, SMA 84064, × 5. Profilstranda, about 130m from base of Olenidsletta Member.

Fig. 12, 14–18. *Cloacaspis ekphymosa* n. gen., n. sp. .... (p. 41)

Fig. 12. Holotype, cranidium, SMA 84065, × 4. Profilstranda, 115m from base of Olenidsletta Member.

Fig. 14, 16. Cranidium, SMA 84066, × 4, Fig. 16 detail of posterolateral part × 15 showing the granulation of the dorsal surface and on the left the postpalpebral furrow. Same bed as holotype.

Fig. 15. Large cranidium, SMA 84067, × 4, from same bed as holotype.

Fig. 17, 18. Pygidium, SMA 84068, × 5, in dorsal and lateral views. Profilstranda, about 110m from base of Olenidsletta Member.

PLATE 11

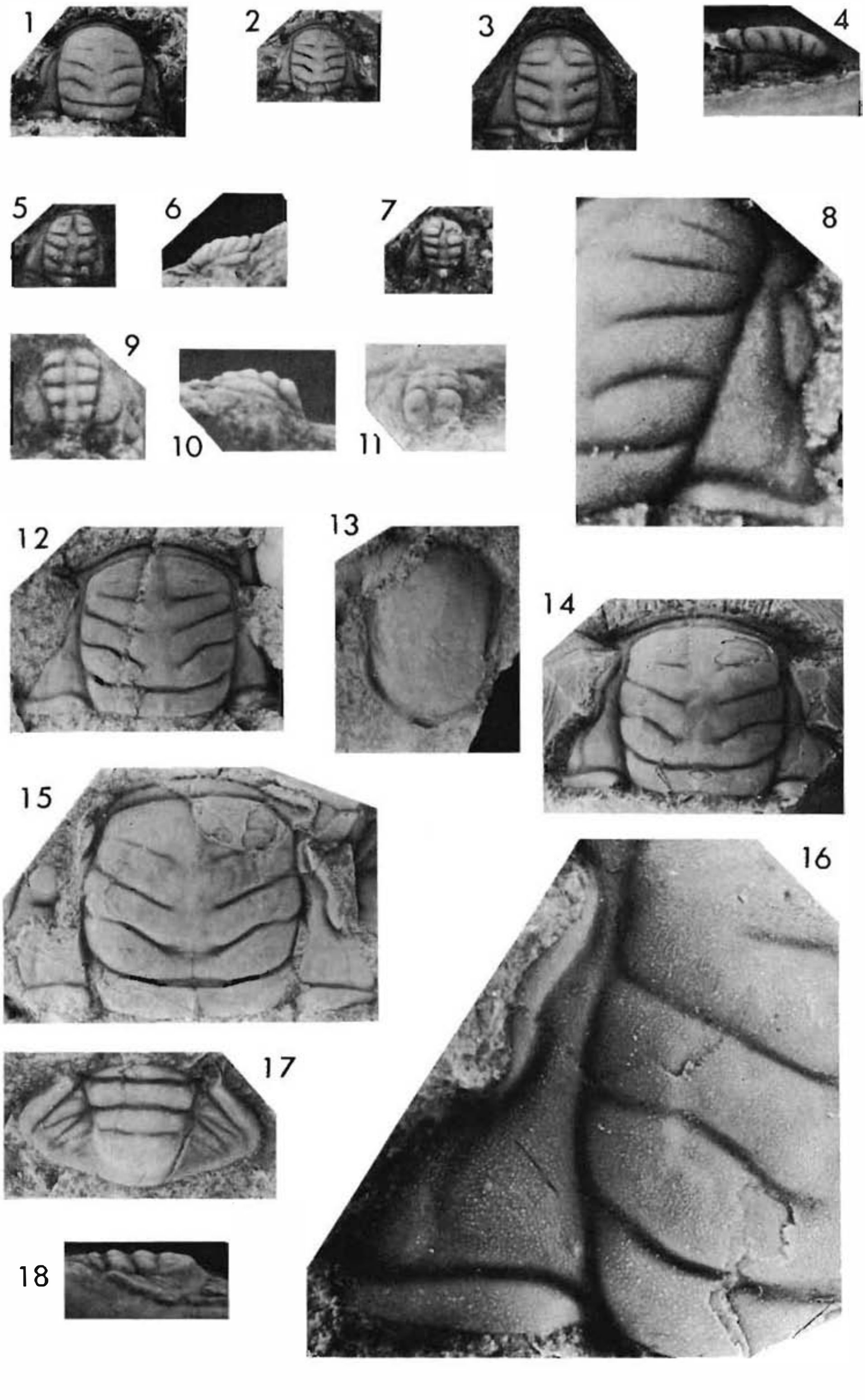


PLATE 12

Fig. 1–6. *Cloacaspis dejecta* n. gen., n. sp. .... (p. 42)

Fig. 1. Latex cast of disarticulated exoskeleton lacking cranidium, PMO NF 1869, × 2. This specimen probably represents the undisturbed parts in moulting position. Shore section along Olenidsletta 30m from base of Olenidsletta Member.

Fig. 2. Holotype, cranidium, PMO NF 2058, × 2. Slightly crushed. Shore section along Olenidsletta, 28m from base of Olenidsletta Member.

Fig. 3. Cranidium, PMO NF 820, × 6. Profilstranda, 38m from base of Olenidsletta Member.

Fig. 4, 5. Pygidium, PMO NF 3034, × 4, in dorsal and lateral views. Profilstranda, about 30m from base of Olenidsletta Member.

Fig. 6. Detail of posterior part of the cranidium in Fig. 3, × 15 showing fine granules confined to the furrows.

Fig. 7. *Cloacaspis senilis* n. gen., n. sp. .... (p. 36)

Fig. 7. Cranidium, PMO NF 2976, × 3. Similarly flattened to specimens of *C. dejecta*, note particularly absence of depressed anterior part of preglabella field, and few, large pits in the border furrow. Olenidsletta, within top 10m of Olenidsletta Member, south of melt stream A.

PLATE 12

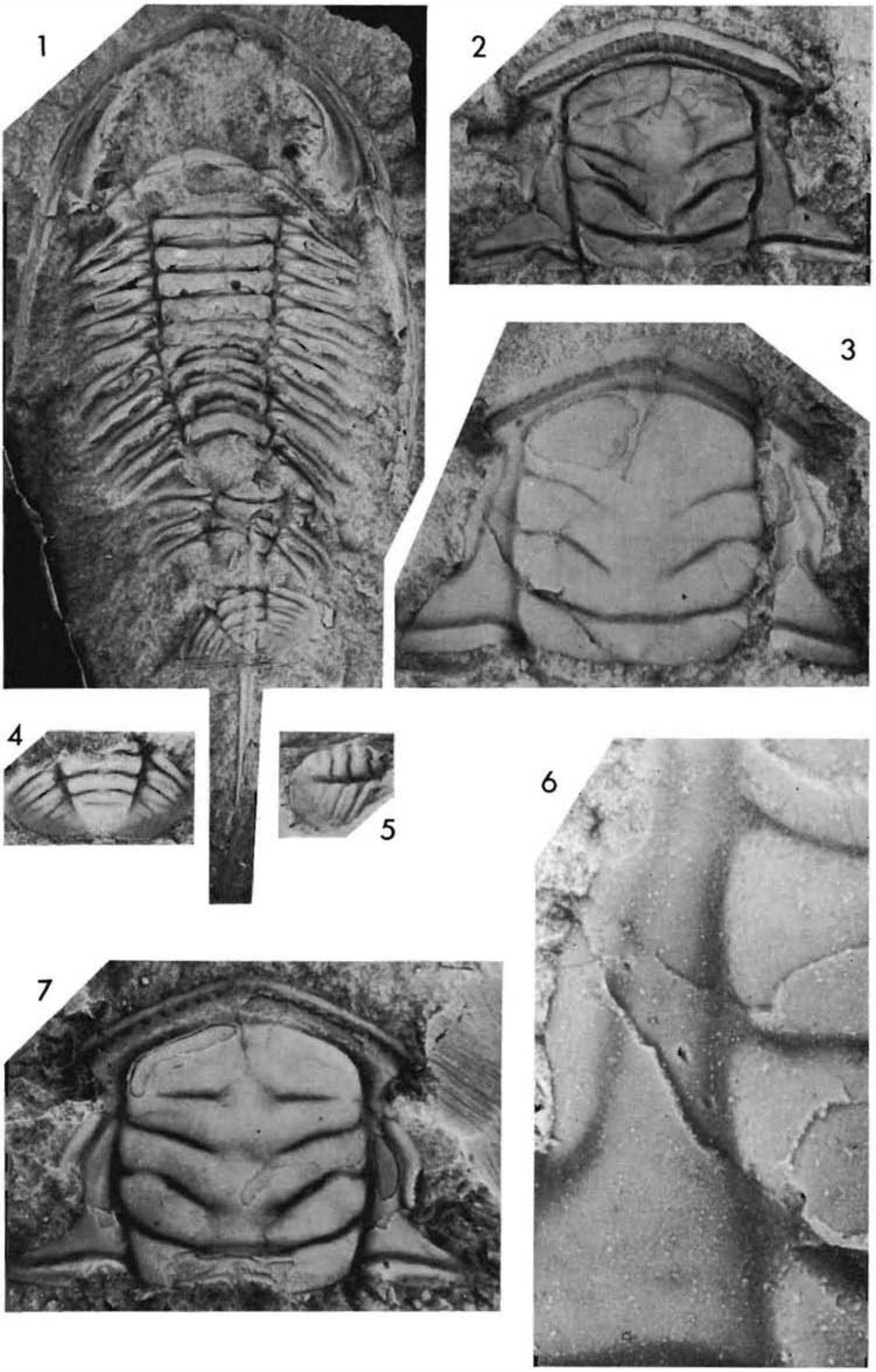


PLATE 13

Fig. 1–9. *Hypermecaspis latigena* n. sp. .... (p. 45)

Fig. 1. Large cranidia, PMO NF 3001, × 4. Profilstranda, 115m from base of Olenidsletta Member. Note extreme thinness of dorsal exoskeleton.

Fig. 2, 8. Holotype, cranidium, PMO NF 3002, × 5, in left lateral and dorsal views. This specimen is surrounded by stipes of *Isograptus* sp. Profilstranda, 115m from base of Olenidsletta Member.

Fig. 3, 4. Incomplete pygidium, PMO NF 1154, × 6, in dorsal, lateral views. Upper part of Olenidsletta Member on Profilbekken.

Fig. 5, 6. Small, partly exfoliated cranidium, SMA 84070, × 6, in dorsal and lateral views.

Fig. 7. Very small cranidium, SMA 84071, × 13, from the same bed as the cranidium in Figs. 5, 6, showing a strong furrow bisecting the frontal lobe of the glabella.

Fig. 9. Right free cheek, PMO NF 3003, × 3, showing broad border, genal spine, and terrace lines on doublure. From the same bed as the holotype.

PLATE 13

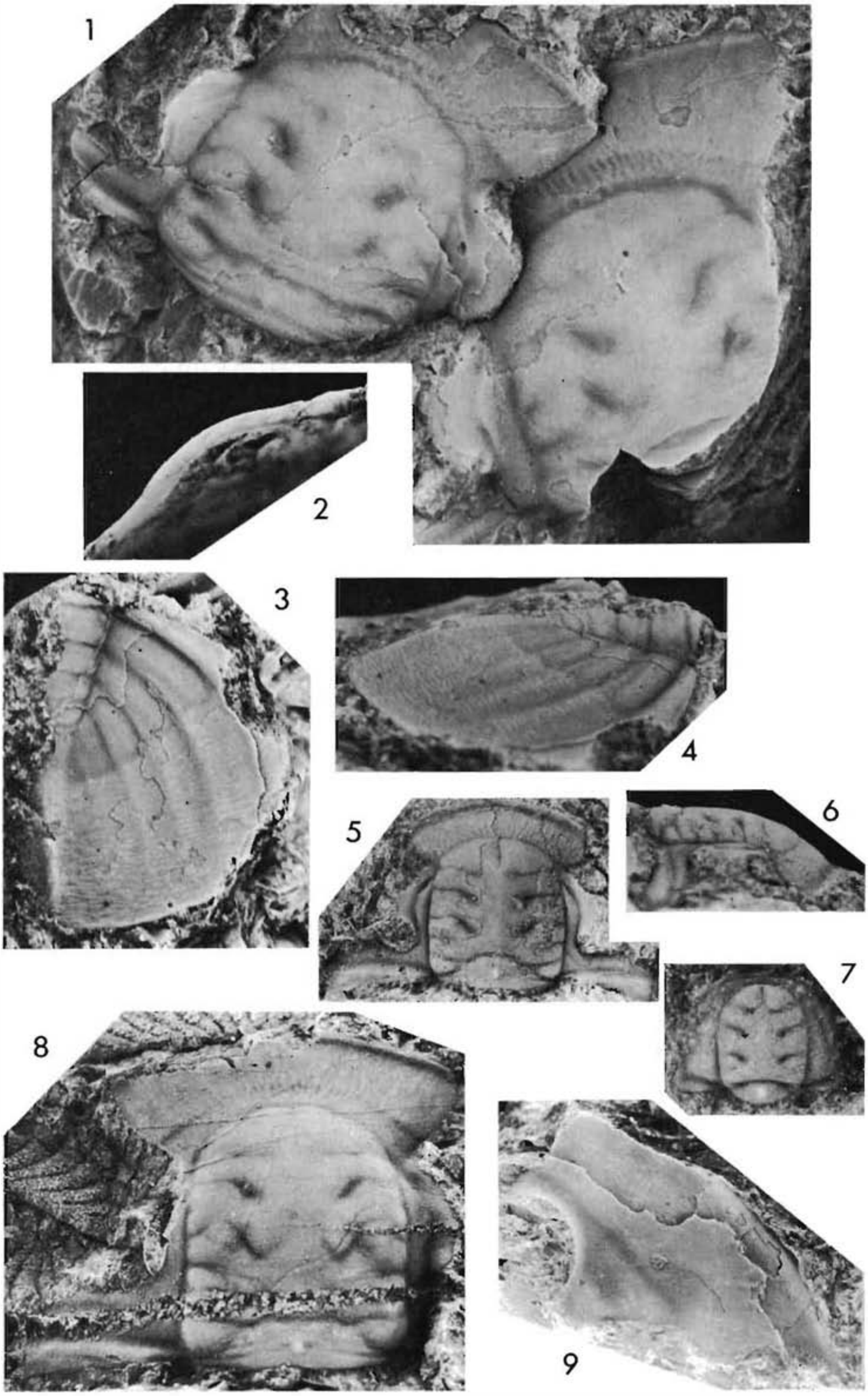


PLATE 14

Fig. 1–9. *Hypermecaspis brevifrons* n. sp. .... (p 48)

Fig. 1, 3. Holotype, cranidium, SMA 84072, in dorsal (× 3) and lateral (× 2) views. Largely exfoliated. Profilbekken, in black limestones from the upper 10m of the Olenidsletta Member exposed there.

Fig. 2. Right free cheek, SMA 84077, × 7. This specimen shows the caeca particularly well, and the principal genal vien cutting across the caeca. Same horizon as the holotype, Figs. 1, 3.

Fig. 3, 5, 6. Pygidium, SMA 84069, × 3, in dorsal, lateral and posterior views. The posterior part of the exoskeleton is exfoliated to reveal the doublure with closely spaced terrace lines. Same horizon as the holotype, Figs. 1, 3.

Fig. 7, 8. Cranidium, PMO NF 434, × 4, in dorsal, anterior views. Stratigraphically earliest specimen with relatively well defined anterior border. Profilstranda, 95m from base of Olenidsletta Member.

Fig. 9. Flattened cranidium, PMO NF 372, × 7. Shore section along Olenidsletta, immediately north of melt stream B, about 115m above base of Olenidsletta Member.

Fig. 10. *Hypermecaspis latigena* n. sp. .... (p. 45)

Fig. 10. Hypostoma, SMA 84079, × 4, in ventral view. Profilstranda, 130m above base of Olenidsletta Member.

PLATE 14

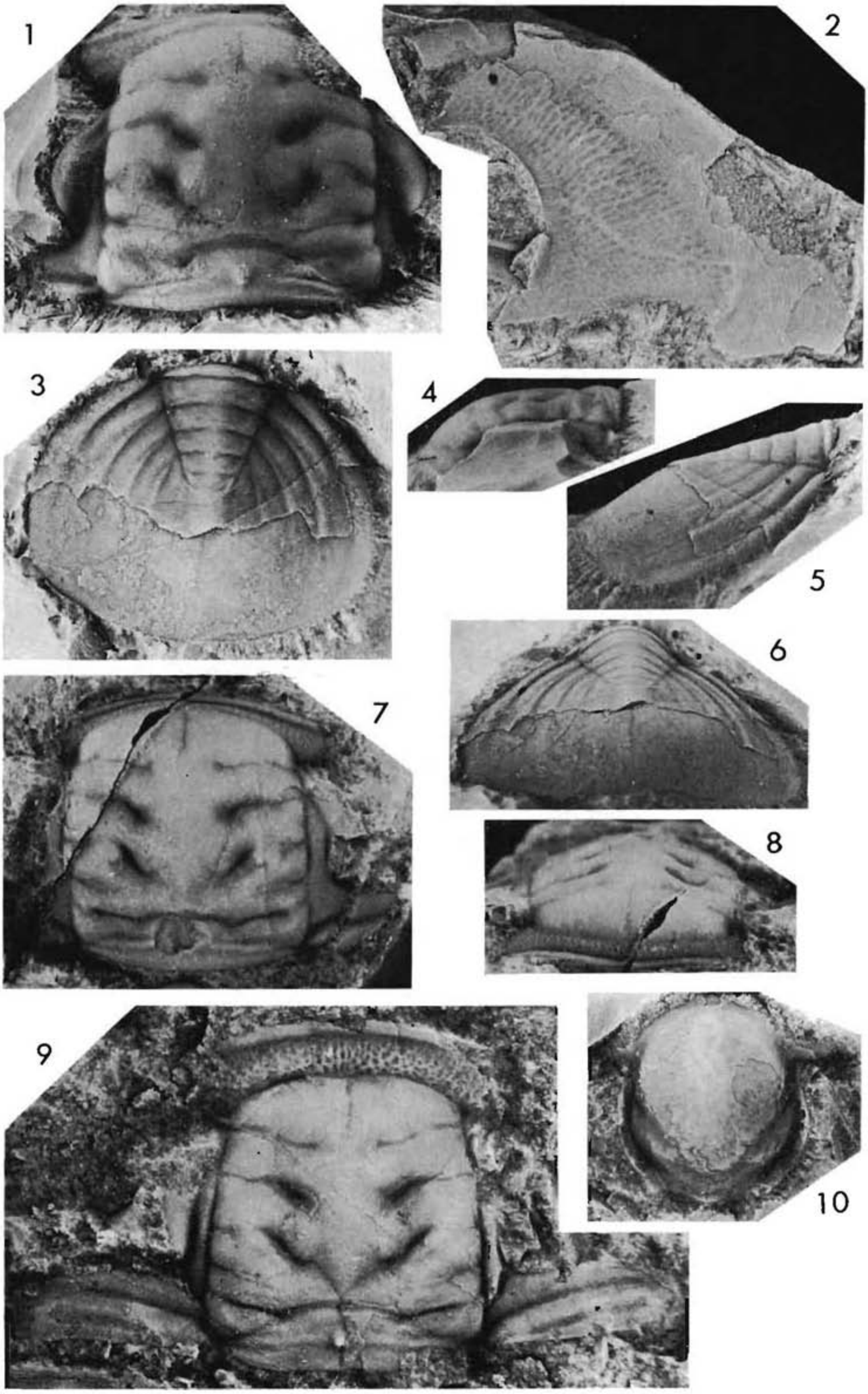


PLATE 15

Fig. 1–9. *Hypermecaspis venulosa* n. sp. .... (p. 49)

Fig. 1, 6. Hypostoma, PMO NF 3013, × 10, ventral view, and detail of macula × 15. Olenidsletta, melt stream D in bed not more than 6m from base of Olenidsletta Member.

Fig. 2, 3. Holotype, incomplete cranidium, PMO NF 12, × 3, in dorsal and lateral views. Note concavity of preglabellar field, and extreme thinness of patches of cuticle retained on glabella. Olenidsletta, melt stream D in bed not more than 6 m from base of Olenidsletta Member.

Fig. 4, 5. Pygidium, PMO NF 16, × 5, in lateral and dorsal views. Same bed as holotype, Figs. 2, 3.

Fig. 7. Latex cast of large pygidium, PMO NF 2783, × 3, showing post-axial ridge and fine terrace lines on doublure. Same bed as holotype, Figs. 2, 3.

Fig. 8. Latex cast of incomplete cranidium, PMO NF 18, × 5. Same bed as holotype, Figs. 2, 3.

Fig. 9. Free cheek, PMO NF 19, × 5, showing course of posterior branch of facial suture and caeca. Same bed as holotype, Figs. 2, 3.

PLATE 15

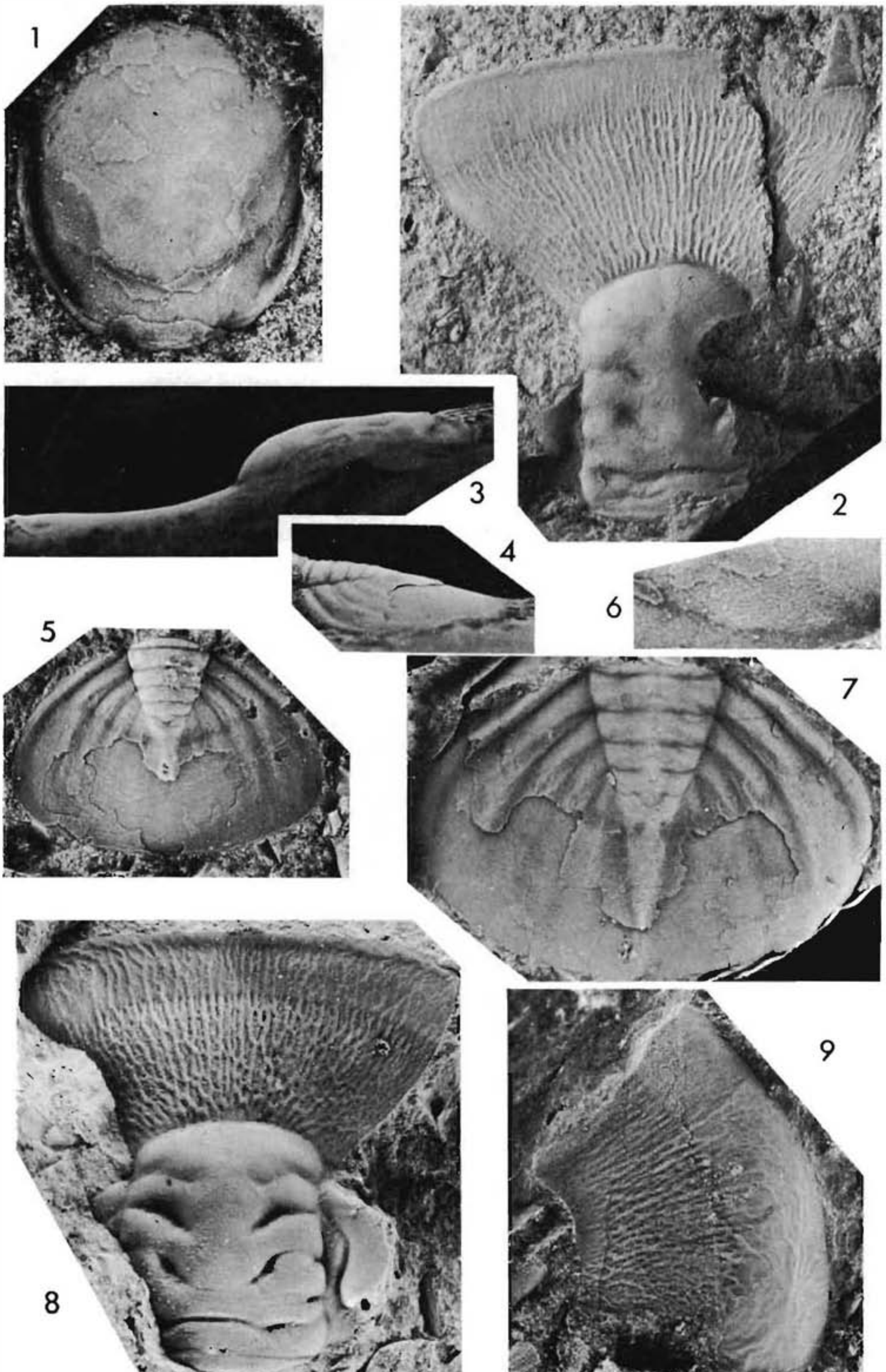


PLATE 16

Fig. 1–5, 7–9. *Tropidopyge alveus* n. sp. .... (p. 51)

Fig. 1, 3. Holotype, incomplete cranidium, PMO NF 487, × 4, in dorsal and lateral views. Profilstranda, 3m from base of Olenidsletta Member.

Fig. 2. Free cheek, PMO NF 477, × 4, showing doublure on right side with traces of genal caeca. The doublure narrows greatly anteriorly. Same bed as holotype, Figs. 1, 3.

Fig. 4. Well preserved pygidium, incomplete on right side, PMO NF 3007, × 3.5. Compare with similar sized pygidium of *T. broeggeri*, Fig. 6. Same horizon as holotype, Figs. 1, 3.

Fig. 5, 8. Cranidium, PMO NF 3008, × 3, in dorsal and lateral views. Same bed as holotype, Figs. 1, 3.

Fig. 7, 9. Pygidium, PMO NF 490, × 3, in dorsal and lateral views. Doublure visible on left. Same bed as holotype, Figs. 1, 3.

Fig. 6. *Tropidopyge broeggeri* (MOBERG and SEGERBERG) .... (see p. 51)

Fig. 6. Holotype, pygidium, Lund University Reg. no. Lo 1836, × 4. Mid part of axis damaged. Ceratopyge limestone, Ottenby, Öland.

PLATE 16

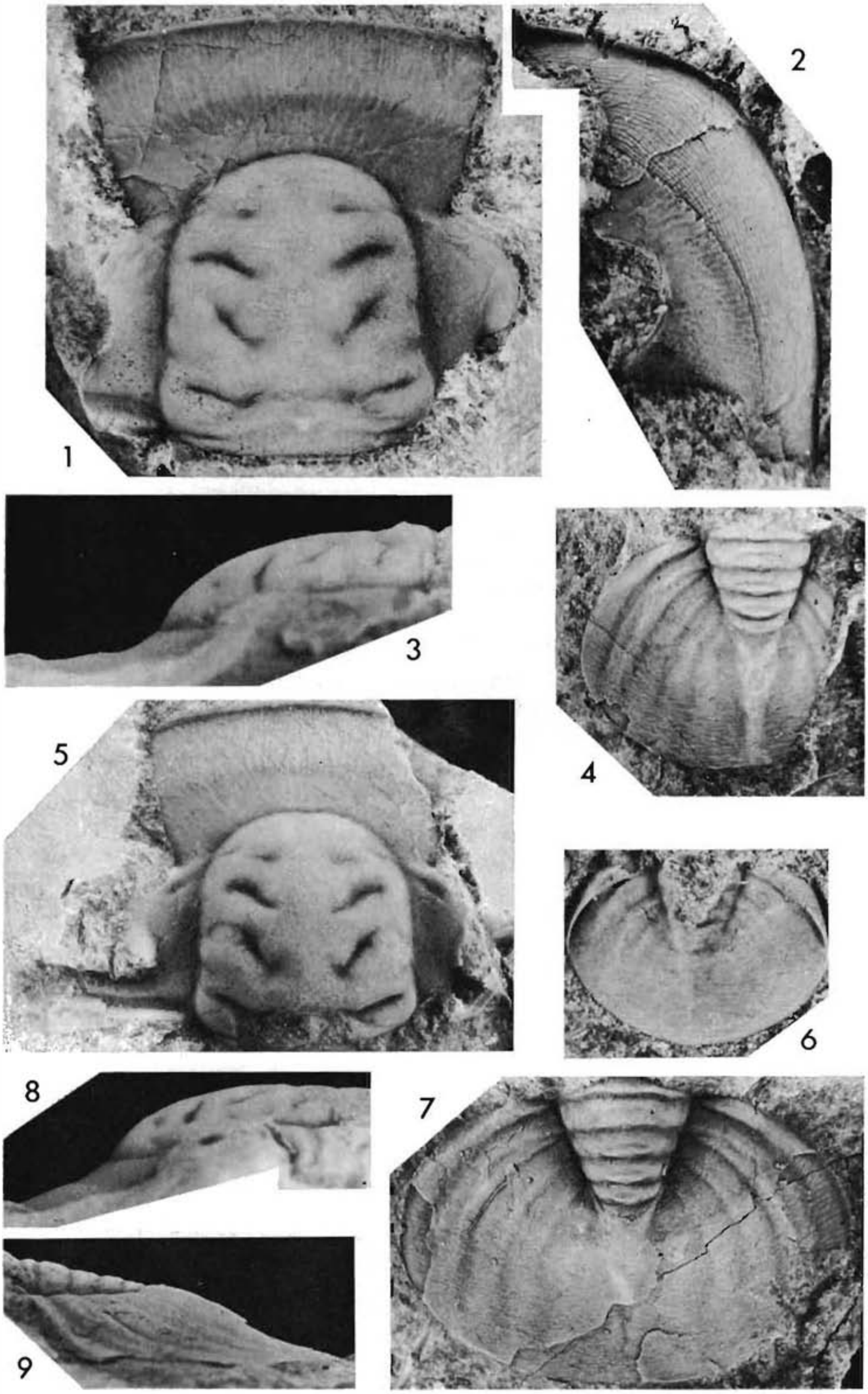


PLATE 17

Fig. 1–10. *Psilocara comma* n. gen., n. sp. .... (p. 55)

Fig. 1, 3, 4. Holotype, partly exfoliated cranidium, PMO NF 2544, × 8, in dorsal, lateral and anterior views. Melt stream C on Olenidsletta, not more than 3m above base of Olenidsletta Member.

Fig. 2, 5. Free cheek, PMO NF 2543, × 6, in dorsal and lateral views. From the same bed as the holotype, Figs. 1, 3, 4.

Fig. 6, 7, 8. Cranidium, PMO NF 2540, dorsal and lateral views × 9, detail or right anterolateral part of cranidium, × 24, showing surface sculpture. From the same bed as the holotype, Figs. 1, 3, 4.

Fig. 9, 10. Pygidium, PMO NF 2541, × 8, from posterior and dorsal views. Note upward arch of posterior margin, and presence of fine raised ridges as on cranidium and free cheek. From the same bed as the holotype, Figs. 1, 3, 4.

PLATE 17

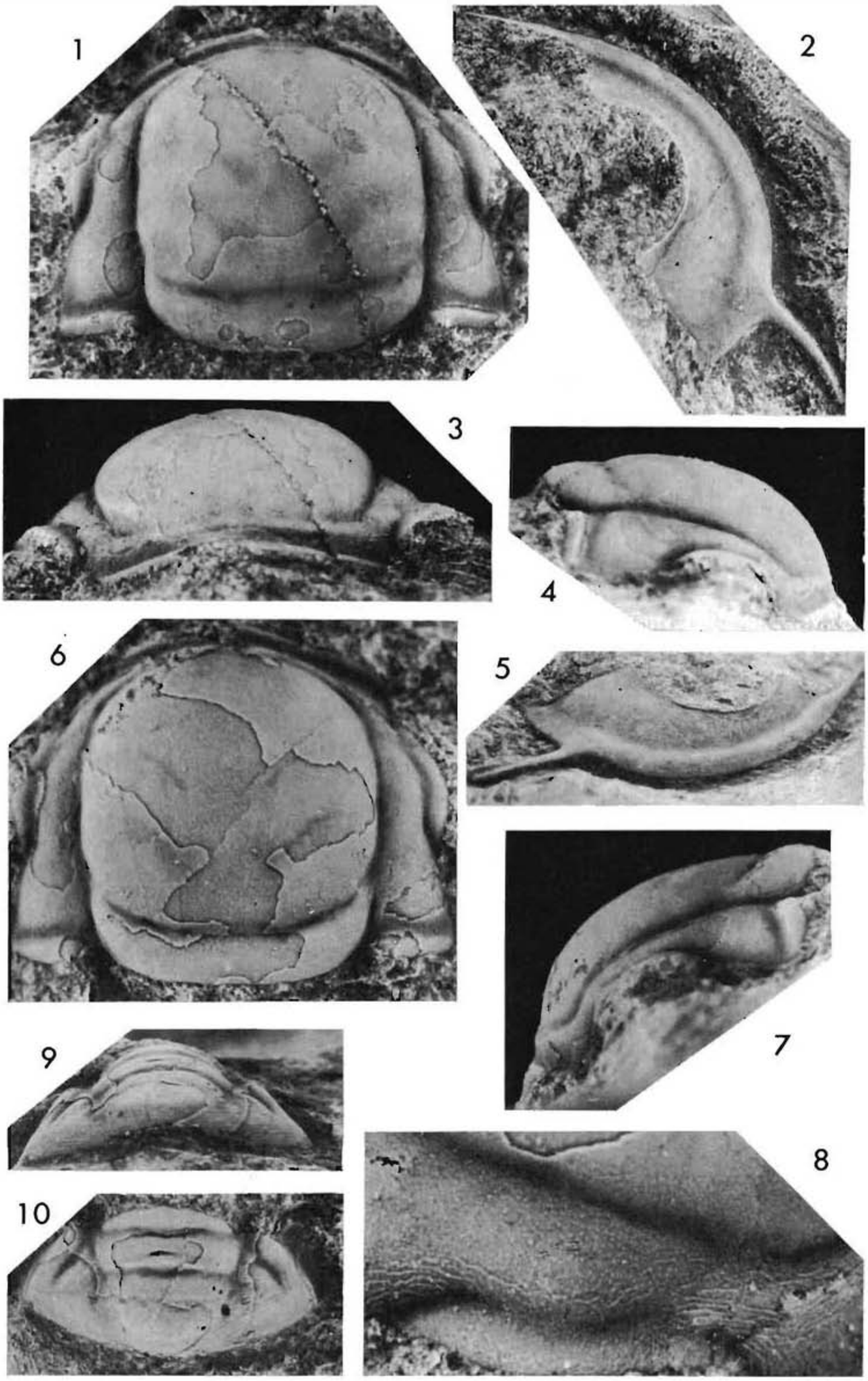


PLATE 18

Fig. 1–12. *Psilocara patagiatum* n. gen., n. sp. .... (p. 57)

Fig. 1, 5. Free cheek, PMO NF 3010, × 12, in dorsal and lateral views. Stream D on Olenidsletta, not more than 9m from base of Olenidsletta Member.

Fig. 2, 7. Very small cranidium, PMO NF 3012, × 12, in dorsal and lateral views. Same bed as free cheek in Fig. 1.

Fig. 3, 4, 6. Holotype, cranidium, PMO NF 2781, × 10, in lateral dorsal and anterior views. Specimen largely exfoliated. Horizon as specimens on Fig. 1 and Fig. 2, Stream D on Olenidsletta, not more than 9m from base of Olenidsletta Member.

Fig. 8, 9. Exfoliated cranidium, PMO NF 3011, × 15, in dorsal and lateral views. Note impressions of glabellar furrows and anterior pits on internal mould. Same bed as holotype, Figs. 3, 4, 6.

Fig. 10. Large cranidium, SMA 84086, × 8. Specimen retains its exoskeleton, and is slightly crushed. From an isolated limestone block.

Fig. 11. Flattened cranidium retaining exoskeleton, PMO NF 645, × 12. Profilstranda, 8m from base of Olenidsletta Member.

Fig. 12. Fragmentary thorax, PMO NF 2784, × 15. From the same bed as the holotype, Figs. 3 4, 6.

PLATE 18

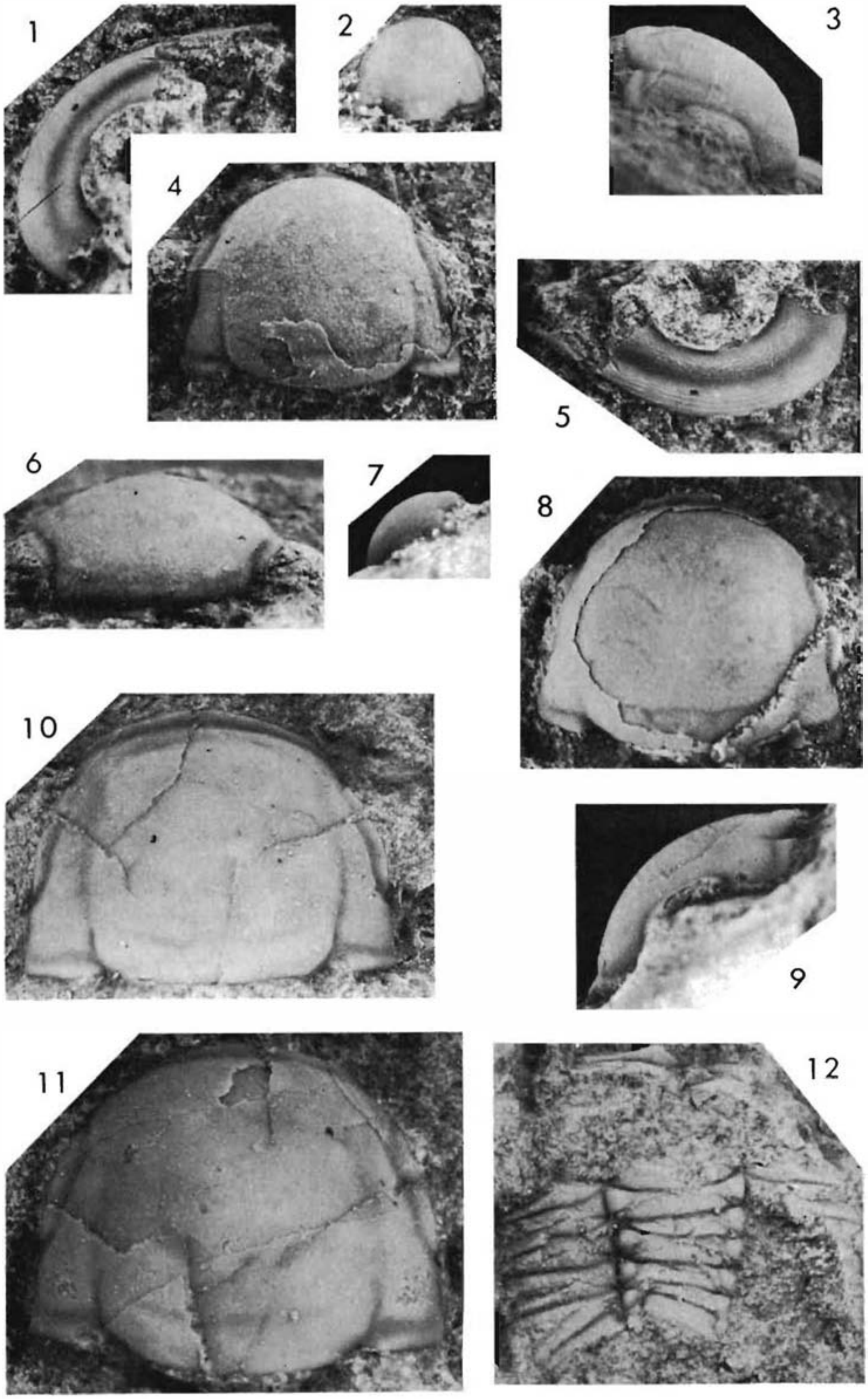


PLATE 19

Fig. 1–10. *Svalbardites lebaxis* n. gen., n. sp. .... (p. 64)

Fig. 1–3. Exfoliated cranidium, PMO NF 3006, × 20, in dorsal, anterior and lateral views, showing faintly defined axial and preglabellar furrows and occipital ring. Profilstranda, 95m from base of Olenidsletta Member.

Fig. 4. Pygidium, PMO NF 3004, × 20. Same bed as cranidium in Fig. 1.

Fig. 5. Small pygidium, PMO NF 3005, × 20. Same bed as cranidium in Fig. 1.

Fig. 6. Holotype, largely unexfoliated cranidium, PMO NF 3009, × 15. Profilstranda, 102m from base of Olenidsletta Member.

Fig. 7, 8. Pygidium, SMA 84134, × 15, in dorsal and lateral views, showing forward bend of mid-part of axial ring particularly well. Profilstranda, about 90m from base of Olenidsletta Member.

Fig. 9. Very small cranidium, PMO NF 731, × 25, exfoliated on right side to show well defined glabella and occipital ring, and glabellar furrows. Horizon as cranidium in Fig. 1.

Fig. 10. Flattened cranidium, PMO NF 1516, × 15, showing cranidial border and palpebral lobe well on left side. Same bed as holotype, Fig. 6.

Fig. 11, 13–15, 18. *Psilocara comma* n. gen., n. sp. .... (p. 55)

Fig. 11. Cranidium, PMO NF 3034, × 12. Melt stream C on Olenidsletta, not more than 3m above base of Olenidsletta Member.

Fig. 13, 15. Small cranidium, PMO NF 2539, × 9, in dorsal and lateral views. Same bed as cranidium, Fig. 11.

Fig. 14, 18. Hypostoma possibly belonging to this species, PMO NF 3035, × 10, ventral and lateral views. From the same bed as other material of *P. comma*.

Fig. 12, 16, 17. *Psilocara patagiatum* n. gen., n. sp. .... (p. 57)

Fig. 12, 16, 17. Exfoliated cranidium, PMO NF 2770, × 10, dorsal, lateral and anterior views. This cranidium is the closest in the population of *P. patagiatum* to *P. comma*, but note ill-defined glabella and very narrow fixed cheeks. Melt stream D on Olenidsletta, about 8m from base of Olenidsletta Member.

PLATE 19

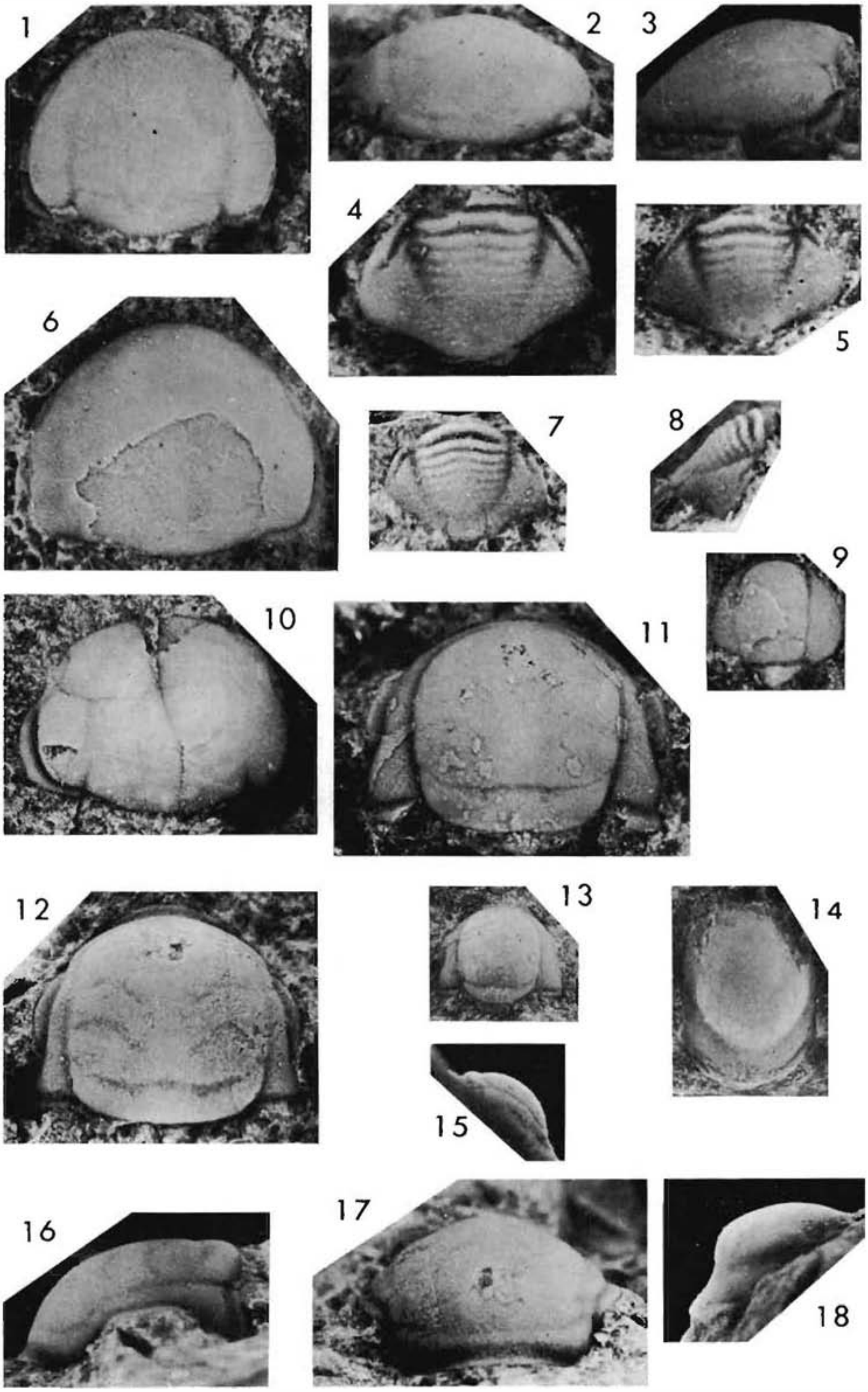


PLATE 20

Fig. 1–12. *Svalbardites hamus* n. gen., n. sp. .... (p. 61)

Fig. 1, 3, 4. Holotype, cranidium retaining exoskeleton, PMO NF 3014, × 20, in dorsal, lateral and anterior oblique views. Profilstranda, 75m from base of the Olenidsletta Member.

Fig. 2. Free cheek, SMA 84131, × 20. About 60m from base of Olenidsletta Member on Profilstranda.

Fig. 5, 6. Exfoliated cranidium, SMA 84126, × 15, in dorsal and lateral views showing hook-like occipital and glabellar furrows. From the same bed as the holotype.

Fig. 7. Internal moulds of cranidia, PMO NF 749, × 7, showing the abundance with which the species can occur. Fragmentary thoracic segment of *Balnibarbi pulvurea* on the left. From the same bed as the holotype, Figs. 1, 3, 4.

Fig. 8. Pygidium retaining exoskeleton, PMO NF 3000, × 30, showing only two axial rings. Same horizon as the holotype, Figs. 1, 3, 4.

Fig. 9, 10, 11. Internal mould of pygidium, SMA 84128, × 15, in dorsal, lateral and posterior views, showing relatively large number of axial rings visible in this preservation. Note small groove running from the region of the tip of the axis to the slightly upward-arched posterior margin.

Fig. 12. Stratigraphically early cranidium, PMO NF 1757, × 15. Dorsal surface not well preserved. Profilstranda, 4m from base of Olenidsletta Member.

PLATE 20

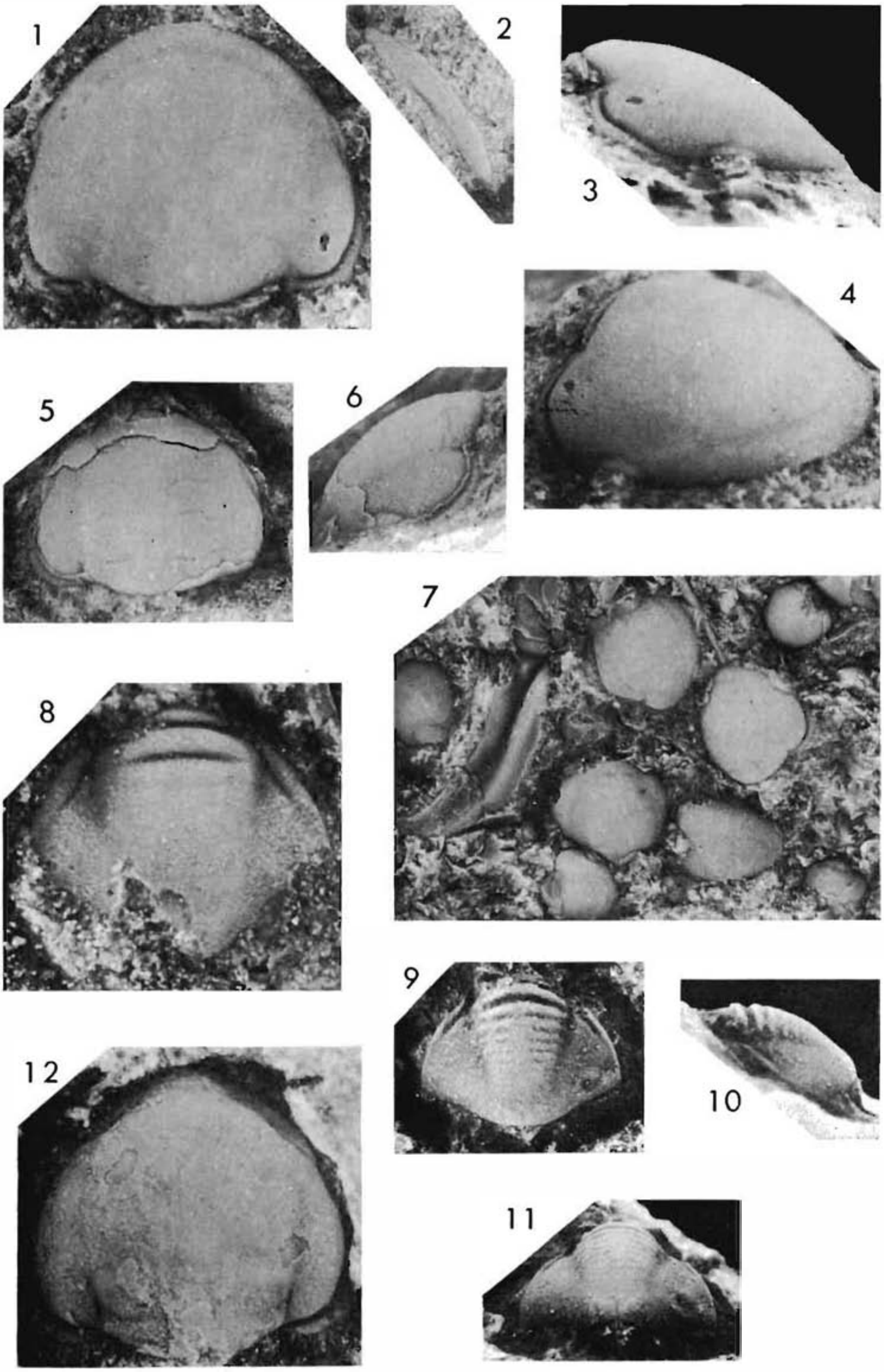


PLATE 21

Fig. 1–7. *Anaximander clavatus* n. gen., n. sp. .... (p. 59)

Fig. 1. Latex cast of external mould of free cheek, PMO NF 1878, × 20. Same bed as dorsal exoskeleton, Fig. 3.

Fig. 2. Holotype, cranidium, PMO NF 815, × 20. Slightly crushed. Profilstranda, 38m from base of Olenidsletta Member.

Fig. 3. Partly disarticulated dorsal exoskeleton, PMO NF 1875, × 12. Largely exfoliated and flattened, with the pygidium detached. Shore section on Olenidsletta, 35m from base of Olenidsletta Member.

Fig. 4–7. Well preserved cranidium, SMA 84122, × 15, in dorsal, anterior, oblique and lateral views. Profilstranda, about 30m from base of Olenidsletta Member.

PLATE 21

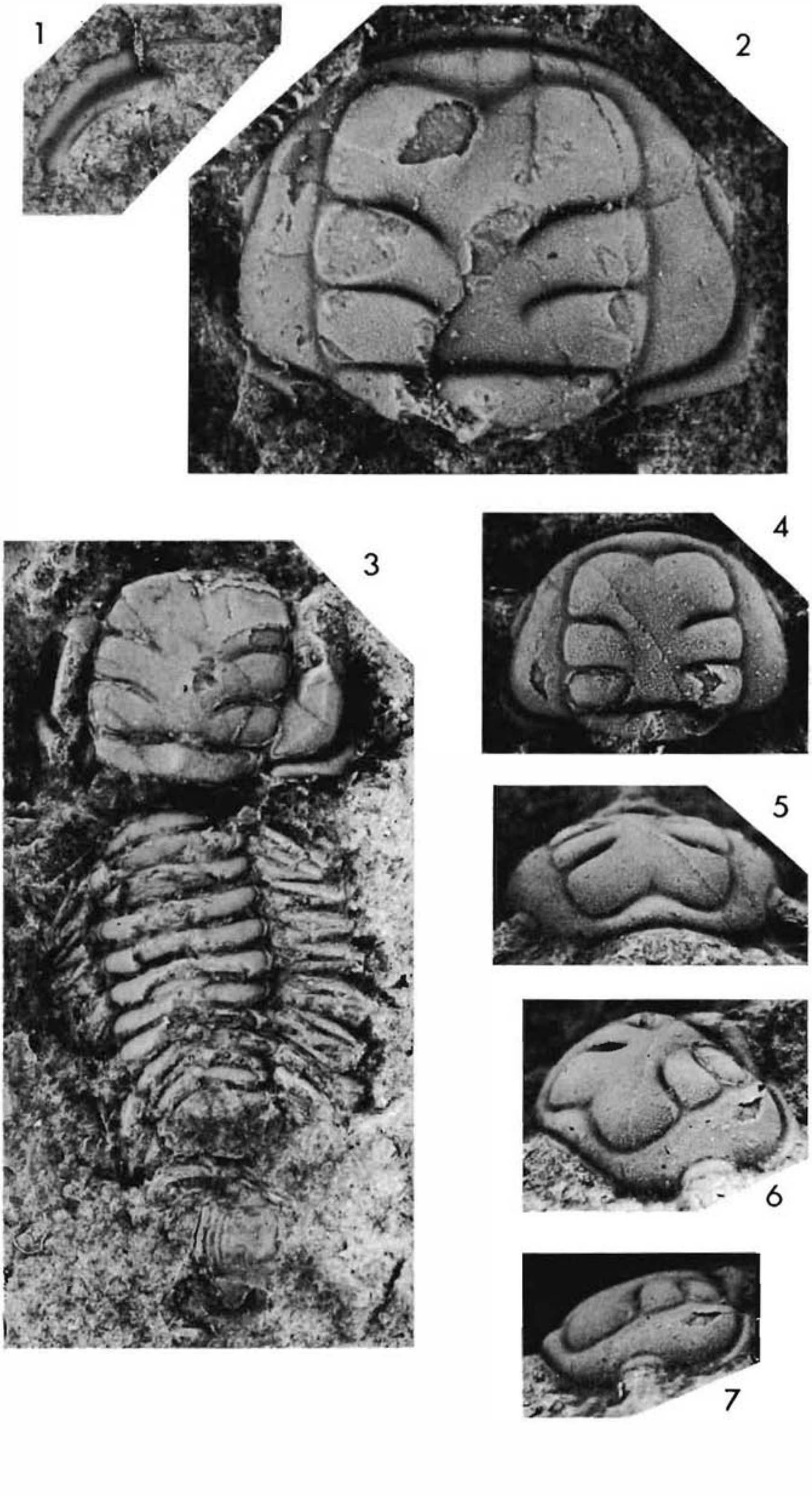


PLATE 22

Fig. 1–15. *Bienvillia stikta* n. sp. .... (p. 66)

Fig. 1. Incomplete dorsal exoskeleton, SMA 84092, × 10, flattened specimen showing ten thoracic segments. Profilstranda, about 90m from base of Olenidsletta Member.

Fig. 2, 3. Holotype, exfoliated cranidium, PMO NF 584, × 8, in dorsal and anterior views. Profilstranda, 75m from base of Olenidsletta Member.

Fig. 4, 5. Convex cranidium, PMO NF 754, × 8, in dorsal and anterior views. From the same bed as the holotype, Figs. 2, 3.

Fig. 6. Fused free cheeks, SMA 84096, × 6, showing absence of median and connective sutures. Profilstranda, about 40m from base of Olenidsletta Member.

Fig. 7, 8. Cranidium of low convexity, PMO NF 761, × 8, in dorsal and anterior views. From the same bed as the holotype, Figs. 2, 3.

Fig. 9. Flattened cranidium, SMA 84098, × 6. From low in the range of the species, about 35m from base of the Olenidsletta Member on Profilstranda.

Fig. 10. Cranidium of low convexity, SMA 84090, × 8, from the same bed as the holotype, Figs. 2, 3.

Fig. 11. Flattened cranidium, SMA 84099, × 6, from high in the range of the species, about 100m from the base of the Olenidsletta Member on Profilstranda.

Fig. 12–14. Pygidium, SMA 84093, × 10, in dorsal, lateral and posterior views. From the same bed as the holotype, Figs. 2, 3.

Fig. 15. Free cheek, SMA 84091, × 6, showing slender genal spine. From the same bed as the holotype, Figs. 2, 3.

PLATE 22

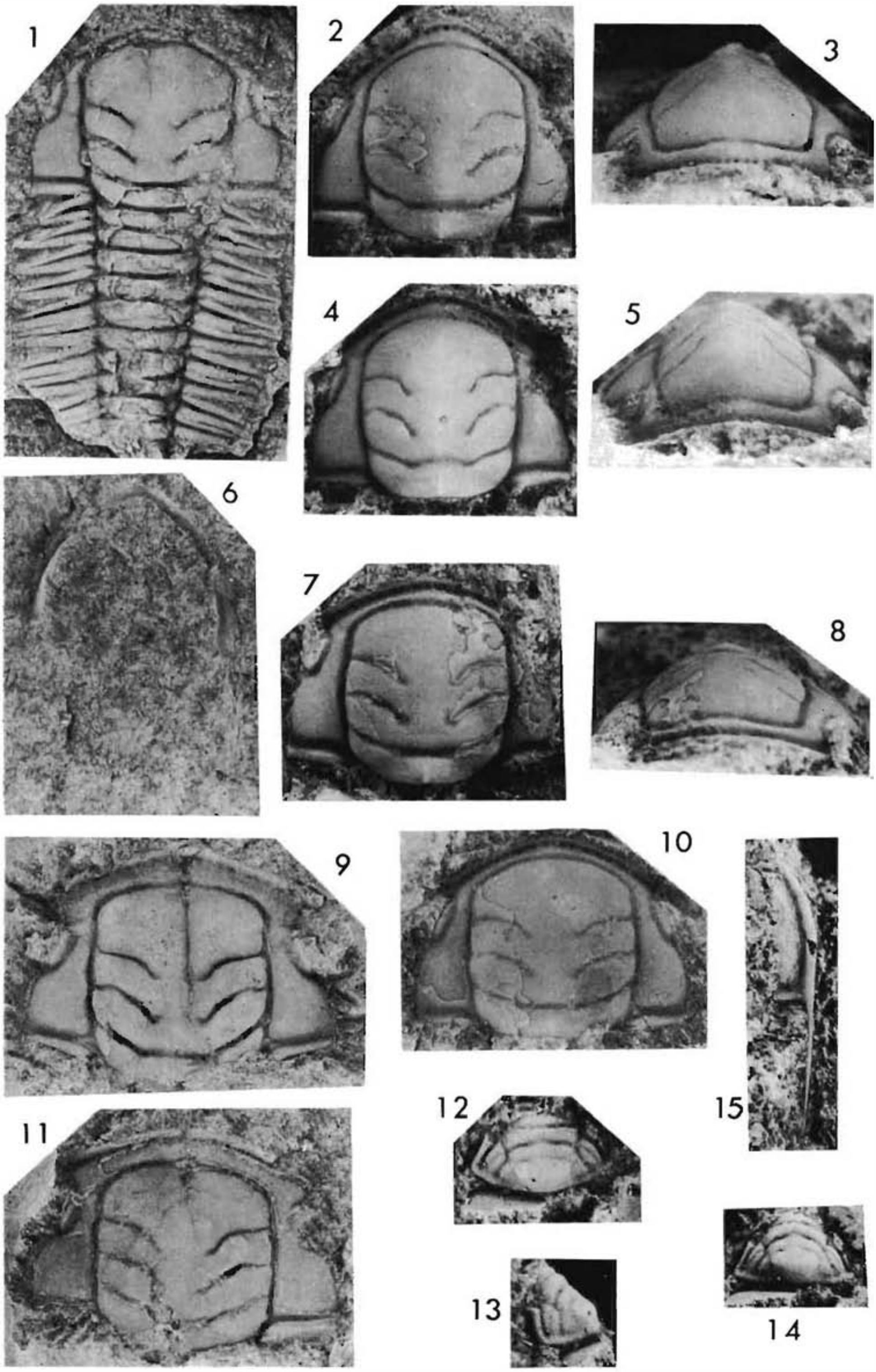


PLATE 23

Fig. 1–11. *Triarthrus papulosus* n. sp. .... (p. 70)

Fig. 1. Holotype, cranidium, SMA 84100, × 12. Slightly crushed, but displaying well the granulate surface sculpture, anteriorly shallowing palpebral furrows and sutural ridges. Profilstranda, 110m from base of Olenidsletta Member.

Fig. 2, 5. Large exfoliated cranidium, SMA 84101, × 7, in dorsal and lateral views. Profilstranda, 124m from base of Olenidsletta Member.

Fig. 3, 4. Small cranidium, SMA 84102, × 10, in dorsal and anterior views. Same bed as holotype, Fig. 1.

Fig. 6, 7. Incomplete pygidium, SMA 84104, × 10, in dorsal and lateral views. From the same bed as the holotype cranidium, Fig. 1.

Fig. 8. Very small cranidium, SMA 84103, × 12. Same bed as holotype, Fig. 1.

Fig. 9. Fused free cheeks, SMA 84105, × 10, in ventral view showing lack of median sutures. Profilstranda, 124m from base of Olenidsletta Member.

Fig. 10. Incomplete and poorly preserved dorsal exoskeleton, SMA 84106, × 6, with small, flattened cranidium, SMA 84107, on right. Profilstranda, 120m from base of Olenidsletta Member.

Fig. 11. Small cranidium, SMA 84108, × 8. Same bed as holotype, Fig. 1.

Fig. 12–23. *Triarthrus thor* n. sp. .... (p. 72)

Fig. 12, 15, 16. Holotype, cranidium lacking exoskeleton, SMA 84109, × 5, dorsal, lateral and anterior views. Profilbekken, in black limestones from the upper 10m of the Olenidsletta Member exposed there, associated with *Hypermecaspis brevifrons*.

Fig. 13. Cranidium, SMA 84110, × 6, incomplete on right side. Same bed as holotype, Fig. 12.

Fig. 14. Small cranidium, SMA 84111, × 6, Same bed as holotype, Fig. 12.

Fig. 17, 18, 22. Small cranidium, SMA 84112, × 10, in dorsal, anterior and oblique views. Note sutural ridge on Fig. 22. From the same bed as the holotype.

Fig. 19. Incomplete pygidium, SMA 84113, × 10. From the same bed as the holotype, Fig. 12.

Fig. 20. Smallest cranidium, SMA 84114, × 10. From the same bed as the holotype.

Fig. 21. Hypostoma, SMA 84115, × 10. Same bed as holotype.

Fig. 23. Protaspis, SMA 84116, × 12. Same bed as holotype, Fig. 12.

PLATE 23

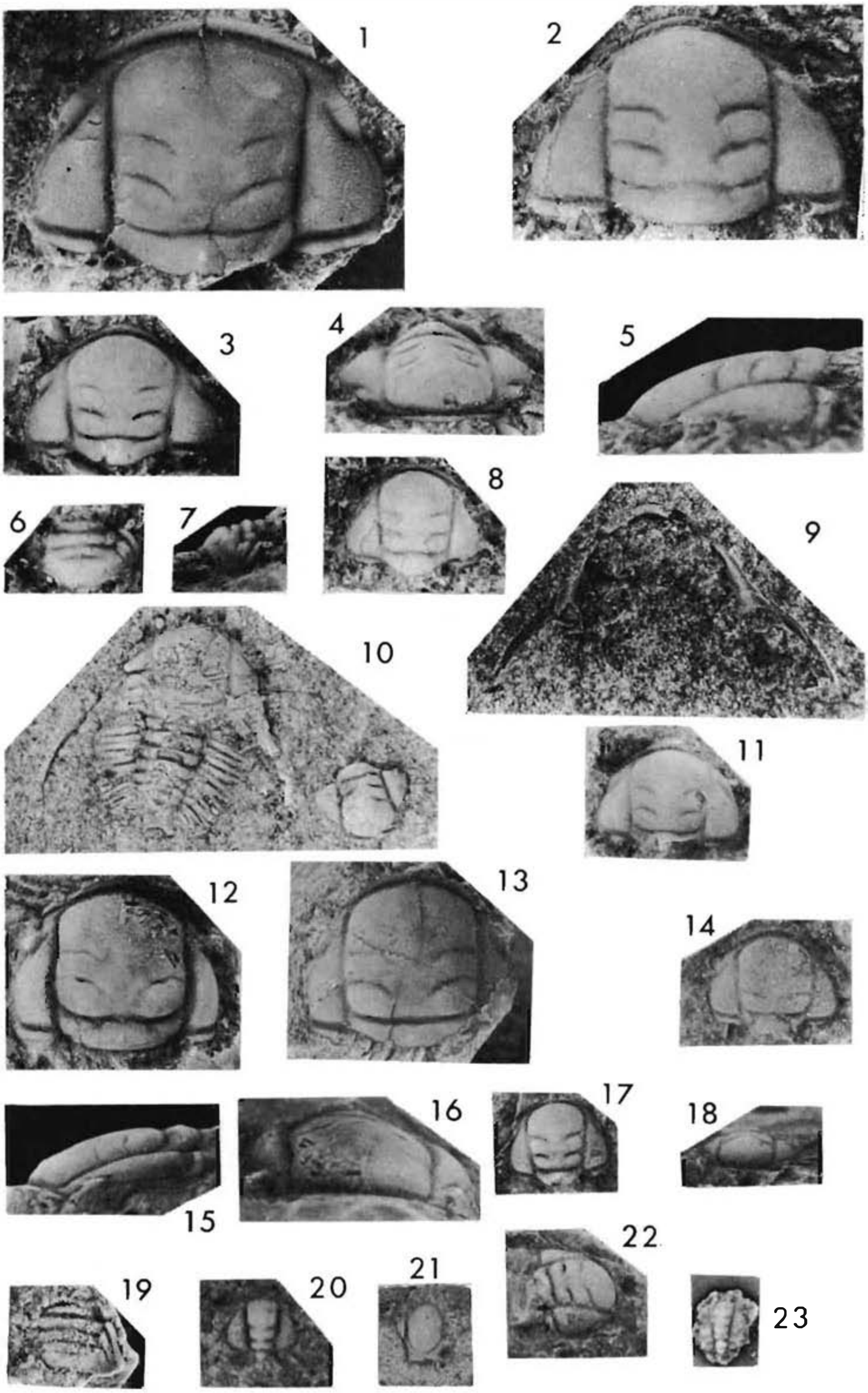


PLATE 24

Fig. 1–4. *Triarthrus parapunctatus* n. sp. .... (p. 74)

1. Holotype, cranidium, SMA 84117, × 16, showing surface sculpture. Profilbekken, 40m from base of the Profilbekken Member.

Fig. 2, 3. Cranidium, PMO NF 1386, in dorsal (× 13) and lateral views. Photograph taken in low, oblique light to emphasize the shallow glabellar furrows of the species. Profilbekken, 30m from base of Profilbekken Member.

Fig. 4. Internal mould of cranidium, SMA 84118, × 12. Profilbekken, 40m from base of Profilbekken Member.

Fig. 5–7. *Bienvillia stikta* n. sp. .... (p. 66)

Fig. 6, 7. Stratigraphically high cranidium, PMO NF 1588, in dorsal and lateral views, × 8. Profilstranda, 102m from base of Olenidsletta Member.

Fig. 5. Detail of right hand side of cranidium of Fig. 6, 7, × 25, showing surface sculpture of fine raised lines.

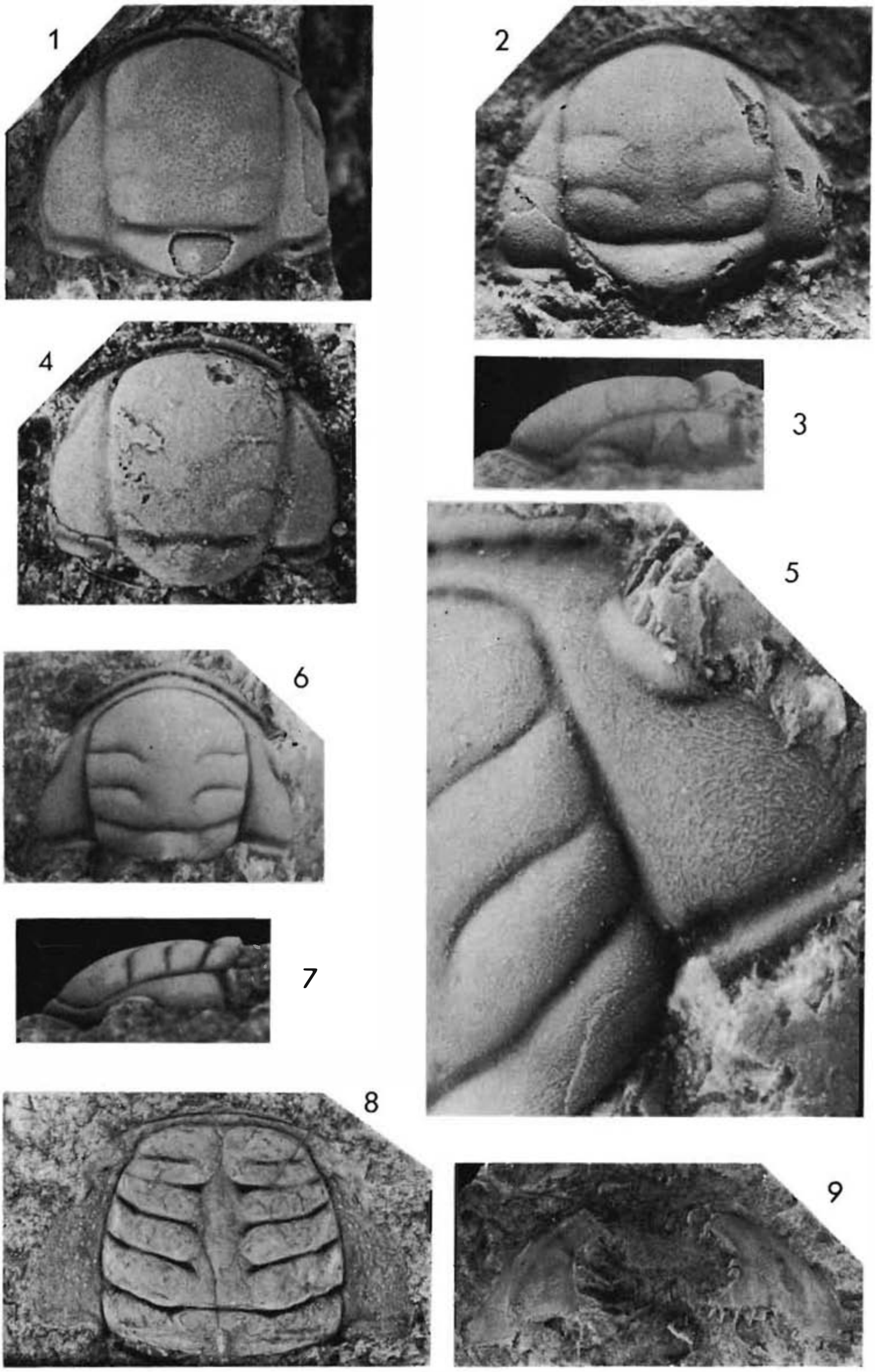
Fig. 8. *Plicatolina* sp. .... (p. 75)

Fig. 8. Flattened cranidium, PMO NF 2064, × 5. Shore section along Olenidsletta, about 30m from base of Olenidsletta Member.

Fig. 9. *Hypermecaspis brevifrons* n. sp. .... (p. 48)

Fig. 9. Fused free cheeks, SMA 84072, × 1.8. Profilstranda, about 135m from base of Olenidsletta Member.

PLATE 24



A.s John Griegs Boktrykkeri, Bergen