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R. A. FORTEY

The Ordovician Trilobites of Spitsbergen

II. Asaphidae, Nileidae, Raphiophoridae and Telephinidae of the Valhallfonna Formation

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Abstract

Thirty-nine species and subspecies of trilobites of Arenig–Llanvirn age are described from the Valhallfonna Formation, north Ny Friesland, Spitsbergen. Of these all but seven are new; five of those known elsewhere are telephinids. Six new genera are defined. Seven asaphid species are assigned to the genera *Niobe* (2 species), *Megalaspides*, *Presbynileus* (*Protopresbynileus*), *Paraptychopyge*, *Ptyocephalus* and *Gog* n. gen. Ten nileid species are assigned to *Nileus* (3 species) *Peraspis* (2 species) *Symphysurus* (1 species) and *Poronileus* n. gen. (4 species). Fourteen raphiophorid species are assigned to *Ampyx* (4 species), *Rhombampyx* n. gen. (2 spp.), *Globampyx* n. gen., *Ampyxoides*, *Mendolaspis*, *Pytine* n. gen., *Endymionia* (2 species), and *Falanaspis*; one is generically undetermined. Telephinids are represented by six species and subspecies of *Carolinites* and two of *Oopsites* n. gen.

Diversity of Raphiophoridae, Nileidae and Telephinidae is matched by no other Ordovician fauna, and permits some comments on the classification of these families. *Endymionia* and related genera are here considered to belong to the subfamily Endymioniinae of the Raphiophoridae. The Telephinidae is revised to include *Carolinites* and related genera.

The genus *Carolinites* and some species of Nileidae are considered to be related in phyletic series; the species–series of *Carolinites* is of stratigraphic importance. The theoretical basis of stratigraphic lineages is discussed.

Asaphidae, Nileidae and Raphiophoridae are characteristic of the Nileid Community of Fortey (1975); Telephinidae are characteristic of the Pelagic Community. Comparison of the Spitsbergen species with their closest-related species indicates connections with Baltoscandia (Asaphid province), North America (Bathyurid province) and, to a lesser extent, South America (Asaphopsis province). The interprovincial mixing can be explained ecologically.

Ontogenetic series of *Symphysurus*, *Globampyx* n. gen. and *Carolinites* are described.

I. Introduction

In this second part of the descriptions of the Ordovician trilobites ot Spitsbergen thirty-nine species and subspecies are described, belonging to the families Asaphidae, Nileidae, Raphiophoridae and Telephinidae. These were collected from the Valhallfonna Formation, north Ny Friesland, from rocks ranging in age from early Arenig to early Llanvirn. Trilobites of these families are an abundant and diverse element in the fauna of the Valhallfonna Formation, second only to the Olenidae described in the previous part. They are particularly important in that they provide evidence of connections with several of the faunal "provinces" of the early Ordovician, and include a number of species of stratigraphic significance. Most of the species are, however, new, and six new genera are defined. They are characteristic of the nileid and pelagic trilobite communities recently described by FORTEY (1975).

Preservation of the material is exceptionally good, and many of the species are known from articulated specimens. Material is also abundant for most of the species described, and is known from detailed bed-by-bed collecting, so that the limits of variation of the species may be well understood. In addition the variety of species of the Nileidae, Raphiophoridae and Telephinidae is sufficient to enable some consideration of the criteria of classification of these families as a whole. The diversity of Nileidae and Raphiophoridae is without parallel in any other Ordovician fauna.

Stratigraphic terminology and locality information follows that given by FORTEY and BRUTON (1973). Figured material is curated in the Palaeontologisk Museum, Oslo (PMO) or the Sedgwick Museum, University of Cambridge (SMA).

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II. Occurrence and Stratigraphy

A. Community types and faunal provinces

The trilobite fauna of the Valhallfonna Formation has recently been described in terms of four major trilobite community types (FORTEY 1975) - termed the olenid, nileid, illaenid-cheirurid and pelagic communities respectively — which are considered to have been widespread in early Ordovician times, and, with the exception of the pelagic community, adapted to different sea bottom conditions, controlled at least in part by a shallow to deep water environmental gradient. Trilobites of the pelagic community occur independently of the other community types.

The species of Asaphidae, Nileidae and Raphiophoridae described herein are almost all characteristic of the nileid community, and many species are represented by sufficiently abundant material, including articulated specimens, to be certain of their autochthonous occurrence. They occur especially in black or brown flat-bedded limestones between 75 m and 103 m from the base of the Olenidsletta Member, and in the lower 80 m of the Profilbekken Member. Two species only, *Peraspis omega* n. sp. and *Endymionia clavaria* n. sp., have their maximum abundances in the upper part of the Valhallfonna Formation in association with many olenids in a black, stinkstone lithology. These species probably occupied niches on that part of the environmental gradient intermediate between the broadly-defined nileid and olenid communities; the maximum abundance of the olenids *Svalbardaspis* and *Bienvillia stikta* (see FORTEY 1975) follows a similar pattern.

The Telephinidae, as redefined in the present work to include *Carolinites*, comprise those species believed to have composed the pelagic community (FORTEY 1975, p. 343). The extraordinary trilobite *Opipeuter inconnivus*, which has been recently described elsewhere (FORTEY 1974a), was also characteristic of the pelagic community. Both Telephinidae and *Opipeuter* are found in equal abundance in rocks bearing olenid and non-olenid trilobites, and, as might be expected from their inferred life habits, are independent of the enclosing lithology.

I have also indicated (FORTEY 1975, p. 348) that the Valhallfonna Formation trilobites are a mixture at the generic level of faunal provinces, as defined for the lower Ordovician by WHITTINGTON and HUGHES (1972). This was explained (FORTEY 1975, p. 349) in terms of decreasing endemicity with increasing depth, the deep water olenid community including genera of wide geographic distribution, the shallow-water illaenid-cheirurid community including genera of restricted (provincial) distribution, and the nileid community with intermediate properties regarding depth and distribution patterns. Oceanic barriers were considered effective only for preventing migrations of the more shallow-water species.

Some justification of this view is obtained by considering where the closest-related species to those of the Valhallfonna Formation occur, since such a close relationship implies a common ancestor, a single population from which migration into Spitsbergen of derived species was possible. A table showing the occurrence of the closest relatives of the species so far described is given in Table 1 (not including species whose closest relatives are to be found among other Spitsbergen species). The provincial occurrence of these close relatives according to WHITTINGTON and HUGHES' (1972) model is also given, together with the community type in which the species occurs. Detailed evidence for the choice of the closely-related species is given in the discussions in the systematic part.

Table 1.

Relationships between the trilobites of the Valhallfonna Formation, so far described, and the early Ordovician faunal "provinces". Trilobite community types of FORTEY *(1975) on left: N—Nileid community; O—Olenid community; P—Pelagic community.*

Species from Spitsbergen	Closest-related species	Faunal province in which related species occur. (WHITTINGTON & HUGHES, 1972)
N *Ampyx porcus*	*Ampyx pater* HOLM — Sweden	Asaphid
N *Ampyx spongiosus*	*Ampyx nasutus* DALMAN — Sweden	Asaphid
N *Ampyxoides inermis*	*Ampyxoides semicostatus* (BILLINGS) — Newfoundland	Bathyurid
O *Anaximander clavatus*	no known relative	—
O *Balnibarbiinae*	*Agalatus* spp. — Kazakhstan	Bathyurid
O *Bienvillia stikta*	*Triarthrus angelini* LINNARSSON — Norway	Asaphid
	Triarthrus parchaensis H. & L. Argentina	Asaphopsis
P *Carolinites genacinaca* ROSS	*C. genacinaca* ROSS — Nevada — N.E. U.S.S.R.	Bathyurid
P *Carolinites killaryensis* (STUBBLEFIELD)	*Carolinites killaryensis* (STUBBLEFIELD) — W. Eire	Bathyurid
P *Carolinites sibiricus* CHUGAEVA	*C. sibiricus* CHUGAEVA — N.E. U.S.S.R.	Bathyurid
O *Endymionia clavaria*	*Endymionia meeki* (BILLINGS) — Newfoundland	Bathyurid
N *Falanaspis extensa*	*Falanaspis aliena* TJERNVIK — Sweden	Asaphid
N *Globampyx trinucleoides*	"*Ampyx*" *linnarssoni* SCHMIDT — Estonia	Asaphid
N *Gog catillus*	*Niobe* sp. N 1 BURSKY 1970 — Pai Khoya	Asaphid
O *Hypermecaspis brevifrons*	*Hypermecaspis inermis* HARRINGTON & LEANZA — Argentina	Asaphopsis

Table 1 — Continued

Species from Spitsbergen	Closest-related species	Faunal province in which related species occur. (WHITTINGTON & HUGHES, 1972)
O *Hypermecaspis latigena* and *H. venulosa*	No closely similar spp.	—
N *Mendolaspis doidyx*	*Mendolaspis salagastensis* RUSCONI — Argentina	Asaphopsis
N *Nileus glazialis costatus*	*Nileus glazialis glazialis* SCHRANK — Sweden	Asaphid
N *Nileus orbiculatoides svalbardensis*	*Nileus orbiculatoides* SCHRANK — Sweden	Asaphid
N *Nileus porosus*	*Nileus? lacunosa* WHITTINGTON — Newfoundland	Bathyurid
N *Niobe occulta*	*Niobe tenuistriata* CHUGAEVA — Kazakhstan	Bathyurid
P *Oopsites hibernicus* (REED)	*Oopsites hibernicus* (REED) — W. Eire	Bathyurid
P *Opipeuter inconnivus*	*Opipeuter inconnivus* FORTEY — W. Eire, Utah	Bathyurid
N *Paraptychopyge disputa*	*Paraptychopyge cincta* (BRØGGER) — Norway, Estonia	Asaphid
N *Peraspis erugata* ROSS	*Peraspis erugata* ROSS — W. U.S.A.	Bathyurid
O *Plicatolina* sp.	*Plicatolina scalpta* HARRINGTON & LEANZA — Argentina	Asaphopsis
N *Poronileus* spp.	? Nileid gen. ind. WHITTINGTON 1965	Bathyurid
?N *Ptyocephalus* cf. *vigilans*	*Ptyocephalus vigilans* WHITTINGTON — Nevada	Bathyurid
O *Psilocara* spp.	*Peltocare* spp. — Norway, Sweden	Asaphid
N *Pytine graia*	Undescribed *Pytine* sp., Sweden	Asaphid
N *Rhombampyx rhombos*	*Raphiophorus ? lamasi* HARRINGTON & LEANZA — Argentina	Asaphopsis
O *Svalbardites* spp.	No obviously related spp.	—
N *Symphysurus arcticus*	*Symphysurus kujandensis* CHUGAEVA — Kazakhstan	Bathyurid
O *Triarthrus papulosus*	*Triarthrus punctatus* (CROSFIELD & SKEAT) — Wales	Selenopeltis
O *Tropidopyge alveus*	*Tropidopyge broeggeri* (MOBERG & SEGERBERG) — Sweden, Norway, Wales	Asaphid, Selenopeltis

Taken as a whole, Table 1 suggests that Spitsbergen had interconnections with all four of the early Ordovician faunal provinces as distinguished by WHITTINGTON and HUGHES (1972). It is of greater interest to clump the Valhallfonna Formation species according to the trilobite community types of FORTEY (1975), shown on Table 2. It must be noted here that the trilobites of the upper part of the Profilbekken Member of the Valhallfonna Formation belonging to the illaenid-cheirurid community have not yet been described, although some genera are listed by FORTEY and BRUTON (1973, p. 2235); these

Table 2.
Relation of community-type to faunal "province" of trilobites listed in Table 1.

Community type (FORTEY 1975)	Number of closest-related species occurring in each early Ordovician Faunal province
Nileid	Asaphid — 9
	Asaphopsis — 2
	Bathyurid — 6
	Selenopeltis — 0
Olenid	Asaphid — 2
	Asaphopsis — 2½*
	Bathyurid — 2
	Selenopeltis — 1½*
Pelagic	Bathyurid — 5
	Others — 0

* Half points are given for two provinces in the cases of *Bienvillia stikta* and *Tropidopyge alveus* which have closely related species in more than one province.

are almost all related to genera occurring in the Bathyurid province. Of the species of the olenid, nileid and pelagic communities so far described, the pelagic community have closely related species only in the Bathyurid province. This is believed to be the case because pelagic trilobites are influenced in their distribution by the ambient temperature conditions, like the shallow-water trilobites of the illaenid-cheirurid community (FORTEY 1975, Fig. 5). The trilobites of the olenid community, by contrast, have close relatives in all four faunal provinces; it is clear that inter-communication between different provinces, whether or not they were separated by oceans, was relatively free for trilobites of the olenid community. This is in accordance with the decrease in endemicity proposed for the deep water community (FORTEY 1975, p. 349), although it should be noted that *Svalbardites* and *Anaximander* cannot at the moment be closely compared with any trilobite outside Spitsbergen. Trilobites of the nileid community may for the most part be compared with near relatives in the Asaphid province, although species similar to those from the Bathyurid province are also important, and there is also a South American (Asaphopsis) province element. Intermigrations between provinces were possible in the nileid community especially between Asaphid and Bathyurid provinces, to a lesser extent extending to the Asaphopsis province, although not to the Selenopeltis province; restrictions on migration were therefore greater than those pertaining in the olenid community, but less than those affecting the pelagic and illaenid-cheirurid community. The evidence from taxonomic comparisons of the Spitsbergen fauna as so far described is consistent with the community model proposed by FORTEY (1975); further comments will be possible when the rest of the Valhallfonna trilobites are described.

B. Stratigraphic distribution of species and correlation

The stratigraphical distribution of the species described in this part is shown on Fig. 1; because most of the trilobites described herein belong to the nileid community, most of the species range through the parts of the Valhallfonna Formation characterised by rocks yielding trilobites of that community, 75 m to 103 m from the base of the Olenidsletta Member, and the lower 60 m of the Profilbekken Member. On the basis of associated graptolites, the Olenidsletta Member is of early Arenig (*deflexus*-zone) to late Arenig (*hirundo* zone) age. The uppermost part of the Olenidsletta Member is of *Isograptus* zone age in North American terms (ARCHER and FORTEY 1974). The fauna from 30 m to 70 m from the base of the Profilbekken Member compares closely with Whiterock age faunas of Nevada, Newfoundland (FORTEY and BRUTON 1973) and Canada (McKEE, NORFORD, and ROSS 1972), particularly that of the *Orthidiella* zone. This part of the section may be as young as the north American zone of *Paraglossograptus etheridgei*, and probably correlates with the early Llanvirn of the British succession. The correlations of trilobites ranges with standard zonal schemes as so far known, are shown also on Fig. 1.

The lower 30 m of the Profilbekken Member is characterised by a particular assemblage of nileid and raphiophorid trilobites, of species related to but distinct from those of the succeeding beds with the typical *Orthidiella* zone Whiterock fauna. This fauna lies above that with presumed uppermost Canadian fossils (zone J of ROSS/HINTZE); it therefore occupies a position between the high Canadian and earliest zone of the Whiterock stage hitherto recognised on shelly fossils. A characteristic trilobite is *Peraspis erugata* ROSS; this species occurs in Nevada in the "Slabby bedded unit" at the base of the Antelope Valley Limestone, Ikes Canyon, Nevada (ROSS 1970, Pl. 20). ROSS included this part of the Antelope Valley Limestone in the *Orthidiella* zone. In the Nevada section *Peraspis* is the only common trilobite in the "Slabby bedded unit" and is succeeded by a rich *Orthidiella* zone fauna; I believe that the *Peraspis*-bearing beds there are the equivalent of the lower part of the Profilbekken Member in Spitsbergen yielding the same species, but that in Spitsbergen a richer associated fauna is present proving the existence of an earlier (pre-*Orthidiella*) Whiterock zone. Characteristic species in this part of the Spitsbergen succession are: *Peraspis erugata* ROSS, *Poronileus fistulosus* n. gen., n. sp., *Nileus orbiculatoides svalbardensis*. n. subsp., *Carolinites ekphymosus* n. sp. and *Ampyx toxotis* n. sp. Several other species from this part of the section remain to be described and further comments on the stratigraphy are best reserved until this work is completed.

C. Stratigraphic importance of *Carolinites*

It has been argued elsewhere (FORTEY 1975) that *Carolinites* species were pelagic, and that this accounts for their wide distribution and independence of sediment type. For present purposes it is pertinent to consider the relevance of the life habits of the genus for stratigraphy. Unlike almost all of the Spitsbergen trilobites described in this and the previous part, many of the *Carolinites* species

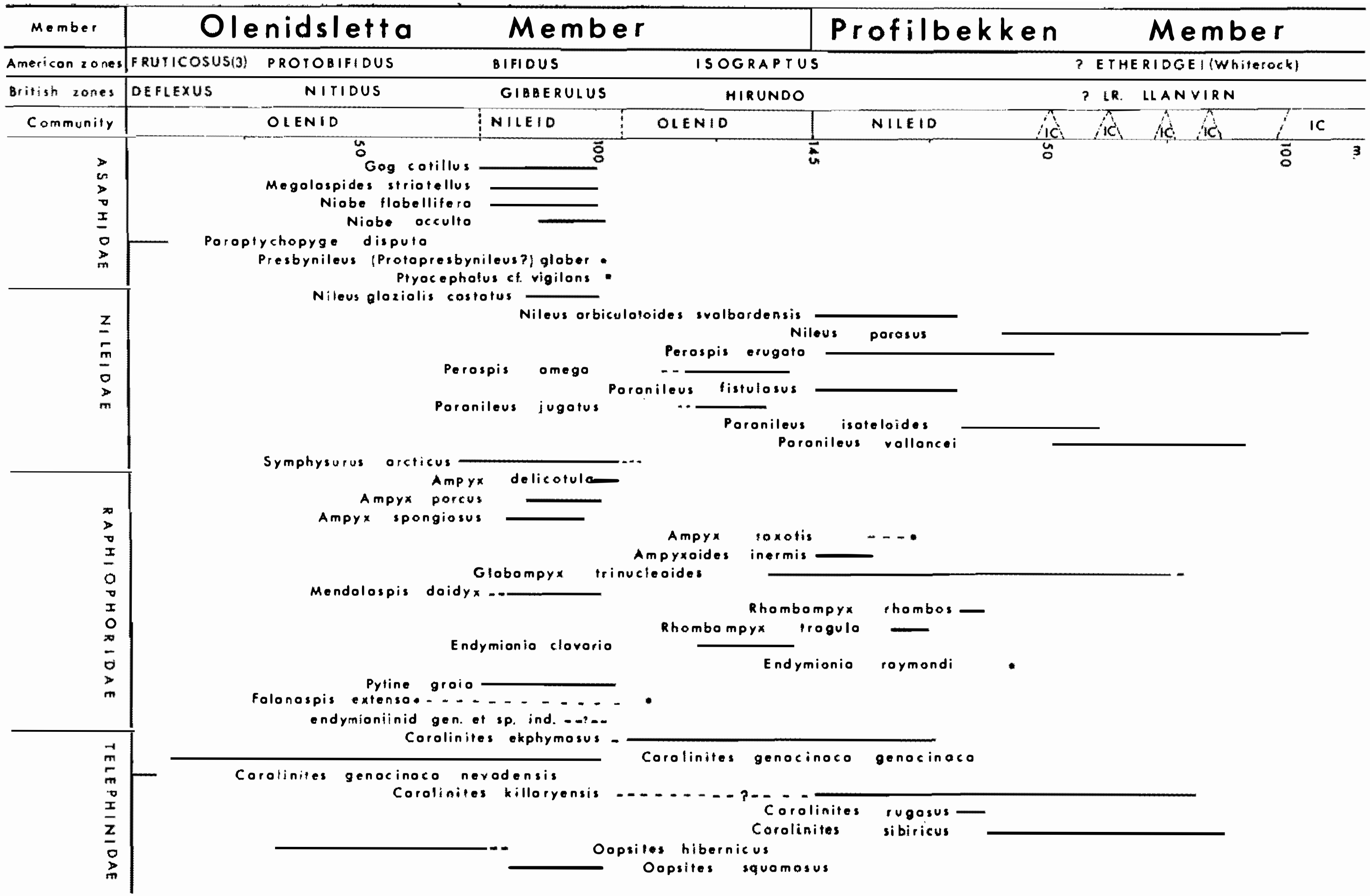

Fig. 1. Stratigraphic ranges of the trilobites described in this paper; genera and species arranged alphabetically. The ranges are calibrated against British and North American graptolite zones, and against the dominant community type of FORTEY (1975). IC — illaenid cheirurid community.

are well-known from other areas. My identifications have been made for all species, except *C. sibiricus* CHUGAEVA, on the basis of comparisons with type and topotype material of described species. The species are believed to be related phyletically as discussed below (p. 101). In support of the proposed phylogeny is the fact that the same species occur in the same order in Utah and Nevada. The fossil record of *Carolinites* is, however, nowhere else as complete as it is in Spitsbergen. The combination of a phyletically related series of species (on the basis of precisely collected successions) with wide distributions of these species approaches the ideal for biostratigraphic purposes, and I attach particular importance to *Carolinites* for correlation with areas outside Spitsbergen. The ambiguity involved with correlations based on gross generic assemblages is that it is difficult to separate the time significance from that of community-type similarity. A fossil assemblage of nileid community type will compare more closely with the same community of different age than with a contemporary illaenid-cheirurid or olenid community fossil assemblage. Since the occurrence of *Carolinites* is independent of these benthic communities I believe that more weight should be attached to correlations made on the occurrence of *species* of this genus, than to the overall generic composition of the trilobite assemblage. Thus the basal part of the Olenidsletta Member of the Valhallfonna Formation is correlated with zone H of the trilobite zones of ROSS (1951) and HINTZE (1953) in Utah and Nevada on the basis of the occurrence there of *Carolinites genacinaca nevadensis* HINTZE, even though this part of the succession is developed in the olenid community type. Similarly, the middle part of the Olenidsletta Member, developed mainly in the nileid community type, is correlated with zone J on the ROSS/HINTZE scheme because of the occurrence of *C. genacinaca genacinaca*. Independent evidence for the correctness of these correlations is provided by the occurrence of graptolites in the same rocks and by the presence of illaenid-cheirurid community fossil assemblages more closely comparable with those of Utah and Nevada below the Olenidsletta Member in the Kirtonryggen Formation, and above in the Profilbekken Member. The wide occurrence of the pelagic trilobite *Opipeuter inconnivus* FORTEY (FORTEY 1974a) is also stratigraphically consistent with that of the *Carolinites* species.

It should be noted that the *upper* limits of the ranges of the youngest species of *Carolinites* from Spitsbergen — *C. killaryensis* (STUBBLEFIELD) and *C. sibiricus* CHUGAEVA — are not known; one or both may range higher in the Whiterock than the *Orthidiella* zone.

Correlations between shelly and graptolitic Ordovician successions based on *Carolinites* have been summarised by FORTEY (1976).

III. Systematic Part

A. Theoretical basis of evolutionary lineages

ELDREDGE (1972, p. 84–5; 1973, p. 289–290) has recently given useful discussion of the methodology used by trilobite workers in the construction of models of phyletic relationships from morphological comparisons without primary regard to stratigraphic occurrence. His approach is based on the "cladistic" model advocated by some theoreticians of phylogeny (HENNIG 1966), dependent on the recognition of nodal (branching) points founded on the presence of shared, derived characters. The identification of such derived characters presumably relies on a priori knowledge, that is, knowledge which does not depend in any way on stratigraphy, of what character-states may be regarded as primitive and what derived.

In my previous discussion of olenid phylogeny (subfamily Balnibarbiinae FORTEY 1974b), and discussions in this paper of *Carolinites* and some of the Nileidae (Figs. 5, 13), emphasis is laid on both morphology *and* stratigraphy in the establishment of phylogenetic models. The Valhallfonna Formation is unusual in its consistently fossiliferous nature through a great thickness of strata and the relatively complete record obtainable therefrom. Even in this favourable circumstance only a relatively few groups of trilobites show *morphological* evidence of falling into phyletic series, and no attempt has been made to "force" species of, for example, *Ampyx* into stratigraphic "series" in the face of morphological opposition. In those series of species that are interpreted phylogenetically I must admit that interpretation would have been impossible without concomitant stratigraphic data. The problem centres on the recognition of "derived" and "primitive" characters. I have proposed here, for example, that *Peraspis* species with genal spines and furrowed pygidia were derived from *Symphysurus arcticus* n. sp. which lacks both features. Yet presumably both genal spines and furrowed pygidia may be regarded as primitive for the Trilobita. Again, the short preglabellar field and small pygidium characteristic of the *Cloacaspis* lineage among the Balnibarbiinae (FORTEY 1974b, p. 17) are probably to be regarded as primitive for the Olenidae (and may be primitive for the Trilobita as a whole on theoretical grounds), yet stratigraphic evidence seems to demonstrate the derivation of such species from a *Balnibarbi* (more "advanced") ancestor. This seems to indicate that what is "primitive" in one subgroup of a family at one time may be "derived" in another subgroup at a different time, but only stratigraphy can elucidate which in fact is the case. In examples where a trilobite does not fit into part of related-species succession - the majority of cases in both the Spitsbergen Ordovician and single horizon collections elsewhere — I believe that we have no alternative but to use purely morphological criteria to assess relationships, against which stratigraphical evidence may be used as a check. The more sporadic the fossil record the more the cladistic approach will be indispensible (it is thus of greatest use for groups with no fossil record at all!); for example, it has been used with success for spasmodically-occurring groups such as fossil fishes. The same applies to trilobites such as *Opipeuter* (FORTEY 1974a, p. 118–120) which are separated by a morphological "jump" from any other trilobite — the only way to form an hypothesis of phyletic relationships is on the basis of adjudged shared, derived characters.

The stratigraphical-morphological species lineage used here for some olenids, nileids and telephinids is surely capable of being tested, and perhaps more importantly is capable of being disproved (POPPER 1965), by every subsequent occurrence of a particular species. But it must be emphasised that such hypotheses can only be based on material from continuous, conformable and fossiliferous sections, where the time relations of each specimen are beyond doubt and not themselves dependent on biostratigraphic criteria. The lineage so established must further fulfil the condition of repeatability of sequence in successions subsequently examined.

The species lineages for the Olenidae (Balnibarbiinae FORTEY 1974b) and Nileidae (*Symphysurus arcticus*, *Peraspis* spp., and *Poronileus* n. gen. spp., see below pp. 36–39) conform well to the patterns expected an allopatric speciation model (ELDREDGE 1971, ELDREDGE and GOULD 1972). Both these families have benthic habits (FORTEY 1975, p. 338) and it is considered that speciation was promoted by isolation of populations on the shallow-deep water environmental gradient. The pelagic *Carolinites* shows, in part at least, more tendencies towards a (possibly relatively slow) "drift" of characters with time, exemplified by the transition from *C. genacinaca nevadensis* to *C. genacinaca genacinaca* (p. 103). Possibly barriers to gene flow among a true pelagic species are not sufficient to allow persistence of geographically isolated populations.

Subspecies

Subspecies are used here when a population differs from the nominate species in only one unequivocal character, but shares with the nominate species distinctive character(s) making a close relationship probable. Such a shared character is, for example, the peculiar pygidial surface sculpture of the *Nileus glazialis* group (p. 41).

B. Terminology and techniques

1. *Terminology*

Intra-palpebral ridge: This term is applied to a ridge on the fixed cheek adjacent to, and parallel with palpebral lobe of *Carolinites*.

Bacculae: This term is applied to inflated areas flanking the base of the glabella of some Raphiophoridae and Telephinidae. Such structures have often been termed "alae" in the past, by comparison with similarly positioned structures on the harpids. However, the homology of these structures between trilobites that are included in different orders is unclear at best. The earliest definition of the term "ala" of which I am aware is by BATHER (1910, p. 116) where it is applied specifically to *Harpes*, an apt (for this family) comparison being drawn with the alae of the human nose. WHITTARD (1955, p. 18–20) has further extended the use of the term ala to designate an area between glabellar and axial furrows on raphiophorids, an area which, as noted by WHITTINGTON (1959, p. 461), is part of the glabella rather than the pleural lobes. The situation in raphiophorids is complicated further by the presence in *Endymionia* of "lateral lobes" adjacent to the glabella which are of extra-glabellar origin (see p. 88, WHITTINGTON 1965, p. 325); these are in a position different from basal glabellar "alae" and it is doubtful whether the same term should be applied.

I propose that the term ala (pl. alae) should be restricted to the distinctive smooth, but not necessarily inflated areas flanking the base of the glabella on harpids. The term bacculae (Öpik 1967, p. 53) is available for swellings adjacent to the base of the glabella on other trilobites, and this usage is adopted here. The "lateral lobes" flanking the glabella of *Endymionia* are described by the non-specific term "lateral inflated areas".

2. *Orientation*

Although it is doubtless desirable to achieve a standard orientation for all trilobites for purposes of comparison and measurement, the extremes of morphological variation within the class make this virtually impossible and I am reluctantly obliged to use orientation suitable for particular families. For the raphiophorids a suitable cranidial orientation has been defined for Trinucleina by Hughes, Ingham and Addison (1975, Fig. 7): for the exterior view of the cranidium the specimen is orientated with the anterior fossulae in the axial furrows and the pits at the extremities of the border furrows in a horizontal plane. This is referred to here as the *fossular view*. Using this view the modifications in the occipital region which are important in the group are not involved in establishing the orientation itself. For the convex nileids the *palpebral view* (Bruton 1968, p. 2) has proved particularly useful. For asaphid and telephinid cranidia, and pygidia of all families, the usual *dorsal view* (Whittington and Evitt, 1954, p. 11) is appropriate, corresponding to the orientation in life of the genera concerned, and giving consistency between entire dorsal shields and fragmentary specimens.

3. *Measurements*

To standardise measurements made on the raphiophorid cranidium a number of angles are defined to measure the expansion of the glabella and its anterior taper, and the degree to which it overhangs the anterior border (Fig. 2). θ is the angle included between the axial furrows in fossular view; φ is the angle enclosed between the anterior margins of the glabella in the same orientation. μ is the angle between the forward part of the glabellar outline and that part of the glabella beneath the frontal spine in lateral view, and ω the angle between this latter part of the glabellar and the anterior border.

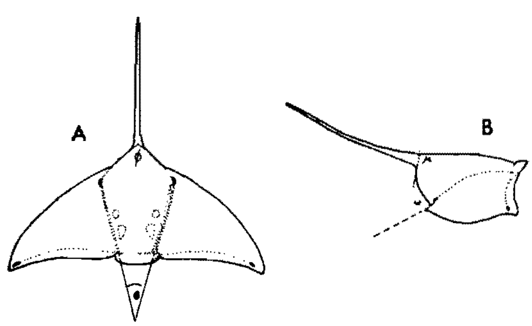

Fig. 2. Angles used in this paper to describe cranidia of *Ampyx* and other Raphiophoridae.

A number of closely-related species occur in Spitsbergen, and it has been found that linear measurements of cranidial and pygidial proportions are not the most sensitive way to discriminate such species when other criteria are available. Emphasis is given in specific diagnoses here to "presence or absence" characters, such as surface sculpture, and presence or not of spines, and to differences in shape, unfortunately not readily quantifiable, such as the differences in the border furrows of *Ampyx* species. Differences in grade, such as the degree of impression of the axial furrows and pygidial border furrow in *Poronileus* n. gen., are inevitably more subjective, and phrases like "well-impressed" or "shallow" have only a general meaning except in conjunction with photographs. Ring light illumination produces a standard, if rather low contrast for the photographs used here, so that the comparative terms are consistent within this work. Number counts, such as the number of terrace lines on a given area, and angular variations, are given with the range of variation within the population on which the species is based. Emphasis is given also to such variation as is found within species in relation to stratigraphic occurrence; within the few kilometres of the Spitsbergen outcrops no geographical variation has been detected.

C. Systematic descriptions

SYSTEMATIC ORDER

Families, subfamilies and genera are treated in alphabetical order. Species are described in an order which facilitates brevity of description, and obviates repetition. Where closely related species are considered, specious description of the second species is not given, points of difference only are discussed; however, a fuller account is given of *Poroniteus* species, which require special care in discrimination.

Family ASAPHIDAE Burmeister 1843

Subfamily ISOTELINAE Angelin 1854

Genus *Megalaspides* Brøgger 1886

Type species. — *Megalaspis dalecarlicus* Holm 1882.

Megalaspides striatellus n. sp.
(Pl. 7, Figs. 1–7)

Stratigraphic range. — Olenidsletta Member 80 m to 100 m; middle Arenig (probable *bifidus* zone).

Material. — Holotype, cranidium with free cheek attached: PMO NF 425; incomplete dorsal exoskeleton: PMO NF 1675; almost complete dorsal exoskeleton, PMO NF 1718; cranidium: PMO NF 520; pygidia: PMO NF 1727, 1856, 509, 1759; hypostoma: PMO NF 460a.

Diagnosis. — A *Megalaspides* species with surface sculpture of fine-scale terrace lines. Anterior branches of facial sutures divergent in front of eyes; posterior border furrows on cranidium deep. Pygidium with ill-defined concave border and wide doublure.

Description. — Elliptical dorsal exoskeleton, about two-thirds as wide as long, and from available unflattened material apparently of low convexity, with the anterior and anterolateral parts of the cephalon, and the posterior margin of the pygidium flattened, pleural regions gently convex, and axial regions but slightly elevated above the rest of the exoskeleton. Glabella about two-thirds cephalic length, best defined in front of the palpebral lobes, front margin hardly rounded across mid-line; posterior part of glabella tapers gently to minimum width adjacent to palpebral lobes. Areas of muscle attachment visible as smooth patches on the anterior part of the dorsal surface of the glabella, faint depressions on internal moulds. 1P depressions adjacent to the anterior parts of the postocular cheeks; on the holotype there is a suggestion of a furrow (?occipital) traversing the glabella at the level of the 1P furrows. 2P depressions relatively deep, placed opposite palpebral lobes at glabellar constriction, subcircular. 3P and 4P faint, straight, outward-backward sloping (4P more so than 3P) and close together, outer end of 3P opposite anterior limit of palpebral lobe. Glabellar tubercle prominent, placed just behind line connecting the posterior limits of the palpebral lobes, at about one quarter glabella (sag.) length. Palpebral lobes slope upwards, such that their outer peripheries are on a level with the highest part of the glabella; their outline is semicircular, length (exsag.) slightly less than one quarter that of glabella. Internal mould shows narrow palpebral rims. Posterior limbs of fixed cheeks of transverse width slightly less than width of basal part of glabella; posterior border furrow deep, broad, delimiting narrow (exag.), flat posterior border. Posterior sections of facial sutures diverge at right angles to the sagittal line behind the eyes, distally curving posteriorly to cut the posterior margins of the cranidium at 90 degrees. Anterior branches diverge at an angle between 10 and 20 degrees in front of the eyes, anteriorly curving adaxially to meet in a point on the mid-line, these parts of the sutures enclosing an angle between 130 and 140 degrees.

Free cheek divided into convex inner part and flat or concave border, the latter narrowing posteriorly and continued into pointed genal spine which extends back at least as far as the fourth thoracic segment. Cephalic doublure broad, occupying the bulk of the width of the cheek, and with surface sculpture of densely-spaced terrace lines; panderian opening near posterior margin of cheek just adaxial to genal spine.

One example of a hypostoma (Pl. 7, Fig. 6 unfortunately partly concealed beneath the preglabellar field of a *Niobe flabellifera* cranidium) undoubtedly belongs with this species, being closely similar to those figured for Swedish *Megalaspides* species (see Tjernvik 1956, Fig. 40, p. 250) characterised by the long, gently arcuate, posteriorly-incurving outline of the lateral borders, and the deep fork in the posterior margin.

Cephalic surface sculpture of fine terrace lines. These have an irregular ripple-like form and run almost transversely across the pre-glabellar field, front part of the glabella (except for median (sag.) smooth line) and adaxial, convex parts of free cheeks; near the lateral margins of the cephalon they are subparallel to the cephalic margin, less anastomosing. Terrace lines are sparse on the posterior part of the glabella.

Thorax with narrow, parallel-sided axis about two-thirds width of adjacent pleurae. Pleural furrows deep, but narrowing adjacent to adaxial part of articulating facets. These latter extend to half the pleural width, and for almost all that width are underlain by the doublure, the inner margin of which is indented where the tips of the pleural furrows cross on the dorsal surface. Prominent panderian openings on the anterior part of facet doublure. Pleural tips blunt.

Pygidium two-thirds as long (sag., including half ring) as wide, with gently convex pleural fields and ill-defined, flattened border. Axis extending to 0.6 pygidial length, anteriorly tapering gently, posteriorly subparallel sided, with up to ten axial rings visible, of which only the first two are defined by ring furrows that cross the axis, the posterior ones indicated by faint depressions on lateral parts of axis. Surface sculpture of very fine anastomosing terrace lines like those on cephalon. Doublure broad, with straight inner margin except where excavated round tip of axis. Terrace lines on doublure increasingly crowded towards inner margin: less than 2 per mm near posterior margin grading to 10 per mm at inner margin. On internal moulds up to six low pleural ribs are visible, each bisected by a shallow rib furrow.

Discussion. — In the possession of a flattened border to the pygidium this species agrees with *Megalaspides nericiensis* WIMAN, which TJERNVIK (1956, p. 251) proposed as type species of the subgenus *Megalaspides* (*Lannacus*), citing the presence of a pygidial border as one of the defining characters of the subgenus. In other characters, however, *M. striatellus* is like the species TJERNVIK assigns to *Megalaspides* (*Megalaspides*) (see TJERNVIK 1956, Pl. 8), for example, the posterior border furrow of the cranidium is relatively deep (in *M.* (*L.*) *nericiensis* it is effaced), the pygidial doublure is broad like that of *M.* (*M.*) *paliformis* TJERNVIK (TJERNVIK 1956, Pl. 8, Fig. 15), and the eyes are placed far back, such that the posterior sections of the facial sutures cross the cephalon transversely behind the eyes. *M. striatellus* is thus intermediate between known species of *Megalaspides* (*Megalaspides*) and *M.* (*Lannacus*). I am inclined to the view that the differences *Megalaspides* (*Lannacus*) *nericiensis* and *Megalaspides* (*Megalaspides*) species are within the range of variation of a group of very closely related species and do not warrant subgeneric separation; *M. striatellus* possesses a new combination of characters within this group. The alternative view, by which *M. striatellus* might be made the type species of another new subgenus of *Megalaspides*, would seem to me to introduce excessive and unnecessary splitting.

M. striatellus differs from other *Megalaspides* species in having surface sculpture of fine terrace lines. The wide pygidial doublure is distinctive, being approached in this respect only by *M. paliformis*, which, however, has the doublure expanding in width posteriorly. It may also be noted that the thoracic axis of *M.* (*M.*) *dalecarlicus* and *M.* (*L.*) *nericiensis* has a zig-zag outline, each axial ring expanding in width slightly backwards; the axial furrows of *M. striatellus* are straight.

Genus *Presbynileus* HINTZE 1954
Subgenus *Protopresbynileus* HINTZE 1954

Type species. — *Pseudonileus willdeni* HINTZE 1953.

The new name *Protopresbynileus* was proposed by HINTZE (1954), because the name *Pseudonileus*, given by HINTZE (1953) for a new genus to accommodate the species *P. willdeni*, was preoccupied. Following JAANUSSON (in MOORE 1959) *Protopresbynileus* is regarded here as a subgenus of *Presbynileus*.

Presbynileus (*Protopresbynileus* ?) *glaber* n. sp.
(Pl. 9, Figs. 1–6)

Stratigraphic range. — A rare trilobite found only in one bed of the Olenidsletta Member, 102 m from base, at or just below base of *hirundo* zone.

Material. — Holotype: almost complete cranidium PMO NF 41. Other material consists of a cranidium: PMO NF 109; pygidia with thoraxes: PMO NF 46, 38 and pygidia: PMO NF 2, 93, 66.

Diagnosis. — A large, smooth asaphid species of relatively low convexity attributed with question to *Presbynileus* (*Protopresbynileus*). Anterior margin of cranidium but slightly flattened; posterior limbs of fixed cheeks wide (trans.). Distinctive sparse cranidial surface sculpture of only five or six terrace lines running transversely across frontal lobe of cranidium near, but not at anterior margin. Pygidium wider than long, axis faintly visible on dorsal surface, extending to two-thirds pygidial length; dorsal surface smooth except for a few terrace lines near posterior margin. Pygidial doublure broad, inner margin convex-forward.

Description. — A large species; one fragmentary pygidium (PMO NF 2) is 7 cm across, suggesting that complete individuals must have exceeded 12 cm in length. Convexity is relatively low, the anterior part of the cranidium is downward-sloping, and for a cranidium 30 mm long the depth in lateral view does not exceed 10 mm. The posterior part of the cranidium forms a near-horizontal plane, from which the palpebral lobes slope slightly upwards, the posterior limbs of the fixed cheeks but slightly downwards. No axial, preglabellar or border furrows may be seen. The maximum width of the cranidium is at the posterior margin; the length of the glabella is about three-quarters this maximum width. The cranidial width across the palpebral lobes is equal to the maximum transverse width across the anterior part of the cranidium at the anterior margin, this width being slightly less than the length of the glabella. Adjacent to the anterior cranidial margin the downward slope of the front part of the cranidium becomes slightly less, thus giving the cranidium a narrow, indistinct anterior concavity. On one specimen (Pl. 6, Fig. 2) a slight antero-median depression is visible. Palpebral lobes semicircular, placed slightly behind mid-length of cranidium, such that the transverse line connecting their mid-points is at 0.4 glabellar length on available material. There are broad, indistinctly defined palpebral rims. Small, median glabellar tubercle posterior to transverse line connecting posterior limits of palpebral lobes. The dorsal surface of the cranidium completely lacks surface sculpture, except for a narrow transverse band running across the anterior, sloping part of the glabella; this sculpture consists of widely spaced terrace lines numbering four to six at any one point. On available material these terrace lines do not extend on to the anterior, slightly concave part of the glabella. Anterior branches of facial suture diverge at 30–40 degrees in front of palpebral lobes, curving at first rather gently adaxially, anterolaterally curving sharply adaxially to run in a uniform arc around the anterior margin to meet on mid line. Posterior sections of the sutures diverge at a right angle to sagittal line behind palpebral lobes, distally curving gently posteriorly to cut posterior margin at an acute angle (about 50 degrees).

Thoracic segments equal in length (sag., exsag.), axis very gently convex, wide, twice the transverse width of the adjacent thoracic pleurae. Axial furrows shallow, parallel, or tapering slightly at last two segments. Inner parts of pleurae horizontal, outer parts steeply down-sloping. Pleural furrows shallowing rapidly abaxially and adjacent to axial furrows, moderately deep only behind articulating fulcrum. Broad triangular facets form outer, sloping part of pleurae. Doublure extends upwards beneath this sloping part, inner margin sloping abaxially posteriorly until crossed by the pleural furrow, behind which it extends adaxially to form a narrow posterior tongue on each segment. Small, circular panderian opening on forward part of doublure, at about its mid-transverse width.

Pygidium of relatively low convexity, steeply downsloping only around its perimeter, posterior outline smoothly parabolic such that its sag. length is about 0.7 maximum width at, or slightly behind anterior margin. Articulating facet similar to those of thorax, backed by prominent half-rib. Apart from this feature the dorsal surface of the pygidium is remarkably smooth. The axis is very faintly visible, extending to about two-thirds pygidial length, evidently tapering very rapidly over a short distance anteriorly to become much narrower than thoracic axis, posteriorly tapering gently (faint axial furrows enclose an angle of about 25 degrees) to rounded tip. Faint mid-axial sagittal ridge visible on one specimen (Pl. 6, Fig. 5). Like the thorax, the pygidium is almost devoid of surface sculpture. Around its posterior margin, however, there are a very few (no more than eight at any one point) terrace lines, which run slightly oblique to the posterior margin. Doublure broad, closely reflexed against dorsal surface, inner margin convex forward, and slightly undulating. Terrace lines on doublure cuesta-like and inward-facing, sparsely spaced near posterior margin (about 1 per mm), becoming 8–10 per mm near the anterior margin.

Discussion. — Discrimination of isotelinid genera is often difficult, and with forms in which the dorsal furrows are almost completely effaced the difficulties are compounded. Discussions concerning the problems of definition of some of the genera involved have been given by SHAW (1968, p. 58) and ROSS and SHAW (1972, p. 19–20). For present purposes it is relevant to note that the species described above has been assigned provisionally to *Presbynileus* (*Protopresbynileus*) because of its resemblance to *P.* (*P.*) *willdeni* (HINTZE) from a slightly earlier horizon in the Fillmore limestone, Utah (HINTZE 1953, Pl. XV, Figs. 14–17). Cranidia of the two species are similar in respect of their evenly rounded anterior outlines, low convexity, and course of the facial sutures, particularly those defining the wide (trans.) postocular cheeks. Pygidia of both species lack borders, and possess a broad, convex-forward doublure. Species of the subgenus *Presbynileus* (*Presbynileus*) are more convex, with narrow (trans.), steeply downsloping postocular fixed cheeks. *Presbynileus* (*Protopresbynileus*) *glaber* differs from *P.* (*P.*) *willdeni* in having a slight anterior concavity on the cranidium, in its distinctive surface sculpture, and in possessing a relatively longer (sag.) pygidium with correspondingly broader (exsag.) doublure. Comparisons with the Utah species are hindered by the smaller size of known material of that species compared with that of *P.* (*P.*) *glaber*, and especially because the free cheek and hypostoma of the Spitsbergen species are not known; for these reasons the assignment of the species described herein to *Presbynileus* (*Protopresbynileus*) must be tentative.

Some resemblance is noted between the cranidium of *P.* (*P.* ?) *glaber* and that of *Anataphrus martinensis* ROSS and SHAW (1973, Pl. 3, Figs. 4–16), from the middle Ordovician Copenhagen Formation of Nevada, particularly with respect to the wide (trans.) postocular fixed cheeks. In this feature *A. martinensis* differs from the type species of *Anataphrus*, *A. borraeus* WHITTINGTON 1954, from the late-middle or upper Ordovician of Baffin Island, which has short (trans.) postocular cheeks. *A. martinensis* differs from the Spitsbergen species, which is considerably earlier, in its greater convexity, the presence of faint cephalic axial furrows, and particularly in having a narrow pygidial doublure, the inner margin of which is concave-forwards.

Genus *Ptyocephalus* WHITTINGTON 1948

Type species. — *P. vigilans* WHITTINGTON 1948.

Ptyocephalus cf. *P. vigilans* WHITTINGTON 1948
(Pl. 4, Figs. 5, 6)

Stratigraphic range. — From a single bed 103 m from the base of the Olenidsletta Member.

Material. — Cranidium, PMO NF 1629; hypostoma, PMO NF 1619.

Discussion. — We have no free cheeks or pygidia of this species, but the cranidium and hypostoma are so very similar to those of *P. vigilans* fully described and illustrated by WHITTINGTON (1948, Pls. 82, 83) that a close relationship between the Spitsbergen species and that from the Pogonip Group is certain, and specific identity likely but unprovable until more parts of the exoskeleton are discovered in the Valhallfonna Formation. In particular the hypostoma has the deep, inverted-U shaped fork, and the rounded postero-lateral extremities of the border illustrated for *P. vigilans* (WHITTINGTON 1948, Pl. 83, Fig. 8), but differing from the truncate posterior tips of the hypostoma of *P. yersini* HINTZE (1953, Pl. XIV, Fig. 8), and lacking the marginal rims characterising *P. declivitus* ROSS (1951, p. 92). On the cranidium palpebral lobes are larger, more strongly curved and further back than those of *P. fillmorensis* HINTZE 1953, *P. accliva* HINTZE 1953 (see HINTZE 1953) and *P. montanensis* LOCHMAN-BALK and WILSON 1967 (see ROSS 1957, Pl. 42, Figs. 5, 6, 8–12).

The occurrence of this species in Spitsbergen is of importance because *Ptyocephalus* species of *vigilans* type are characteristic in Utah and Nevada of upper Canadian beds of zone "J" age. *P.* cf. *vigilans* is found in Spitsbergen with the stratigraphically youngest specimens of the typical zone "J" pelagic trilobite *Carolinites genacinaca* ROSS.

Subfamily NIOBINAE JAANUSSON 1959

Genus *Gog* n. gen.

Type species. — *Gog catillus* n. sp.

Diagnosis. — Large niobinid trilobites of low convexity. Relatively long glabella narrowest at about the level of the eyes with characteristic crescentic (long axis sag.) basal pair of furrows. Occipital ring well defined by transverse occipital furrow; glabellar tubercle well in front of occipital furrow. Eyes small, medially placed. Posterior limbs of fixed cheeks wide, of transverse width equal to that of the occipital ring; bacculae prominent adjacent to the basal part of the glabella. Hypostoma with very shallow notch; middle furrows backward sloping. Anterior thoracic segments blunt-tipped, posterior thoracic segments pointed. Pygidium much like that of *Ogygiocaris*, with six to eight pairs of gently curved pleural ribs, and undulating inner margin to doublure. Surface sculpture of raised lines. Species included in the genus: *Gog catillus* n. sp., *Gog explanatus* (ANGELIN 1851), *Niobe?* sp. N 1 BURSKY 1970.

Discussion. — This genus possesses features transitional between niobinid and ogygiocarinid trilobites. The pygidium is very similar to that of *Ogygiocaris* species (compare that of *G. catillus* with that of *Ogygiocaris sarsi sarsi* ANGELIN (HENNINGSMOEN 1960, Pl. 4, Fig. 5) in having narrow ribs and a crenulate inner margin of the doublure. Similarly the transversely wide posterior fixed cheeks and elongate glabella are also matched in *Ogygiocaris* species. However the position of the glabellar tubercle, distinct occipital ring, presence of bacculae and gently notched hypostoma, and lack of genal spines suggests affinities with *Niobe* species rather than those of *Ogygiocaris*. These features, and also in particular the presence of a panderian opening on the thoracic doublure, have indicated to the writer that *Gog* should be included within the Niobinae rather than the Ogygiocaridinae.

Gog is also probably related to the little-known Tremadoc genus *Niobina* LAKE from Wales (LAKE 1946, p. 334), Argentina (HARRINGTON and LEANZA 1957, p. 180) and Sweden (TJERNVIK 1956, p. 234) which also possesses a transverse occipital furrow, wide (trans.) posterior fixed cheeks, broad pygidium with a narrow axis and many segments, and in *N. taurina* HARRINGTON and LEANZA a surface sculpture of fine lines (HARRINGTON and LEANZA 1957, Fig. 91, 1a). However *Niobina* species have the eyes in a relatively anterior position compared with *Gog*, possess a posteriorly pointed hypostoma, and deep interpleural furrows on the pygidium. The similarities between *Ogygiocaris*, *Gog* and *Niobina* suggest a derivation of the ogygiocaridids from a *Gog*-like ancestor, possibly during the early Arenig.

Gog catillus n. sp.
(Pls. 1–3; Fig. 3)

Stratigraphic range. — Olenidsletta Member 75 m to 100 m (middle Arenig, probable *bifidus* zone).

Material. — Holotype, dorsal exoskeleton lacking free cheeks, melt stream E on Olenidsletta PMO NF 1679. Among abundant further material are 2 dorsal exoskeletons lacking free cheeks PMO NF 1673, 531; cranidia: PMO NF 421, 465, 350, 423, 537, 2633, 442, 2760, SMA 84360 — 84365; free cheeks: PMO NF 439, 532–3, 2626, 1015, SMA 84366; pygidia: PMO NF 444, 536, 2659, 454, 466–7, 451–3, 445, 436, 438, 2022 and hypostomata: PMO NF 426, 459, 1939, 2040, 1726.

Diagnosis. — A *Gog* species with surface sculpture of extremely fine raised lines, about three times more densely spaced on dorsal surface of exoskeleton than terrace lines on doublure. Pygidium with eight pairs of pleural ribs, broad doublure with strongly undulating inner margin.

Description. — This is the largest of the trilobites of the Valhallfonna Formation; the holotype has a length of 13 cm, but fragments of larger specimens indicate that some individuals may have approached 20 cm in length. Cephalon and pygidium are equal in length; the thorax relatively slightly shorter. Much of the material of this species is flattened, but the convexity is low and flattening in this species does not greatly alter its proportions. In unflattened cranidia the glabella and palpebral lobes stand above the rest of the cranidium, the preglabellar field forms a horizontal rim around the front of the glabella, while the postocular cheeks slope gently downwards. The glabella is fusiform in outline, with a sagittal length between 1.4 and 1.75 times the width across the occipital ring on available material. The glabella is narrowest adjacent to the eyes and in front of the bacculae, anteriorly with a broadly parabolic outline. The occipital ring occupies about one-tenth total length of glabella; occipital furrow running transversely across the glabella and slightly backward-bowed medially, where the occipital ring is slightly narrower. Four pairs of glabellar furrows; 1P crescentic (with long axis sag. and concave side of crescents facing outwards) and deepest posteriorly, placed about one third across the glabella with anterior limits opposite base of palpebral lobe; 2P deep, transverse, opposite mid-part of palpebral lobe; 3P sloping gently backwards-outwards, outer end opposite anterior limit of palpebral lobe; 4P shallow and close to 3P, shorter, and sloping backwards more steeply (approximately 70 degrees to sag. line). Outer ends of 2P, 3P and 4P are progressively closer to the axial furrows, which 4P almost touches. Axial furrows shallow, but become exaggerated by flattening and then appear deep. Minute glabellar tubercle on mid line between bases of 1P furrows, and well in front of occipital furrow.

Prominant bacculae adjacent to the basal part of the glabella, extending forwards from where the occipital furrow joins the axial furrows to behind the palpebral lobes. Preglabellar field narrows medially, where it is of about the same width (sag.) as the occipital ring. Palpebral lobes placed at mid-length of glabella, horizontal, with a semicircular outline, anterior limits almost touching the axial furrows, posterior limits slightly further away from glabella, distance from anterior to posterior limits between 0.16–0.19 length of glabella on available material. Poorly defined, broad palpebral rim visible on some specimens. The wide, triangular fixed cheeks are slightly below the level of the posterior border. Posterior border furrows meet the axial furrows posterior to the junction of those furrows with the occipital furrow. Posterior border widens rapidly abaxially, and laterally is divided by a furrow parallel to the posterior border furrow. Anterior branches of facial sutures diverge at between 21 and 28 degrees to sagittal line in front of the eyes, anteriorly curving adaxially to converge forwards in front of the preglabellar field (enclosing an angle of about 150 degrees), passing supra-marginally to meet at the cephalic border on the mid line. In small cranidia the sutures are niobiform and they meet at a point; in larger cranidia such a distinct point is not usually visible and the facial sutures may have been tangential to the cephalic margin medially. Posterior branches diverge at a high angle behind the palpebral lobes, laterally curving in a uniform arc posteriorly to cut the posterior border at a high acute angle.

Free cheeks lacking genal spines and with rounded genal angle. Eye surrounded by low eye socle. Doublure underlies most of the free cheek and the paradoublural line is strongly reflected on the dorsal surface. Inner margin of doublure subparallel to the cephalic border, gently undulating. Terrace lines strong on ventral surface of doublure, more weakly reflected on dorsal surface (Pl. 1, Fig. 2) and number a maximum of 20 at the anterolateral part of the cheek. Anteriorly the doublure narrows around the hypostomal suture almost coincident with the preglabellar furrow; median suture short. The anterior

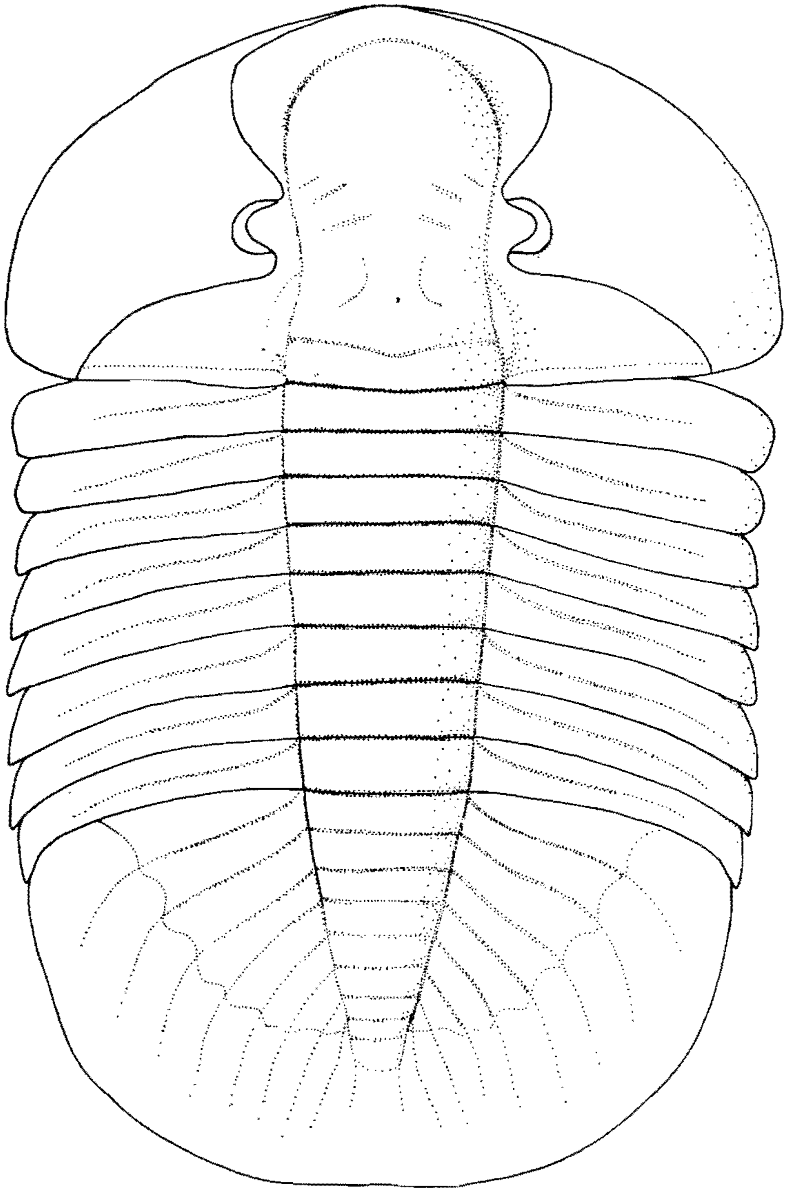

Fig. 3. Reconstruction of *Gog. catillus* n. gen., n. sp. Approx. natural size.

margin of the hypostoma indicates that the hypostomal suture was medially pointed. No specimen has been found which shows the panderian opening on the doublure of the free cheek.

Hypostoma of maximum width (just anterior to middle furrows) about 0.8 sagittal length, with prominent oviform middle body, tapering gently posteriorly and particularly convex in front of the hypostomal suture, where there is a subcircular, median inflated area (Pl. 2, Fig. 4). Deep middle furrows, which slope outwards and backwards with steep, backward-facing facets, divide the middle body into a large anterior, and much smaller posterior lobe. The lateral border begins at about mid-length of middle body, expands rapidly in width and is downward arched adjacent to middle furrows, tapers posteriorly where it merges with the narrow (sag.) posterior border. Anterior wings almost vertical; if we are correct in assuming that the anterior margin of the hypostoma was ventrally correspondent with the preglabellar furrow then it seems probable that the dorsal edges of the anterior wings were adpressed against the axial furrows. Posterior margin of hypostoma very gently notched.

Thorax with parallel sided axis two-thirds width of pleurae. Anterior pleurae with rounded tips, posteriorly progressively more pointed. Tips of anterior segments overlap, these segments possessing a broad, depressed facet; in this way the expanded lateral parts of the posterior cephalic border extend over the first thoracic segment. Pleural furrows deep, almost transverse, dying out on a line coincident with the ventral extension of the doublure. The form of the doublure is similar to that described in *Niobe quadricaudata* (BILLINGS) by WHITTINGTON (1965, Pl. 24, Fig. 6) with the narrow posterior adaxial extension of the doublure, except that the inner margin is deeply notched where crossed by the pleural furrow. Minute panderian opening on the anterior part of the doublure (Pl. 3, Fig. 3).

Pygidium has a length/width ratio (sag. length excluding half ring) varying between 0.54 and 0.66 on available material, gently convex pleural fields and flattened border. Axis tapers gently, the axial furrows enclosing an angle of about 25 degrees. Well preserved material retaining the exoskeleton shows nine axial rings, but the last ring furrow is shallow and only visible medially; many flattened specimens only show eight rings. Ring furrows curve backwards medially. Axis extends to about three-quarters pygidial length but its posterior margin is not defined, the axial furrows becoming subparallel distally so that the terminal piece merges with the posterior border. The nine pairs of pleural furrows do not reach the posterior margin of the pygidium, distally becoming shallow and backward-deflected; successive pairs slope backwards more steeply, so that the anterior pair is parallel to the last pleural furrows on the thorax, the ninth pair (often not visible on flattened specimens) almost parallel to the sagittal line. On a few specimens weak interpleural furrows are also developed. Paradoublural line prominent on the dorsal surface of the exoskeleton. Inner margin of doublure undulating; the v-shaped troughs are at the points where the doublure is crossed by the pleural furrows. After the sixth pleural furrow the margin runs transversely towards the axial furrows, before its invagination around the tip of the axis.

Surface sculpture over the greater part of the dorsal exoskeleton consists of fine raised lines. These are sparser over the posterior part of the glabella and do not pass over areas of muscle attachment; on the pygidial axis such areas are finely punctate (Pl. 3, Fig. 6). True terrace lines occur on the ventral surface of the doublure and are more closely spaced marginally, often with finer terrace lines intercalated towards the inner margin of the doublure; their spacing is three or four times more sparse than that of the dorsal raised lines.

Discussion. — The species *Niobe explanata* ANGELIN (1851, p. 15, Pl. XI, Fig. 4; Pl. XII, Fig. 2) from the early Ordovician of Skåne, Fågelsång, Sweden, possesses the combination of characters whereby *Gog* is distinguished from other niobines, and is referred to the new genus. The lectotype cranidium (here selected, Ar 24085) differs from that of *G. catillus* in having a shorter preglabellar field which continues the anterior slope of the frontal lobe of the glabella (Pl. 4, Fig. 1), paradoublural line not distinct on the dorsal surface of the pygidium, and the inner surface of the doublure less crenulate. Terrace lines are more widely spaced on the dorsal surface of cranidium and pygidium. Unfortunately this species was not precisely stratigraphically localised by Angelin although on the basis of the black limestone lithology in which *G. explanatus* occurs it is probable (Dr. TJERNVIK, written communication 1973) that the species occurs in the *limbata* or *expansus* zones at the top of the Arenig, i.e. younger than *G. catillus.*

Pygidia closely comparable to that of *Gog catillus* occur in the *planilimbata* zone (early Arenig) of central Sweden; one of these, kindly lent to me by Dr. TORSTEN TJERNVIK, is illustrated on Pl. 4, Fig. 3. They differ from those of *G. catillus* only in being relatively longer, with a very narrow border, and scarcely cranulated inner margin to the doublure. A pygidium probably of this type was illustrated by WIMAN (1905, Pl. 2, Fig. 13).

The genus is almost certainly present in Arenig rocks in Pai-Khoya, north Arctic Urals. The *Ogygiocaris* sp. figured by BURSKY (1970, Pl. 15, Fig. 1) has a pygidium similar to that of *planilimbata* zone species from Sweden, and in spite of distortion the deep occipital furrow typical of *Gog* (but unlike *Ogygiocaris*) is visible. The pygidia figured by BURSKY (Pl. 14, Figs. 6, 9) as *Niobe?* sp. N 1 are similar to those of *Gog catillus*, in dimensions and number of pleural ribs, and are apparently of the same age, but their preservation is too poor to be sure of specific identity.

Genus *Niobe* ANGELIN 1851

Type species. — *Asaphus frontalis* DALMAN 1827.

Discussion. — The type species of *Niobe, N. frontalis* (DALMAN 1827), has been redescribed by BOHLIN (1955, Pl. VI, Figs. 5–9). Two species attributed to the genus occur in Spitsbergen, and these are similar to the type species in cranidial features, such as the outline of the glabella, position of the palpebral lobes, and distribution of muscle areas and surface sculpture. They also possess prominent bacculae, a character which WHITTINGTON (1965, p. 349) suggested may be of importance in distinguishing *Niobe* species from those of *Niobella* (*sensu* TJERNVIK 1956, p. 228). The pygidial pleural fields of the Spitsbergen species are crossed by deep pleural furrows, but the posterior borders are not clearly defined as in the type species. Two other small differences may be noted: the glabellar tubercle on the type species is very prominent, whereas on the Spitsbergen species it is minute, and on the latter the postocular fixed cheeks are wider (trans.), and laterally defined by sigmoidal sutures. The relatively small differences are not considered sufficient to warrant the separation of the Spitsbergen species from *Niobe*.

Niobe flabellifera n. sp.
(Pl. 5, Figs. 1–5)

Stratigraphic range. — Olenidsletta Member 80 m to 100 m Middle Arenig, beds underlying *hirundo* zone.

Material. — Holotype, incomplete dorsal exoskeleton lacking free cheeks, PMO NF 457; cranidia: PMO NF 460a, 424, 534; pygidia: PMO NF 535, 54, 462, 2066, 534 (same block as cranidium), 521; free cheek: PMO NF 420.

Diagnosis. — A *Niobe* species with relatively small eyes, preglabellar field about one-fifth glabellar length (sag.), postocular fixed cheeks wide (trans.). Pygidial doublure very broad; four pairs of pygidial pleural furrows, the posterior three very short; pygidial border poorly-defined. Surface sculpture of very fine terrace lines without interspersed pits.

Description. — Exoskeleton about two thirds as wide as long, cephalon, thorax and pygidium approximately equal in length. Most cephalic material is flattened, but from unflattened pygidia it is apparent that convexity of this species was low. Cranidium widest posteriorly, about twice the width at the posterior margin compared with the maximum preocular width (trans.) at about midlength of frontal lobe of glabella. Glabella narrowest at midlength, length 1.4 times width across occipital ring, front margin truncate transversely. Glabellar muscle impressions appear as smooth patches and faint depressions, anterior pair adjacent to axial furrow in front of palpebral lobe, 2P and 3P transverse, opposite palpebral lobes, and 1P revealed by ill-defined depressions opposite anterior parts of bacculae. Occipital ring narrows medially, defined by an occipital furrow which is deep for its medial, backward-bowed part, shallows greatly near the axial furrows. Minute glabellar tubercle about midway between occipital furrow and transverse line connecting posterior limits of palpebral lobes; on the dorsal surface this tubercle shows four symmetrically disposed pits (Pl. 5, Fig. 5), which are similar in arrangement to the occipital organ of *Raymondaspis* (WHITTINGTON 1965, Pl. 58, Fig. 10) and odontopleurids (WHITTINGTON 1956, p. 177). Bacculae prominent adjacent to the posterior, anteriorly-tapering part of the glabella, relatively deeply defined by the axial furrows on their inner sides, and merging with the fixed cheeks on their outer sides, suggesting that they are a structure belonging more to the genal than to the axial regions of the species.

Palpebral lobes medially placed, fairly small, one-fifth glabellar length (exsag.). Postocular fixed cheeks wide (trans.), but slightly less than the transverse width of the occipital ring. Shallow posterior border furrow more or less bisects the postocular cheek. Preglabellar field relatively broad for *Niobe*, about one fifth glabellar length (sag.) on available material, widest laterally and medially. Anterior branches of facial suture curve outwards in front of the eye lobe, thence curving uniformly adaxially to meet on the midline, and at the margin of the cephalon at an obtuse-angled point. Posterior branches sigmoidal, flaring out almost at right angles to the sagittal line, laterally curving posteriorly to become parallel to the posterior parts of the axial furrows, and finally curving outwards again to cut the posterior margins at an angle of about 30 degrees.

Free cheek with rounded genal angle, eye socle deep; the greater part of the cheek is underlain by broad doublure, and the paradoublural line is prominent on the dorsal surface. Terrace lines on the anterior part of the doublure continuous and strong, cuesta-like, with steep slopes posterior. This is in contrast to the terrace lines on the dorsal exoskeleton (Pl. 5, Fig. 2) which are fainter and more crowded, discontinuous and anastomosing, steep slopes facing anteriorly. Doublure narrows medially where its inner margin ventrally corresponds with the anterior margin of the glabella. Fine terrace lines continue on preglabellar field and on postocular fixed cheeks; on the glabella they are present along the sagittal line and, more scattered and weak, between muscle impressions exsagittally. No hypostoma can be attributed with certainty to this species.

Thorax with gently tapering axis of transverse width less than pleurae. Pleurae with diagonal furrows which stop at broad, downward-sloping facets; terrace lines on adaxial part of pleurae run approximately sagittally, on facets transversely. Construction of thoracic doublure identical to that figured by WHITTINGTON (1965, Pl. 24, Fig. 6) for *N. quadraticaudata* (BILLINGS 1865).

Pygidium almost two-thirds as wide as long, with a quadratic outline, and posteriorly a broad, ill-defined and gently sloping border. Axis tapers gently at 20–25 degrees, reaching to about two-thirds pygidial length, with six axial rings usually visible, the posterior three but faintly defined by shallow ring furrows which are not impressed laterally. Of the four pairs of pleural furrows only the first crosses the paradoublural line to die out before reaching the lateral margin of the pygidium, the three posterior pairs slope progressively steeply backwards and are progressively shorter, such that the very short, most posterior pair is almost parallel to the sagittal line. Pygidial doublure broad, inner margins converging backwards at about 70 degrees to sagittal line, outline slightly indented where approached by pleural furrows and excavated around tip of the axis. Surface sculpture on pleural fields of fine irregularly anastomosing terrace lines, running transversely and oblique to the pygidial margin; similar terrace lines are present especially on the mid-part of the axis. Terrace lines on doublure stronger, more widely spaced, subparallel to posterior margin.

Discussion. — The distinctive pygidium of this species, with its short pleural furrows, ill-defined border and sculpture of fine, anastomosing lines at once distinguishes it from late Tremadoc-Llanvirn Scandinavian *Niobe* species, *N. frontalis* (DALMAN 1827), *N. insignis* LINNARSSON 1869, *N. incerta* TJERNVIK 1956 and *N. emarginula* ANGELIN 1851 (the last three described by TJERNVIK

1956). In addition the transversely wide postocular fixed cheeks of *N. flabellifera* and its relatively broad, halo-like preglabellar field separate it from these species. Similar wide fixed cheeks are present on *Niobe morrisi* (Billings 1865) (Whittington 1965, Pl. 28, Figs. 1, 3, 4) from the middle Table Head Formation, but this species has a short preglabellar field, different cephalic surface sculpture, and a pygidium with a narrow doublure, relatively long axis, and longer pleural furrows than *N. flabellifera.*

N. flabellifera is undoubtedly closely related to *N. occulta* n. sp., discussed below. The two forms occur together and may represent sexual dimorphs of the same species. Detailed collecting has shown, however, that *N. occulta* n. sp. extends its range into higher beds within the Olenidsletta Member than *N. flabellifera* and it seems more probable, therefore, that it is indeed a distinct species.

Niobe occulta n. sp.

(Pl. 4, Fig. 4; Pl. 6, Figs. 1, 2, 4–6; Pl. 23, Fig. 8)

Stratigraphic range. — Olenidsletta Member, 90 m to 103 m, uppermost part of range extending into earliest beds with graptolites of *D. hirundo* zone.

Material. — Holotype, incomplete dorsal exoskeleton PMO NF 106; cranidia: PMO NF 78, 2181, 49; hypostoma: PMO NF 107; free cheeks: PMO NF 2206, 2183, 10; pygidia: PMO NF 2192, 2130, 2111, 1623, 7, 104, 2718.

Diagnosis. — A *Niobe* species with relatively small eyes, preglabellar field about one-fifth glabellar length (sag.), postocular fixed cheeks wide (trans.). Pygidial doublure of moderate width; five pairs of pygidial pleural furrows; narrow, poorly-defined pygidial border. Surface sculpture of very fine terrace lines without interspersed pits.

Discussion. — This species is best considered in relation to *Niobe flabellifera* to which, as the diagnosis indicates, it is very close. The distinctions between the two species may be summarised as follows:

1. In *N. occulta* the glabella is less conspicuously waisted adjacent to the palpebral lobes and its front margin is more uniformly rounded; terrace lines are completely distributed over the surface of the glabella except in muscle impressions. Terrace lines are also present on the palpebral lobes, which in *N. flabellifera* are smooth.
2. The free cheek of *N. occulta* seems to be wider than that of *N. flabellifera*, but it should be remarked that only one specimen of the cheek of *N. flabellifera* is known, and the intraspecific variation in width is therefore not known.
3. The pygidial axis of *N. occulta* shows eight axial rings (with traces of a very narrow ninth ring shown by a smooth area on some specimens) compared with six on the axis of *N. flabellifera.*
4. Five pairs of pygidial pleural furrows are present on *N. occulta*, the fifth

pair very short, compared with four on *N. flabellifera*. The pleural furrows of *N. occulta* are continued, faintly, behind the paradoublural line.

5. The pygidial doublure of *N. occulta* is much narrower than that of *N. flabellifera*; its inner margins converge backwards more steeply (about 40–45 degrees to sag. line), but before meeting axis curve sharply forwards. 13–17 terrace lines present across its widest part (exsag.).

The pygidium of this species resembles that of *Niobe tenuistriata* CHUGAEVA (CHUGAEVA 1958, Pl. 4, Figs. 7–9) from the late Arenig Kopalinsky Formation of the Chu-Ili Mountains, Kazakhstan, in its general outline, length of pleural furrows and surface sculpture. *N. tenuistriata* differs in having a long fifth and short sixth pair of pleural furrows, and possibly also in not having the paradoublural line clearly visible on the dorsal surface. Comparisons of the cranidia of *N. occulta* and *N. tenuistriata* are hampered due to distortion of the Kazakhstan material, although CHUGAEVA's species clearly shows the transversely wide postocular fixed cheeks found on *N. occulta*. Like the stratigraphically high specimens of *N. occulta*, *N. tenuistriata* occurs with the graptolites *Tristichograptus ensiformis* and *Isograptus*, and a late Arenig age is possible for the Kopalinsky Formation. It is important to note that *N. tenuistriata* occurs also with a nileid which is certainly closely related to *Symphysurus arcticus* n. sp. the range of which species overlaps that of *Niobe occulta* in Spitsbergen.

The lithology of the Kopalinsky Formation (shales and limestone nodules, see CHUGAEVA 1958, Fig. 2) and the occurrence therein of nileids and raphiophorids in variety, as well as *Niobe*, indicates the presence of the nileid community (FORTEY 1975, Fig. 6), possibly of the same age as the upper part of the Olenidsletta Member, which for the most part yields the faunas of the olenid community in Spitsbergen.

Another comparable species is *Niobe ornata* (REED 1945) from the Tourmakeady Limestone, Western Ireland. The type and only specimen of this species is an incomplete pygidium, here refigured (Pl. 6, Fig. 3), from which the similarity to *N. occulta* in the form of the pygidial pleural furrows and sculpture will be apparent. *N. ornata* is distinguished by the straight, rather than undulating outline of the paradoublural line, and by the density of the terrace lines on the doublure (22–23 compared with 13–17 on *N. occulta*), but further comparison is not possible due to the fragmentary nature of the Tourmakeady material. The evidence supports the assignment of Reed's species to *Niobe* as indicated by WHITTINGTON (1968, p. 56) rather than to *Bathyurellus* (REED 1945, p. 61). The similarity of the Valhallfonna and Tourmakeady species is of interest because *N. occulta* occurs with *Opipeuter inconnivus* FORTEY and *Oopsites hibernicus* (REED) in the Olenidsletta Member, both of which species are present also in the Tourmakeady Limestone.

Some comparison in the general form of the pygidium may also be made with *Niobella* cf. *lignieresi* (BERGERON) from the Couches du Landeyran inférieures (Arenig) of the Montagne Noire as figured by DEAN (1966, Pl. 15, Figs. 2, 4). This species has at least one more pair of pygidial pleural furrows than *N. occulta*, and an hour glass-shaped glabella quite unlike that of the Spitsbergen species.

A single hypostoma (Pl. 23, Fig. 8) may be referred to *N. occulta*; it is of typical *Niobe* form (cf. *N. quadraticaudata* see WHITTINGTON 1965, Pl. 26, Figs. 1, 2, 6–8), but with a relatively shallow notch in the posterior margin.

Subfamily PTYCHOPYGINAE BALASHOVA 1964

Discussion. — The subfamily Ptychopyginae was erected by BALASHOVA (1964, p. 4) to include *Ptychopyge*, and a number of genera species of which were formerly included in *Ptychopyge sensu lato*, and separated from that genus by BALASHOVA, together with *Pseudoasaphus* SCHMIDT and *Pseudobasilicus* REED. The species included in the subfamily are the product of an evolutionary radiation during the Arenig-Llandeilo centred on Scandinavia and the Russian platform. One species from the early Arenig of the Valhallfonna Formation is considered to be closer to the ptychopygines than other asaphid subfamilies.

Genus *Paraptychopyge* BALASHOVA 1964

Type species. — *Ptychopyge plautini* SCHMIDT 1904.

Paraptychopyge disputa n. sp.
(Pl. 8, Figs. 1–9)

Stratigraphic range. — One of the characteristic trilobites of the lowest part of the Valhallfonna Formation, pygidia being commonly found in the basal 3m. The range of the species extends up to 8 m from the base of the Olenidsletta Member, where it intermingles with the early olenid community. Early Arenig (*fruticosus*-3 zone).

Material. — Holotype, cranidium preserving cuticle PMO NF 2488. Free cheeks: PMO NF 794, 1291, 2609, 2520; pygidia: PMO NF 797–8, 790, 812, 1766, 2596.

Diagnosis. — A *Paraptychopyge* species with a very short preglabellar field; surface sculpture of widely spaced terrace lines on cheeks and anterior part of glabella. Genal spines lacking. Posterior border furrow on cranidium almost effaced. Pygidium with gently convex border, emarginate, pleural furrows faint or absent. Surface sculpture of terrace lines more closely spaced than on *P. cincta*. Pygidial doublure broad.

Description. — Only one example of a cranidium is known, although free cheeks and pygidia of this species are numerous. Width across posterior margin of cranidium about twice maximum width in front of the eyes on a level with front margin of glabella. The frontal part of the glabella slopes steeply downward; the rest of the cranidium is relatively horizontal, although the posterior fixigenal limbs are slightly declined. Glabella faintly defined by shallow axial furrows, narrowing forward to reach minimum width at mid-point of palpebral lobes, anterior to which it expands again to same width as at posterior margin;

anterior margin gently rounded. Transverse convexity of glabella is also greatest at the anterior, downsloping part. Muscle impressions faint; one pair, subelliptical in outline (exsag.) lie immediately in front of the glabellar tubercle adjacent to the posterior part of the palpebral lobes; two pairs are anterior to this, subadjacent to axial furrows (long axis trans.), one pair opposite the anterior part of the palpebral lobes, the second immediately in front of same. Ridges run transversely across the glabella immediately behind the glabellar tubercle, and short distance in front of posterior glabellar margin: the area between these ridges may represent the basal (1P) glabellar muscle areas. Glabellar tubercle small, on a level with the posterior limits of the palpebral lobes. Preglabellar field short, and very narrow adjacent to the frontal lobe of the glabella. Palpebral lobes incompletely preserved, evidently upward-inclined, distance between anterior and posterior limits about one-quarter length of cranidium. Posterior limbs of fixed cheeks narrow (exsag.), and of transverse width slightly less than that of glabella at posterior margin; posterior border furrow weakly-defined and narrow, outlining narrow posterior border which widens abaxially. Anterior branches of facial suture diverge at about 30 degrees in front of palpebral lobes, anteriorly curving rather abruptly adaxially to meet on mid line at a point. Posterior branches diverge at right angles to sag. line distally curving in an even arc posteriorly to cut posterior margin of cranidium at a high acute angle. Cuesta-like terrace lines (steep slope backward-facing) are present on the anterior perimeter of the frontal lobe of the glabella, preglabellar field and postocular cheeks, widely spaced, about three per mm. The mid-line of the frontal lobe, adjacent to the preglabellar furrow, forms a smooth, slightly depressed area. Hypostoma and thorax unknown for this species.

Free cheek convex adaxially, anteriorly sloping down into a narrow, flattened border, which becomes narrower backwards and indistinct before reaching the genal angle. The lenses are not preserved on the semi-circular eye. Genal angle rounded, posterior and lateral margins of cheek enclosing approximately a right angle. Terrace lines on dorsal surface subparallel to outer margin of eye. Doublure broad, closely reflexed against dorsal surface, inner margin following outline of cheek, but backward-curved sharply posteriorly. Terrace lines on doublure twice as closely-spaced as on dorsal surface. Panderian opening circular, small (Pl. 8, Fig. 5) at about mid-width of doublure near posterior margin.

Pygidium with maximum transverse width between 1.75 and 1.85 sagittal length on available material (all unflattened), emarginate. Axis narrow, at anterior margin occupying one-fifth maximum pygidial width, anteriorly gently narrowing backwards (axial furrows enclosing an angle of 20–30 degrees), posteriorly subparallel-sided, and extending to about three-quarters pygidial length. A maximum of six very faint axial rings are visible on the axis. Axial furrows shallow on large specimens, more deeply incised on smaller specimens. Pleural fields convex, downward-sloping laterally as far as flattened or gently convex border; this border is widest posterolaterally, narrowing behind axis. Some specimens show up to four pairs of pleural furrows separated by narrow ridges, of which only the first pair are sufficiently impressed to cross the paradoublural line. Posterior margin of pygidium gently upward-arched at median emargination. Surface sculpture of fine cuesta-like terrace lines, spaced as on cephalon, subparallel to posterior margin, sparse or absent on anterior part of axis and adjacent pleural field. Doublure very broad and closely reflexed against dorsal exoskeleton; inner margin convex forwards, and slightly undulating. Terrace lines more closely spaced than on dorsal surface.

Discussion. — This species is assigned here to *Paraptychopyge* because of its close resemblance to *Paraptychopyge cincta* (BRØGGER 1886). *P. disputa* particularly resembles *P. cincta* in having an exceptionally short preglabellar field (see BALASHOVA 1964, Pl. IV, Figs. 1a, 3a), an almost unfurrowed pygidium with a border of identical form (see especially SCHMIDT 1904, Pl. 8, Fig. 8) and broad doublure of similar outline (SCHMIDT 1904, Pl. 8, Fig. 7). *P. disputa* differs from *P. cincta* principally in lacking genal spines and in having weakly developed posterior border furrows on the cranidium, and in the anterior branch of the facial suture curving more sharply adaxially. The pygidial axis is relatively wider in *P. cincta*, and the terrace lines on the dorsal surface are more widely spaced in that species, and run transversely (BALASHOVA 1964, Pl. IV, Fig. 4b). The other species assigned to *Paraptychopyge* by BALASHOVA (1964, p. 11–14) differ from both *P. cincta* and *P. disputa* in having strongly furrowed pygidia.

Dr. TORSTEN TJERNVIK has shown me an undescribed species from the early Ordovician of Sweden which is clearly related to *P. disputa.*

Family NILEIDAE ANGELIN 1854

Discussion. — Trilobites belonging to this family are a particularly abundant element of the Valhallfonna faunas, 10 species being represented in the collections. As with other families in which the dorsal furrows are subdued (Illaenidae, certain asaphids) the identification of species and their generic classification presents particular problems. In the account which follows the following features have been found especially useful:

(i) outline of glabella in lateral view; this may vary from gently and uniformly downsloping (*Poronileus* n. gen.) through more or less horizontal posteriorly and steeply downsloping anteriorly (typically *Peraspis*) to uniformly steeply sloping (*Nileus*).

(ii) width (sag.) of doublure connecting free cheeks.

(iii) shape of the adult pygidium; varies from relatively wide (*Nileus*) to relative long (*Poronileus* n. gen.).

(iv) taper and length of the pygidial axis and the number of muscle scars upon it (often seen only on internal moulds); axis may be funnel-shaped (some *Peraspis*) to gently and uniformly tapering (*Poronileus* n. gen.), long, or short and rapidly tapering (*Nileus*).

(v) outline and width of pygidial doublure; may be narrow and concave-forward, with an anterior margin parallel to that of the pygidial margin

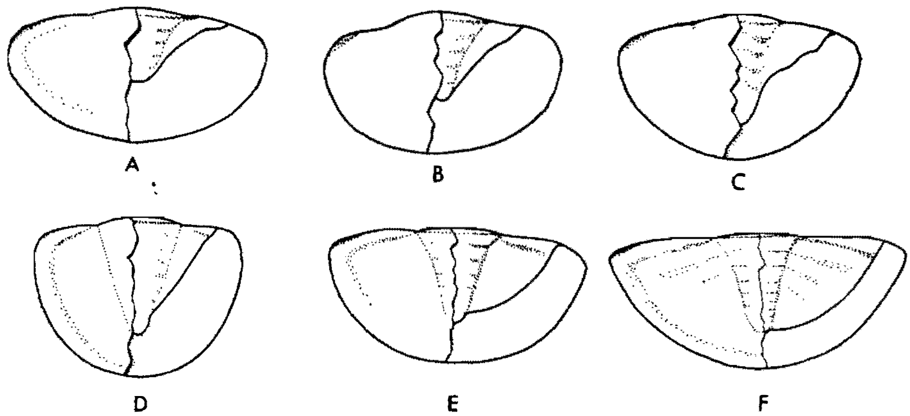

Fig. 4. Variation in pygidia of nileids, outline of doublure on right. A. *Nileus porosus*. B. *Nileus orbiculatoides svalbardensis*. C. *Nileus glazialis costatus*. D. *Poronileus fistulosus*. E. *Symphysurus arcticus*. F. *Peraspis erugata*.

(*Symphysurus*, *Peraspis*), almost straight-sided (*Poronileus* n. gen.) to convex forward (*Nileus*) (Fig. 4).

(vi) shape of the posterior branch of the facial suture; may be convex or concave forwards, straight or sigmoidal.

(vii) distribution of the surface sculpture on cephalon and pygidium — and on the cephalic and pygidial doublure. Nileids may exhibit combinations of pitting and terrace lines but are apparently never granulate.

Some non-nileid genera, especially *Varvia* (TJERNVIK 1956), have a remarkable similarity to species of *Nileus* itself. *Varvia* resembles *Nileus* notably in the shape of the cephalic doublure and the associated hypostoma, which is closely similar to that of such nileids as *N. exarmatus* (TJERNVIK 1956, Pl. 2, Fig. 16) and *N. affinis* BILLINGS (WHITTINGTON 1965, Pl. 31, Fig. 6). The differences are principally the possession of a marginal rim on the cranidium in *Varvia*, and an apparent median ventral suture. Most nileids have a supramarginal preglabellar suture, with a marginal rim developed at the edge of the narrow strip of dorsal exoskeleton connecting the free cheeks. It would require only the smallest anterior migration of the preglabellar suture to a marginal position to incorporate the rim in the cranidium. BRUTON (1968) has shown in *Panderia* the ventral sutures may become non-functional and the free cheeks united as a single piece. It is possible that the resemblance of *Varvia* to the nileids may indicate a closer relationship than their present incorporation in different families suggests.

Nileids such as *Peraspis* WHITTINGTON and *Poronileus* n. gen. are very asaphid-like in gross morphology, while retaining the characteristic nileid cephalic doublure and hypostoma. Asaphids are absent in the Profilbekken Member of the Valhallfonna Formation where these two genera are common, and it is possible that the ecological niches normally occupied by asaphids were occupied there by similarly adapted nileids.

Evolution of the Nileidae in Spitsbergen (Fig. 5)

Like that of the Olenidae (FORTEY 1974b, p. 15–21) the fossil record of the Nileidae in the Spitsbergen successions is exceptionally complete, with a high species diversity and abundant material from those parts of the section yielding the remains of the nileid community. Some of these nileid species occur in series believed to be phyletically related, and their evolution may be described in detail.

Species of *Nileus* itself appear quite suddenly in the Spitsbergen sections, *Nileus glazialis costatus* at 85 m from the base of the Olenidsletta Member, *N. orbiculatoides svalbardensis* low in the Profilbekken Member, and they seem to invade the area from the Baltoscandian region, where very closely related forms occur, and where evolution of these related species appears to have been continuous and complete (SCHRANK 1972, p. 353). This affords further evidence of free faunal interchange with the Scandinavian region, as indicated also by some of the asaphids and raphiophorids described elsewhere in this paper.

On the other hand the species here attributed to *Poronileus* n. gen. and *Peraspis* appear to have a common origin in *Symphysurus arcticus* n. sp. and in so far as they occur elsewhere appear to be related to species occurring in the Ordovician of the north American region (and possibly also Kazakhstan, p. 63). They apparently cannot be matched in the Arenig-Llanvirn rocks of Sweden or the Russian platform.

The earliest species, *Symphysurus arcticus* n. sp., from the mid-part of the Olenidsletta Member has relatively well-defined axial furrows, a wide pygidium with a funnel-shaped axis, doublure with concave outline, and surface sculpture of fine terrace lines. The hypostoma is subquadrate in outline, posterior section of facial suture sigmoidal, and genal spines are lacking. Stratigraphically high populations of this species include a number of specimens in which the posterior border furrow of the pygidium is well defined, especially posterolaterally (Pl. 21, Fig. 8). This provides the first evidence of a feature important in the lines leading to *Peraspis* and *Poronileus* n. gen. A nileid population occurring at about 115 m above the base of the Olenidsletta Member, present as thin band within the upper olenid community, contains the earliest species of *Poronileus* and *Peraspis*. Both species retain the funnel-shaped pygidial axis, terrace lines, concave outline of pygidial doublure and rather rectangular glabella similar to *Symphysurus arcticus*. In other respects the two species have already established the characteristic features of their respective genera. The convex pygidial border of *Poronileus jugatus* n. sp. is defined by deep furrows posterolaterally, the pygidium is relatively long (sag.) the eyes are large and the characteristic punctate surface sculpture is present on the glabella, although on a very fine scale; posterior branches of facial sutures retain a sigmoidal outline. Conversely, *Peraspis omega* n. sp. has a flattened pygidial border, the pygidium is relatively wide with a narrow axis, and the convexity is low, less than that of *S. arcticus* or *Poronileus jugatus*; although pleural furrows are not clearly visible on the pygidial pleural fields, the annulations on the axis are distinct on material retaining the dorsal exoskeleton. The eyes are relatively smaller than those of *S. arcticus*, and, although genal spines are not present on large free cheeks, they are still present on specimens over 0.5 cm long, posterior branches of facial suture slightly concave in outline. An increase in overall size compared to *Symphysurus* appears to be characteristic of both *Peraspis* and *Poronileus* from their inception; some pygidia of *Peraspis omega* n. sp. exceed 5 cm in transverse diameter.

Peraspis erugata Ross succeeds *P. omega* near the base of the Profilbekken Member, and differs from that species principally in retaining genal spines in the adult, in having faint pleural ribs on the pygidium, and the eyes further back; some evidence of the transitional nature of the change from the earlier species to the later is provided by the earliest members of *P. erugata* having only very short genal spines on the cheeks. The species *Peraspis lineolata* (RAYMOND) (WHITTINGTON 1965, Pls. 34, 35) takes the tendencies seen in the transition *P. omega* to *P. erugata* still further, with well defined pygidial pleural ribs and stout genal spines, eyes far back, and very low convexity. The series *omega* — *erugata* — *lineolata* is also characterised by a progressive increase in the density of the terrace lines on the dorsal surface, and the hypostoma loses the tripartition of the posterior margin, which becomes pointed medially. Apart from the sculptural changes, most of the changes occurring in this lineage are neotenous, for example, genal spines are probably a general feature of immature nileids, and in the *Peraspis* species lineage they are present at progressively later stages in ontogeny. Similarly, the flattened border characteristic of *Peraspis* is present in early ontogenetic stages of *Symphysurus arcticus* n. sp. (p. 62).

The changes occurring from species to species on the *Poronileus* lineage are concerned with subtle alterations in surface sculpture; the three species involved — *P. fistulosus*, *P. isoteloides* and *P. vallancei* — succeed one another in order through the Profilbekken Member. The earliest species, *P. fistulosus*, exhibits a few modifications from *P. jugatus*, changes which remain consistent with the succeeding species. The pygidial axis becomes uniformly tapering, losing the funnel-like appearance of that of *P. jugatus* (derived from *Symphysurus arcticus*) and the inner margin of the pygidial doublure is straight; the eyes are slightly further back and the posterior section of the facial suture is straight, cutting the posterior margin of the cephalon at an acute angle. Cephalic surface sculpture of *P. fistulosus* consists of fine pits and terrace lines, and on the dorsal surface of the pygidium terrace lines are closely spaced. The succeeding species, *P. isoteloides* is extremely similar to *P. fistulosus*, but the surface sculpture on the cranidium consists only of punctae, and the terrace lines on the pygidium are more widely spaced. Spacing of pygidial terrace lines also decreases during ontogeny, so that small pygidia of *P. isoteloides* are more closely similar to large pygidia of *P. fistulosus*: this tendency exhibits the peculiar evolution by "recapitulation" with regard to surface sculpture, such as was noted in the transition from *Cloacaspis ekphymosa* — *C. senilis* among the olenids (FORTEY 1974b, p. 41). One transitional population between *P. fistulosus* and *P. isoteloides* is known; cranidia from this horizon exhibit terrace lines on the glabella only at the extreme anterior margin, the rest of the cranidium being pitted as in *P. isoteloides* (Pl. 15, Fig. 10). The youngest *Poronileus* species, *P. vallancei*, carries

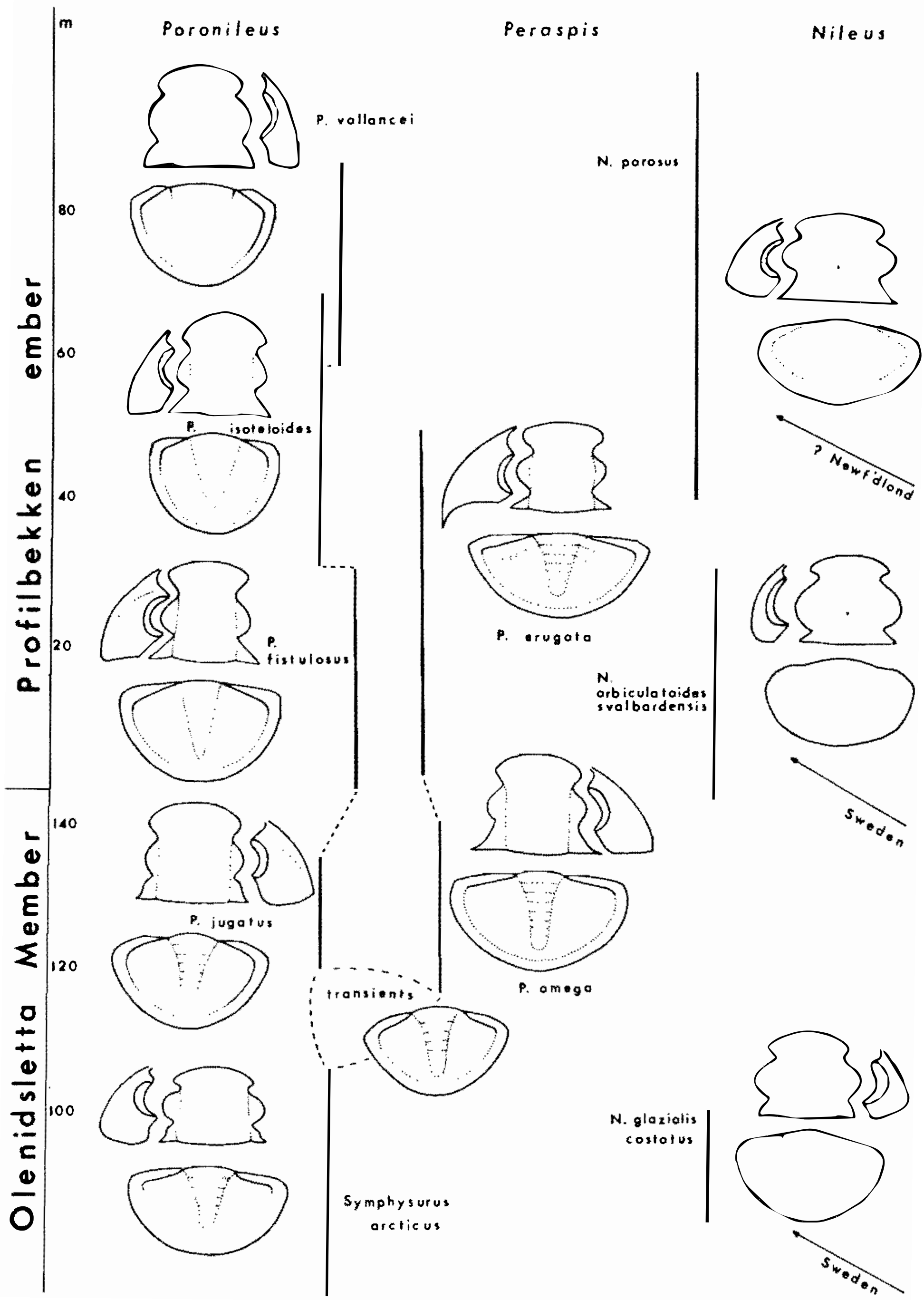

Fig. 5. Evolutionary history of the Nileidae through the Valhallfonna Formation.

the tendency towards reduction and simplification of surface sculpture further: on the glabella very fine pits are concentrated at the anterior margin of the cranidium, palpebral lobes and free cheeks, while terrace lines on the pygidium are sparse and present only around the posterior margin of the pygidium, the median part being smooth. This species in addition has a convex outline of the postocular facial suture.

As with the subfamily Balnibarbiinae of the Olenidae described in the previous part (FORTEY 1974b, p. 20) in the nileid phylogeny the period of duration of a species in the Arenig-Llanvirn of the Valhallfonna Formation is believed to have been relatively long compared with the period of derivation from the ancestral species. Populations with recognisable transitional forms are hard to discover, even with the most punctilious bed-by-bed collecting; one such has been found between *Poronileus fistulosus* and *P. isoteloides*. Where such populations occur they do so only in a single bed, and probably represented a very rapid change. Change from one species to another does not correspond with any major changes in the fauna as a whole, nor with any evidence of non-sequence. Indeed in the case of the *Poronileus* lineage the changes between the three species *P. fistulosus* — *P. isoteloides* — *P. vallancei* is coincident with the range of the single species of raphiophorid, *Globampyx trinucleoides* n. gen., n. sp. The evolution of these nileids was evidently relatively rapid compared with some other trilobites in the same community type.

The fossil record of this family in Spitsbergen thus seems to define discrete palaeontological species which can nonetheless be related in phyletic series. This pattern of evolution is consistent with the allopatric model of speciation. It is possible that the marginal populations in which speciation took place were related to the community types recently proposed by FORTEY (1975). It seems probable, for example, that the change from *Symphysurus arcticus* to *Poronileus jugatus* occurred in the "fringe" areas between the nileid and olenid communities — since the populations of the latter species occur interbedded with a typical olenid community in the upper part of the Olenidsletta Member. It may be proposed that marginal populations of *Symphysurus arcticus* became modified (*Poronileus jugatus*) in adaptation to the marginal olenid environment, the environmental gradient (FORTEY 1975, p. 341) inducing a barrier to gene flow with the populations of *Symphysurus arcticus* in the nileid community *forma typica*. Subsequent species of *Poronileus* were able to invade the nileid community later when Profilbekken Member was deposited — their large size and gross morphology indicating a convergence with, and possible niche replacement of asaphids which they parallel in most features. Asaphids are absent in the nileid community in the Profilbekken Member, although common in the nileid community of the Olenidsletta Member. The change *P. isoteloides* — *P. vallancei* is associated with the first appearance of elements of the Illaenid — cheirurid community, and may therefore represent an adaptation to relatively shallower water conditions.

Genus *Nileus* DALMAN 1827

Type species. — *Nileus armadillo* DALMAN 1827.

Diagnosis. — Nileid trilobites with broad cephalon and pygidium. Cranidium of width between palpebral lobes equal to or exceeding the length of the cranidium in dorsal view, and sagitally convex. Axial furrows faint or absent on dorsal surface of cranidium. Glabellar tubercle visible on internal moulds anterior to a line connecting the posterior limits of the palpebral lobes. Postocular fixed cheeks minute. Eyes large to very large, free cheeks narrow (trans.) lacking genal spines in larger individuals. Cephalic doublure narrow to very wide. Hypostoma of width exceeding length, with short pit-like maculae, posterior border tripartite. Pygidium about twice as wide as long, with or without border, axis poorly defined or not visible on dorsal surface, on internal moulds more clearly visible, short, with four or five axial rings. Doublure broad, anterior outline curving forward.

Discussion. — Species included in this genus are: *Nileus armadillo* DALMAN 1827, *N. depressus* (SARS and BOEK 1838), *N. affinis* BILLINGS 1865, *N. macrops* BILLINGS 1865, *N. scrutator* BILLINGS 1865, *N. limbatus* BRØGGER 1882, *N. tengriensis* VEBER 1948, *N. exarmatus* TJERNVIK 1956, *N. orbiculatus* TJERNVIK 1956, *N. transversus* LU 1957, *N. armadilloformis* LU 1957, *N. symphysuroides* LU 1957, *N. latus* PERFILYEV and LEVITSKY 1963, *N. planus* BALASHOVA 1966, *N. pamiricus* BALASHOVA 1966a, *N. hesperaffinis* ROSS 1967, *N. deynouxi* DESTOMBES 1970, *N. nesiotes* DEAN 1971, *N. globicephalus* SCHRANK 1972, *N. glazialis* SCHRANK 1973, *N. platys* SCHRANK 1972, *N. gabata* DEAN 1973b. Of these species *N. latus*, *N. planus* and *N. pamiricus* are insufficiently known for complete comparison with the species described below.

To characterise this confusing group of trilobites adequately it is important to have well-preserved material showing both the internal and external features, indeed the internal mould of the cranidium and pygidium is in some examples as important in the definition of species as the dorsal surface. Three typical *Nileus* species are known from the Valhallfonna Formation in Spitsbergen. SCHRANK (1972) has recently described the Baltic region *Nileus* species from material obtained from erratic boulders; I am indebted to Dr. TORSTEN TJERNVIK for demonstrating to me the *in situ* occurrence of these species in southern Sweden.

Nileus glazialis glazialis SCHRANK 1973

1972 *Nileus exarmatus lineatus* n. subsp. — SCHRANK, p. 363–4, Pl. 3, Fig. 13; Pl. 5, Figs. 3–6.

1973 *Nileus exarmatus glazialis* nom. nov. — SCHRANK, p. 1186.

Discussion. — SCHRANK (1973) proposed the new name *Nileus exarmatus glazialis* for the subspecies he had previously (1972) named *N. exarmatus lineatus*, as the latter name had been previously used. Dr. TORSTEN TJERNVIK (personal communication 1973) has demonstrated to me that there are several distinct *Nileus* populations in the early Ordovician of Sweden which have pygidia possessing a sculpture of numerous raised lines, considered diagnostic of the forms assigned by SCHRANK to the subspecies *glazialis* of *Nileus exarmatus* TJERNVIK. These populations are of stratigraphic significance. It seems preferable, therefore, to regard SCHRANK's material as of specific rank, and to describe these variants as subspecies: one such is known from abundant material in the Valhallfonna Formation.

Nileus glazialis costatus n. subsp.
(Pl. 10; Pl. 16, Fig. 8)

Stratigraphic range. — Mid-part of the Olenidsletta Member 85 m to 100 m from base in beds probably to be correlated with the zone of *D. bifidus* (M. Arenig) *sensu* BERRY (1960).

Material. — Holotype, pygidium with exoskeleton, PMO NF 1651. Abundant further material includes cranidia: PMO NF 431, 432, 1479, 2713, 1614, 1652, 57–8, 1571, SMA 84275, 84278; pygidia: PMO NF 1567, 1644, 1663, 2710, SMA 84270–3; free cheeks: PMO NF 1566, SMA 84279.

Diagnosis. — A subspecies of *Nileus glazialis* with cranidium moderately convex (sag.), lateral profile of glabella arcuate, anterior outline strongly rounded on mid-line, axial furrows not visible, even on internal moulds. Eyes very large. Cephalic doublure relatively narrow, with strong terrace lines on ventral surface. Pygidium lacking border, with rounded posterior outline, surface sculpture of grooves, axis not visible on dorsal surface. Pygidial doublure very broad, inner margin gently undulating, with only about eight to twelve widely-spaced terrace lines.

Description. — Cranidium of maximum width between the palpebral lobes, which also exceeds the cranidial length, gently convex (trans.). The lateral profile is arcuate, steeply downwards-sloping. Anterior outline broadly rounded on mid-line. Palpebral lobes large, about half length of cranidium, outline semicircular, transverse line connecting their posterior limits at 0.2 cranidial length. Axial furrows not visible. Glabellar tubercle prominent. Facial sutures diverge at 60–70 degrees to the sagittal line in front of the palpebral lobes, at an equal or slightly smaller angle behind the palpebral lobes to delimit a minute, short (exsag.), narrow (trans.), triangular postocular fixed cheek. On the posterior margin of internal moulds of the cranidium, opposite the posterior ends of the palpebral lobes (exsag.), there are deep pits, presumably situated at the lateral limits of the glabella and representing the articulating sockets in the axial furrows. Cephalic doublure (Pl. 10, Fig. 7) narrow (sag., exsag.), gently convex, with very prominent terrace lines, 6 on mid line.

Free cheeks fairly narrow (trans.), width (excluding eye) about equal to the length of the palpebral lobe. Genal angle obtuse, rounded. Faint lateral border which does not reach the genal angle and dies out anteriorly. Eyes large, crescentic, elevated above the free cheeks on a narrow rim, deeper anteriorly.

Dorsal surface of cranidium finely punctate, lacking the grooves which are so conspicuous on the pygidium; internal moulds smooth.

Pygidium about twice as wide as long, semicircular, lacking posterior border. Surface sculpture of distinctive, deep grooves which are reflected more faintly on internal moulds. Axis not defined by furrows on dorsal surface, but its general shape may be made out as a triangular smooth area. On internal moulds the axis is faintly visible, gently tapering, reaching about two thirds pygidial length, with indications of four axial rings. Anterior facet narrow (exsag.), steeply downturned, almost reaching (trans.) the narrow articulating half ring. Doublure very broad, inner margin convex forwards, undulating, deeply excavated around tip of axis. Terrace lines widely spaced, more distinct towards the front margin of the doublure, numbering only 8 to 12.

Transitory pygidium (Pl. 10, Fig. 16) of very low convexity with a narrow axis, very gently tapering, which almost reaches the posterior margin. There are at least 6 axial rings, and interpleural furrows of the anterior four segments are visible on the internal moulds of the broad pleural fields. This pygidium differs from those of *Symphysurus arcticus* n. sp. of comparable size in lacking a concave border.

Discussion. — *N. glazialis* is distinguished from others of the genus by its distinctive pygidial sculpture, the broad pygidial doublure with undulating inner margin and sparse terrace lines. There is some cephalic similarity to *Nileus macrops* BILLINGS (WHITTINGTON 1965) which also has large eyes (even larger than those of *N. glazialis costatus* n. subsp.) and the axial furrows effaced. Strikingly similar in general proportions is the *Nileus* sp. described by WHITTINGTON (in NEUMAN 1964, p. 27, Pl. 5, Figs. 11, 12, 15, 17–19) from Ordovician Tuffs, North Eastern Maine. The pygidium is similar in outline, convexity, and width of doublure; the size of the eyes and shape of the cranidium are closely similar, and the cephalic doublure, like that of *N. glazialis costatus* n. sp., is rather narrow (sag.). Further comparisons are not possible, unfortunately, because of the poor preservation of the Maine material. *N. glazialis costatus* differs from *N. glazialis glazialis* (SCHRANK 1972, Pl. 5, Figs. 3–6) in lacking a pygidial border. TJERNVIK (written communication 1973) has informed me that a nileid close, or even identical to *N. glazialis costatus* occurs in the "Limbata limestone" of Sweden (also late Arenig). Only one pygidium (PMO NF 112, Pl. 10, Fig. 17) occurring stratigraphically above the populations of *N. glazialis costatus* at 103 m from the base of the Olenidsletta Member, shows the presence of a concave border, and may therefore belong to *N. glazialis glazialis*. The specimen is, however, incomplete.

Different sculpture on cephalon and pygidium is not uncommon among nileids, as shown also by *Poronileus* species described below, and the other *Nileus* species from Spitsbergen. This species is rather variable in the relative length and convexity of the pygidium, some specimens (Pl. 10, Figs. 11, 13) noticeably longer and deeper than others (Pl. 10, Figs. 12, 14). All internal moulds clearly reflect the characteristic surface sculpture, and there are all intermediates between the extreme examples, and it is therefore considered unlikely that more than one species is represented.

Nileus orbiculatoides svalbardensis n. subsp.
(Pl. 11, Figs. 1–13)

Stratigraphic range. — Lower 30 m of the Profilbekken Member, associated with *Poronileus fistulosus*, but not continuing upwards into typical *Orthidiella* zone fauna.

Material. — Holotype, exfoliated cranidium, PMO NF 2412. Other material includes cranidia: PMO NF 2469, 345, 2409, 2469, 2478; incomplete cephalon: PMO NF 2407; pygidia: PMO NF 342, 344, 358, 355, 2471, 2349, 2415; free cheek: PMO NF 2477; hypostoma: PMO NF 2417.

Diagnosis. — A subspecies of *N. orbiculatoides* SCHRANK 1972, with facial sutures not meeting in a point on mid-line, cephalic surface sculpture minutely punctate. Dorsal furrows effaced.

Discussion. — SCHRANK (1972, p. 261–2, Pl. 4, Figs. 1–4; Pl. 5, Figs. 1, 2) has described *Nileus exarmatus orbiculatoides* from *geschiebe* material originating from Arenig rocks of the Baltic region. The species under discussion shares many features with SCHRANK's material, and it is proposed here to elevate *orbiculatoides* to specific rank, and to describe the Spitsbergen material as a new subspecies. In particular, *N. orbiculatoides orbiculatoides* and *N. orbiculatoides svalbardensis* may have identical pygidia with regard to convexity, outline of axis and number of terrace lines (compare Pl. 11, Fig. 8 with SCHRANK's holotype, SCHRANK 1972, Pl. 4, Fig. 1). Some of the pygidia illustrated by SCHRANK, however, have a distinct, slightly convex posterior border, a feature not shown by any of the pygidia from the Profilbekken Member, and some of the latter may have up to 30 terrace lines (Pl. 11, Fig. 11) exceeding in density any specimens of *N. orbiculatoides orbiculatoides*. The most important distinguishing feature of the Spitsbergen subspecies is the lack of an angulate junction of the anterior branches of the facial suture on the mid-line (compare SCHRANK 1972, Pl. 4, Figs. 3a, 4). The axial furrows of the Spitsbergen subspecies are completely effaced on the dorsal surface of the cranidium, but are visible on internal moulds, slightly bowed outwards between anterior and posterior limits of palpebral lobes. Small cranidia are punctate on cranidium and free cheeks, the latter bearing very short, posterolaterally directed genal spines. Fine-scale punctae are present also on the forward part of large cranidia. *N. orbiculatoides orbiculatoides* and *N. orbiculatoides svalbardensis* are similar with regard to size and position of the eye and outline of facial sutures, and width of cephalic doublure. The width of the free cheek, particularly that part in front (exsag.) of the eye, may prove to be consistently greater for the Spitsbergen species.

Hypostoma (Pl. 11, Fig. 3) much like that of *N. orbiculatoides orbiculatoides*

(SCHRANK 1972, Pl. 4, Fig. 3c) but with larger maculae, and apparently lacking convex rim around the periphery of the lateral and posterior borders. In view of the similarities and intergradations between SCHRANK's species and the populations from Spitsbergen a subspecific distinction is all that seems to be justified on present knowledge on the basis of the difference in the anterior junction of the sutures. Moreover, Dr. TJERNVIK informs me that *orbiculatoides*-like forms continue into *hirundo* zone strata in Sweden, and may therefore be near contemporaries of the Valhallfonna subspecies. *Nileus exarmatus obsoletus* CHANG and FAN 1960 (see LU et al. 1965, p. 520, Pl. 107, Figs. 12–15) appears to have a pygidium externally similar to that of *N. orbiculatoides svalbardensis,* but the internal mould shows a pair of tubercles at the tip of the pygidial axis which have not been seen on any specimen from Spitsbergen.

The relationships between the Spitsbergen and Scandinavian forms may be clarified further when more details of the pygidium of the latter are known. As shown on internal moulds, the axis of *N. orbiculatoides svalbardensis* has 4–5 axial rings, tapers backwards posteriorly to no more than half pygidial length (axial furrows enclosing an angle of 25–35 degrees), posterior margin of axis transversely truncate. The pygidial doublure is very broad, typical of *Nileus,* inner margin broadly curved forwards, and carrying about 10 terrace lines.

Both *N. orbiculatoides svalbardensis* and *N. glazialis costatus* appear quite suddenly in the Spitsbergen sections, and are unrelated to the other nileids for which a phylogeny has been proposed (p. 36). They are believed to have been derived from the Scandinavian forms to which they are closely allied, perhaps by migrations within the nileid community type between the different areas.

Nileus porosus n. sp.
(Pl. 12, Figs. 1–14)

Stratigraphic range. — Upper part of Profilbekken Member, 40–100 m from base, with typical Whiterock (*Orthidiella* zone) fauna.

Material. — Holotype, partly exfoliated cranidium, PMO NF 1357. Other material includes cranidia: PMO NF 328, 1306, 1357, 1354, 1290, SMA 84285; free cheeks: PMO NF 3160, SMA 84289–90; pygidia: PMO NF 333, 1302, 1304–5, 1361, SMA 84286–9; hypostomata: PMO NF 322, 325.

Diagnosis. — A *Nileus* species with cephalic surface sculpture of dense punctae, pygidium smooth, except for terrace lines around posterior margin, and sparsely on pleural fields. Cranidium of low convexity, with small palpebral lobes for the genus, medially placed; posterior sections of facial sutures diverge at a low angle to sag. line behind palpebral lobes. Pygidium twice as wide as long, with indistinct, broad border, axis (visible on internal moulds) with five axial rings, first two distinct, and very broad, forward-curving doublure. Hypostoma with ill-defined middle body, prominent pit-like maculae at about (sag.) mid-length.

Description. — This species is less obviously related to Scandinavian *Nileus* species than those described above. It is associated with *Poronileus isoteloides* n. gen., n. sp. and *P. vallancei* n. sp. but extends higher than these species in the Profilbekken Member. Cranidium of low convexity, only that part anterior to the palpebral lobes downward-sloping, posteriorly almost horizontal. Front margin gently rounded about mid-line, less strongly curved than *N. glazialis costatus* or *Poronileus* spp. Palpebral lobes medially positioned, 0.4–0.5 cranidial length. Axial furrows not visible on dorsal surface, on internal moulds present as shallow furrows parallel to sagittal line joining anterior and posterior limits of palpebral lobes. Median glabellar "tubercle" prominent on internal moulds, opposite posterior parts of palpebral lobes (at about 0.4 cranidial length in palpebral view). Facial sutures diverge at 27–35 degrees to sagittal line behind the palpebral lobes, and at a greater angle in front of the palpebral lobes, posterior section running straight to posterior margin of cranidium. Surface sculpture of fine, closely spaced punctae. Free cheeks gently convex (trans.), lacking lateral border, with broadly rounded genal angle. Cephalic doublure upward-turned in anterior view, and broad (sag.), carrying closely-spaced terrace lines.

Hypostoma almost two-thirds as long as wide (trans.). Middle body poorly defined, backward tapering, very gently convex (trans.), transverse width at anterior margin (excluding anterior wings) approximately equal to sagittal length of hypostoma. Maculae present as broad-based depressed pits on edge of middle body at about half (sag.) hypostomal length. Wide (trans.) lateral borders, gently concave, lateral margins almost straight and converging backwards. Posterior margin of typical tripartite *Nileus* form with broadly triangular median process. Junction of lateral and posterior borders angulate, about 140 degrees.

Pygidia exhibit few distinguishing characters from those of other smooth *Nileus* species. Width/length ratio varies between 1.8 and 2.1 on available material. Indistinct, slightly concave border wider laterally, obsolete or faint behind axis on dorsal surface, more clearly visible on internal moulds. Latter also show the pygidial axis, which is short, reaching to slightly more than half pygidial length (sag.), and tapers rapidly anteriorly, faint impressions of axial furrows enclose an angle of about 40 degrees posteriorly. Five axial rings are visible, of which only the first two pass completely across the axis, separated by wide (sag.), shallow furrows. Posterior rings are separated by short (trans.) pits which do not reach midline of axis. Pygidial doublure broad, and arched forwards (exsag.), with 12–15 terrace lines, which are wider-spaced posteriorly, and run subparallel to posterior margin. Behind the axis there is a shallow groove in the doublure, not reaching posterior margin. Terrace lines on dorsal surface present around posterior margin of pygidium, to which they are parallel, and behind articulating facet, where they are almost normal to pygidial margin. A few of the latter run up on to the anterolateral parts of the pleural fields, which are otherwise smooth. One transitory pygidium (Pl. 12, Fig. 7) shows two thoracic segments as yet unreleased; posterior proportions of the pygidium are similar to those of holaspides.

Discussion. — This species is closer to the type species, *N. armadillo* (DALMAN), from latest Arenig/early Llanvirn of Sweden, than the other species of *Nileus* from Spitsbergen. *N. armadillo* has recently been re-described by SCHRANK (1972, p. 365–7, Pl. 6, Figs. 1–3, 5, 6) from which the close similarity of pygidia of *N. armadillo* and *N. porosus* is apparent. MOBERG (1902, Pl. 3, Fig. 2) illustrated a fine punctate surface sculpture on the cranidium of *N. armadillo*. The major differences on the cranidium are the smaller palpebral lobes of *N. porosus*, which are further forward and therefore define a longer (exsag.) postocular fixed cheek, defined by sutures which diverge at a smaller angle behind the eyes. The hypostoma of *N. armadillo* as described and figured by LINDSTRÖM (1901, p. 62, Pl. 5, Fig. 13) possesses broadly rounded lateral borders with a distinct rim, and lacks the posterolateral angulations seen in that of *N. porosus*. *N. depressus* (SARS and BOEK) not only has larger eyes than *N. porosus*, but narrower free cheeks, and a longer, more convex pygidium, with convex border defined behind the axial region (see SCHRANK 1972, Pl. 7, Figs. 1, 2). Of the species from the Middle Table Head Formation, Newfoundland, *Nileus? lacunosa* WHITTINGTON closely resembles the Spitsbergen species in respect of its low cranidial convexity and punctate surface sculpture (WHITTINGTON 1965, p. 362–3, Pl. 36, Figs. 1–10), but has much larger eyes extending far back to delimit a short (exsag.) postocular cheek. Genal spines are present on the cheeks of the Newfoundland species, but as the specimens are all small it is possible that these represent early growth stages, and that such spines are not present on larger individuals. *Nileus affinis* BILLINGS (WHITTINGTON 1963, Pl. 9, Figs. 7, 9–12; Pl. 10, Figs. 1–7, 10, 13; 1965, Pl. 30, Figs. 1, 3, 5, 7; Pl. 31, Figs. 1–6, 8, 10) shares with *N. porosus* the convex cephalic doublure, and has a cranidium of similar convexity, but differs particularly in lacking the cephalic pitting, and in having a broader hypostoma, with relatively few terrace lines, and maculae much closer to the anterior margin.

Comparison with *Nileus hesperaffinis* ROSS (ROSS 1967, p. 13–14, Pl. 4, Figs. 18–25) from the Antelope Valley Limestone of Western United States, is hampered by the small size and silicified preservation of the specimens on which that species is based, so that sculptural details are obscured. The palpebral lobes of *N. hesperaffinis* are larger than those of *N. porosus* and extend further back, thereby defining narrower (exsag.) prong-like postocular fixed cheeks. The margins of the lateral borders of the hypostoma of *N. hesperaffinis* converge backwards more noticeably than is the case in *N. porosus* such that the transverse width of the posterior border of the hypostoma does not greatly exceed the width of the anterior margin.

N. transversus LU 1957 (Pl. 151, Figs. 4–6; also LU et al. 1965, Pl. 108, Figs. 11–13) has palpebral lobes of similar length to those of *N. porosus* but the anterior outline of the cranidium of *N. transversus* is strongly forward-bowed, and the pygidium possesses a concave border of equal width around its posterior perimeter.

Genus *Peraspis* WHITTINGTON 1965

Type species. — *Peraspis lineolata* (RAYMOND 1925).

Peraspis erugata Ross 1970
(Pl. 19, Figs. 1–9, 11)

1970. *Peraspis erugata*; Ross, p. 72, Pl. 14, Figs. 21, 22; Pl. 15, Figs. 1–5.

Stratigraphic range. — Lower part of Profilbekken Member 2–50 m from base, lower part of range with graptolites of *Isograptus* zone (probable *D. hirundo* zone), upper part with Whiterock (*Orthidiella* zone) faunas.

Material. — Includes a complete dorsal exoskeleton SMA 84304; exoskeleton, lacking free cheeks and hypostoma PMO NF 1827; fused pairs of free cheeks SMA 84306–7; pygidia: SMA 84305, 84308, PMO NF 332b, 335, 1388.

Description. — Exoskeleton elliptical, twice as long as wide, of very low convexity. Cephalon semicircular, one third the sagittal length of the exoskeleton. Cranidium occupying about one third the cephalic width at the posterior margin, its width between the palpebral lobes 0.7 its length, sloping very gently downwards anteriorly. Axial furrows shallow, joining the inner ends of the palpebral lobes, and bowed outwards slightly opposite their mid-point. Glabellar "tubercle" situated on mid-line opposite posterior limit of the palpebral lobe. Palpebral lobes large, over one third glabellar length, outline semicircular, transverse line connecting their posterior limits at about one quarter glabellar length. Facial sutures supramarginal in front of glabella, diverging at about 60 degrees to the sagittal line behind the eyes to cut the posterior border at a low acute angle (about 30 degrees), in front of the eyes diverging at about 45 degrees to sagittal line and curving adaxially anteriorly to meet on the mid line.

Free cheeks broad, with a gently concave lateral border which becomes faint anteriorly. On small specimens the genal spines are narrow, pointed; on larger specimens broader and shorter. Strip of dorsal exoskeleton connecting free cheeks very narrow (sag., exsag.). Surface sculpture of numerous very fine terrace lines only present on the outer parts of the free cheeks.

Ventral doublure connecting the free cheeks fairly narrow (about 0.2 cephalic length on sagittal line), widest exsagittally, gently convex, reflexed sharply beneath ventral surface of the free cheeks. 8–9 terrace lines on mid-line subparallel to the anterior border, coarser than those on the dorsal surface of the free cheeks. Hypostoma sub-square in outline, attached anteriorly to the median transverse hypostomal suture and reaching posteriorly at least as far as the glabellar mid-point. Middle body broadly oval (long axis sag.), very gently inflated, with a pair of short, deep middle furrows, which curve gently backwards from about the mid-point of the middle body. The characteristic nileid tripartition of the posterior border is weakly developed on this species. Anterior wings long, narrow, attached to the exsagittal, upturned part of the ventral doublure (Pl. 19, Fig. 8). External surface with very fine terrace lines, of a comparable scale to those on borders of the free cheeks.

Thorax with seven segments, of uniform width (trans.). Axis tapering very gently, each axial ring tapering to the posterior margin of the preceding one, so that the shallow axial furrows have a zig-zag outline. Pleurae of transverse width equal to that of the axis anteriorly, greater than that of the axis posteriorly, bluntly pointed. Pleural furrows extend for two thirds the width of the pleurae, deeper abaxially, directed obliquely backwards from the axial furrow. Articulating facet narrow (exsag.), triangular, over half the width of the pleurae. Doublure extending ventrally at least as far as the tip of the pleural furrow, with shallow transverse vincular notch.

Pygidium of very low convexity with arcuate posterior outline, about twice as wide as long. Axis clearly defined on dorsal surface, occupying 0.2 pygidial width at anterior margin and 0.75 pygidial length, funnel shaped, tapering more rapidly anteriorly, axial furrows becoming parallel to the sag. line posteriorly, its tip rounded. There are indications of four axial rings (perhaps five on some specimens) defined by shallow ring furrows which are absent over the median third of the axis. Pleural fields gently convex, surrounded by a narrow, concave border of uniform width. There are two pairs of pleural ribs, variably developed, on most specimens rather faint. Anterior border convex, sloping backwards parallel to the pleural furrows, with a wide (trans.), narrow (exsag.) facet similar to those of the thorax. The narrow doublure has a concave outline, parallel to the posterior margin of the pygidium except where excavated around the tip of the axis. Particularly in flattened material the paradoublural line is conspicuous on the dorsal surface. Dorsal sculpture of very fine terrace lines subparallel to the posterior margin.

Discussion. — This species closely resembles the type material described by Ross (1970) from the "slabby bedded unit" near the base of the Antelope Valley limestone, Ikes Canyon, Nevada. Dr. Ross (written communication 1971) has kindly confirmed the great similarity to the Nevada species. One minor difference is that most pygidia of type material of *P. erugata* have rather straight-sided pygidial axes (Ross 1970, Pl. 14, Figs. 21, 22), not funnel-shaped as in the Spitsbergen material. Others, however (Ross 1970, Pl. 15, Fig. 2), are so extremely similar that I see no reason to separate the Spitsbergen material from the Nevada species. The shape of the pygidial doublure is quite different from that of typical species of *Nileus* (Fig. 4). The pygidial doublure of *Symphysurus arcticus* n. sp. resembles that of *Peraspis erugata* in being narrow, inner margin parallel to the posterior border of the pygidium, but cephalic characters are quite different. The differences between *P. erugata* and *P. yukonensis* Dean, from an early Ordovician fauna in the Yukon, have been summarised by Dean (1973b, p. 21). The weak development of the posterior trilobation of the hypostoma of *P. erugata* appears to be characteristic of the genus, the hypostoma of the type species being similar (Whittington 1965, Pl. 35, Fig. 6), as is that of *P. yukonensis* Dean (Dean 1973b, Pl. IV, Fig. 1). It may be noted here that the hypostoma tentatively assigned by Ross to *P. erugata* does not belong with that species (see also Dean, 1973b, p. 21). Collections of topotype material of *P. erugata* from Nevada show that the species there possesses a hypostoma identical to that figured from Spitsbergen material.

Peraspis omega n. sp.
(Pl. 20, Figs. 1–11)

Stratigraphic range. — Olenidsletta Member, upper part, 117–140 m from base, with *Isograptus* zone graptolites (upper Arenig, *D. hirundo* zone).

Material. — Holotype, cranidium, PMO NF 374; other material includes cranidia: PMO NF 360, 361, 368, SMA 84312, 84316; pygidia: PMO NF 374–5, 362, 366–7, 1889, 2256, 2237, 2178, SMA 84313–4; free cheeks: PMO NF 370, 377, 365, 3151; hypostoma: PMO NF 364.

Diagnosis. — A large *Peraspis* species with a narrow glabella defined by distinctly defined axial furrows which pass well inside the posterior limits of the palpebral lobes. Palpebral lobes of moderate length with a distinct, narrow rim. Cranidium lacking surface sculpture. Facial sutures diverge at a low angle behind the eyes curving abaxially near posterior border. Semi-circular pygidium with a very narrow, funnel-shaped axis, and ill-defined, concave border, with many terrace lines on dorsal surface.

Description. — Cranidium with maximum width at posterior margin, width between palpebral lobes less than its length (sag.), its anterior one third downsloping. Glabella of width at mid-point two thirds its length (sag.), gently convex (trans.), defined by shallow axial furrows. These run backwards parallel to the sagittal line from the anterior limits of the palpebral lobes, passing well *inside* the posterior limits of the palpebral lobes. Behind the palpebral lobes they are invaginated into the glabella producing a distinct constriction, posterior to which they diverge slightly to the posterior margin. Palpebral lobes of moderate length, about one third that of glabella, outline arcuate, a line joining their posterior limits at 0.3 glabellar length. There is a narrow palpebral rim, outlined by a shallow furrow, which is slightly broader and better defined posteriorly. Postocular cheeks triangular, relatively long (exsag.) compared with the other nileids described herein.

Internal moulds (Pl. 20, Fig. 3) show the impressions of a variety of structures developed on the ventral surface of the exoskeleton. There is a small median glabellar "tubercle" which is just posterior to a line connecting the posterior limits of the palpebral lobes. Running forward from the "tubercle" on the sagittal line there is a low ridge (a groove on the ventral surface of the exoskeleton), which is continued near the anterior margin as an elongate pit (representing a short ridge on the ventral surface). Symmetrically disposed to the median ridge-groove are a complex pattern of ridges and depressions representing grooves and thickened areas on the ventral side of the glabella. Of those most prominent are a pair of grooves which run outwards and forwards from the median groove towards the anterior parts of the palpebral lobes. Immediately in front of these grooves is a thickened area of exoskeleton, itself subdivided by grooves. The anterior mid-part of the glabella bears a series of grooves apparently radially arranged, separated by thickened areas of exoskeleton. A pair of transverse thickened areas of exoskeleton are present posterior to the glabellar tubercle. The thickened areas may have represented sites of muscle attachment. The grooves are not likely to have been connected with the musculature, and their function is uncertain. Possibly they served as ducts for circulatory fluid or nervous tissue.

Facial sutures diverge at a low angle (about 30 degrees) to the sagittal line in front of, and behind the palpebral lobes, the posterior section straight until almost at the posterior margin, where it curves sharply abaxially to cut the posterior margin at a low angle.

Hypostoma similar to that of *Symphysurus arcticus* (p. 61), but with maculae in a more posterior position, posterior margin narrower (trans.), tripartition hardly developed.

Free cheeks broad (trans.) and gently convex, retaining short and slender genal spine on specimens up to 10 mm in length. Larger free cheeks, known from fragmentary specimens, lack such spines, and carry a few terrace lines around lateral margin.

Pygidium almost twice as wide as long, semicircular, very gently convex. Axis very narrow, occupying 0.2 pygidial width at anterior margin, funnel shaped, well defined on dorsal surface, extending to 0.7 pygidial length. Four axial rings, of which the first two are more distinct, of equal length (sag.). Ring furrows shallow, not noticeably fainter medially. Broad pleural fields gently convex. An indistinct, gently convex border is present posterolaterally, dying out towards the mid-line. Anterior border convex, wider laterally. Doublure fairly broad, inner margin parallel to the posterior margin of the pygidium, except where excavated about the tip of the axis. External surface with closely-spaced terrace lines which extend on to adaxial part of pleural fields (50–60 adjacent to the axis).

Discussion. — This species is closest to *Peraspis*, but with several features indicating that it is transitional between *Symphysurus arcticus* n. sp. and *Peraspis erugata* Ross (see p. 36). The cranidium is distinguished from that of the type species *P. lineolata* (Raymond) (see Whittington 1965, Pls. 34, 35; Pl. 36, Figs. 11, 12), and also that of *P. erugata* Ross and *P. yukonensis* Dean (1973b, p. 19–22, Pl. 3, Figs. 10, 11; Pl. 4, Figs. 1–10; Pl. 5, Figs. 3, 8–11), by the axial furrows passing inside the posterior limits of the palpebral lobes, by the small size of these lobes and their forward position, and by the relatively low divergence of the posterior sections of the facial suture. Only *P. lineolata* has as wide a pygidium with a narrow axis, but the latter does not have a funnel-like outline as in the Spitsbergen species, and the pleural fields of *P. lineolata* are crossed by distinct pleural furrows. Only small (up to sag. length 10 mm) free cheeks of *P. omega* retain genal spines. Pygidial surface sculpture resembles that of *P. erugata*, *P. lineolata* having very dense, and *P. yukonensis* sparse terrace lines on the dorsal surface.

Genus *Poronileus* n. gen.

Type species. — *Poronileus fistulosus* n. gen., n. sp.

Diagnosis. — Large nileid trilobites with cranidium longer than wide, of low convexity, shallow axial furrows connecting inner ends of palpebral lobes. Eyes large. Genal angles approximately 90 degrees in large specimens. Hypostoma as long (sag.) as wide. Pygidium of low convexity, about two-thirds as long as wide, with relatively long, gently tapering pygidial axis defined on dorsal surface of exoskeleton. Posterior border of pygidium gently convex, best defined laterally. Internal moulds show 7–8 pairs of muscle impressions on the pygidial axis. Cephalon with prominent punctae on dorsal surface. Pygidial doublure broad, inner margin straight (except where notched around the tip of the axis).

Included species: *P. fistulosus* n. sp., *P. isoteloides* n. sp., *P. jugatus* n. sp., *P. vallancei* n. sp., ?Nileid gen. ind. (WHITTINGTON 1965, p. 166).

Discussion. — This genus is erected to include four distinctive species from Spitsbergen: *P. fistulosus* n. sp., *P. vallancei*, *P. isoteloides* n. sp., and the less closely related *P. jugatus* n. sp. The relatively long cranidium, pygidium of low convexity with a straight inner margin to the doublure, the long, gently tapering pygidial axis, and convex posterolateral border to the pygidium, and relatively long (sag.) hypostoma, distinguish species of *Poronileus* n. gen. from those of *Nileus*. *Peraspis* WHITTINGTON (1965) has a wider, furrowed pygidium, and free cheeks with genal spines in the later growth stages. *Symphysurus* (*Kodymaspis*) PRANTL and PŘIBYL (1949) (type species *S.* (*K.*) *puer* (BARRANDE 1872)) has a similar cranidium to that of *Poronileus* n. gen. A cast of the original of PRANTL and PŘIBYL (1949, Pl. II, Fig. 1) is here refigured (Pl. 19, Fig. 10). PRANTL and PŘIBYL believed (op. cit.) that *S.* (*Kodymaspis*) possesses an occipital furrow — an unusual feature among nileids — defining a broad occipital ring. It is clear from the specimen illustrated that what was interpreted as an occipital ring is in fact the axis of a thoracic segment which has been pushed slightly beneath the cranidium. The glabella (seen on the right side) is of normal nileid type, faintly defined by furrows joining the inner ends of the palpebral lobes, and in its general proportions is similar to that of *Poronileus fistulosus* n. sp. However, *Symphysurus* (*Kodymaspis*) apparently has broad genal spines, and a *Symphysurus*-type pygidium different from that of *Poronileus* n. gen.

Poronileus fistulosus n. sp.
(Pl. 13, Figs. 1–9; Pl. 14, Figs. 1–5; Pl. 16, Fig. 6; Pl. 41, Figs. 3, 6; Fig. 6)

Stratigraphic range. — Basal beds of the Profilbekken Member 0–30 m from the base of the Member, at least the lower part of its range corresponding to the upper part of the *hirundo* zone (U. Arenig).

Material. — An abundant species throughout its range with abundant cranidia, pygidia and free cheeks represented in the collections. Holotype, cranidium, PMO NF 2440; other material includes external mould of cephalon: SMA 84238, 84239; thorax and pygidium: PMO NF 123; cranidia:

PMO NF 2357, 216, 382, 384–5; pygidia: PMO NF 166–7, 156, 1333, 2433, 2439, 343, 346, 208, 291, 2368, 2380, 2381; free cheeks: PMO NF 257, 296, 2366, 2467, 2474, 352; hypostomata: PMO NF 348, 217, 2499.

Diagnosis. — A *Poronileus* species with surface sculpture on cephalon of minute punctae and terrace lines, both occurring intermixed on glabella and free cheeks. Free cheeks with convex lateral border, dying out posteriorly. Eyes large, far back. Pygidium of low convexity, with long gently tapering axis, well defined on dorsal surface. Pygidial surface sculpture of close terrace lines, about twice as many as those on *P. isoteloides*.

Description. — Cephalon semicircular in outline, of low convexity. Cranidium slopes down gently and uniformly anteriorly, of width between palpebral lobes 0.8–0.9 its length (sag.), anterior outline gently rounded. Glabella defined by faint axial furrows joining the limits of the palpebral lobes, gently inflated posteriorly (trans.) of width about 0.6 its length. Axial furrows slightly deeper and wider in front of the posterior end of the palpebral lobes, and continued faintly posteriorly to the posterior margin. Palpebral lobes large, one-third length of the cranidium, posterior limit one-sixth cranidial length (sag.) from the posterior margin. Very faint and narrow palpebral rims can be seen on this species, defined by very shallow palpebral furrows posteriorly. The palpebral lobe has a characteristic outline, the anterior part of the suture bounding its lateral edge curving inwards at a lower angle to the sagittal line than the posterior part. Facial sutures strongly divergent both behind, and in front of the eyes, the postocular section straight, cutting the posterior border at a low acute angle (25 degrees), preocular section sigmoidal, curving adaxially anteriorly to meet across the mid-line, supramarginal. Minute glabellar "tubercle" visible on internal moulds, but not on the dorsal surface, on the mid-line of the glabella near the posterior limits of the palpebral lobes. Anterior to the glabellar tubercle there is a median smooth line running forward on the sagittal line on to the front of the cranidium but not reaching the anterior margin. Three pairs of muscle impressions, visible as shallow depressions in the dorsal exoskeleton. 1P consisting of a pair of closely spaced (exsag.), elongate (trans.) depressions opposite the posterior limit of the palpebral lobes, 2P a similar pair of depressions immediately behind the anterior limit of the palpebral lobes, 3P a broad depression immediately in front of the palpebral lobes.

Free cheeks broad, downsloping, united as a single piece, surrounded by a very narrow, horizontal rim. Rounded genal angle, approximately 90 degrees. Gently convex lateral border, defined by a broad furrow, wider anteriorly (exsag.) and dying out posteriorly. The anterior part of the furrow defining the border curves adaxially to pass in front of the eye. The large semi-circular eye is deeper anteriorly than posteriorly, and is raised above the level of the cheek on a narrow socle. The minute lenses are arranged in files (vertically) of about 30 anteriorly and 24 posteriorly (total number of lenses about 2400). Posterior margin curves gently backwards to the genal angle. Surface sculpture on cephalon of densely spaced punctae arranged in irregular rows between

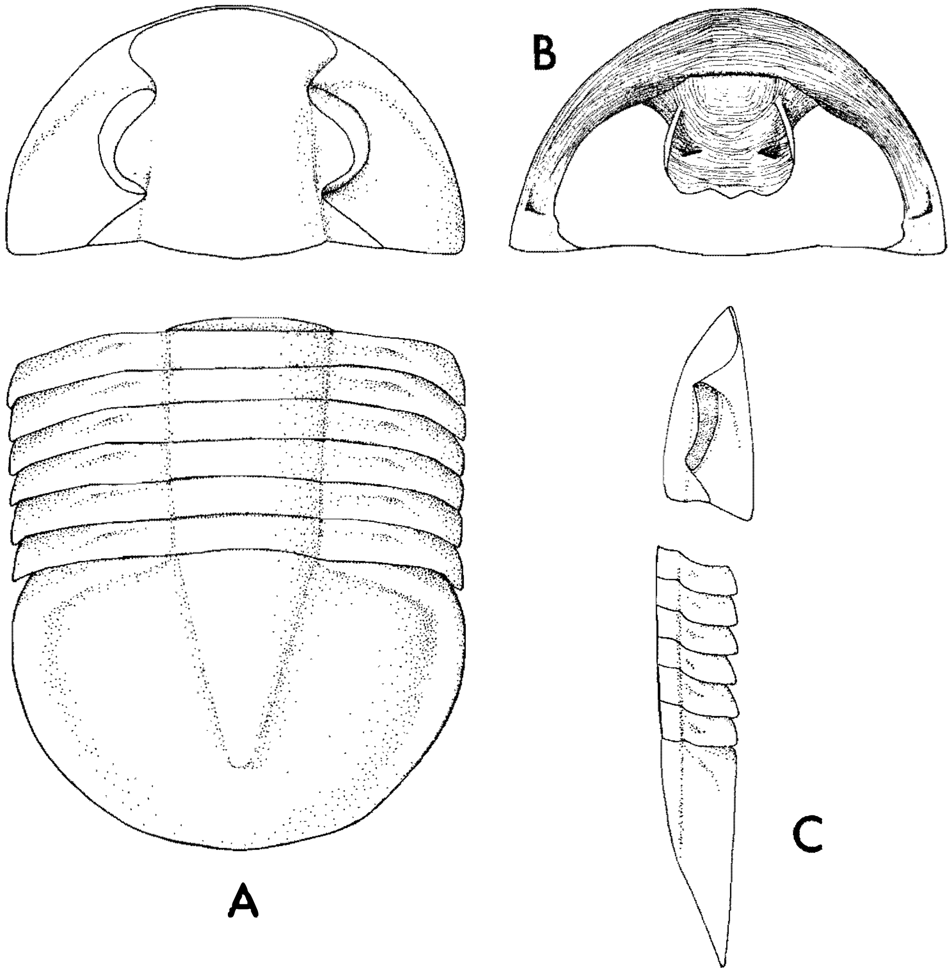

Fig. 6. Reconstruction of *Poronileus fistulosus* n. gen., n. sp., about twice natural size. A. dorsal view, B. ventral view of cephalon showing doublure and hypostoma. C. lateral view to slightly smaller scale.

terrace lines, well-developed on the cheeks and especially the front of the cranidium, fainter over the muscle impressions.

Doublure about 0.25 cephalic length, broadest medially, where it is reflexed horizontally beneath the cranidium, laterally upturned beneath the free cheeks. The lower surface bears closely set terrace lines parallel to the anterior margin (about 20 on the mid line), which are absent on the area immediately anterior to the median hypostomal suture, this area being also slightly depressed. Vincular notch (Pl. 41, Fig. 6) prominent on posterolateral part of doublure, consisting of an L-shaped depression, the base of the "L" deep, transverse. Postero-laterally the doublure widens, its inner margin curving adaxially to meet the posterior margin almost at the point where it is cut by the suture. Near the posterior border the inner margin of the doublure is notched (Pl. 41, Fig. 6).

Hypostoma almost as long as wide, anterior margin gently bowed forwards. Posterior margin tripartite, with a pointed median projection, flanked by broadly rounded lobes. Oval middle body (long axis sag.) ill defined posteriorly, not greatly inflated. Middle body cut laterally at two thirds its length by a pair of deep elongate pits ("maculae") which run transversely to about one quarter the (trans.) width of the middle body. Relatively shallow lateral border furrows run anteriorly from the outer ends of the transverse pits. Lateral borders very steep medially, not reaching the anterior margin of the hypostoma, and very low posterior to the lateral pits. Broad, triangular anterior wings, the anterior margins of which are believed to have fitted against the exsagittal cephalic doublure where it becomes reflexed beneath the cheeks away from the mid line (see Fig. 6). External surface of the hypostoma covered with very closely spaced terrace lines similar to those on the cephalic doublure, which are very generally subparallel to the lateral and posterior margins but cut the anterior margin at a high angle.

Pygidium with broadly rounded posterior outline, of length two-thirds width, gently convex, pleural fields sloping downwards at a low angle laterally from the axis, more steeply sloping behind the axis. Narrow axis occupies about 0.2 pygidial width at anterior margin, tapering gently (25 degrees) posteriorly to about two thirds pygidial length, defined quite clearly on dorsal surface by shallow axial furrows. Convex anterior border defined by a broad furrow which slopes gently backwards at an angle of about 80 degrees to the sagittal line, and which, near the anterolateral corner of the pygidium, curves posteriorly through 90 degrees to outline a flat or very slightly convex border; the border becomes less distinct posteriorly, so that the posterior pleural field slopes down uniformly to posterior margin. Small triangular articulating facet, fairly narrow (trans.), steeply downsloping.

Surface sculpture of very closely set terrace lines (about 65 between the posterior and anterior borders adaxially) which do not continue on to the smooth axis. They are approximately parallel to the posterior margin, but have a lower radius of curvature, so that they approach the margin obliquely. On internal moulds up to seven faintly impressed pairs of muscle impressions can be seen on the lateral parts of the axis. Doublure broad, sharply reflexed against the dorsal exoskeleton beneath the greater part of the pleural areas of the pygidium, its inner margin straight, passing inwards and backwards from the anterior border (at an angle of 30 degrees to sag. line), except where excavated around the tip of the axis. Surface sculpture of some 20–30 terrace lines, more widely spaced than those on dorsal surface.

Discussion. — Characteristic of this species are the fine pit — and — terrace cephalic surface sculpture, well-defined lateral borders on the free cheeks, and the numerous terrace lines on the dorsal surface of the pygidium, features which particularly distinguish *P. fistulosus* from the closely related succeeding species *P. isoteloides*. It should be noted that small pygidia of the latter species have more terrace lines on the pleural fields than larger ones, and so resemble larger pygidia of *P. fistulosus* more closely. It is also important to distinguish small cranidia of *P. fistulosus* from those of *Nileus orbiculatoides svalbardensis* n. subsp. (compare Pl. 13, Fig. 7 with Pl. 11, Fig. 5). Small cranidia of *P. fistu-*

losus have a similar punctate surface sculpture to that of *N. orbiculatoides svalbardensis* (terrace lines on cranidia of *P. fistulosus* are lacking below about sag. length 4 mm), but that part of the cranidium in front of the palpebral lobes is longer (sag.), and on internal moulds the glabellar "tubercle" is conspicuously smaller.

An intermediate population, stratigraphically and morphologically, between *P. fistulosus* and *P. isoteloides* has been found on melt stream A on Olenidsletta 31 m from the base of the Profilbekken Member. Cranidia (Pl. 16, Fig. 6) show terrace lines only on the anterior part of the glabella, but the pitting is more similar in density to that on *P. isoteloides* forma typica.

Poronileus isoteloides n. sp.
(Pl. 14, Figs. 6–8; Pl. 15, Figs. 1–9, 11; Pl. 16, Figs. 1–5, 7, 9, 10;
Pl. 41, Figs. 1, 2, 5, 7)

Stratigraphic range. — Profilbekken Member, 31–70 m from base; transitional population with *P. fistulosus* at 31 m. A typical nileid of the Whiterock (*Orthidiella* zone) stage in Spitsbergen.

Material. — Holotype, large, almost complete cranidium with exoskeleton, PMO NF 24. Other material includes cranidia: PMO NF 72, 1365, SMA 84247; free cheeks: SMA 84250, PMO NF 336; hypostoma: PMO NF 337; pygidia: PMO NF 338, 23, SMA 84054–8.

Diagnosis. — A *Poronileus* species with surface sculpture on cranidium of coarse punctae, with a few terrace lines in addition on free cheeks. Eyes smaller, and further forward, than those of *P. fistulosus.* Pygidial axis faint on larger specimens, long and gently tapering. Posterolateral border of pygidium convex, fainter posteriorly. Pygidial surface sculpture of rather widely spaced terrace lines, about half as many as *P. fistulosus* at a given size.

Description. — Cranidium of length exceeding the width between the palpebral lobes, sloping gently and evenly downwards anteriorly, front margin rounded on mid line. Glabella very gently convex (trans.) defined by shallow furrows joining the inner ends of the palpebral lobes. These furrows are deeper on internal moulds. Palpebral lobes of length rather more than 0.3 that of glabella, posterior limit at 0.25 glabellar length. No palpebral rims are visible, the lateral outline of the horizontal palpebral area being rather less curved than that of *P. fistulosus.* Facial sutures diverge strongly in front of the eyes, curving gently adaxially anteriorly to meet on mid line, supramarginal. Behind the eyes on larger cranidia the suture is initially subparallel to the sagittal line, rapidly curving outwards and running straight to the posterior border which it cuts at an acute angle of about 35 degrees. The narrow (exsag., trans.), triangular postocular fixed cheek is indistinctly set off from the glabella, more by a change in slope than by any definite furrow.

Free cheeks united as a single piece, sloping downwards from the eye, edged by an extremely narrow, horizontal rim. Genal angle rounded on larger specimens, approximately 90 degrees. The crescentic eye is raised above the level of the cheek on a low eye socle, deeper anteriorly than posteriorly, with some 2000 lenses on a large specimen. Doublure broad, upturned on the mid-line sufficiently to be visible when the free cheeks are viewed anteriorly. The median one-third of the doublure is horizontal, corresponding to the hypostomal suture, laterally the horizontal part narrows gradually, the posterior part of the doublure being reflected upwards close against the ventral surface of the free cheek. Near the posterior margin the doublure widens, its inner margin curving adaxially (Pl. 41, Fig. 5). Shallow vincular furrow of similar form to that of *P. fistulosus*.

Hypostoma (Pl. 15, Fig. 7) shows sculpture of terrace lines and pitting similar to free cheek. There are about half the number of terrace lines compared with the hypostoma of *P. fistulosus*, and, although the posterior margin is medially pointed, the margin is not tripartite like that of *P. fistulosus*. Macula steeply forward-sloping and smooth, neither terrace lines nor pitting passing on to its surface.

Surface sculpture on cephalon consisting of coarse, rather closely spaced punctae (Pl. 41, Fig. 2), with rather widely spaced terrace lines in addition on the lateral parts of the free cheeks. The glabellar "tubercle" is not visible on the dorsal surface, but is a prominent feature of internal moulds, that is, it represents a marked thinning of the dorsal exoskeleton. It is positioned on the mid-line opposite the posterior parts of the palpebral areas. Running forwards on the mid-line from the position of the glabellar tubercle there is a median smooth line where the punctae are absent. A similar line is developed on *P. fistulosus*, and it corresponds in position with the internal median groove of other nileids (see *P. vallancei*, Pl. 18, Fig. 12, *Nileus porosus*, Pl. 12, Fig. 5). Internal mould smooth, but on the free cheeks with faint genal caeca radiating from the eye region (Pl. 41, Fig. 7). The ventral surface of the doublure bears strong terrace lines (about 20 on the mid-line) which are subparallel to the border, absent in front of the hypostomal suture and on the posterolateral corner of the doublure. These terrace lines are reflected faintly on the dorsal surface of the doublure.

Larger (sag. length greater than 1 cm) pygidia resemble those of *P. fistulosus* in general form but are more convex. Axis occupies 0.3 pygidial width at anterior margin, tapering at about 30 degrees posteriorly to two-thirds or slightly more pygidial length, faintly defined on the dorsal surface, on some larger specimens (length greater than 2.5 cm) hardly visible. On internal moulds the axis is quite clear, except for the posterior tip, and bears eight pairs of narrow (exsag.) muscle impressions which occupy one-third the width of the axis, and are progressively fainter and narrower (trans.) posteriorly. Pleural fields near-horizontal adaxially, sloping rather steeply downwards laterally, posterolaterally, and especially behind the axis to the broad and shallow posterior border furrow. Posterior border distinct laterally, where it is gently convex, becoming horizontal and narrower posteriorly. Anterior border convex; articulating facet triangular, steeply downturned, occupying half the width of the pleural field. Doublure broad, with a similar straight inner margin to that of *P. fistulosus.* Surface sculpture of terrace lines, quite widely spaced, with no more than 30 adaxially between the anterior and posterior margins, sparser on the largest specimens. Smaller pygidia (length 2 cm or less) are minutely punctate also (see Pl. 14, Fig. 8), this punctation being finer and denser than that on the cephalon. Small free cheeks are narrower (trans.) and bear genal spines. There is a faint lateral border comparable to that of *P. fistulosus* on the smaller free cheeks. Genal spines disappear on specimens of cephalic length exceeding 5 mm. The punctae, which are distributed evenly over the surface of even the smallest cranidia and free cheeks, do not alter in size through ontogeny, although smaller specimens have the punctae rather more densely spaced than the adults.

Smaller pygidia are relatively wider than those described above, the width being almost twice the length (dimensions usual for other nileids). The narrow pygidial axis is similar to that of larger specimens, well defined on dorsal surface, but is relatively longer, more closely approaching the posterior margin. The posterior border furrow is continuous around the tip of the axis, parallel to the posterior margin, delimiting a gently convex posterior border, which is of equal width (sag., exsag.) along its length. Up to seven pairs of muscle scars are visible on the axis on internal moulds. One pygidium (Pl. 16, Fig. 5) shows the presence of one unreleased thoracic segment. The pygidium + segment approaches the proportions of the adult pygidium, and it might be suggested that later in ontogeny the segment may have been incorporated in the pygidium to give the relatively long pygidium characteristic of the genus. It may be noted that the seventh segment in *Symphysurus arcticus* n. sp. seems to be released at a rather late stage in the ontogeny.

Discussion. — This species is distinct from the type species in a number of details, although the overall resemblance is such that they are obviously closely related. The cephalic sculpture of the two species is, however, quite different. The eyes of *P. fistulosus* are larger, and *P. isoteloides* lacks the convex lateral border to the free cheeks (except on small specimens). The postocular suture of the type species cuts the posterior border at a lower angle than that of *P. isoteloides.* The pygidium of *P. isoteloides* has half the number of terrace lines on the dorsal surface compared with comparably sized pygidia of *P. fistulosus,* that of *P. isoteloides* has a broader, more markedly tapering axis and a more distinct, convex posterolateral border.

Poronileus vallancei n. sp.
(Pl. 18, Figs. 1–16; Pl. 41, Fig. 4)

Stratigraphic range. — Profilbekken Member, upper part, 60–90 m from base, associated with Whiterock (*Orthidiella* zone) faunas.

Material. — Holotype, cranidium retaining cuticle, SMA 84263. Other material includes cranidia: SMA 84264–5, 84267, PMO NF 3148, 3149; free cheeks: SMA 84266; pygidia: SMA 84268, PMO NF 129, 1350, 1355, 1294, 1237, 1229, 1259.

Diagnosis. — A *Poronileus* species with a surface sculpture on the cephalon of minute, scattered punctae on the palpebral lobes, the front of the glabella, and the free cheeks. Axial furrows hardly defined on dorsal surface of cranidium and pygidium. Eyes very large. Postocular sutures diverge strongly behind the eyes curving adaxially distally to cut the posterior border at a high angle. Pygidium similar to that of *P. isoteloides*, but relatively broader, more convex, with shorter, more rapidly tapering axis visible on internal mould, and few terrace lines only near posterior margin.

Description. — Cranidium moderately convex, of width between palpebral lobes about equal to its length, anterior margin rounded on mid-line. Axial furrows joining inner ends of the palpebral lobes hardly visible on the dorsal surface, glabella very gently convex (trans.). Palpebral lobes with gently arcuate outline, one third the length of the glabella. Facial sutures diverge strongly in front of, and behind the palpebral lobes. The posterior branch diverges behind the palpebral lobe at about 60–70 degrees, then curves posteriorly to cut the posterior border at a high acute angle on larger cranidia. Thus bounded by the sutures, the postocular cheeks are shaped like a quadrant of a circle, of width 0.2 that of the glabella at posterior margin. On internal moulds (Pl. 18, Fig. 13) the axial furrows are more distinct, converging very slightly forwards. The glabellar tubercle is prominent on internal moulds, but it is not visible on the dorsal surface (that is, it represents an internal thinning of the exoskeleton), on a level with the posterior parts of the palpebral lobes. Running forward from the tubercle along the mid-line of the internal mould there is a narrow ridge, which corresponds to a ventral groove in the exoskeleton. This groove occupies the same position as the median smooth line on the dorsal surface of other *Poronileus* species (Pl. 41). A broad band on the mid-line forms a depressed area on the internal mould (Pl. 18, Fig. 12), symmetrically disposed to the median ridge, representing a ventral thickened band of the exoskeleton. Six pairs of transverse thickened bars, not reaching the axial furrows, branch off from this median band. The anterior pair, just in front of the palpebral lobes, are the longest; the three pairs behind are progressively shorter, the fourth pair close to the glabellar tubercle. These thickened areas may represent sites of muscle attachment, although their close proximity to sagittal line is unusual, and it seems probable that their function was quite different. Where the axial furrows meet the posterior margin they are deepened into apodemes internally.

Free cheeks narrower than those of *P. isoteloides* or *P. fistulosus*, sloping down steeply from the eye, the front margin surrounded by a narrow convex rim. Very large gently crescentic eye raised above the level of the cheek on a low rim, with about 1600 minute lenses. Doublure broad, of similar form to that of *P. isoteloides*, but with the anterior part turned up dorsally to a greater degree towards the mid-line.

Surface sculpture on the cephalon consisting of minute, scattered punctae, on the cranidium only on the palpebral lobes and the most anterior part of the glabella, evenly scattered over the free cheeks (Pl. 41, Fig. 4), which, laterally, also have widely spaced terrace lines. The punctae are more dense on smaller cranidia. Internal moulds are smooth.

Pygidium semicircular, of width slightly exceeding its length, very similar to that of *P. isoteloides*, apart from having terrace lines absent on pleural fields, sparse on posterior border. Axis occupying 0.25 pygidial width at anterior margin, shorter than that of *P. isoteloides*, and not visible on dorsal surface, with up to 8 pairs of muscle impressions visible on internal moulds. Doublure broad, inner margin straight or slightly sigmoidal, with about 16 terrace lines on mid-line.

Small cranidia are more convex than large cranidia, flexed downwards on a transverse line across the posterior ends of the palpebral lobes, so that in palpebral view they appear more similar to larger cranidia (compare Pl. 18, Fig. 4 with Fig. 5). The palpebral lobes are relatively longer, while the post-ocular suture runs in an almost straight line to cut the posterior border at an acute angle.

No hypostoma can be undoubtedly attributed to this species.

Discussion. — This species most closely resembles *P. isoteloides*, from which it is distinguished by its different surface sculpture, faint axial furrows, larger, less curved palpebral lobes and different postocular suture, narrower free cheeks with larger eyes. The great similarity of the pygidia of these two species has been discussed above. *Nileus tengriensis* VEBER (1948) has a generally similar cranidium, but with the glabellar tubercle further back, and a pygidium which is much wider, less convex, with broader axis. It is also interesting to note the resemblance of the cranidium of *P. vallancei* to that described by DEAN (1973b, p. 22, Pl. 5, Figs. 8–12) as "Asaphid genus and species indeterminate" from the Ordovician of the Keele Range, Yukon; it seems possible that this might belong to another, related *Poronileus* species.

Poronileus jugatus n. sp.
(Pl. 17, Figs. 1–9)

Stratigraphic range. — Upper part of the Olenidsletta Member 120 m to 135 m (late Arenig, *hirundo* zone = *Isograptus* zone of N. America) the only nileid trilobite to occur abundantly interbedded with the upper olenid-bearing beds with *Cloacaspis* and *Triarthrus*.

Material. — Holotype is a perfectly preserved external mould of a pygidium, PMO NF 2964. Other material assigned to this species includes cranidia: PMO NF 2977, 2976 (block including well-preserved cranidia of *Cloacaspis senilis* FORTEY), 2967, 2963; pygidia: PMO NF 2965, 2973, 2946, 2954, 2971, 2945, 1837, SMA 82321–2; free cheeks: PMO NF 2967.

Diagnosis. — A *Poronileus* species with surface sculpture of minute punctae distributed over all the surface of cephalon. Anterior part of cranidium slopes more steeply downwards than that of other *Poronileus* species. Posterior section of facial suture sigmoidal. Pygidium with markedly convex border, well-defined except behind tip of axis; terrace lines present on border, absent or dying out rapidly on pleural fields.

Discussion. — As indicated above in the discussion of the phylogeny of the nileids in Spitsbergen, this species presents intermediate characters between *Symphysurus arcticus* n. sp. and the other *Poronileus* species described above, and it is best discussed in relation to these species rather than described separately. The pygidium of *P. jugatus* is distinctive, with its "rolled" posterior border defined by deep border furrows which shallow rapidly behind the pygidial axis, and relative lack of surface sculpture. Some stratigraphically high specimens of *Symphysurus arcticus* possess a gently convex posterior border, but this does not extend as far towards the sagittal line as on *Poronileus jugatus*; there is a general proportional difference between pygidia of the two species, the width/length ratio of *S. arcticus* (which do not exceed 10 mm in length) being in the range 1.8 to 2.2, that of *P. jugatus* (most specimens of which are about 15 mm in length) in the range 1.5 to 1.7 and comparable to other *Poronileus* species. On the other hand the pygidial doublure of *P. jugatus* is concave-forwards like *S. arcticus*, but unlike later *Poronileus* species, which have an almost straight inner margin. Cranidia resemble those of *S. arcticus* particularly in the shape of the postocular suture, but carry the typical *Poronileus* sculpture of fine pits, which continue on to the free cheeks. Three or four axial rings are visible on the dorsal surface of the pygidial axis. *Peraspis omega* n. sp., which occurs with *Poronileus jugatus*, may have shared *Symphysurus arcticus* as a common ancestor (see p. 38). It may be at once distinguished from *P. jugatus* by its different surface sculpture on cephalon and pygidium, concave outline of the posterior branch of the facial suture, pygidium with narrower axis and less distinct, flattened border.

Genus *Symphysurus* GOLDFUSS 1843

Type species. — *Asaphus palpebrosus* DALMAN 1827, designated by BARRANDE 1852.

Symphysurus arcticus n. sp.
(Pl. 21, Figs. 1–16)

Stratigraphic range. — Olenidsletta Member 70 m to 103 m, ?106 m. Range extending into earliest *Isograptus* zone (forms transitional with *Peraspis omega*), but most of the range of the species in *bifidus* (*sensu* BERRY 1960) zone.

Material. — An abundant species, represented by some hundreds of specimens. Holotype, dorsal exoskeleton lacking free cheeks, PMO NF 538; among other material are exoskeletons (mostly lacking free cheeks): PMO NF 2642, 2035, 2041, 2029, 1814, 2039; SMA 84292–3, 84301; cranidia: PMO NF 2696, 407, 496a–d, 511, 63, SMA 84295–6; pygidia: PMO NF 1435, 2146, 1668, 522, 61; free cheeks and hypostoma: PMO NF 2118; hypostomata: PMO NF 496e, SMA 84276.

Diagnosis. — A *Symphysurus* species with moderately large eyes, axial furrows quite well defined, glabella wider at posterior margin than between palpebral lobes, posterior branch of facial suture sigmoidal. Pygidium lacking distinct posterior border, axis well defined on dorsal surface and coming to a point posteriorly, 4–5 axial rings visible on internal moulds. Pygidial doublure narrow, inner margin subparallel with the posterior margin of pygidium, sharply excavated around tip of the axis.

Description. — Dorsal exoskeleton elliptical, almost two thirds as wide as long, of low convexity (sag., trans.). Cephalon semicircular, sagittal length about equal to that of the thorax and that of the pygidium. Cranidium of maximum width at the posterior margin, width between palpebral lobes exceeding sagittal length, down-sloping rather steeply in front of the palpebral lobes, posteriorly horizontal. Axial furrows distinct on larger cranidia, running backwards from the anterior ends of the palpebral lobes parallel to the sagittal line, becoming fainter and curving outwards to the posterior ends of the palpebral lobes. Immediately behind the palpebral lobes the furrows are not well defined, but near the posterior margin of the cranidium are quite distinct, converging backwards slightly, the distance (trans.) between them greater than that between the palpebral sections of the axial furrows. The glabella so defined is thus wider near the posterior margin than opposite the palpebral lobes, gently convex (trans.), with a small glabellar "tubercle" visible on internal moulds just anterior to a line connecting the posterior limits of the palpebral lobes. Running forwards on the sagittal line from the glabellar tubercle there is a line of short transverse ridges, this being the only surface sculpture on the cranidium, and corresponding in position with a ventral groove, seen as a ridge on some internal moulds. Palpebral lobes semicircular, horizontal, one-third glabellar length, a transverse line joining their posterior ends at about one quarter glabellar length. Facial sutures diverge at 30–60 degrees to the sagittal line in front of palpebral lobes, behind the palpebral lobes initially diverging at a similar angle, posteriorly curving adaxially, and near the posterior margin swinging outwards to cut it at an acute angle. The posterior branch of the facial suture thus has a sigmoidal outline, which is present even on degree 6 meraspides (Pl. 21, Fig. 16). Small postocular fixed cheeks of transverse width slightly less than length (exsag.).

Hypostoma of maximum width exceeding its length (sag.), with subcircular middle body, gently inflated, poorly defined by shallow, broad lateral and posterior border furrows, the former deepest and narrower anteriorly. Maculae developed as narrow (exsag.), short pits backwards sloping, straight, transverse line connecting their outer ends at hypostomal midlength. Lateral borders steep, anteriorly widening and flattening out posteriorly. Posterior border with well-developed tripartition as in *Nileus*, with 25–30 terrace lines (sag.). Anterior wings broader (exsag.) and more rounded than those of *Nileus affinis* (compare WHITTINGTON 1965, Pl. 31, Figs. 2–4).

Free cheeks about half the width of the cranidium at posterior margin, genal angles broadly rounded. Narrow lateral border, variably developed. Eyes moderately large, deeper and wider anteriorly. Surface sculpture lacking, except in genal angles which have closely spaced terrace lines. Doublure connecting free cheeks fairly broad, about 0.2 cephalic length, with terrace lines on ventral surface, about 12 on mid-line. Hypostomal suture broad, gently curved forwards.

Thorax of 7 segments, axis of equal width (trans.) to pleurae, posterior three axial rings tapering very slightly. Axial rings of equal width (sag.) tapering forwards to the posterior margin of the preceeding axial ring, so that the well-defined axial furrows have a slightly zig-zag outline. Long narrow articulating half rings extend beneath (sag.) one-third of the preceeding axial ring. Adaxial one-third of pleurae horizontal, laterally downsloping, bluntly pointed. Pleural furrows fairly shallow, sloping backwards from axial furrow and dying out half way across pleurae. Articulating facets broad (trans.), triangular, narrowing adaxially, wider (exsag.) on anterior segments.

Pygidium twice as wide as long, semicircular, border lacking. Axis well-defined on dorsal surface, 0.25 pygidial width at anterior margin, gently tapering (at about 30 degrees) to a pointed tip at about two-thirds pygidial length. On internal moulds there are four pairs of narrow (exsag.) muscle impressions, which do not cross the middle of the axis, defining four axial rings of decreasing width (trans.) posteriorly. Anterior border convex, its width increasing and convexity decreasing laterally. Articulating facet steeply downturned, narrow (exsag., trans.). Doublure moderately broad, its width increasing posteriorly, inner margin concave, subparallel to the posterior margin of the pygidium, deeply excavated around the tip of the axis, with 10–13 rather widely spaced terrace lines parallel to the posterior margin.

Pygidial surface sculpture on stratigraphically early specimens of relatively few (8–12) terrace lines around posterior part of pygidium only; stratigraphically higher specimens have twice as many terrace lines which cover a greater part of the pygidium, but do not extend on to the adaxial part of the pleural fields. Internal moulds (Pl. 21, Fig. 5) show the impressions of caeca of two sizes — broader caecum confluent with ring furrow where it joins axial furrow, narrower caecum meeting axial furrow at about mid-length (exsag.) of axial ring.

Ontogeny. — Smallest cranidium (Pl. 21, Fig. 14) sag. length (in palpebral view) 1.2 mm differs from holaspid cranidia in its greater convexity, and longer (exsag.) palpebral lobes. Axial furrows are faint, but incised sufficiently near posterior margin to show narrow (trans.) glabella, occupying only about half the width of the cranidium, with axial furrows passing well inside palpebral lobes. Pygidium of similar length to the small cranidium is (Pl. 21, Figs. 10, 12) of low convexity, and is surrounded by a narrow, concave posterior border. The axis is narrower than in larger pygidia, tapers backwards almost to posterior border. The articulating facets are transversely much shorter than on large pygidia, so that the horizontal, adaxial part of the pleural regions is much extended. This would also apply to any thoracic segments at this stage of development. The axial narrowing on very early growth stages seems to be general for nileids from Spitsbergen, although small transitory pygidia of other species (Pl. 10, Fig. 16) do not possess a concave border.

Cranidia with sag. length 2 mm (palpebral view), are not greatly different from those of holaspides (Pl. 21, Fig. 13), slightly more convex, with a more strongly curved anterior outline. Cranidia of about 3 mm in length are associated with degree 6 meraspides (Pl. 21, Fig. 16) which are similar to holaspides in general proportions, but show evidence of the retention of the seventh segment in the pygidium.

Small growth stages associated with other nileid species from Spitsbergen are similar to those described above, but their assignment to particular species is difficult because of the co-occurrence of several species in the same beds. Small pygidia of *Nileus* lack the concave border seen on *S. arcticus*.

Discussion. — This species differs from the type species, *S. palpebrosus* (DALMAN), as figured by ANGELIN (1851, Pl. XVI, Fig. 4; see also JAANUSSON in MOORE 1959, Fig. 267) in having shallower axial furrows, less convex (trans.) glabella, and in possessing a pointed, rather than bluntly rounded pygidial axis. The same characters distinguish *S. arcticus* from other *Symphysurus* species from Norway, Sweden and the Russian platform, all of which are in need of revision, and from other species of the genus which occur widely through Europe and Asia. Only *Symphysurus kujandensis* CHUGAEVA (1958, p. 66–7, Fig. 14, Pl. 7, Figs. 15–19) from the late Arenig or early Llanvirn Kopalinsky Formation of Kazakhstan, possesses a combination of the diagnostic characters of *S. arcticus*. Comparisons are hindered by the fact that the Kazakhstan species is known only from flattened material; this compares very closely with similarly preserved material from Spitsbergen (see also FORTEY 1975, Fig. 8). Two differences are considered sufficient to justify specific separation of *S. arcticus*: the postocular section of the facial suture of *S. kujandensis* appears to be straight or slightly concave, rather than sigmoidal as in *S. arcticus*; the facets on the pygidium have only about half the relative transverse width of the Spitsbergen species. A similar difference on the thoracic pleurae results in a wider, horizontal adaxial part of each pleura. As discussed above (p. 31) a *Niobe* species closely related to *N. occulta* n. sp. also occurs in the Kopalinsky Formation.

Stratigraphically high populations of this species show certain features, manifest particularly on the pygidium, indicating a transitional nature with *Peraspis omega* n. sp. and *Poronileus jugatus* n. gen., n. sp. These species, and hence other species of their respective genera, are believed to have been derived (p. 36) from such transitional populations of *S. arcticus*. A convex, posterolateral pygidial border (Pl. 21, Fig. 8) is present on such specimens, and fine terrace lines occur on the pygidial pleural fields. There is, however, every gradation between these "advanced" pygidia and *S. arcticus forma typica*, and cranidial features are constant, so that taxonomic distinction of these populations is not considered appropriate.

Family RAPHIOPHORIDAE ANGELIN 1854

Diagnosis. — Blind trilobites of the suborder Trinucleina with triangular or subcircular cephalon and pygidium. Glabella expanding forward, with median spine in some genera, or glabellar tubercle. Facial sutures run in curved course along the margins of the triangular fixed cheeks. Free cheeks long, narrow, lacking median or connective sutures, bearing long genal spines.

Discussion. — ANGELIN's (1854) original definition of this family included the genera *Raphiophorus*, *Ampyx* and *Lonchodomas*, the type species of which were redescribed by WHITTINGTON (1950), who also included in the family *Raymondella* and *Ampyxina*. To these five genera were added *Anisonotella* WHITTINGTON (1952), *Cnemidopyge* WHITTARD (1955), *Mendolaspis* RUSCONI (see HARRINGTON and LEANZA 1957), *Bulbaspis* CHUGAEVA (1956). WHITTINGTON (in MOORE 1959 p. 0427) transferred *Edmundsonia* COOPER (1953) from the Dionididae to the Raphiophoridae. The number of genera in the family was further extended by the addition of *Ampyxinella* KOROLEVA (1959), *Ampyxella* DEAN (1960), *Ampyxoides* WHITTINGTON (1965), *Miaopopsis* LU (type species *M. whittardi* (YI) figured LU et al. 1965, p. 1127, Fig. 6) and *Malongullia* WEBBY, MOORS and McLEAN (1970). Raphiophorids are abundant in the Valhallfonna Formation, no less than 14 species are found here, and the discovery of three new genera (*Globampyx* n. gen., *Rhombampyx* n. gen. and *Pytine* n. gen.) and well preserved material of a fourth, little known genus (*Mendolaspis* RUSCONI) permits some consideration of the classification of the group as a whole.

The family Endymioniidae RAYMOND 1920 (including *Endymionia* and *Salteria*, WHITTINGTON in MOORE 1959) is here regarded as a subfamily of the Raphiophoridae. WHITTINGTON (1965) has illustrated the appearance of the lateral inflated areas of *Endymionia* during ontogeny, and in the new species of this genus described below, these areas are poorly defined in the adult and do not appear until quite late growth stages. Small cranidia resemble those of *Pytine* n. gen. The presence of lateral inflated areas is not regarded as being of fundamental importance and the separation of *Endymionia* from the raphiophorids seems unwarranted. The new genus *Pytine* is similar in some ways both to *Endymionia* and *Anisonotella* (see p. 91). The latter genus also resembles *Salteria* notably in having pit-like glabellar furrows, and a large pygidium with many segments. The genera *Endymionia*, *Salteria*, *Anisonotella* and *Pytine* n. gen. thus appear to be rather closely related and together constitute the subfamily Endymioniinae as here defined. All are characterised by possessing 7 thoracic segments, lacking a frontal spine, and in having a prominent glabellar tubercle far back on the glabella. To these four genera may possibly be added *Typhlokorynetes* SHAW (1966) regarded by the original author as belonging to a separate family possibly allied to the illaenids. This genus has a glabella of similar form to

Endymionia, faint lateral infalted areas, and a hypostoma which is more consistent with raphiophorid than illaenid affinities.

Other raphiophorid genera are included in the subfamily Raphiophorinae. Within the subfamily the morphological variation is considerable. There is a group of genera with five thoracic segments and a short pygidium, which is generally strongly furrowed, including *Raphiophorus*, *Ampyxina*, *Ampyxoides*, *Raymondella*, *Miaopopsis* and *Globampyx* n. gen. Median spine may be present (*Raphiophorus*, *Ampyxoides*) or absent on later growth stages (*Ampyxina*, *Raymondella*) or throughout ontogeny (*Globampyx* n. gen.): bacculae may be prominent (*Ampyxina*, *Raymondella*) or lacking (*Ampyxoides*, *Globampyx* n. gen.). A second group of genera have six thoracic segments and relatively longer pygidium, which is generally smooth (except *Cnemidopyge*), including the genera *Ampyx*, *Cnemidopyge*, *Edmundsonia*, *Bulbaspis*, *Mendolaspis*. A median spine is usually prominent, but is lacking in *Mendolaspis* and *Edmundsonia*. Connecting these two groups are *Lonchodomas* and *Ampyxella* DEAN 1960, which have five thoracic segments, but otherwise more closely resemble trilobites of the second group. Within such an intergrading series of genera distinction of further subfamilies is not possible until more is known of their phylogenetic relationships.

The genus *Ampyxinella* KOROLEVA (1959) (placed by the original author in a separate subfamily, Ampyxinellinae) apparently has six thoracic segments, but in other respects appears to be closest to *Raymondella*. It is tentatively considered to belong to the Raphiophorinae.

Subfamily RAPHIOPHORINAE ANGELIN 1854

?Ampyxininae HUPÉ 1955, Ampyxinellinae KOROLEVA 1959

Diagnosis. — Raphiophorid trilobites with five or six thoracic segments, glabella expanding forwards and inflated anteriorly, usually with anteromedian spine, or with tubercle in comparable forward position. Pygidium triangular, with minimum of three axial rings. Pleural fields smooth to strongly furrowed. Included genera: *Ampyx* DALMAN 1827, *Raphiophorus* ANGELIN 1854, *Lonchodomas* ANGELIN 1854, *Ampyxina* ULRICH 1922, *Raymondella* REED 1935, *Cnemidopyge* WHITTARD 1955, *Mendolaspis* RUSCONI 1951, *Edmundsonia* COOPER 1953, *Bulbaspis* CHUGAEVA 1956, *Ampyxella* DEAN 1960, *Ampyxoides* WHITTINGTON 1965, *Globampyx* n. gen., *Rhombampyx* n. gen., ?*Ampyxinella* KOROLEVA 1959, *Miaopopsis* LU (date of authorship uncertain).

Genus *Ampyx* DALMAN 1827

Type species. — *Ampyx nasutus* DALMAN 1827.

Discussion. — The type species of *Ampyx*, *A. nasutus*, was redescribed by WHITTINGTON (1950, p. 554, Pl. 74, Figs. 3–9). For the purposes of comparison with the species included in the genus from Spitsbergen, the following features of the type may be noted: 1. thorax and pygidium of approximately the same length, 2. lateral outline of thorax gently curved, 3. posterior thoracic segments with pleural furrows concave towards front, 4. pygidium smooth except for anterior pair of pleural furrows, which, like those of the thorax, are concave forwards, 5. glabella convex, elevated well above cheeks immediately in front of occipital ring, 6. muscle scars on the glabella deeply impressed, 7. anterior border of cranidium wide (trans.), 8. free cheeks wide enough (trans.) to give facial sutures concave-forwards outline. Species similar to the type species in these features, which may be regarded as belonging to *Ampyx sensu stricto*, include: *Ampyx austini* PORTLOCK 1843 (see WHITTARD 1940), *A. laeviusculus* BILLINGS 1865 (see WHITTINGTON 1965), *A. salteri* HICKS 1875 (see WHITTARD 1955), *A. americanus* SAFFORD and VOGDES 1889 (see COOPER 1953), *A.* ? *hastatus* RUEDEMANN 1901, *A. camurus* RAYMOND 1925 (see COOPER 1953), *A. priscus* THORAL 1935 (see DEAN 1966a), *A. serguncovae* VEBER 1948 (see also CHUGAEVA 1958), *A. virginiensis* COOPER 1953 (see also WHITTINGTON 1959), *A. linleyensis* WHITTARD 1955, *A. depressus otradinca* BALASHOVA 1959 (see BALASHOVA 1960, Pl. 1) and *A. nunezi* BALDIS and BLASCO 1973.

Six *Ampyx*-like species occur in the Valhallfonna Formation, testifying to a vigorous diversification of this group of raphiophorids in the early Ordovician. Only one of these, *A. spongiosus* n. sp., fits most closely into the concept of *Ampyx sensu stricto* based on the type species. The other species exhibit great variation, particularly in the following features:

a. degree of forward protrusion of the glabella.
b. form of muscle impressions on glabella.
c. degree of inflation of the posterior part of the glabella, and particularly the extent to which the occipital ring is defined.
d. depth, completeness and curvature of the posterior border furrow, with corresponding changes in the form of the posterior border on the cranidium.
e. relative size of the pygidium and the degree to which the pleural fields are furrowed.
f. surface sculpture, which may be almost any combination of pits, raised lines, and grooves.

Two species are so different from *A. nasutus* that their incorporation in the same genus is not possible — these are assigned to the new genus *Rhombampyx*, type species *R. rhombos* n. sp. Other species are included for the moment in *Ampyx sensu lato*. They are tentatively included in informal "species groups" on the basis of probable shared derived characters. Further knowledge of *Ampyx* species from other areas in the early Ordovician is necessary before separating new genera, but I have no doubt that the *sensu lato* concept of *Ampyx* used here includes several groups of only distantly related species.

A. Ampyx sensu stricto

Ampyx spongiosus n. sp.
(Pl. 22; Pl. 23, Figs. 1, 3, 4, 5)

Stratigraphic range. — Olenidsletta Member, 80–96 m from base, middle Arenig, approximately equivalent to *bifidus* zone of BERRY (1960).

Material. — Holotype, mould of dorsal exoskeleton lacking free cheeks, PMO NF 2021. Among numerous other specimens are dorsal exoskeletons lacking free cheeks: PMO NF 1853, 2646, SMA 84137; cranidia: PMO NF 446, 2652, SMA 84130–9, 84141; pygidia: PMO NF 440, 2661, SMA 84140; free cheek: PMO NF 1847; hypostomata: PMO NF 437, 458, 406, 408.

Diagnosis. — An *Ampyx* species with thorax less than one third sagittal length. Cranidium very wide, posterior border furrows broad, faint adaxially. Frontal spine very long, exceeding length of cranidium (sag.) curving slightly downwards. Thorax increases in width rather abruptly backwards to third thoracic segment, posteriorly tapering more gradually. Width of pleurae greatly exceeding that of axis, pleural furrows faint. Pygidium large; long, narrow axis tapering to a point with up to 17 faintly defined axial rings. Pleural fields lacking furrows on dorsal surface. Posterior border greatly upward arched on mid-line. Surface sculpture of densely spaced punctae.

Description. — Exoskeleton subelliptical, length (sag.) approximately equal to transverse width of cranidium. Cranidium broadly triangular, occupying 0.4 length of exoskeleton, width at posterior border about 2.5 times its sagittal length (excluding median spine). Glabella convex (trans.) expanding gently in width (θ in range 26–30 degrees on 12 measured specimens) and increasing in transverse convexity forwards, front margin tapering rapidly (φ close to 90 degrees). Mid-line of glabella almost horizontal, may be obscurely carinate on internal moulds, continuing anteriorly into a stout, tubular anteromedian spine which tapers rapidly at first and is directed slightly upwards, distally slender, and gently downward-directed. Beneath the spine the front margin of the glabella slopes steeply downwards such that μ is about 75 degrees, this steep anterior slope continuing in the preglabellar field (ω almost 180 degrees). Three pairs of muscle impressions visible as smooth patches on dorsal surface of exoskeleton and as slightly depressed areas on internal moulds (Pl. 22, Fig. 8). 1P and 2P close together, on sides of glabella just above axial furrows, anterior limit of 2P opposite mid-point (sag.) of glabella, 1P elliptical (long axis sag.), 2P subcircular. 3P is halfway between 2P and the fossula in the axial furrow, lies adjacent to the axial furrows, rather small and semicircular. Smooth areas adjacent to base of glabella may represent an additional pair of muscle impressions. Occipital ring wider medially, not forward sloping, of transverse width 0.7 maximum width of glabella. Occipital furrow deepening abaxially. Visible on internal moulds between the lateral parts of the occipital ring and the mid-part of muscle impressions 1P there are elongate (sag.) very slightly inflated bacculae, narrowest medially. Axial furrows fairly shallow, except where deepened into prominent fossulae, curving sharply abaxially posteriorly, and not separating posterior border from occipital ring.

Fixed cheeks wide (trans.), triangular, forwards sloping, progressively so anteriorly, the very steep anterior slope continuing in front of the glabella. Anterior margin arching upwards considerably towards mid-line where it is almost confluent with the anteromedian part of glabella. The cheeks are crossed by a pair of genal "ridges" which are in fact grooves in the internal surfaces of the cheeks, diverging gradually from the axial furrow adjacent to furrow 3P and crossing the cheek towards the posterolateral corner of the cranidium. Posterior border furrow very wide (exsag.), not defined axially, laterally terminating in a rather small pit almost at posterolateral corner of cranidium. Posterior border widening laterally and steeply forward sloping. Facial sutures running along the length of the lateral margin of the cranidium.

Narrow free cheeks produced into a very long genal spine which is initially laterally directed, distally curving posteriorly to become parallel to the sagittal line, and exceeding the length of the rest of the dorsal exoskeleton. The spine is grooved on the dorsal surface.

The surface of the cranidium is covered with rather coarse punctae, which extend into the posterior border furrow; anterior margin of cranidium with grooves interspersed with punctae. On the anterior part of the glabella the punctae are replaced by a honeycomb-like pattern, this being due to an expansion of the punctae at the expense of the intervening exoskeleton, which assumes the appearance of low ridges. Around the front margin of the glabella, and extending onto the anteromedian spine, the honeycomb pattern gives way to parallel, closely spaced ridges (Pl. 22, Fig. 7).

Hypostoma (Pl. 22, Figs. 3, 4) with the general characters of raphiophorid hypostomata listed by Whittington (1959, p. 461), but length (sag.) exceeding maximum width, which is posterior to anterior margin. Narrow lateral and anterior borders, posteriorly convex, anterolaterally steeply inward-sloping. Middle body smooth and oval with maximum width at about one third hypostomal length, middle furrows visible only as faint depressions contricting sides of middle body at two-thirds length of hypostoma.

Thorax of six segments, short and wide, occupying only a quarter of the sagittal length of the exoskeleton, expanding in width backwards rather rapidly to a maximum at the posterior margin of the second thoracic segment, and tapering rather more gently posteriorly. The sixth thoracic segment is narrower (trans.) than the first. Axis parallel sided; axial rings of equal width (sag., exsag.), defined by straight ring furrows which are deepest to either side of the mid-part. Pleurae at least half as wide again as axis, blunt tipped, edged by a narrow, downturned strip of exoskeleton. Pleural furrows are only at all well defined on anterior two segments, those of first segment running in an almost straight line from the adaxial anterior margins of the pleurae to the posterolateral corners, those of second segment running along the middle of the pleurae distally. Only the outer parts of the pleural furrows of the posterior three segments are clearly visible, these running just posterior to the mid-line of each pleura, not reaching the tip, deepened distally. Punctate surface sculpture as on fixed cheeks.

Pygidium large, triangular, sagittal length exceeding that of thorax. Axis narrow, width at anterior margin 0.21 that of pygidium, tapering gently posteriorly, tip pointed. Axial rings visible as transverse smooth bands on dorsal surface of pygidium, on internal moulds gently convex, outlined by shallow furrows anteriorly and by muscle scars posteriorly. Up to 17 axial rings are visible. Muscle impressions paired, the inner impression is in the ring furrow, the furrow in fact joining the inner ends of the scars, while the outer impression is on the axial ring immediately behind (Pl. 22, Fig. 9). Axial furrows shallow. Pleural fields lacking furrows on dorsal surface, except for transverse first pleural furrow, which is impressed laterally. On internal moulds the first pleural furrow is more distinct, and there are faint indications of several more pairs of similar furrows. Posterior border deepest postero-laterally, sloping downwards at a steep angle, arched up greatly medially. Posteriorly it is not separated from the pleural fields other than by a change in slope; antero-laterally the pleural fields are edged by a narrow (exsag.) ridge. Surface sculpture on pygidium consisting of punctae slightly finer than those on the rest of the exoskeleton, posterior border with closely-set terrace lines, which extend on to the posterior part of the pleural field. On internal moulds a small furrow extends from the tip of the axis to the posterior margin (Pl. 22, Fig. 10).

Discussion. — This species differs from the type species (WHITTINGTON 1950, p. 554, Pl. 74, Figs. 3–9; in MOORE 1959, p. 0425) in having a short (sag.) thorax with a strongly curved outline, pleural furrows not concave posteriorly, in possessing a relatively wider cranidium with a steeply upward-arched anterior margin, genal ridges, and in having a relatively larger pygidium with a long, pointed axis with over twice as many axial rings, and a straight anterior pygidial pleural furrow. The same features distinguish this species from most other species assigned to the genus. *Ampyx volborthi* SCHMIDT 1894 (*sensu* SKJESETH 1952, Pl. 5) from the Lower Didymograptus series of Norway, of similar age to that part of the Valhallfonna Formation containing *A. spongiosus* n. sp., is strikingly similar to the new species in the general proportions of the cranidium and pygidium. I have examined material of *A. volborthi* in the Paleontologisk Museum, Oslo, which shows that paired genal ridges are present. The pygidial axis has about 18 axial rings. *A. volborthi* may be distinguished from *A. spongiosus* n. sp. by its apparently prismatic frontal spine, well impressed muscle scars, and in having the posterior border of the pygidium but slightly upward arched on the mid-line. The surface sculpture on the pygidial pleural fields (Pl. 23, Fig. 2) is distinct from that of *A. spongiosus* n. sp., widely spaced terrace lines being interspersed among the very fine punctae. POULSEN (1965, p. 100-101) indicates, however, that SKJESETH's material may not be identical with the type material of SCHMIDT. "*Raphiophorus*" *akdjaricus* LISOGOR (1965) from the Middle Ordovician of Kazakhstan is probably also closely related to *Ampyx spongiosus* n. sp. with generally similar cranidium and pygidium, and a thorax of identical outline, but differing in having deeply impressed 1P furrows on the glabella, and in possessing a distinct rim around the posterior margin of the pleural fields of the pygidium.

B. Porcus species group

Definition. — *Ampyx* species with posterior border furrow effaced adaxially; occipital ring and posterior part of glabella scarcely elevated above fixed cheeks. Glabellar muscle impressions not deeply impressed and adjacent to axial furrows, 1P and 2P tending to form a confluent, oval depression near base of glabella. Facial sutures nearly marginal, outline convex-forwards. Pleural furrows on posterior thoracic segments and pygidium transverse, rather than concave-forward as on *Ampyx* s.s.

Ampyx porcus n. sp.
(Pl. 24, Figs. 1–8)

Stratigraphic range. — Olenidsletta Member, 85–100 m from base, a characteristic associate of *Gog catillus*, *Niobe flabellifera* and *Ampyx spongiosus*, probably corresponding to the Middle Arenig (*bifidus* zone).

Material. — Holotype, dorsal exoskeleton lacking free cheeks, PMO NF 502; other material includes cranidia: PMO NF 2691, 2017, SMA 84147–8, 84150; exoskeletons lacking free cheeks: PMO NF 2745–6, 524–5, 1758; pygidia: PMO NF 1659, 514, SMA 84149, 84151.

Diagnosis. — An *Ampyx* species with an extremely low, narrow (sag.) occipital ring. Glabella in front of the occipital ring not elevated above fixed cheeks. Muscle impressions 1P and 2P confluent, forming a long (exsag.), slightly depressed area along sides of glabella. Posterior border furrow not defined adaxially. Surface sculpture on cranidium consisting of widely spaced punctae on fixed cheeks (not on posterior border), and very widely spaced, loosely branching ridges on glabella. Triangular pygidium with low axis ill defined posteriorly, anterior pleural furrow straight, dorsal surface with lines of widely spaced pits representing pleural and interpleural furrows.

Description. — Cranidium broadly triangular, width twice sagittal length (excluding spine). Glabella immediately in front of occipital ring not elevated above cheeks, expanding gradually and evenly in width and convexity anteriorly (θ 25–32 degrees). In lateral view outline of top surface of glabella is gently and evenly arcuate, sloping downwards anteriorly. Front part of glabella extends beyond anterior border, lower surface sloping downwards (both φ and μ large obtuse angles), meeting the preglabellar field at a high angle (ω approximately 80 degrees). Frontal spine circular in cross section, horizontal or slightly declined. Occipital furrow narrow, straight and rather shallow, dying out laterally. Occipital ring very low, narrow, gently convex, slightly wider on mid-line, nearly twice the width of that part of the glabella immediately in front of the occipital ring. Between the lateral parts of the occipital ring and muscle impressions 1P on the glabella there are small triangular bacculae, gently inflated and ill defined laterally. Muscle impressions 1P and 2P fused, forming an elliptical (long axis sag.), depressed area along side of glabella adjacent to axial furrow, reaching almost to half glabellar length. 3P impressions are smaller, a short distance in front of 2P. Axial furrows shallow, except at anterolateral corners of glabella where they are deepened into pits. Cheeks triangular, gently convex. Posterior border furrow narrow and deep, only present on outer two thirds of the fixed cheek, shallowing rather abruptly adaxially, laterally terminating in a deep pit almost at posterolateral edge of cranidium. On internal moulds the posterior border furrow can be traced faintly adaxially, meeting the axial furrow almost at posterior margin. Posterior border increases in width laterally, rather narrow, gently convex. Surface sculpture very distinctive, consisting of widely spaced punctae on the fixed cheeks, and very widely spaced, loosely bifurcating ridges on the glabella, absent on the posterior midpart (Pl. 24, Fig. 5). Preglabellar field narrow, sloping down to narrow (sag., trans.), horizontal anterior border.

Thorax shows six segments, length slightly less than one-third that of entire exoskeleton, lateral outline bowed outwards, with maximum width at third segment. Axis of low convexity (trans.), parallel-sided except for last segment which tapers to anterior width of pygidial axis. Pleurae broader than axis, of equal width (exsag.). Posterior pleural furrows narrow (exsag.) running transversely across middle of each pleura, almost to tip, and deepening laterally. Pleural furrow of anterior thoracic segment runs across pleura from anterolateral margin of axial ring to posterolateral extremity of pleura. Sculpture in pleural furrows of scattered pits like those on fixed cheeks and pleural fields of pygidium.

Pygidium triangular, of width 2.1–2.7 sagittal length. Axis narrow, about one quarter pygidial width at anterior margin, tapering gently posteriorly, not greatly elevated above pleural fields, bluntly rounded tip reaching posterior border. Only the most anterior axial ring is visible on the dorsal surface, on the internal mould up to eight rather obscure rings can be seen. Axial furrows shallow on dorsal surface. Pleural fields horizontal. Anterior pleural furrow fairly deep, straight, well defined on internal moulds. Further evidence of pleural segmentation is obscure on internal moulds, but on the dorsal surface transverse lines of widely spaced pits probably correspond with pleural and interpleural furrows, indicating the presence of at least four segments in the pleural fields. Posterior border steeply down-sloping, fairly deep, arched up slightly on mid-line.

Discussion. — This species differs from the type species (and related species listed on p. 66) in having the posterior part of the glabella very low, occipital ring narrow and of low convexity, posterior border furrow dying out adaxially, muscle areas 1P and 2P conjoined, not deeply impressed, and the anterior pleural furrow on the pygidium straight, transverse. The Scandinavian species

Ampyx pater HOLM 1882 (see SKJESETH 1952, TJERNVIK 1956), *A. glaber* POULSEN 1965, and *A. nasutoides* RÉGNELL 1940 are closest to the new species, all having the posteriorly low glabella with muscle impressions scarcely incised, and the straight anterior pleural furrow on the pygidium. In none of these species is the occipital ring as low as in *A. porcus* n. sp., nor the posterior border furrow so effaced adaxially. In material I have examined of *A. pater* and *A. glaber* I have found no indication of similar sculptural type of *A. porcus* n. sp.

It is noteworthy that *A. porcus* n. sp. and the species to which it has been compared are all of similar age (mid-Arenig to top Arenig, or earliest Llanvirn for *A. glaber*). Further study may show that the several differences that the porcus species-group exhibit when compared with the type and allied species may be of more than specific significance.

Ampyx delicatulus n. sp.
(Pl. 25, Figs. 1–7)

Stratigraphic range. — Olenidsletta Member, 98 to 103 m from base, extending into earliest beds with *Isograptus* zone graptolites.

Material. — Holotype, cranidium with three thoracic segments, PMO NF 1; other material includes cranidia: PMO NF 2198, 2202, 2235, 1616, 1630, 1618, 1624, 2223, 2210, 2198, 2247, 2251, 2176, 1526–7; pygidia: PMO NF 1619, 1626, 2234, 2205.

Diagnosis. — An *Ampyx* species cranidium of which resembles that of *A. porcus* in having a low occipital ring, adaxially effaced posterior border furrow, and differs from that species in having the front part of the glabella highly elevated above the fixed cheeks, and in having a complex surface sculpture of lines and fine punctae. Pygidium with deeper posterior border than that of *A. porcus*, more upward-arched on mid-line, and lacking pitted sculpture.

Discussion. — A full description of this species is not necessary as it resembles *A. porcus* in most characters, those features by which it is most easily distinguished being listed above. *A. delicatulus* occurs in the Olenidsletta Member immediately above *A. porcus* and it is tempting to assume that there is an ancestor-descendent relationship between the two species; although there is no doubt that *A. delicatulus* is more closely related to *A. porcus* than any other Spitsbergen *Ampyx*, the differences between the two species are considered to embrace too many features to make such a simple relationship likely. *A. delicatulus* is found in beds transitional between the nileid and olenid communities, the former community including *A. porcus* and the latter lacking raphiophorids. It seems probable that *A. delicatulus* is a species (? with a common ancestor with *A. porcus*) specifically adapted to these transitional conditions on the environmental gradient (FORTEY 1975, Fig. 5).

The surface sculpture on the fixed cheeks of *A. delicatulus* is distinctive (Pl. 25, Fig. 3): incised grooves, each surrounded by a smooth area, loosely bifurcating and subparallel to the anterior margin of the cranidium, the areas between the grooves being minutely pitted (pitting finer than any other *Ampyx* from Spitsbergen), pitting continuing into the posterior border furrow. The form of the glabella is similar to that of *A. porcus* with regard to muscle impressions, forward expansion (θ) and anterior outline (φ), but the anterior elevation is greater such that μ is between 90–100 degrees on measurable specimens; ω is difficult to measure due to the narrowness of the anterior border, but is a large obtuse angle, about 150 degrees. Pygidia of *A. porcus* and *A. delicatulus* are similar, except that the posterior border of the latter is deeper, more upward-arched on mid-line, and the dorsal surface is apparently without surface sculpture.

Ampyx toxotis n. sp.
(Pl. 26, Figs. 1–11)

Stratigraphic range. — Lower part of Profilbekken Member, occurring in one bed on shore section of Profilstranda, approximately 22 m from base of Member.

Material. — Holotype, cranidium, PMO NF 261; other cranidia: PMO NF 189, 215, 218, 188, 233, 1321; pygidia: PMO NF 281, 223.

Diagnosis. — An *Ampyx* species with posterior border furrows only defined laterally where they curve forwards from the posterolateral corners of the cranidium bisecting the posterolateral angle. Glabella obtuse anteriorly, not greatly inflated; anterior spine slender, gently declined.

Description. — The front margin of the cranidium is curved in a gentle and uniform arc, such that the transverse width at the posterior margin is about 2.8 sagittal length. Glabella expands gently and uniformly forwards (θ 18 to 21 degrees) anteriorly tapers rapidly so that it does not protrude greatly beyond the anterior margin of the cranidium in standard view (φ 110–125 degrees). Posterior part of glabella gently convex above fixed cheeks; occipital ring of similar transverse elevation, narrow, indistinctly defined laterally. Muscle impressions on glabella weak, aligned adjacent to axial furrows: 1P subcircular, a short distance in front of the occipital furrow, 3P a slightly deeper pit about the same distance behind the anterolateral corner of the glabella, 2P very shallow, midway between 1P and 3P. In lateral view the glabella is not greatly inflated anteriorly (μ obtuse) and only just overhangs the narrow, vertical preglabellar field (ω large obtuse angle, about 150–160 degrees). Axial furrows shallow; anterior fossulae small. Anterior spine slender, circular, horizontal or slightly declined in front of glabella. Front margin of cranidium scarcely upward-arched about mid-line, of transverse width equal to maximum width of glabella. Fixed cheeks downward-sloping around anterior perimeter, posterolateral corners rounded. Posterior border furrow curves forward to about mid-width of cheek, bisecting posterolateral angle; adaxially it becomes very faint, but curves again posteriorly; on no specimen can the border furrow be traced as far as the junction with the occipital furrow. The posterior border so defined is gently convex and forward-sloping laterally. The posterior border furrow terminates in a pit as in all *Ampyx* species. Surface sculpture of fine, occasionally anastomosing terrace lines, which run transversely, subparallel to the margins of the fixed cheeks. Similar terrace lines are present on the glabella, especially anteriorly, except in muscle impressions. The cuticle of this species is thin, and unlike other *Ampyx* from Spitsbergen the sculpture is also weakly reflected on internal moulds. The slender anterior spine of this species is gently downward-declined.

Pygidium three times as wide as long with unfurrowed pleural fields, at least on the internal mould. The narrow axis reaches, but does not spill on to the posterior border, and there are indications of at least 8 pairs of muscle impressions. The posterior border is only slightly arched about mid-line, and bears fine terrace lines like those on the cranidium.

Discussion. — The peculiar, forward-arched posterior border furrow at once distinguishes this species from other *Ampyx* from Spitsbergen and elsewhere. While the species compares with *A. porcus* and *A. delicatulus* in the adaxial effacement of the border furrow, the anteriorly truncate glabella and wide posterior border set it apart from those species and make a close relationship unlikely. However, *A. toxotis* seems to be closer to the porcus species group than *Ampyx* sensu stricto.

Genus *Ampyxoides* Whittington 1965

Type species. — *Ampyx semicostatus* Billings 1865.

Ampyxoides inermis n. sp.
(Pl. 30, Figs. 10–15)

Stratigraphic range. — Profilbekken Member, lower 12 m only, in melt streams A and B on Olenidsletta; graptolites occurring in the same bed indicate *Isograptus* (probably late *hirundo*) zone.

Material. — Holotype, small but well preserved cranidium, PMO NF 1825; other material consists of cranidia: PMO NF 1870, 1830, 1322, 1824 (block including at least three examples); pygidium: PMO NF 1826.

Diagnosis. — An *Ampyxoides* species with frontal spine lacking, glabella less inflated anteriorly than other species of the genus; axial furrows with concave outline. Posterior part of glabella only slightly elevated above fixed cheeks, and occipital ring low; posterior border furrow very shallow. ω approximately a right angle.

Description. — A small species, known only from internal moulds of cranidia and pygidium. Cranidia are of less convexity (sag., trans.) than other *Ampyx*-like species described here; anterior outline of cranidium semicircular in fossular view. Glabella is not highly vaulted transversely, nor greatly elevated above the fixed cheeks in front of the occipital ring. The shallow axial furrows diverge gently forwards (θ 25–30 degrees on available material) to define the slightly concave sides of the glabella; φ acute (c. 65–80 degrees). The front part of the glabella is not greatly inflated, so that in lateral view the upper surface of the glabella is seen to slope in a uniform curve downwards (Pl. 30, Fig. 13); this part of the glabella is produced well beyond the front of the cranidium, overhanging the narrow and steep preglabellar field (μ acute, approximately 60 degrees, ω close to 90 degrees on the two specimens where it can be seen). Muscle impressions on the glabella are very shallow and details are not possible to discern: it is probable that the 1P scar lies adjacent to the posterior, subparallel sided part of the glabella by analogy with other early raphiophorinids. There is no evidence for a frontal spine in this species, although the forward-protruding form of the glabella is usually associated with such a structure in raphiophorids; it is possible that on the *external* surface a small spine was present, but this seems unlikely as on other raphiophorids from Spitsbergen and elsewhere the anterior spine is hollow and therefore distinguishable on internal moulds. Small anterior fossulae in axial furrows next to widest part of glabella. Occipital ring narrow and of uniform width (sag., exsag.), defined by distinct occipital furrow which is deeper than the posterior border furrows of the cranidium, transverse width exceeding that of base of glabella, but with similar transverse convexity. Posterior edge of occipital ring bulges backward relative to posterior margins of fixed cheeks.

Fixed cheek shaped like quarter circle; posterior border furrow shallow, transverse, not terminating in an obvious pit, outlining narrow posterior border which is almost horizontal over most cranidial width, near lateral border flexed sharply downwards. This change in slope occurs at the point where the thorax articulates with the cranidium.

Pygidium known from a single example, short, at least three times as wide as long, with deep posterior border upward-arched on mid-line. Axial furrows taper posteriorly to enclose an angle of 40 degrees, but axis is not defined around its tip, which spills over on the posterior border. Four, and a faint fifth, rings are defined by shallow ring furrows which do not pass across middle of axis. Pleural fields are smooth on the internal mould, except for faint, transverse anterior pleural furrow, but it remains possible that pleural furrows were deeper on dorsal surface.

Minute fragments of cuticle adhering to the internal mould indicate that the surface sculpture of this species included fine raised ridges on the front of the glabella, and strong, closely spaced terrace lines on posterior border of the pygidium.

Discussion. — Although lacking a frontal spine, this species is considered to be closest to *Ampyxoides*, by comparison with the type species *A. semicostatus* Billings, as redescribed by Whittington (1965, p. 319–321, Pl. 12, Figs. 13-20, Pl. 13, Figs. 1–8, 10, 12) from the Middle Table Head Formation, Newfoundland, and *A. occipitalis* Dean (1973b, pp. 4–6, Pl. 1, Figs. 7–9, 13, 15, 16) from beds of comparable Whiterock age in the Yukon. As stated by WHITTINGTON (1965, p. 319) *Ampyxoides* appears to be closest to *Ampyxina*, species of which may have the anterior spine reduced in holaspides (WHITTINGTON 1959, Pl. 34). The species under discussion resembles *Ampyxina* in this respect, but in other features is closer to *Ampyxoides*, notably in lacking bacculae. The narrow (exsag.) posterior border on the cranidium, and the narrow (sag.) and backward-bowed occipital ring defined by a distinct occipital furrow also seem to be characteristic of the genus. Apart from lacking a frontal spine *A. inermis* differs from *A. semicostatus* and *A. occipitalis* in the shallowness of the posterior border furrow on the cranidium, and the high degree of forward protrusion of the glabella, such that φ is an acute angle. *A. occipitalis* possesses a distinctive posterior glabellar inflation not seen on the Spitsbergen species (compare DEAN 1973b, Pl. 1, Fig. 8). The pygidium of *A. inermis* is closely similar in outline and proportions to that of *A. occipatalis* but the pleural fields are unfurrowed; however the Spitsbergen specimen is an internal mould, and it is not known whether the dorsal surface carried such furrows.

Genus *Globampyx* n. gen.

Type species. — *Globampyx trinucleoides* n. sp.

Diagnosis. — Small raphiophorinid trilobites having five thoracic segments, short, wide triangular pygidium. Bacculae lacking. Glabella flask-shaped, extremely inflated anteriorly, lacking frontal spine throughout ontogeny, but with glabellar tubercle at highest point of glabella. Posterior border furrow faint adaxially, deeper laterally, not terminating in a pit at lateral extremity. Cephalon covered with dense punctae. Five thoracic segments with convex axial rings, pleural furrows deep, running along middle of pleurae. Pygidium with rather low axis reaching posterior border, up to six axial rings, indistinctly defined. Pleural and interpleural furrows faint on pygidial pleural fields. Posterior border fairly deep, arched upwards markedly medially. Included species: *G. trinucleoides* n. sp., "*Ampyx*" *obtusus* MOBERG and SEGERBERG 1906, "*A.*" *linnarssoni* SCHMIDT 1894.

Globampyx trinucleoides n. sp.
(Pl. 29, Figs. 1–21; Fig. 7)

Stratigraphic range. — Olenidsletta Member 135 m (extremely rare, 1 specimen only SMA 84154), abundant throughout lower 75 m of the Profilbekken Member, outnumbering all other raphiophorids in most beds.

Material. — The most abundant trilobite of the Profilbekken Member. Holotype, dorsal exoskeleton lacking free cheeks, SMA 84152. Other figured material consists of cranidia: PMO NF 319, 334, 314; pygidia: PMO NF 3157–8, 1369, 225. Dorsal exoskeleton, badly weathered but showing genal spines, PMO NF 1762; fused free cheeks: PMO NF 332a, 1770.

Diagnosis. — See that of genus.

Description. — Exoskeleton subcircular, convexity of cranidium greatly exceeding that of the thorax and pygidium. Cranidium roughly semicircular, length (sag.) 0.4 to 0.5 width at posterior margin. Glabella flask-shaped, extremely convex (sag., trans.), convexity increasing anteriorly so that the glabella overhangs the preglabellar field. The highest point of the glabella bears a prominent glabellar tubercle. Two pairs of subcircular muscle impressions a short distance above axial furrows, 1P in the "neck" of the glabella, 2P a short distance in front of 1P. There are indications of a third pair of muscle impressions on the sides of the glabella opposite the glabellar tubercle. Occipital ring narrow (sag.) straight, of transverse width slightly less than maximum width of glabella; occipital furrow rather shallow. Axial and preglabellar furrows continuous, fairly shallow and broad, deepened just anterior to the point of maximum width of the glabella into deep apodemal pits. On dorsal surface axial furrows notably shallower and broader adjacent to mid-part of glabella (Pl. 29, Fig. 1). Fixed cheeks broad, sloping gently forwards posteriorly, more steeply outwards and forwards anteriorly and laterally. Posterior border furrow narrow (broader on internal moulds), curving slightly forward, faint or absent adaxially, deepening gradually laterally, not terminating in a pit as on other raphiophorids. Posterior border gently forwards-sloping, widening gradually laterally. Preglabellar field fairly narrow, sloping downwards to very narrow (sag.) anterior border. Internal moulds show a curious horizontal "rim" running along the lateral edge of the cranidium (see Pl. 29, Fig. 10). This is not seen on the edge of cranidia retaining the exoskeleton. It is believed to represent the external mould of the facial suture, extending forwards as far as the anterior border. This suture is not normal to the surface of the exoskeleton, but is a horizontal plane cutting the exoskeleton obliquely. External surface of cranidium densely punctate (except on posterior border), punctae smaller on glabella. Internal moulds are also punctate (representing granules on the

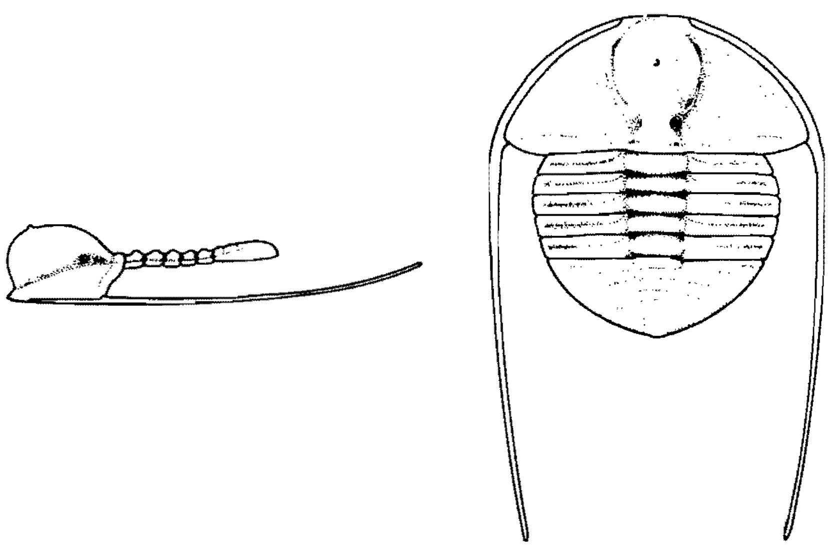

Fig. 7. Reconstruction of *Globampyx trinucleoides* n. gen., n. sp., × 8, lateral and dorsal views.

internal surface of the exoskeleton), but the punctae are more scattered than on the dorsal surface, and it does not seem likely that the dorsal and ventral sculptures are directly related. Small smooth areas present adjacent to the axial furrows and just posterior to the anterior pits, from which a smooth line passes laterally across the cheeks towards the posterolateral angle of the cranidium (Pl. 29, Fig. 1).

Free cheeks united as a single piece by narrow (sag., exsag.) doublure, which is smooth anteriorly, but with slightly inflated posterior band carrying a few terrace lines (Pl. 29, Fig. 16). Long genal spines with subcircular cross section, exceeding length of dorsal exoskeleton, and parallel to sag. line.

Thorax of five segments, increasing slightly in width to third segment, tapering gently to pygidium. Axis convex, of width (trans.) slightly less than pleurae, each axial ring tapering slightly backwards, with prominent articulating half ring. Ring furrows deepening and widening laterally. Axial furrows fairly deep and narrow (appearing very deep on internal moulds), and deepened into a pit at the posterior edge of each thoracic segment, this possibly representing a socket articulating with a slight projection on the anterior margin of the thoracic segment behind. Pleurae in contact along their length, tips rounded. Pleural furrows narrow and rather deep, deeper laterally, on external surface, on internal moulds appearing much broader, curving backwards from anterior adaxial limit of pleurae, rapidly becoming transverse and running along centre of pleurae almost to tips.

Pygidium broadly triangular, like the cranidium rather variable in width, ranging between 2.4 and 3.0 times the sagittal length. Axis not as convex as axial rings of thorax, tapering very gently posteriorly and reaching posterior border, tip rounded, ill defined. Up to six axial rings are visible, of which the anterior two are most distinct. The ring furrows defining the first two rings pass across the axis, posteriorly the rings are defined by faint paired muscle impressions. Axial furrows shallow. Pleural fields concave, sloping gently backwards and inwards from the posterior border, with up to four pairs of extremely faint pleural and interpleural furrows, of which only the first pair of pleural furrows are visible on internal moulds. Posterior border steeply downsloping, fairly deep, bulging slightly backwards behind axis, arched up considerably towards mid-line. Surface sculpture of closely spaced parallel terrace lines, which extend on to posterior part of pleural fields.

On small cranidia (Pl. 29, Figs. 20, 21) the glabella is more convex (trans.), outline in anterior view deeply parabolic, expanding in width less markedly anteriorly, muscle impressions distributed more evenly along length of glabella. This suggests that the expansion of the glabella later in ontogeny occurs anterior to 2P. Glabellar tubercle very prominent, posterior to which there is a sagittal ridge. Fixed cheeks punctate, punctae of equal size to those of large cranidia (posterior border smooth). Transverse smooth line passes from axial furrow on to fixed cheek opposite anterior part of glabella (compare *Endymionia clavaria* n. sp. Pl. 32, Fig. 6). Posterior border furrows deeper than on large cranidia, reaching axial furrows.

Transitory pygidia (Pl. 29, Fig. 9) very wide, axis with well defined axial rings, ring furrows not reaching axial furrows, deepened laterally into distinct pits. Pleural furrows deep, transverse, not reaching posterior border. Interpleural furrows indicated by rows of pits parallel to the lateral parts of the pleural furrows.

Discussion. — Probably congeneric are *Ampyx obtusus* Moberg and Segerberg 1906 (see Tjernvik 1956, Pl. XI, Figs. 16–18) and *A. linnarssoni* Schmidt 1894. I have examined material of the former species, from early Arenig beds of Sweden, from which the general resemblance of cranidium and pygidium to *Globampyx* n. gen. is apparent. It is, however, immediately distinguishable from *G. trinucleoides* in possessing a peculiar (sag.) ridge on the glabella, and in having granulate surface sculpture along the glabellar mid-line. *A. linnarssoni* Schmidt (Schmidt 1894, p. 83, Pl. VI, Figs. 21–23) probably occurs in the zone of *Megistaspis estonica* in Estonia and thus is older than *Globampyx trinucleoides*; it is closely similar, the only obvious differences apparent from Schmidt's account being a greater anterior glabellar inflation and a relatively longer (sag.) pygidium in the Estonian species. The same differences are apparent on *Geschiebe* material identified as *A. linnarssoni*, illustrated by Neben and Krueger (1971, Pl. 2, Figs. 7–9; Pl. 3, Figs. 9–10).

As indicated above this species is rather variable in width (see Fig. 8A). The stratigraphically earliest specimen has fixed cheeks of considerably greater width than those of the holotype (Pl. 29, Fig. 19) and broader axial furrows. This specimen occurs some 5 m below the next specimens, and we have insufficient material from the lower horizon to indicate whether it represents a second species. Measurements made on the abundant material from the top of the Valhallfonna Formation, fail to show any relation between stratigraphic occurrence and relative width of cranidium (Fig. 8).

The presence of distinct furrows on the transitory pygidia is similar to early growth stages described by Whittington (1959, p. 473) of *Ampyx americanus* Billings. I have not seen any indication of a frontal spine on even the smallest

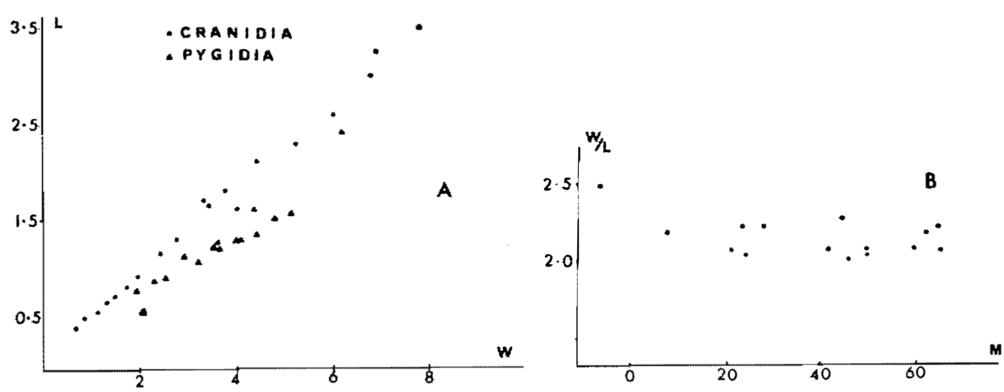

Fig. 8. A. Relation of length (L) to width (W) of cranidia and pygidia of *Globampyx trinucleoides* n. gen., n. sp. B. Relation of width/length ratio (W/L) of cranidia of *Globampyx trinucleoides* to stratigraphic occurrence (metres above base of Profilbekken Member).

cranidia, *Globampyx* n. gen. contrasting in this respect with *Ampyxina* and *Raymondella* (WHITTINGTON op. cit.) which only lose such spines on larger cranidia.

Genus *Mendolaspis* RUSCONI 1951

Type species. — *Mendolaspis salagastensis* RUSCONI 1951.

Mendolaspis doidyx n. sp.
(Pl. 30, Figs. 1–9)

Stratigraphic range. — Olenidsletta Member, ?75 m, 80–100 m from base.

Material. — Holotype, dorsal exoskeleton lacking free cheeks PMO NF 1283. Other material includes: dorsal exoskeletons lacking free cheeks: SMA 84162, 84168; cranidia: PMO NF 504, 505, SMA 84163, 84165; pygidium: PMO NF 3152.

Diagnosis. — A *Mendolaspis* species with convex glabella expanding evenly forward and rounded in front, with minute glabellar tubercle anteriorly. Bacculae very small. Thorax of six segments, maximum width (trans.) at second or third segment. Pygidium with narrow axis indenting posterior border, very faint pleural ribbing. Posterior border not arched up on mid-line.

Description. — Exoskeleton with thin cuticle, elliptical, cephalon occupying 0.4 sagittal length. Length of cranidium 0.4 width, anterior outline arcuate. Glabella about one-fifth width of cranidium at occipital ring, expanding evenly forwards (θ 24–28 degrees), highly convex (trans.), in profile sloping very steeply downwards anteriorly, but not overhanging anterior border (ω almost 180 degrees). Front margin of glabella obtusely rounded about mid-line (ϕ about 130 degrees). Two pairs of muscle impressions adjacent to axial furrows, of which 1P is deepest, semicircular, constricting the posterior part of the glabella slightly, 2P a shallow furrow sloping backwards at about 45 degrees to the sagittal line and not reaching one third of the way across the glabella; a transverse line joining the outer ends of the 2P furrows is almost exactly at glabellar mid-point (sag.). Faint indications of 3P furrow mid-way between 2P and the anterior fossula. Flattening deepens and artificially exaggerates the furrows. Minute glabellar tubercle on mid-line anteriorly, at about the point of origin of the median spine on other raphiophorinids. Beneath this tubercle on internal moulds (Pl. 30, Fig. 8) a triangular tuberculate area may be an area of muscle attachment. Occipital ring sloping anteriorly, narrow medially, very narrow near axial furrows where it continues without a break into the posterior border. Occipital furrow broad (sag.), shallower medially. Axial and pre-glabellar furrows fairly broad and deep, with prominent pit immediately anterior to anterolateral corner of glabella. Fixed cheeks wide, triangular, almost horizontal adaxially, sloping downwards laterally and anteriorly.

Small bacculae adjacent to the posterior parts of the axial furrows. Preglabellar field narrow, narrowest on mid-line, gently convex, medially continuing downward slope of glabella. Anterior border very narrow (sag.), of width (trans.) less than maximum width of glabella. Posterior border furrow fairly narrow and shallow, widening and deepening laterally, and terminating in a pit almost at the posterolateral corner of the cranidium. Posterior border narrow, forward sloping, its lateral one-third (that part projecting beyond thorax) rather wider. Facial suture passing along lateral edge of cranidium, presumably becoming marginal medially, and passing in front of the anterior border. Free cheeks not known. External surface of cephalon smooth, except that area on the cheek anterior to a line passing from the anterolateral corner of the glabella to the posterolateral corner of the cranidium which bears prominent genal caeca.

Thorax of six segments, occupying 0.8 cranidial width at anterior margin, expanding in width rather rapidly to second or third segment; after the third segment tapering more gently to the pygidium. Axis about two thirds the width of the pleurae, not tapering, axial rings convex, of approximately uniform width (sag., exsag.) curving slightly forwards laterally. Ring furrows narrow, deepened laterally to form an apodeme, shallower medially. Pleurae in contact along their whole length, blunt tipped, turned downwards sharply distally. Pleural furrows shallow, running obliquely backwards from anterior adaxial margin of pleurae, that of the first segment running backwards to the abaxial posterior margin of the pleura, those of segments 2–6 curving horizontally and running almost to the tip of the pleurae.

Pygidium triangular, about 0.3 sagittal length of the exoskeleton, over twice as wide as long. Axis occupying slightly less than one quarter pygidial width at anterior margin, tapering gently backwards and indenting posterior border but not reaching posterior margin of pygidium, with 7 axial rings, the first four of which are more distinct. Ring furrows between first four axial rings extend across the axis, posterior to which they are faint medially. Pleural fields horizontal with about six pairs of very faint, straight, backward-sloping ribs; pleural furrows, except for the anterior one, are even fainter. Posterior border steeply downsloping, widening gradually medially, set off from the pleural fields by a low ridge, which follows the outline of the posterior margin. Surface sculpture on posterior border of closely spaced terrace lines.

Note that on flattened material the posterior border is pushed outwards and so appears broader. Flattening of the glabella tends to overdeepen the glabellar furrows, and the basal bacculae may be obscured.

Discussion. — This species differs from the type species (Harrington and Leanza 1957) in having more distinct muscle impressions on the glabella, small bacculae, and a faintly furrowed pygidium with posterior rim. It also resembles *Edmundsonia* (see Cooper 1953) in lacking an anteromedian spine, having caecate fixed cheeks and 6 thoracic segments. *Edmundsonia* differs in having a much longer, distinctly furrowed pygidium, with many segments, and apparently different glabellar furrows.

Genus *Rhombampyx* n. gen.

Type species. — *Rhombampyx rhombos* n. gen., n. sp.

Diagnosis. — *Ampyx* — like trilobites with relatively small, furrowed pygidia. Glabella lacking deeply impressed muscle scars, highly convex (trans.) in occipital region. Facial sutures with outline convex-forwards. Posterior border furrow deep and broad, reaching axial furrows, outlining wide, forward-sloping posterior border with articulating socket about halfway between axial furrows and posterolateral corner of cranidium. Thorax narrowing greatly forward, so that thorax and pygidium together have a subcircular outline, with six segments; posterior pleural furrows transverse. Pygidium short (sag.) with distinct transverse pleural furrows. Hypostoma (known only in *R. tragula* n. sp.) with broad anterior border and prominent maculae. Included species: *R. rhombos* n. sp., *R. tragula* n. sp., "*Raphiophorus*" *lamasi* HARRINGTON and LEANZA 1957.

Discussion. — This genus is erected to include two distinctive species from Spitsbergen and a third, believed to be closely related, from south America, which show combinations of characters which place them outside *Ampyx*, even in the *sensu lato* concept of the genus used above. Most obvious of these distinguishing features are the small pygidium with well-marked pleural furrows, and the anteriorly narrow (trans.) thorax. The glabella shows an unusual degree of occipital inflation, reaching its maximum expression in *R. tragula* n. sp., where the occipital ring is effaced and the posterior part of the glabella bulges backwards. The very deep posterior border furrow and steeply forward-inclined posterior border also appear to be characteristic, and on the latter the relatively adaxial position of the articulating socket can be seen, marking the attachment of the thorax to the cranidium (cf. *Ampyx sensu stricto*, see WHITTINGTON 1959, Pl. 29, Fig. 4). In addition the two Spitsbergen species have an unusual surface sculpture consisting of pits in the border and axial furrows, terrace lines on the anterior part of the fixed cheeks. While the glabellar furrows are less deeply incised than those of the type species of *Ampyx*, *A. nasutus* (WHITTINGTON 1950, Pl. 74, Fig. 3), they are little different in this respect from those species of the *porcus* species group included above in *Ampyx sensu lato*, and earlier species of *Ampyx sensu stricto* (such as *A. laeviusculus* BILLINGS, as figured by WHITTINGTON 1965, Pl. 12, Fig. 5). I note also that the pleural furrows of the posterior five thoracic segments and pygidium are straight and transverse, rather than concave.

Although only the species named above can be certainly assigned to *Rhombampyx* n. gen. some unnamed fragments show features suggestive of the new genus: the "*Ampyx* sp." pygidium described by ROSS (1967, p. 22, Pl. 7, Figs. 20, 21), and the cranidium figured by DEAN (1973a, Pl. 2, Figs. 1, 4, 7, 11) are examples.

Rhombampyx rhombos n. sp.
(Pl. 27, Figs. 1–10; Fig. 9)

Stratigraphic range. — Profilbekken Member 30–35 m from base, with earliest *Orthidiella* zone fauna.

Material. — Holotype, dorsal exoskeleton lacking free cheeks, SMA 84143; cranidia: 84144, 84145, PMO NF 1378, 1112 & 1117 (part and counterpart with several specimens); pygidia: SMA 84146, PMO NF 1192.

Diagnosis. — A *Rhombampyx* species having cranidium with deep, wide, forward-bowed posterior border furrow, surface sculpture of closely spaced punctae most prominent on posterior border furrow, terrace lines on anterior parts of cheeks and glabella. 1P deeply impressed, constricting sides of glabella. Occipital furrow visible over mid-part of glabella. Pygidium with short axis; pleural fields with at least two pairs of deep, straight pleural furrows, fainter interpleural furrows. Posterior border relatively deep, arched upwards very slightly on mid-line.

Description. — Sagittal length of exoskeleton (excluding median spine) about equal to the width of the cranidium, convexity of cranidium greatly exceeding that of thorax and pygidium. Cranidium (excluding median spine) half the length of the exoskeleton, and of width at posterior margin twice its (sag.) length. Glabella highly convex (trans.) expanding gradually (θ 30 degrees) in width from in front of the occipital ring to its anterolateral corners, in front of which it tapers more rapidly (φ about 80 degrees) almost to a point at the base of the median spine, this anterior part of the glabella overhanging the anterior margin. In lateral view the dorsal outline of the glabella is gently arcuate, the anterior third gently downsloping, while the anterior part of the glabella beneath the median spine slopes downwards and backwards at a high angle, at 90 degrees to the anterior part of the dorsal surface, and meeting the preglabellar field at a high obtuse angle (ω of the order of 160 degrees).

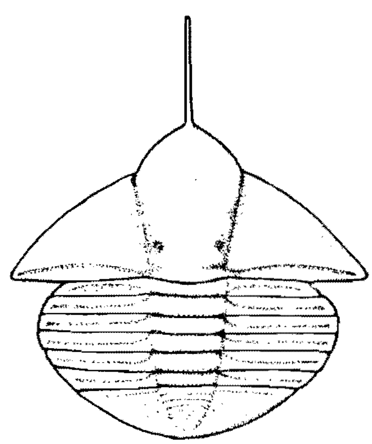

Fig. 9. Reconstruction of *Rhombampyx rhombos* n. gen., n. sp., × 10.

Median spine slender, with circular cross section, upwardly directed, of a length probably less than that of glabella. Occipital ring rather low, widening medially, of a transverse width only slightly less than the maximum width of the glabella. Occipital furrow fairly wide, deepening laterally. Of the muscle impressions only 1P is clearly visible, subcircular, indenting the sides of the glabella at about one third glabellar length. Axial furrows broad and shallow, except where deepened into apodemal pits at anterolateral corners of glabella. Fixed cheeks triangular, anterior margin curved, sloping more noticeably backwards near posterolateral angle, convexity of cheeks increasing forwards. Posterior border furrow deep and wide (exsag.) mid-part convex forward, terminating posterolaterally in a deep pit near the edge of the cranidium. The posterior border is widest and most convex medially, forward sloping, confluent with the occipital ring (Pl. 27, Fig. 10). Surface sculpture of deep, closely set punctae, which are concentrated along the posterior part of the cheeks, especially in the posterior border furrow, and terrace lines on the anterior part of the cheeks, which are subparallel to the anterior margin. Similar terrace lines are present on the anterior part of the glabella. Sculpture on the posterior part of the glabella not known, as all specimens are exfoliated in this region. Preglabellar field narrow and downsloping, not arched upwards on mid-line. No indication of an anterior border has been seen on this species. Internal moulds are punctate on a minute scale, this presumably representing minute, needle-like invaginations of the exoskeleton, and paired genal "ridges" are visible on the fixed cheeks. "Ridge" is a misnomer for this structure, which is not visible on the dorsal surface, and is a ridge only on the internal mould, representing a groove in the ventral surface of the exoskeleton. Free cheeks not known, presumably long and narrow as defined by the marginal facial sutures.

Thorax of six segments, one third sagittal length of exoskeleton, maximum width at third segment, to which the thorax expands rapidly, tapering more gently posteriorly. Width of first thoracic segment only two thirds that of cranidium. Axis convex, tapering gently, transverse width less than that of adjacent pleurae except on the first thoracic segment. Axial rings of uniform width (sag., exsag.) separated by deep ring furrows, with prominent crescent shaped articulating half rings of almost equal width (sag.) to axial rings. First pair of pleural furrows wide and deep, similar in form to the posterior border furrow of the cranidium. Pleural furrows of segments 2–6 commence almost at adaxial anterior limit of pleurae, very rapidly curving to run transversely just posterior to the mid-line (trans.) of the pleurae. Tips of pleurae truncate, with a minute vertically downturned edge.

Pygidium triangular, three times as wide as long. Axis occupying about one quarter pygidial width at anterior margin, tapering gently, posterior margin not clearly defined. There are four fairly well defined axial rings of decreasing width (sag.) posteriorly, and faint indications of a fifth ring on the dorsal surface; internal mould shows up to seven rings. Pleural fields horizontal or slightly concave with two pairs of straight, deep pleural furrows, the first of which is almost twice as long as the second, and two pairs of shallow, narrow interpleural furrows, posterior to which are several more pairs of obscurely defined furrows. Internal moulds also show the presence of the deep pleural furrows, and, like the cranidium, are minutely pitted; seven (?8) pairs of muscle impressions are visible on the anterolateral parts of the axial rings. Posterior border deep, and steeply downsloping, with sculpture of strong, subparallel, anastomosing terrace lines. Posterior margin slightly upward arched on mid-line.

Discussion. — The short, wide, strongly furrowed pygidium, and distinctive thoracic outline distinguish this species immediately from those attributed to *Ampyx sensu lato* as understood herein. *Raphiophorus* ? *lamasi* HARRINGTON and LEANZA 1957, although much less well preserved than the species described above, is closely similar, having six thoracic segments of identical outline (see HARRINGTON and LEANZA 1957, Fig. 116,2, right hand side of holotype), and a short, wide pygidium with a relatively broad posterior border. These two species are probably not related to *Raphiophorus* (see WHITTINGTON 1950, Pl. 74, Figs. 1, 2; 1968, p. 95, Fig. 6), species of which have five thoracic segments, quite different thoracic outline, and a short pygidium with a characteristically truncate posterior outline. Both *Rhombampyx rhombos* n. sp. and *Raphiophorus ? lamasi* are of probable Arenig age, whereas *Raphiophorus* species appear to be characteristic of Caradoc and later strata.

Rhombampyx tragula n. sp.
(Pl. 28, Figs. 1–9)

Stratigraphic range. — Profilbekken Member, lower part, on melt stream A on Olenidsletta, 16–24 m from base of Member.

Material. — Holotype, cranidium (internal mould) PMO NF 2476, counterpart PMO NF 2459; other material consists of cranidia: PMO NF 2399 (3 specimens on block); hypostoma: PMO NF 2427.

Diagnosis. — A *Rhombampyx* species with extremely convex (trans.) glabella, occipital furrow obsolete, back part of the glabella inflated and protruding backwards. Glabellar furrows not deeply impressed.

Discussion. — This species is known from cranidia and hypostoma only, and is clearly related to *R. rhombos*, occurring stratigraphically below that species in the Profilbekken Member. The differences from *R. rhombos* may be summarised as follows:

1. The inflation of the posterior part of the glabella is such that the occipital ring is effaced on large cranidia; even on small cranidia the occipital furrow does not pass over the mid-part of the glabella.
2. The posterior margin of the glabella protrudes strongly backwards with an almost semicircular outline.
3. Muscle impressions are not deeply impressed in the sides of the glabella; in particular 1P is not defined as a furrow. The "occipital" muscle impression is small and subcircular; of preoccipital impressions 1P and 2P almost

touch, the latter is larger than the former and slightly higher on the sides of the glabella. As in most raphiophorids (WHITTINGTON 1959, p. 460) 3P is a small subcircular depression far forward and adjacent to the axial furrow, just posterior to the anterior fossulae, which in this species are particularly deep and conspicuous (Pl. 28, Fig. 3).

4. The minutely pitted internal mould of the holotype does not show the paired genal ridges seen on *R. rhombos*.
5. The surface sculpture of the two species is similar — large scale pitting in the border furrow with fine terrace lines on the forward part of the fixed cheeks. External surfaces of both *R. rhombos* and *R. tragula* are difficult to prepare but on comparably sized specimens of both species the terrace lines of *R. tragula* are coarser and more widely spaced: how much intraspecific variation may be involved here is not known.

Hypostoma (Pl. 28, Fig. 6) found in the same bed as the holotype, is sufficiently large to make it improbable that it belongs to any raphiophorid other than *R. tragula*. While agreeing with the general features of raphiophorid hypostomata as listed by WHITTINGTON (1959, p. 461–2) this hypostoma differs from all others ascribed to the family in having the anterior border expanded (sag., exsag.) to form a halo-like, gently down-sloping anterior band. This band runs into the narrow (trans.) backward-converging lateral borders. Posterior border convex (sag.), outline gently arcuate backwards. Middle body transversely convex, bearing prominent maculae.

The convex, backward-protruding occipital region of this species distinguishes it from other raphiophorids. In its posterior cranidial features the species lies at the opposite morphological pole to the *porcus* species group of *Ampyx* in which the occipital ring is scarcely elevated above the fixed cheeks, the posterior border furrow obsolete adaxially, and the posterior border narrow, and hardly convex. Why this particular region in *Ampyx*-like species should be susceptible to such extremes of variation is not known, but the fact that they fall into groups defined on such characters, and that such groups are linked by other common morphological features, seems to indicate that such cranidial features are of real value in the discrimination of "natural" generic groupings within the *Ampyx* complex.

Subfamily ENDYMIONIINAE RAYMOND 1920

? Typhlokorynetidae SHAW 1966

Diagnosis. — Raphiophorid trilobites with seven thoracic segments; glabella not greatly inflated anteriorly, not overhanging anterior border. Glabellar tubercle at about mid-length of glabella.

Included genera: *Endymionia* BILLINGS 1865, *Salteria* W. THOMSON 1864, *Anisonotella* WHITTINGTON 1965, *Pytine* n. gen., ? *Typhlokorynetes* SHAW 1966. *Malongullia* WEBBY, MOORS and MCLEAN 1970 may also belong here, but only has six thoracic segments (see discussion in WEBBY 1974, p. 232).

Genus *Endymionia* BILLINGS 1865

Type species. — *Endymion meeki* BILLINGS 1862.

Endymionia clavaria n. sp.
(Pl. 32, Figs. 5–15)

Horizon. — Olenidsletta Member, upper part, 120–140 m from base, with graptolites indicative of early *Isograptus* zone (probably equivalent to the *hirundo* zone of British scheme).

Material. — Holotype, dorsal exoskeleton lacking free cheeks, PMO NF 1735 (counterpart PMO NF 1741); cranidia: SMA 84173–6, SMA 84177; pygidium: SMA 84178.

Diagnosis. — An *Endymionia* species with lateral inflated areas which are only faintly defined abaxially. Posterior border expands in width greatly laterally. Posterior border very faint or absent adaxially. External surface of cranidium smooth. Pygidial axis ill-defined posteriorly, with four axial rings. Two pairs pleural furrows on pygidium. Posterior border deep, arched upwards slightly on mid-line.

Description. — Width of cranidium 2.1 to 2.3 times its length (sag.), anterior margin arcuate. Glabella gently convex (trans.), curving evenly downwards anteriorly, not overhanging anterior border. Occipital ring tapers forwards, in front of which the glabella expands in width very slightly, then tapers equally gently to a point at about its mid-length (sag.). Anterior to this it expands in width sharply to reach maximum width at rounded anterolateral corners, 0.35–0.4 width of cranidium. Anterior margin gently rounded. Median glabellar tubercle just posterior to glabellar mid-point (sag.). Axial and preglabellar furrows narrow and fairly deep. Minute anterior pits in lateral parts of preglabellar furrows. Occipital ring narrow, forwards sloping. Lateral inflated areas spindle-shaped, sloping outwards-forwards, extending anteriorly as far as anterolateral corners of glabella, maximum transverse width less than half that of posterior part of glabella. Fixed cheeks broad, sloping downwards gently adaxially, more steeply laterally. Preglabellar field fairly broad, of uniform width (sag., exsag.), continuing downward slope of anterior part of glabella, bearing pair of tubercles. Very narrow (sag.) anterior border of transverse width slightly less than that of the front of glabella. Posterior border furrow very faint or scarcely visible adaxially, deepening and widening laterally, terminating in a deep pit almost at the rounded posterolateral angle of the cranidium. Border furrow curves slightly forwards on most specimens. Posterior border narrow adaxially, widening rather abruptly at about its mid-point (trans.), and narrowing again slightly at its lateral extremity. External surface of the cranidium quite smooth. Facial sutures passing along the edge of the cranidium and outside the anterior border to meet on mid-line, slightly upwards arched anterolaterally (Pl. 32, Fig. 10). Free cheeks not known.

Pygidium three times as wide as long, axis occupying one quarter pygidial width at anterior margin. Axis tapering gently posteriorly, tip ill defined, merging with posterior border. Four axial rings of similar width (sag.). Ring furrows faint laterally. Pleural fields horizontal, edged posteriorly by narrow, convex rim (except postaxially). Two pairs of straight pleural furrows, of which the second pair slope more steeply backwards. Posterior border deep, sloping downwards at a high angle, slightly upward arched on mid-line.

Discussion. — This species differs from others of the genus (*E. meeki*, *E. raymondi*, *E. shuckerti*, see WHITTINGTON 1965) in having the lateral inflated areas weakly defined on their outer sides, and in the greater expansion of the posterior border (exsag.) laterally. It is particularly close to *E. meeki* BILLINGS, which has a very similar pygidium, and cranidium of similar proportions, with forward curving posterior border furrow. Note that one cranidium of *E. clavaria* n. sp. has the posterior border furrow laterally directed, in this respect resembling *E. raymondi* WHITTINGTON (compare Pl. 32, Fig. 11 with WHITTINGTON 1965, Pl. 15, Fig. 25). Since this specimen agrees in other diagnostic characters with other specimens of *E. clavaria* n. sp., I believe that this difference is probably due to intraspecific variation.

Small cranidia lack lateral inflated areas (Pl. 32, Figs. 6, 9) which originate abaxially and as they increase in size constrict the posterior part of the glabella. The inflated areas do not appear until the cranidia are quite large. One specimen 6 mm wide still lacks lateral lobes. The same specimen (Pl. 32, Fig. 6) shows a faint "eye ridge" passing transversely from the anterior corner of the glabella on to the fixed cheek, comparable in position with the eye ridges of the Hapalopleuridae (HARRINGTON and LEANZA 1957), and the transverse genal furrows of *Pytine* n. gen. and *Anisonotella*. Small cranidia are similar to the adult cranidia of *Pytine graia* n. gen., n. sp., in having the glabella rather evenly forward expanding, of greater convexity (trans.) than larger cranidia.

Endymionia raymondi WHITTINGTON 1965
(Pl. 32, Figs. 1–4)

1914, *Endymionia meeki* (BILLINGS) — RAYMOND, p. 526.
1925, *Endymionia meeki* (BILLINGS) — RAYMOND, p. 42–44.
1965, *Endymionia raymondi* — WHITTINGTON, p. 326, Pl. 15, Figs. 21, 22, 25.

Stratigraphic range. — Profilbekken Member, 42 m from base, with typical Whiterock assemblage.

Material. — Cranidium, PMO NF 319.

Diagnosis. — An *Endymionia* species with narrow glabella, steeply downward-sloping preglabellar field which bears terrace lines. Horizontal cranidial border narrower (trans.) than other species due to relatively adaxial course of facial sutures.

Discussion. — The single specimen from Spitsbergen occurs well above *E. clavaria*, in the Profilbekken Member. WHITTINGTON (1965, p. 326) proposed the name *E. raymondi* for some specimens from the Shumardia Limestone, Quebec, originally identified by RAYMOND (1914, p. 526) as *E. meeki* (BILLINGS 1862); WHITTINGTON demonstrated that these specimens differed in several details from the holotype of *E. meeki*. The cranidium from Spitsbergen agrees exactly with that from the Shumardia Limestone. The glabella is less forward-expanded than that of *E. schucherti* RAYMOND and *E. meeki* (BILLINGS) (see WHITTINGTON 1965, Pl. 15, Figs. 1–20, 23, 24) and has a relatively narrower anterior border. The steeply sloping preglabellar field bears terrace lines like those on *E. raymondi*, but unlike other species of the genus. There seems no reason to doubt the specific identity of the Spitsbergen and Quebec material. Paired tubercles (Pl. 32, Fig. 4) are present on the preglabellar field of *E. raymondi*, as on other *Endymionia* species, and the glabellar tubercle seems to be larger and more diffuse than that of *E. schucherti* and *E. meeki*.

Genus *Pytine* n. gen.

Type species. — *Pytine graia* n. sp.

Diagnosis. — Endymioniinid trilobites with broad cephalon and short, wide pygidium. Glabella expanding forwards, rounded anteriorly, with prominent median tubercle. Axial furrows very wide posteriorly, opposite glabellar tubercle having short, transversely directed branch, anterior to which the axial furrows are narrower. Three pairs of muscle impressions of which 1P is the deepest, pit-like. Prominent bacculae within the axial furrows. Surface sculpture of strong anastomosing raised ridges. Thorax of 7 segments, greatest width at second or third segment. Pleural furrows broad, straight. Pygidium with axis extending to edge of posterior border, having at least 5 axial rings. Pleural fields wide (trans.) and short (exsag.) with two pleural ridges. Posterior border very deep.

Pytine graia n. sp.
(Pl. 23, Fig. 7; Pl. 31, Figs. 1–11; Fig. 10)

Stratigraphic range. — Olenidsletta Member, 75 m to 103 m from base.

Material. — Holotype, well preserved dorsal exoskeleton, PMO NF 40. Other material includes three almost complete, but poorly preserved specimens: PMO NF 1936 (2 specimens) SMA 84170; exoskeletons lacking free cheeks: PMO NF 2638, 1876, SMA 84171, 84172; cranidia: PMO NF 2639, 2153, 1863, 2135, SMA 84167–9.

Diagnosis. — As for genus.

Description. — Exoskeleton elliptical, cephalon occupying 0.4 sagittal length, pygidium about 0.2 sagittal length. Cephalon about 2.7 times as wide as long (sag.), anterior margin arcuate. Glabella highly convex (trans.) increasing gradually in width and convexity forwards (θ 20 degrees), sloping steeply downwards anteriorly and not overhanging anterior border, front margin rounded. Prominent glabellar tubercle just in front of transverse mid-line of glabella. Three pairs of muscle impressions, of which 2P and 3P are faint, 1P prominent, developed as a deep subcircular pit a short distance in front of the occipital ring. 2P and 3P are faint depressions in the sides of the glabella, 3P just anterior to the glabellar tubercle. Axial furrow deep and wide posteriorly, and widening backwards, with a short transverse furrow running into the fixed cheek at right angles to the sagittal line, branching from the axial furrow at a point opposite the glabellar tubercle. Anterior to this furrow the axial furrows and preglabellar furrows are narrower and not so deep, except immediately in front of anterolateral corners of the glabella where there is a deep fossula. Within the posterior part of the axial furrows and immediately in front of the posterior border furrows there is a pair of prominent oval bacculae. Fixed cheeks gently convex adjacent to the axial furrows, laterally and anterolaterally steeply downsloping. Posterior border furrow fairly broad and deep adaxially, widening, shallowing and curving forwards for its lateral one-third, and terminating in a pit. Posterior border narrow immediately in front of the thorax, expanding considerably and inclined forward laterally. Preglabellar field gently convex, sloping downwards steeply. Very narrow horizontal anterior border, of transverse width about equal to that of glabella.

Facial sutures run along lateral and anterolateral margins of cranidium to anterior border, meeting in front of the anterior border on the mid-line. Free cheeks long and narrow (exsag.) bearing long, slender genal spines which curve backwards at least as far as the front margin of the pygidium. Surface sculpture

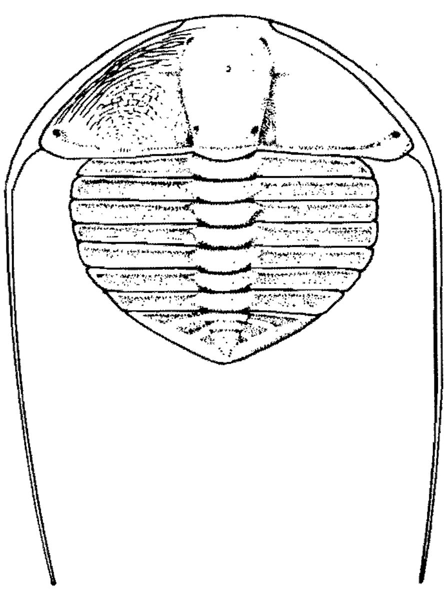

Fig. 10. Reconstruction of *Pytine graia* n. gen., n. sp. × 6. Surface sculpture indicated on left hand side.

on cephalon is distinctive, consisting of concentric fine ridges on the glabella centred about glabellar tubercle, on the anterior part of the cheeks coarse anastomosing ridges, and posterior to a line connecting the short transverse furrow with the posterolateral corner of the cranidium, a finer, somewhat reticulate pattern of ridges. Fine granules in axial and posterior border furrows.

Thorax of seven segments, width at anterior margin about 0.7 that of cephalon, with maximum width at second or third segment, tapering posteriorly. Convex axis of width (trans.) about 0.6 that of pleurae, hardly tapering posteriorly. Inter-ring furrows deep and straight. Pleurae in contact along their whole length, blunt tipped, with deep, broad (exsag.), straight pleural furrows which reach very nearly to the tip of each pleura. Posterior margin of each pleura is a narrow (exsag.) transverse ridge, anterior margin with a similar transverse ridge, immediately in front of which there is a narrow depressed area abutting the posterior ridge of the preceeding segment (Pl. 31, Figs. 1, 4).

Pygidium about four times as wide as long, axis narrow, occupying 0.2 pygidial width at anterior margin, tapering gently posteriorly (angle enclosed by axial furrows about 25 degrees) and extending on to the posterior border. Axial rings number five, before reaching posterior border, of which the first three are more distinct. The first two ring furrows reach the axial furrows, posteriorly they are represented by transverse pits. Pleural fields narrow (exsag.), with two pairs of slightly backward-sloping interpleural ridges, of which the anterior pair is much longer and more prominent. Deep, pleural furrows between the anterior ridge and the front of the pygidium, and between the two ridges, which become slightly broader laterally. Posterior border very broad (exsag.). Posterior margin not arched up on mid-line, with surface sculpture of closely spaced parallel terrace lines.

Discussion. — This remarkable trilobite resembles no other raphiophorid closely. It is most similar to *Anisonotella* (see WHITTINGTON 1965, Pl. 14, Figs. 1–6, 8) which has a glabella of similar shape and possesses similar transversely directed furrows partly incised into the fixed cheeks from the axial furrows. Position of the glabellar tubercle and glabellar furrows 1P are also comparable on *Pytine* n. gen. and *Anisonotella.* However, the muscle impressions on *Anisonotella* are much deeper and isolated within the glabella and pygidia of the two genera are completely different, that of *Pytine* n. gen. being more like that of *Endymionia.* Small cranidia of *Endymionia* (Pl. 32, Fig. 9) are quite similar to those of *Pytine* n. gen. and it is possible that the two genera may be more closely related than comparisons of adult individuals might suggest.

Endymioniinid gen. and sp. indet.
(Pl. 33, Figs. 4–7)

Stratigraphic range. — Melt stream B on Olenidsletta, exact horizon not known, but between 80–100 m from base of Olenidsletta Member.

Material. — Two cranidia, PMO NF 1880, 2121.

Discussion. — Although known from only two examples this species shows a number of interesting features which deserve some discussion. In its general outline, form of the posterior border furrow and anterior border, the cranidium most resembles that of *Endymionia clavaria* of the raphiophorids described here, although the glabella lacks the lateral lobes characteristic of that genus. An indistinct, subcircular pair of 1P glabellar furrows are present. However, as discussed above, the lateral lobes of *E. clavaria* are a late feature of the ontogeny, and it seems possible that this species represents an earlier stage in the morphological history of the genus. It is interesting to note in this connection that the cranidium under discussion occurs in that part of the Olenidsletta Member underlying the first appearance of *E. clavaria*. Like that of *Endymionia* the glabella of this species is of low convexity, with a frontal lobe that slopes down uniformly into the preglabellar field, and with the anterior fossulae in the preglabellar furrow.

There is a superficial resemblance also to the cranidium of *Hapalopleura longicornis* HARRINGTON and LEANZA 1957 notably in the shape of the glabella and border furrow, although our cranidium lacks eye ridges and palpebral lobes, and the sutures are marginal. Eye ridges are, however, present on immature cranidia of *Endymionia clavaria* (see Pl. 32, Fig. 6). The similarities suggest that future discoveries may indicate that there is a closer relationship between the hapalopleurids and endymioniinids than is at present recognised.

The combination of cranidial features of this species are sufficiently different from that of any other raphiophorid to necessitate its description under "open" nomenclature. But I do not feel that the material at present known is sufficient to form the basis of a new genus.

Subfamily UNCERTAIN

Remarks. — Although *Seleneceme* and *Falanaspis* have been included in a separate family Alsataspidiae in the *Treatise* (WHITTINGTON in MOORE 1959, p. 0428), it is doubtful whether enough is known of their relationships to justify such a separation from either the raphiophorids or hapalopleurids. Several authors (HARRINGTON and LEANZA 1957, p. 207, WHITTARD 1959, p. 118) have noted the resemblance of *Seleneceme* to hapalopleurids (particularly *Hapalopleura longicornis* HARRINGTON and LEANZA 1957), while the marginal facial sutures and lack of eyes seem to place the genus closer to the Raphiophoridae, especially the subfamily Endymioniinae. Examination of casts of the types of *Hapalopleura longicornis* lacking free cheeks (HARRINGTON and LEANZA 1957, Figs. 112, la, b) has shown that there is no sign of the anterior spine on such specimens, which is evidently present on entire exoskeletons: it is tempting to conclude that the anterior spine originates from the cephalic doublure as on *Seleneceme* and *Falanaspis*.

A species of *Falanaspis* occurs in the Spitsbergen Ordovician; it is provisionally placed in Raphiophoridae *incertae sedis*.

Genus *Falanaspis* TJERNVIK 1956

Type species. — *Falanaspis aliena* TJERNVIK 1956.

Discussion. — I am doubtful whether *Falanaspis* is truly distinct from *Seleneceme* (type species, *S. propinqua* CLARK 1924). WHITTARD (1958, p. 117) has stated that the median frontal spine of *S. acuticaudata* (HICKS) arises from the anterior cephalic doublure, rather than from the front of the cranidium (WHITTINGTON in MOORE 1959, p. 0428), a condition similar to that pertaining in *Falanaspis aliena* (TJERNVIK 1956, Pl. 11, Fig. 21). It is probable also that the diagnostic "median furrow" bisecting the frontal lobe of the glabella in *Seleneceme* is a feature due to flattening — material of *Seleneceme* species tends to be indifferently preserved in a crushed condition in graptolitic shales. An irregular crack rather than a true furrow is indicated by CLARK (1924, Pl. 9, Fig. 10) for the type species, TURNER (1940, p. 516) states that on *S. bakeri* (TURNER) the glabella is "somewhat crushed, divided into two lateral lobes, which may be quite accidental", Kindle's (1942) illustration of *S. evansi* (KINDLE) clearly shows that the furrow is neither straight nor median, while no such furrow is present at all on *S. acuticaudata* (HICKS) (WHITTARD 1958, Pl. 16, Fig. 4). I retain *Falanaspis* here pending a full description of the type species of *Seleneceme.*

KINDLE (1942, p. 33) and WHITTARD (1958, p. 118) note the association of *Seleneceme* with graptolitic deposits. Described species of *Falanaspis* and *Seleneceme* occur in the Arenig/Llanvirn of Bathyurid, Asaphid and Selenopeltis provinces; their distribution is therefore nearly cosmopolitan. In Spitsbergen *Falanaspis* is associated with the olenid community (and with graptolites) which, as has been noted elsewhere (FORTEY 1975, p. 349), might be predicted to include more widespread genera. It is noteworthy that *Seleneceme* is characterised by a multiplication of thoracic segments compared with other raphiophorid — like trilobites, a condition that may be associated with life in deep water, deoxygenated conditions of the olenid environment (cf. FORTEY and OWENS 1975, p. 237).

Falanaspis extensa n. sp.
(Pl. 33, Figs. 1–3)

Stratigraphic range. — Olenidsletta Member, 60 m to 110 m from base, occurring with abundant olenid trilobites.

Material. — Holotype, incomplete cranidium, PMO NF 2255 (counterpart PMO NF 2260); one other cranidium PMO NF 850.

Diagnosis. — A *Falanaspis* species with wide (trans.) fixed cheeks, preglabellar field steeply downward-sloping to horizontal anterior border. Posterior border furrow present laterally, effaced near glabella.

Description. — This species is known from only two cranidia, of which one is not well preserved, but clearly represents a new species distinct enough to justify its formal recognition here. Cranidia are almost three times as wide as long, convex. The glabella has an almost perfectly circular outline, is low and flat, scarcely elevated above the fixed cheeks; on the poorly preserved specimen the glabella can scarcely be discerned. Glabellar furrows are not visible on available material, but there is an obscure median tubercle towards the front of the glabella. Minute apodemal pits are present in the preglabellar furrow. Preglabellar field continues the downward slope of the front of the glabella, of width (sag.) about one-sixth length of glabella. Flat, narrow (sag., exsag.) anterior border of transverse width slightly less than that of glabella. Posterior border furrow only defined near lateral edge of cranidium, obsolete adaxially; posterior border so defined flat, or slightly forward-inclined.

Discussion. — This species differs from the type species *F. aliena* (TJERNVIK 1956, p. 273, Pl. 11, Figs. 20, 21) in having much wider fixed cheeks, shorter (sag.) preglabellar field, in possessing a distinct anterior border, and in having the posterior border furrow obsolete adaxially.

Family TELEPHINIDAE MAREK 1952

Carrickiinae, DEAN 1971b, p. 48.

Diagnosis. — Pelagic trilobites with greatly developed eyes, occupying the major part of the free cheeks. Glabella very convex, smooth, or with two to four pairs of muscle impressions, of which 1P may be deepened at its inner end (in some species of *Telephina*) to form a furrow subparallel to sagittal line. Occipital furrow deep, defining wide (sag.) occipital ring. Fixed cheeks with broad (trans.) palpebral lobes, occupying the major part of the cranidial length. Anterior border arched, with circular cross section, or modified as a pair of spine-like projections. Free cheeks with prominent borders, laterally or posterolaterally bearing long tubular or blade-like genal spines. Thorax (where known) of 9 or 10 segments, axis extremely convex, pleurae short. Pygidium convex, with prominent axis having 2–4 axial rings; terminal piece may bear a long spine. Doublure narrow.

Included genera: *Oopsites* n. gen., *Carolinites* KOBAYASHI 1940, *Goniophrys* ROSS 1951, *Telephina* (*Telephina*) MAREK 1952, *Carrickia* TRIPP 1965, *Telephina* (*Telephops*) NIKOLAISEN 1963.

Discussion. — This family has hitherto included only the genus *Telephina* MAREK 1952 (WHITTINGTON in MOORE 1959, p. 0–297), but discovery of early relatives of this genus, included herein in *Oopsites* n. gen., demonstrates the close relationship between *Telephina* and certain genera included in the *Treatise* in the Komaspididae. Such a relationship has already been suggested by NIKOLAISEN (1963). It is proposed here to extend the Telephinidae to include the genera *Goniophrys* Ross 1951, *Carolinites* KOBAYASHI 1940, and *Carrickia* TRIPP 1965. The evolutionary relationship of these genera to the Cambrian komaspidids has yet to be clarified, and since the Cambrian genera differ from the telephinids (as here understood) consistently in, for example, the possession of transverse glabellar furrows, they are considered to represent a separate family. The genus *Benthamaspis* POULSEN 1946, formerly included in the Komaspididae (HENNINGSMOEN in MOORE 1959), is here exluded from the Telephinidae, as it lacks both the well-defined occipital ring and broad (trans.) palpebral rims typical of the family. Is is probably most closely related to a group of Upper Canadian trilobites including *Strigigenalis* WHITTINGTON and Ross 1953, "*Platycolpus*" sp. Ross 1951, and "new genus aff. *Strigigenalis*" BERRY 1960 (Pl. 1, Figs. 1, 3).

Oopsites n. gen. is apparently confined to the early Ordovician, and is the morphological and stratigraphic intermediate between *Goniophrys prima* Ross 1951 and early species of *Telephina*. The glabella of *Oopsites* and *Goniophrys* are very similar, and both possess a rather wide, arched anterior border; the pygidium of *Oopsites gladiator* n. sp. with its convex axis with two axial rings and broad (trans.) pleural field is similar to that of *Goniophrys prima* Ross. The long palpebral rims of *Goniophrys* bend inward posteriorly, and it was probably the exaggeration of this inward bend that produced the characteristic form of the telephinid fixed cheek. In *Oopsites* n. gen. the posterior border is still relatively wide (trans.), especially on smaller cranidia (see Pl. 33, Figs. 14, 18), which, except for the telephinid-like palpebral lobe, are remarkably *Goniophrys*-like. In *Telephina* itself the posterior border becomes very narrow (trans.), in some species reduced to a spine (*T. americana* (BILLINGS), see WHITTINGTON 1965, Pl. 37, Fig. 18). Corresponding with this change the lateral ends of the arched anterior border migrate adaxially, becoming very close together, and modified in many species to form a pair of tubular spines. These changes allow for a greater extension anteriorly and posteriorly of the visual surface of the eye, changes no doubt connected with a better adaptation to the pelagic mode of life. It should be emphasised that the transition between *Oopsites* and *Telephina* is gradational. One transitional species is *T. bicuspis* HADDING (material of which I have been able to examine) in which the anterior border is of *Oopsites* type, but with the lateral tips steep and rather close to the sagittal line.

The probable derivation of *Carolinites* from *Goniophrys prima* through *Carolinites* sp.A HINTZE 1953 has been discussed by HINTZE (1953, p. 147, 156) and CHUGAEVA (in CHUGAEVA, ROZMAN and IVANOVA 1964). The close similarity of *Goniophrys* to *Carrickia* TRIPP 1965 has been emphasised by Ross and INGHAM (1970, p. 396), who regarded the latter genus as a junior synonym of *Goniophrys*. Cranidia of species attributed to *Carrickia* (TRIPP 1965, SHAW 1968, DEAN 1971b) differ from *Goniophrys prima* in having wider fixed cheeks with less curved palpebral lobes and I follow DEAN (1971b, p. 60) in accepting *Carrickia* as a valid genus.

All genera of the Telephinidae (as here defined) can therefore be reasonably derived from a species close to *Goniophrys prima* Ross 1951. Within such a natural group the separation of *Telephina* in a family of its own seems to intro-

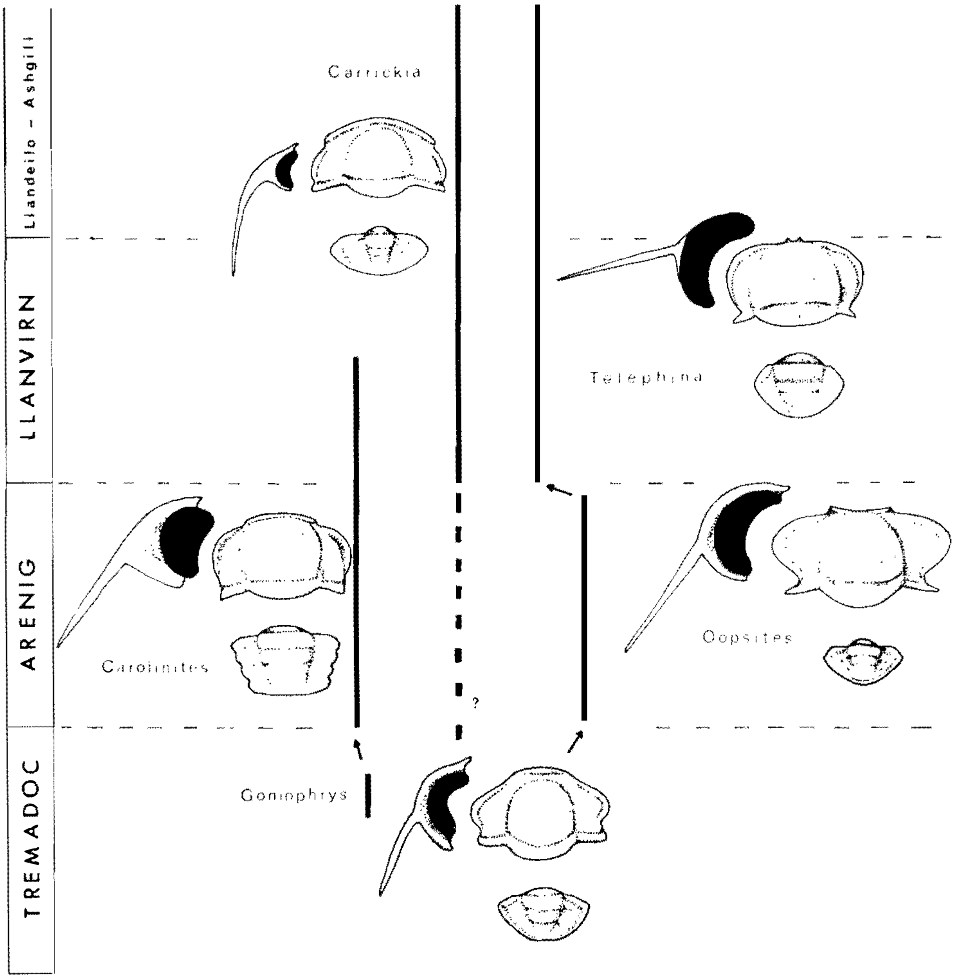

Fig. 11. Phylogeny of the Telephinidae as redefined in the present work. The possible continuation of the record of *Carrickia* into the Tremadoc is based upon DEAN's (1971b, p. 50) assignment of "Undetermined genus and species A" of ROSS (1951, Pl. 18, Figs. 21, 23, 24) to this genus.

duce excessive splitting. The evolutionary relationships are shown diagrammatically in Fig. 11.

DEAN (1971b, p. 48) has introduced a subfamily Carrickiinae of the Komaspididae to include *Carrickia* and *Goniophrys*. If the view of the relationships of the genera included here in the Telephinidae is correct (Fig. 11), including separation from the Cambrian komaspidids, then the concept of the Carrickiinae seems to be included within the Telephinidae in the present revision.

Genus *Oopsites* n. gen.

Type species. — *Oopsites hibernicus* (REED 1909).

Diagnosis. — Telephinid trilobites having convex glabella tapering forward and rounded in front. Fixed cheeks of similar form to *Telephina*, but wider (trans.) and with broad palpebral rims. Anterior border convex, arched, of width (trans.) about two-thirds that of occipital ring. Postocular fixed cheeks narrow (exsag.), with a relatively wide (trans.) convex posterior border. Free cheeks with large crescentic eyes, borders fairly wide, with long, downwardly directed, backward pointing genal spines. Thorax of more than 8 segments, pleurae as wide (trans.) as axis. Pygidium wider than long, with convex, gently tapering and posteriorly rounded axis with two axial rings and terminal piece. Pleural fields downsloping, with narrow, slightly concave posterior border. Dorsal surface tuberculate.

Oopsites hibernicus (REED 1909)
(Pl. 33, Figs. 8–19; Pl. 34, Figs. 1–7; Figs. 12A, B)

1909 *Telephus hibernicus* sp. nov.; REED, p. 149, Pl. VI, Figs. 10, 11.
1968 *Telephina hibernica* (REED 1909); WHITTINGTON, p. 56.

Stratigraphic range. — Olenidsletta Member; 30 m — 75 m ?80 m from base (approximately *protobifidus* zone).

Material. — Includes cranidia: PMO NF 580, 587, 588a, 629, 635, 747, 749; SMA 84179, 84182, 84185–8; incomplete dorsal exoskeleton SMA 84180; free cheek: SMA 84181; pygidia: PMO NF 917, SMA 84183–4.

Diagnosis. — An *Oopsites* species with surface sculpture on cranidium of very low, scattered tubercles. Anterior border broadly arched, transverse width about two-thirds that of occipital ring. One pair of shallow elliptical muscle impressions visible on internal moulds. Free cheeks with broad border, and long, gently tapering genal spine. Pygidium with convex axis with two axial rings, pleural fields with narrow, horizontal adaxial region, sloping down laterally to narrow rim; one pair pleural furrows.

Description. — Cranidium with maximum width between palpebral lobes, this being about 1.8 times the sagittal length. Glabella highly convex, maximum width at occipital ring equal to sagittal length, tapering very gently forwards and broadly rounded anteriorly. Maximum convexity on mid-line, sloping gently downwards anteriorly. One pair of muscle impressions, visible on internal moulds as shallow elliptical furrows, sloping backwards at about 20 degrees to sagittal line, not reaching axial furrows, inner ends at about mid-length of glabella. Occipital furrow deep across middle of glabella and laterally, exsagittally shallower and wider at sites of occipital muscle impressions. Occipital ring broad (sag.), about one quarter glabellar length, its mid two-thirds widest and of uniform width (sag., exsag.), laterally narrowing slightly. Axial and preglabellar furrows continuous, deep, and rather narrow, shallowest adjacent to occipital ring. Maximum transverse width of fixed cheeks adjacent to forward part of glabella. Fixed cheeks wide (trans.), triangular, sloping gently downwards anteriorly. Palpebral rims broad, outlined by deep furrows and narrowing posteriorly. Postocular cheeks narrow (exsag.), triangular, steeply downsloping, posterior border furrow deep, straight, outlining highly convex posterior border. The adaxial part of the fixed cheek opposite and in front of the anterolateral part of the occipital ring is elevated into a semi-circular facet sloping steeply down into the axial furrows, representing a large muscle attachment area. Preglabellar field absent on mid-line, laterally a slightly inflated subtriangular area. Anterior border broadly arched, cross section circular, transverse width about two-thirds that of occipital ring. Facial suture running inwards at a high angle from posterior border, curving sharply abaxially at posterior limit of palpebral lobe to run outwards at about 30 degrees to sagittal line, then curving evenly adaxially around lateral extremity of palpebral lobe to run almost transversely along its anterior margin. Anterior branch curves downwards to cut the anterior border at an acute angle.

Free cheeks fairly broad, outline approximately semicircular. Eye extremely large, crescentic, transverse outline strongly curved, with rather large, hexagonal lenses arranged in vertical files of about 20 lenses with a total of about 45 such rows. Lateral and posterior borders with circular cross section. Lateral border curves rather evenly backwards, posterior border much shorter, running slightly forwards to obtuse genal angle. Border furrows very deep except at genal angle where they shallow abruptly. Genal spine sloping backwards and downwards, extremely long, cross section elliptical proximally, circular distally. When the cheek is reconstructed attached to the cranidium in life position it slopes downwards quite steeply, projecting below the level of the thorax and pygidium.

Thorax of at least 8 segments, the first three expanding in width, the last five tapering, pleurae of transverse width about equal to that of axis. Axis convex, gently tapering. Axial rings of uniform width (sag., exsag.) with prominent articulating half rings at least half the width of the axial rings. Axial furrows deep. Pleurae of first three segments pointed, those of last four segments blunt tipped. Pleural furrows of anterior segments oblique, those of posterior segments running transversely along middle of pleurae.

Pygidium triangular, very convex, over twice as wide as long. Axis extremely convex anteriorly, decreasingly so posteriorly, tapering very gently, tip not well defined and bluntly rounded. Two axial rings, the anterior one slightly wider (sag.), of uniform width. Ring furrows deeper laterally. Terminal piece sub-semicircular, sloping down to posterior border, bearing a pair of slightly elevated nodes separated by a shallow, depressed groove on mid-line. Axial furrows deep anteriorly, shallowing considerably posterior to the second axial ring. Pleural fields with narrow (trans.) horizontal area adaxially, steeply downsloping laterally. One pair of fairly shallow, transverse or slightly backwards-sloping pleural furrows, which almost reach posterior margin. Posterior to the pleural furrows the edge of the horizontal adaxial part of the pleural field is marked by two tubercles, the posterior of which is very close to the axis.

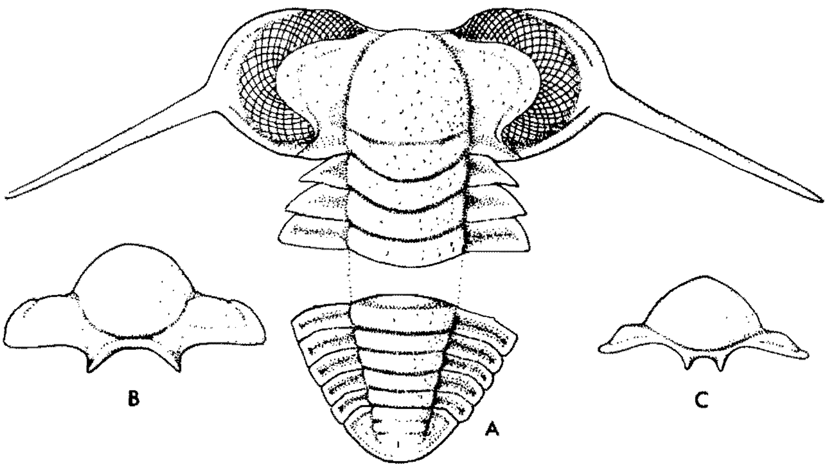

Fig. 12. A. Reconstruction of *Oopsites hibernicus* (REED) in dorsal view, × 6. B. Cranidium, anterior view, × 6. C. Anterior view of the cranidium of the type species of *Telephina*, *T. fracta* (BARRANDE), based on casts of the type material, to show diagnostic difference in the anterior border from that of *Oopsites*.

Posterior border narrow, slightly concave, edged by very narrow, slightly convex rim, more distinct posteriorly.

Surface sculpture consisting of depressed tubercles on fixed cheeks and palpebral rims, and on the occipital ring, but very sparse or absent on the preoccipital part of the glabella of larger cranidia. A similar sculpture is developed on the anterior axial rings. Other parts of the exoskeleton, including the pygidium, appear to be smooth. Tubercles are more prominent on smaller cranidia, rather widely spaced.

Small cranidia (sag. length 3 mm or less) differ from larger cranidia in being generally shorter and wider with broader (trans.) fixed cheeks, which posteriorly do not curve so far adaxially, not closely approaching the glabella at their posterior limits. The glabella tapers more noticeably forwards. Posterior border wide, approaching width of glabella.

Discussion. — REED's original description of *O. hibernicus* (REED 1909, p. 149, Pl. VI, Figs. 10, 11) from the Tourmakeady Limestone, Western Ireland, is not sufficiently clear to evaluate the relationships of the Spitsbergen material. The best-preserved, least distorted cranidium from REED's original collection is here refigured (Pl. 33, Fig. 8), and selected as lectotype (SMA 10398). The similarity of the Tourmakeady cranidia and those of comparable size from the Olenidsletta Member is remarkable. The wide fixed cheeks, broadly arched anterior border and relatively long (trans.) postocular fixed cheeks, features characteristic of *Oopsites* n. gen., are similarly developed on the Irish material. The 1P furrows are visible on the holotype as faint depressions, but as on the Spitsbergen material their development is variable. Perhaps most strikingly the scattered tubercular sculpture is of identical density on the Tourmakeady and Olenidsletta Member material, much sparser than on comparably-sized cranidia of *O. squamosus*. In short there seems no reason to give a separate specific name to the Spitsbergen *Oopsites*. I have recently found a pygidium and free cheek for the Tourmakeady species which further support this conclusion. The identity is of interest because the equivalence in age of the Tourmakeady and the mid-part of the Olenidsletta Member is supported also by the occurrence there of *Opipeuter inconnivus* (FORTEY 1974a) and a *Niobe* extremely close to *N. occulta* n. sp. (p. 31).

Oopsites squamosus n. sp.
(Pl. 35, Figs. 1–11)

Stratigraphic range. — Olenidsletta Member, beds above *O. hibernicus*, typically 80–100 m from base; probably *bifidus* (*sensu* BERRY 1960) zone.

Material. — Holotype cranidium, PMO NF 1579, other material includes cranidia: PMO NF 1286, 2647, 2635, SMA 84189; free cheeks: PMO NF 102, SMA 84192; pygidium: PMO NF 1579.

Diagnosis. — An *Oopsites* species with surface sculpture on cranidium of prominent, densely spaced tubercles interspersed with finer granules. Two pairs of smooth muscle areas on glabella, and prominent occipital impressions. Glabella tapering forwards more rapidly than that of *O. hibernicus*. Free cheeks with narrow border, rapidly tapering genal spine. Pygidium similar to that of *O. hibernicus*, but transversely narrower.

Discussion. — This species continues stratigraphically later than *O. hibernicus* which it resembles rather closely, and from which it may have been derived. It differs from the type species notably in its surface sculpture, relatively broader based, more rapidly tapering glabella, and narrower border on the free cheek. Pygidia of the two species are closely similar, but that of *O. squamosus* is of a length (sag.) approaching maximum transverse width. Muscle impressions are particularly well shown as smooth areas on the sides of the glabella, 1P in a similar position to that of *O. hibernicus*, and in addition a subcircular, smaller impression 2P, far forward on glabella. The occipital muscle impression is also prominent (Pl. 35, Fig. 8). The muscle impressions of *Telephina americana* (BILLINGS) (WHITTINGTON 1965, Pl. 37, Fig. 18) include a prominent smooth area on the glabella immediately in *front* of the pit in the occipital ring. I believe that this impression is homologous to that on the occipital ring of *Oopsites squamosus* and *O. hibernicus* and that the *Oopsites-Telephina* transition was accompanied by its anterior migration. Note also that on *T. americana* the posterior impression on the fixed cheek adjacent to the axial furrow is broader and longer, not developed as a distinct facet as in *Oopsites* n. gen.

Genus *Carolinites* KOBAYASHI 1940

Type species. — *Carolinites bulbosus* KOBAYASHI 1940.

Discussion. — This genus includes the following species: *C. minor* (SUN 1931), *C. bulbosus* KOBAYASHI 1940, *C. killaryensis* (STUBBLEFIELD 1950), *C. genacinaca*

Ross 1951 (and subsp. *nevadensis* Hintze 1953), C. sp.A (Hintze 1953), *C. macrophthalmus* Harrington and Leanza 1957, *C. popovkiensis* Balashova 1961, *C. sibiricus* Chugaeva 1964 (= *C. angustagena* Ross 1967 see below), *C. indentus* Ross 1967, and *C. parma* Ogienko 1972. Two new species, *C. rugosus* n. sp. and *C. ekphymosus* n. sp. are described here, while the identity of several previously described species may be questioned on the basis of abundant and well-preserved material from Spitsbergen.

Carolinites species are of very wide geographic distribution, this probably being due to a pelagic mode of life (p. 10, Fortey 1975, p. 343). They are thus of outstanding stratigraphic importance. *C. genacinaca* Ross has been recorded from Utah, Nevada, East Greenland, East Siberia, Novaya Zemlya, and Arctic Canada, and occurs also in Spitsbergen. *C. sibiricus* Chugaeva is recorded from Spitsbergen herein, occurring also in Siberia, Western Ireland (see Pl. 40, Fig. 7) and Western U.S.A. (as *C. angustagena* Ross 1967). *C. killaryensis*, from the top of the Spitsbergen section, is known also from Western Ireland and the Basin ranges, Western U.S.A. (Ross 1967, p. D.11). All these occurrences in other areas are consistent with the stratigraphic succession of species in the Valhallfonna Formation.

Growth stages described below show that the species *C. indentus* Ross 1967 represents a growth stage of a species of *Carolinites* with a "normal" anterior border. Since several species of the genus pass through an "*indentus*" stage it is not possible to be certain of the status of Ross' species at the present time. *C. sibiricus* and *C. killaryensis* are coeval in the top part of the Spitsbergen section.

The probable derivation of *Carolinites* from *Goniophrys prima* Ross 1951 by way of *Carolinites* sp.A of Hintze (1953) has already been discussed by Hintze (1953, p. 147, 156) and Chugaeva (in Chugaeva, Rozman and Ivanova 1964). As discussed above, a species close to *Goniophrys prima* is also believed to have given rise to *Oopsites* n. gen., and through species of this genus to *Telephina*. *Carolinites* is thus rather close to the telephinid trilobites, and they are included in the same family here.

Phylogeny of Carolinites species in Spitsbergen (Fig. 13).

The Valhallfonna Formation has yielded six species and subspecies of *Carolinites*, which is one of the most abundant genera throughout the sections, being present in virtually every bed examined (Fortey 1975, p. 336). The continuous stratigraphic record enables a phylogenetic model to be proposed here. Most features of the cranidium, free cheek and pygidium are involved, and the changes that occur appear to fall on a more nearly intergradational morphological series than was the case either with the Olenidae (Fortey 1974b, p. 19–21) or the Nileidae (p. 36).

The earliest species is *C. genacinaca nevadensis* Hintze 1953, occurring in the basal 3 m of the Olenidsletta Member, its range there extending upwards from the top few metres of the Kirtonryggen Formation. Diagnostic features are its very small bacculae which scarcely indent the base of the glabella, fixed cheeks of relatively narrow (trans.) width for the genus. The free cheek has a straight

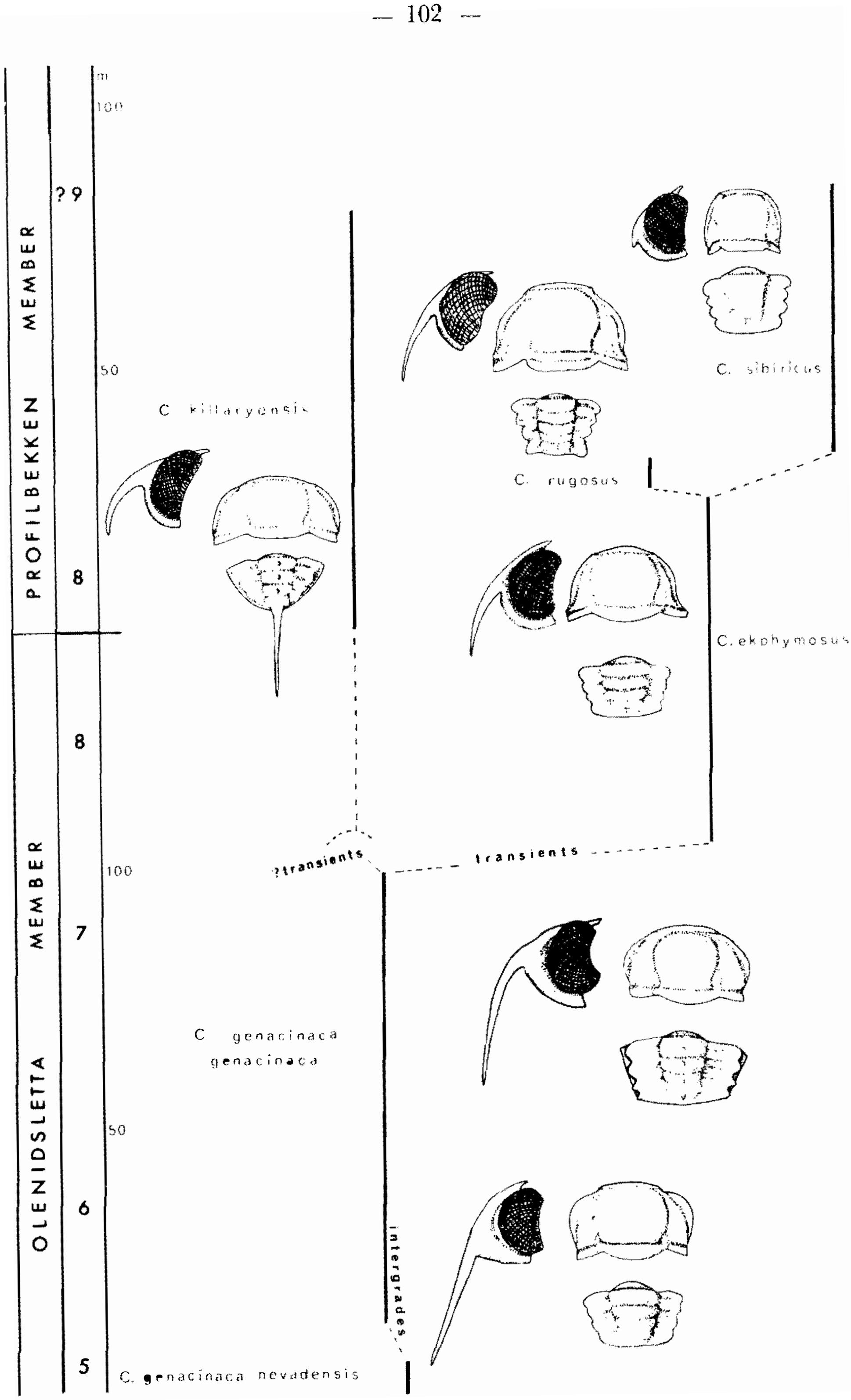

Fig. 13. Phylogeny of *Carolinites* species through the Valhallfonna Formation. Modified from FORTEY 1976, Fig. 2.

genal spine, which originates far back, and perhaps most diagnostic of all, carries a distinctive inflated band parallel to the base of the eye (Pl. 38, Fig. 10; HINTZE 1953, Pl. 20, Fig. 4). The pygidium tapers very slightly; only two axial rings are clearly defined by deep ring furrows.

The succeeding species, *C. genacinaca genacinaca* ROSS 1951, has slightly larger bacculae which indent the base of the glabella more noticeably, so that on larger cranidia the glabella expands forwards. The fixed cheeks are slightly wider (trans.), the expansion in width occurring at the posterior margin, and marked by an abaxial flexure of the intra-palpebral ridge. The genal spine on the free cheek originated further forward than on *C. genacinaca nevadensis*, and is typically curved, broadly-based, and tapering distally. The inflated band characteristic of *C. genacinaca nevadensis* is absent. The pygidium tapers posteriorly; the pygidial axis with two prominent axial rings defined by deep ring furrows, but a third, much fainter ring is also visible. The axial rings and terminal piece carry small, median tubercles. This description applies to stratigraphically late populations of *C. genacinaca genacinaca* which compare exactly with ROSS' (1951) type populations. Stratigraphically early populations (Pl. 38, Fig. 1) show features intermediate with *C. genacinaca nevadensis*: the inflated circumocular band is still present, although much reduced; the pygidium shows three axial rings like *C. genacinaca genacinaca*, but the median tubercles characteristic of that subspecies are lacking. The intergradation between the sub-species appears to be perfect; there is no evidence of a morphological jump between *nevadensis* and *genacinaca* morphology between any two successive beds. Two species are derived from *C. genacinaca genacinaca*: *C. killaryensis* (STUBBLEFIELD) and *C. ekphymosus* n. sp.

C. killaryensis further developes the tendency of *C. genacinaca genacinaca* towards wide (trans.) fixed cheeks, although the bacculae remain at about the same size. The free cheeks of the two species are similar in form, although the lenses of *C. killaryensis* are coarser, and comparable-sized eyes therefore have about half the number of lenses as *C. genacinaca genacinaca*. The pygidium retains and increases the posterior taper of *C. genacinaca genacinaca*, but the median tubercles are developed into spines, and that on the terminal piece of the pygidial axis greatly produced posteriorly. Again it is possible that there is a complete intergradation between *C. genacinaca* and *C. killaryensis*; although associated pygidia are lacking in the uppermost part of the Olenidsletta Member cranidial proportions intergrade between the two species, and the pygidial spines of early *killaryensis* are relatively delicate.

C. ekphymosus n. sp. shows the opposite morphological developments to those involved in the *genacinaca genacinaca* — *killaryensis* transition. The fixed cheeks become narrower, and the bacculae more inflated, and therefore occupy a greater proportion of the fixed cheeks; it is still possible, however, to see a small area of fixed cheek between the bacculae and the intra-palpebral ridge. Surface sculpture is granulate, with small, mound-like protruberances developed adjacent to the intra-palpebral ridges. The free cheek retains the same general form as that of *C. genacinaca genacinaca*; the pygidium is also closely similar to that of the earlier species but lacks the median tubercles characteristic of stratigraphically high *C. genacinaca genacinaca*, tapers less posteriorly, and has the three axial rings almost equally well-defined, and pleural and interpleural furrows equally distinct on the horizontal pleural fields. *C. rugosus* n. sp., which unlike the other species discussed here appears rather suddenly in the Profilbekken Member, shares almost exactly the proportions of *C. ekphymosus* but has greatly deepened dorsal furrows; in particular the occipital and axial rings are bisected transversely by furrows which do not reach the axial furrows. The pleural and interpleural furrows of the pygidium are deepened so that the segments of the pygidium closely resemble thoracic segments. The genal spine is shorter and more slender than that of *C. ekphymosus* and the lenses on the eye are larger. Surface sculpture consists of fine ridges which are present on the small, mound-like protruberances on the fixed cheeks. This affords another example of a phyletic sculptural transition from granulate to ridged sculpture which has already been noted in the transition from *Balnibarbi pulvurea* to *B. tholia* among the Olenidae (FORTEY 1974b, p. 18).

Carolinites sibiricus CHUGAEVA retains many of the characters of *C. ekphymosus*, following that species in the Profilbekken Member, but carries the tendency towards inflation of the bacculae and narrowing of the fixed cheeks to completion, so that the bacculae abut directly against the intrapalpebral ridge, and the base of the glabella may appear "waisted". The genal spine becomes reduced on large free cheeks. The pygidium is closely similar to that of *C. ekphymosus*, with four axial rings, equally well-defined by transverse ring furrows, posterior margin transversely truncate. Again the "boundary" between *C. ekphymosus* and *C. sibiricus* is difficult, if not impossible, to define, specimens 32–37 m from the base of the Profilbekken Member appearing to be transitional. *C. ekphymosus*, *C. rugosus* and *C. sibiricus* share as an apomorphic character a bisected terminal piece on the pygidial axis.

C. killaryensis and *C. sibiricus* occur together almost to the top of the fossiliferous part of the Profilbekken Member. Of species that occur outside Spitsbergen of the same age or younger than these species derivation from *C. killaryensis* is more probable than from *C. sibiricus*. The subspecies distinguished by HINTZE (1953, p. 145, Pl. 20, Figs. 10–13) as *C. killaryensis utahensis*[1] retains a similar pygidium to *C. killaryensis killaryensis*, and bacculae of similar proportions, but the fixed cheeks are relatively narrower. The unnamed tuberculate species illustrated by WHITTINGTON (1965, Pl. 39, Fig. 3, 4, 11; 7, 12, 13) and DEAN (1973b, Pl. 3, Figs. 3, 6, 7, 9, 12) all have fixed cheeks of width (trans.) comparable to, or exceeding that of *C. killaryensis killaryensis*.

Most authors have tended to emphasise the width of the fixed cheeks as an obvious character to distinguish *Carolinites* species. The preceding discussion shows that almost all exoskeletal features are involved in the species-lineages proposed here. Fig. 14 shows the relative width of the fixed cheeks of *Carolinites* species (defined on the plexus of characters used here) as related to strati-

[1] HINTZE (1953) records this subspecies from zone M (Whiterock), but YOUNG (1973, p. 98, Pl. 101, Figs. 18–20, 23, 24, 28–31) identifies the subspecies as early as zone H. But note that the free cheek illustrated by YOUNG shows the subocular ridge characteristic of *C. genacinaca nevadensis* (zone H).

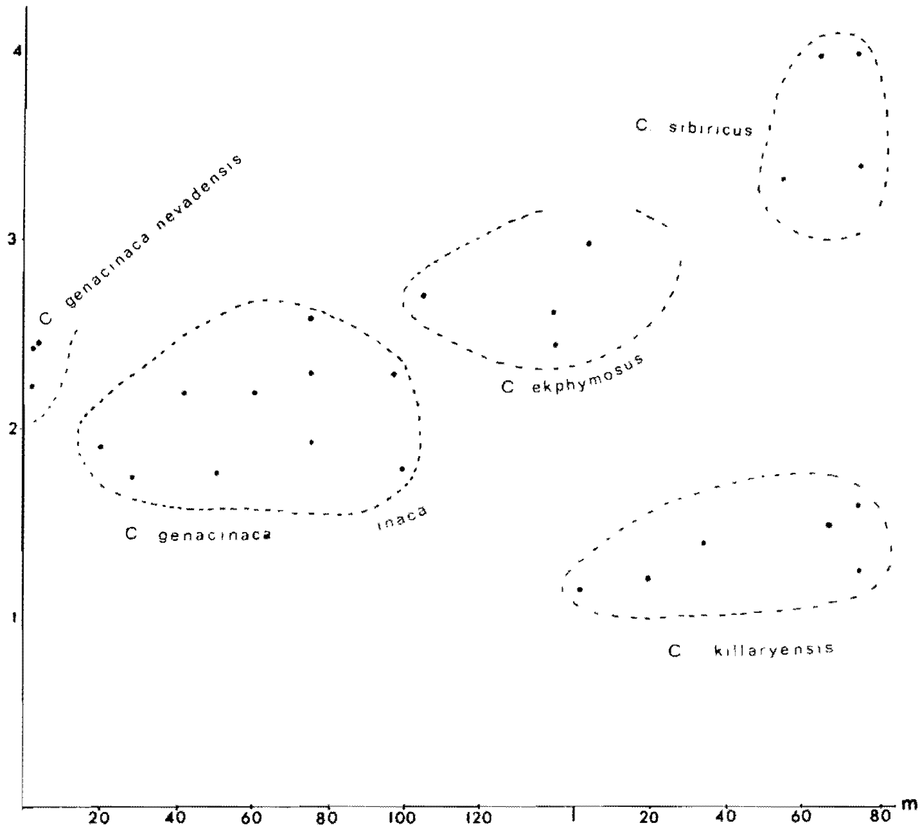

Fig. 14. Relative width of fixed cheeks of perfectly preserved *Carolinites* cranidia plotted against stratigraphic occurrence. WG — maximum transverse width of pre-occipital glabella. WC — transverse width of fixed cheek at posterior border measured from axial furrow. For the sake of clarity *C. rugosus*, with proportions similar to those of *C. ekphymosus*, has been omitted.

graphical occurrence. The intergradational nature of the changes in this dimension is apparent from the graph, but the dichotomy into the *killaryensis* line with broad fixed cheeks and the *ekphymosus-sibiricus* line with narrow fixed cheeks is obvious. The front margin of the glabella of *Carolinites* species often shows a median depression; this feature is highly variable and is considered of dubious value as a specific character.

Carolinites rugosus n. sp.
(Pl. 34, Figs. 8–10; Pl. 36, Figs. 1–19)

Stratigraphic range. — Profilbekken Member 30–36 m from base.

Material. — Holotype, cranidium, SMA 84195. Other material includes thorax and free cheeks: PMO NF 1374, cranidia: SMA 84197, 84202–5, PMO NF 1190, many specimens on blocks PMO NF 1192, 1200; pygidia: SMA 84198, 84200, 84208, PMO NF 1189, 1184; free cheeks: SMA 84196, 84206, PMO NF 1209.

Diagnosis. — A *Carolinites* species with narrow fixed cheeks and large bacculae. Prominent median transverse furrows on occipital ring, axis of thoracic segments, and axial rings of pygidium. Pygidium with four axial rings, interpleural and pleural furrows deep. External surface covered with a sculpture of fine to coarse anastomosing ridges, especially prominent on fixed cheeks and posterior part of the pygidium.

Description. — Cranidium convex, trapezoidal in outline, widest at posterior border, maximum length (sag.) almost two thirds maximum width. Glabella highly convex (sag., trans.), sloping steeply downwards anteriorly, almost as broad as long. It occupies over half cranidial width at occipital ring, and is narrowest in front of the occipital ring adjacent to the bacculae, in front of which it expands rapidly to its maximum width. Anteriorly it tapers gently to broadly rounded anterolateral corners. The front margin is straight. Occipital furrow deep and straight, narrowing medially. Occipital ring slightly below the level of the glabella in lateral view, widest on mid-line, with a prominent median (trans.) furrow which just fails to reach the axial furrows. Axial furrows shallow except adjacent to the bacculae, where they curve up the sides of the glabella.

Surface sculpture on the glabella consisting of fine raised ridges running for the most part parallel to the axial furrows, but crossing transversely over the mid-line, where they break up into minute granules. Adjacent to the areas of muscle attachment the ridges "open out" into a fine network. These muscle impressions are defined by conspicuous smooth and sunken patches on the cuticle and are in places deepened sufficiently to form shallow furrows. Their shapes are quite irregular, but they fall into four main areas (Pl. 34, Figs. 8, 10): — 1P is a transverse linear depression commencing near, but not touching, the axial furrow, and running up the side of the glabella to about one-quarter its width. Near its inner end it is deepened to form a short, shallow furrow. The second area 2P is the largest and most complex, developed on that part of the glabella opposite the bacculae. The anterior part is a highly irregular oval (long axis trans.) approximately parallel with 1P, and like that area almost, but not quite, reaching the axial furrow. The part of 2P nearest the axial furrow, and subparallel to it, is deepened, so that a short furrow is produced parallel to the edge of the glabella. The inner end of the smooth area 2P is continued backwards as a narrow, shallow, vermiform impression which is expanded into a disc-shape posteriorly. Around this disc shape there is a circlet of peculiar small pits (Pl. 34, Fig. 10). 3P is ovate, long axis parallel to the anterior oval part of 2P, although extending a lesser distance across the glabella, and like 2P almost reaching the axial furrow and very slightly deepened at its outer end. 4P is a circular depression at the anterolateral corner of the glabella, and further away from the axial furrow than either 3P or 2P. The outer end of the furrow running transversely across the middle of the occipital ring is also widened as a depressed smooth area (Pl. 34, Fig. 10) and it is considered that this represents another muscle area. These impressions are apparently constantly developed on all specimens preserving the exoskeleton.

Similar impressions can be made out, though less clearly, on *C. ekphymosus*. The anterior sloping part of the frontal lobe of the glabella has a median smooth line (Pl. 34, Fig. 8) which continues in line with the mid-line sculptural deflexion described above: the former is analogous to the median indentation of the front of the glabella of *C. sibiricus* (p. 111), while the latter occupies the same position as the median internal groove (ridge on internal mould) seen in some specimens of *C. ekphymosus* (Pl. 39, Fig. 4), that is they are the external, surface expressions of an internal structure.

The narrow fixed cheeks are widest at the posterior margin, posteriorly sloping downwards and outwards, anteriorly downwards and forwards. Bacculae large, occupying the bulk of the width of the fixed cheek. The inner edge of the palpebral furrow is bounded by a prominent ridge (referred to hereafter as the intra-palpebral ridge), which anteriorly is almost adjacent to the glabella, posteriorly running outwards at about 30 degrees to the sagittal line before swinging outwards sharply near the posterior border to run out almost to the posterolateral corner of the cranidium. The palpebral rim follows the line of this ridge, running the whole length of the cranidium. It is of rather uniform width except at its extremities, and is on a level slightly below that of the palpebral ridge, from which it is separated by a broad and shallow palpebral furrow. Posterior border furrow deep and narrow behind bacculae, slightly broader laterally, at distal extremity separated from the palpebral lobe only by the intra-palpebral ridge described above. Posterior border narrow and low near axial furrow, curving downwards, broadening and flattening abaxially, laterally developing a shallow, oblique median furrow. Preglabellar field developed as narrow triangular areas in front of the rounded, anterolateral corners of the glabella, absent anterior to mid-part of glabella. Arched anterior border is expanded distinctly (sag.) on mid-line, with surface sculpture of parallel raised lines. Sculpture on fixed cheeks complex, consisting of coarse ridges and mounds each of which is covered with fine raised ridges similar to those on the glabella. The abaxial sides of the bacculae are covered by irregular raised ridges, while the intra-palpebral ridges bear subparallel anastomosing fine raised lines. Palpebral lobes, and axial and posterior border furrows, are smooth.

Free cheek consisting of an enormous globular eye surrounded by a convex border. The inner margin of the eye is straight where it abuts the palpebral lobe. Hexagonal lenses rather coarse (long diameter 0.025 mm) arranged in files of 30–34 across (trans.) the eye, the number of lenses, totalling about 1300 in eyes of length (sag.) about 0.5 cm. Lenses hexagonal, but 5–7 sided polygons are not uncommon. With the eye in presumed life position some lenses are facing upwards, a large number laterally, while the back and front parts of the eye have many lenses in such a position as to command an anterior and posterior view. Furthermore the cheek border is directed downwards at such a steep angle that the lower part of the eye has lenses directed *downwards* with a ventral field of view. Border separated from the eye by a narrow (trans.) depressed area widest just posterior to genal spine and narrowing rapidly round the anterior and posterior parts of the eye. The border itself is convex, subparallel to the dorsal outline of the eye, widest immediately in front of the genal spine and narrowing rapidly in front of the anterior part of the eye. It carries the genal spine at its mid-point, which is strong and blade-like, curving outwards and backwards and downwardly directed. Doublure turned up sharply inside the border, narrow, and continued anteriorly as a narrow strip which is attached at the connective suture below the anterior border of the cranidium. Facial suture runs in an almost straight line from posterior to anterior margins of the cranidium, anteriorly turning sharply adaxially to run along the edge of the anterior border.

Hypostoma (Pl. 36, Fig. 17) preserved between a pair of free cheeks on one specimen that represents a moulted arrangement of the parts of the exoskeleton. The cheeks are rotated so that the genal spines point forwards, the hypostoma is both inverted and reversed so that its posterior margin now points anteriorly. Such an orientation is consistent with the moulting habits discussed for *C. genacinaca genacinaca* (p. 114), the inversion of the hypostoma accompanying that of the cranidium. The free cheeks remain in a position consistent with the view that the genal spines were used as levers during the shedding of the eyes. The hypostoma is similar to that of *C. genacinaca genacinaca*, described below, except that the middle furrows are hardly developed; anterior margin not preserved. The hypostomata of both species differ from that of *Telephina*, as figured by WHITTINGTON (1965) and ULRICH (1930), in having a broader posterior margin.

Thoracic segments very convex, with arched-up axis of similar outline to occipital ring, pleurae horizontal for a short distance adaxially, curving down steeply laterally. Pleural furrow a broad median depression dying out abaxially. The tip of the pleura is blunt, and continued anteriorly as a small rounded projection. On silicified specimens a very short (tr.) doublure can be seen.

Pygidium wider than long, tapering gently posteriorly to almost straight (trans.) posterior margin, highly convex, with the axis standing well above pleural fields. Axis occupies one-third of the pygidial width at its anterior end, tapering gently posteriorly. Four axial rings well defined by ring furrows which curve forward adjacent to the axial furrows, and are bowed slightly backwards on mid-line. The fourth ring furrow does not quite reach the axial furrows. A shallow furrow runs transversely across the middle of each axial ring, dying out before reaching the axial furrows. The terminal piece of the axis, occupying less than one sixth of its length, is bisected by a longitudinal furrow, and slopes down almost vertically and without a break into the postaxial field. The pleural regions consist of a flat platform with three distinct, bluntly pointed segments looking very like thoracic segments but for their fusion. Both pleural and interpleural furrows are strongly developed on the first three segments; interpleural furrows transverse, narrow and rather deep adaxially; pleural furrows directed backwards at a low angle, broader than interpleural furrows, not reaching the border. The fourth pleural furrow is directed backwards at about 45 degrees to sagittal line, while the fourth pleural tip is an elevated node, backward pointing and projecting slightly beyond the posterior margin. The steeply sloping posterior part of the pygidium and the terminal piece of the axis with which it is contiguous are excavated into a distinctive arrangement of pits and ridges (Pl. 36, Fig. 8) rather like those on the fixed cheeks. Beneath, and adaxially to, the jutting out tips of the pygidial pleurae there is a smooth vertical "wall" which surrounds the pygidium and is itself edged by a narrow out-turned border. From its relative ventral position beneath the pleural fields it seems possible that this represents part of a modified doublure.

Ontogeny. — Smallest cranidium (0.5 mm long) probably represents an early meraspis (Pl. 36, Fig. 15). The glabella is twice as long as wide, almost pointed anteriorly. Preglabellar field broad, bisected by median sagittal furrow. Anterior border flat and straight. Palpebral lobes relatively short, about one third the cranidial length (sag.), and are quite far forward, posterior end opposite glabellar mid-point. Posterior border expands outwards to obtuse genal angle, anterior to which there is a short lateral border, i.e., the facial suture at this size is proparian.

Cranidia about 1 mm long have the glabella parallel sided posteriorly, anteriorly tapering to rounded front (Pl. 36, Fig. 14). The flat anterior border has a narrow median indentation. Fixed cheeks much wider than in adult cranidia, especially anteriorly, and the palpebral lobe is only about half the length of the cranidium. A faint eye ridge is visible, passing transversely from the anterior end of the palpebral lobe almost to the front of the glabella. The bacculae typical of the adult cranidia are not present.

Cranidia about 1.5 mm long have bacculae visible as the merest swellings on the fixigenal side of the axial furrows (Pl. 36, Fig. 13) not indenting the glabella, which expands forwards only slightly to broadly rounded anterior margin. The lateral parts of the preglabellar field — those parts corresponding to the anterolateral triangular areas on the adult — become slightly inflated, these inflated parts separated by a median depression, in the comparable position to the sagittal furrow of the smallest cranidium. Anterior border with a prominent median indentation, not arched upwards. Palpebral lobes reach neither the anterior nor the posterior borders: the eyes thus continue to be smaller than in the adult.

Cranidia 2–3 mm long are more similar to those of the adult, but the glabella does not expand forward so markedly and is rounded anteriorly. Bacculae are small, not indenting the sides of the glabella. The fixed cheeks are relatively wider compared with those of larger cranidia, and the palpebral lobes are bowed outwards slightly. Anterior border is arched and convex, but with the lateral extremities forwardly deflected, giving cranidia of this size a resemblance to *Carolinites indentus* Ross 1967. A narrow, downsloping preglabellar field is present.

Ross (1951, p. 83) has commented on the resemblance of smaller cranidia of *Carolinites* to those of *Goniophrys*, and postulated an extra-glabellar origin for the bacculae. His conclusions are confirmed by the present ontogenetic series. The bacculae originate on the adaxial part of the fixed cheeks on cranidia about 1.5 mm long and through later ontogeny increase in size to indent the base of the glabella. The origin of the arched anterior border is of particular interest, the first trace of the arch being a slight indentation of the anterior border on the mid-line, this indentation gradually increasing in transverse width, the border at the same time becoming bowed upwards, increasingly convex, and progressively closer to the glabella. The fixed cheeks become narrower, this change corresponding with an increase in the size of the eye. The usual tendency during ontogeny is for the eye to become relatively smaller, and it is suggested that this retention and exaggeration of a larval feature is perhaps further evidence of the planktonic or free swimming mode of life.

The semicircular transitory pygidium is relatively wide compared with that of the adult and includes 7 well defined segments outlined by distinct interpleural furrows. Pleural furrows visible on first two segments only. The tip of each pleura bears the nub characteristic of the adult thoracic segment.

Discussion. — An indented front margin of the cranidium was used by Ross (1967, p. 11) as the diagnostic feature of his species *C. indentus.* Such a feature, as we have seen, is characteristic of a particular ontogenetic stage (it is well displayed also on *C. ekphymosus*, Pl. 39, Fig. 9), which may well be found on many species of *Carolinites.* The true identity of *C. indentus* must await the discovery of larger cranidia from the same horizon. *C. indentus* also possesses the relatively wide preglabellar field characteristic of early growth stages. *C. rugosus* is distinguished from all other *Carolinites* species by its distinctive surface sculpture, the median furrows on occipital ring, thoracic and pygidial axis, and the deep interpleural furrows on the pygidium. Both this species and *C. ekphymosus* n. sp. resemble *C. popovkiensis* BALASHOVA (1961) rather closely. This species is known only from one badly preserved cranidium which does not show the surface sculpture, and its relationship to the Spitsbergen species must at the moment remain unresolved.

Carolinites ekphymosus n. sp.
(Pl. 39, Figs. 1–13)

Stratigraphic range. — Characteristic of the upper part of the Olenidsletta Member above the last occurrence of *C. genacinaca genacinaca*, 105 m from base to top of Member, and lower 25 m of Profilbekken Member below earliest typical *Orthidiella* zone fauna (probable late Arenig — *hirundo* zone).

Material. — Numerous specimens occur throughout stratigraphic range. Holotype, cranidium with five thoracic segments SMA 84212. Other figured material includes cranidia: SMA 84210–1, 84214–5, 84217; pygidia: SMA 84218, PMO NF 1320, 351; free cheek: 84213.

Diagnosis. — A *Carolinites* species with narrow fixed cheeks but not as narrow as those of *C. sibiricus*, and with large bacculae. Surface sculpture of fine granules, and with low ridges on the posterior parts of the fixed cheeks. Gently tapering pygidium with four axial rings defined by transverse ring furrows with faint pleural and interpleural furrows.

Discussion. — This species strongly resembles *C. rugosus* in the general proportions of the cranidium and pygidium. It differs from that species in several minor details, particularly in the form of the surface sculpture, which is granulate, and is lacking the transverse mid-occipital and mid-axial ring furrows characteristic of *C. rugosus*. The ridges and coarse tubercles developed on the fixed cheeks of *C. rugosus* are seen also on those of *C. ekphymosus* but are less prominent (Pl. 39, Fig. 1). The gently tapering pygidium is similar in form but with only faint pleural and interpleural furrows. Small cranidia (Pl. 39, Figs. 8, 9) show well the indented anterior border of this (*C.* "*indentus*") stage in the ontogeny. Muscle impression preserved as smooth patches on the side of the glabella are of similar form to *C. rugosus*. Well preserved internal moulds are minutely pitted (Pl. 39, Fig. 11), that is the inside of the dorsal exoskeleton bears scattered granules. This feature has been observed on other species of *Carolinites* and may be characteristic of the genus. There is also a ventral groove on the mid-line of the glabella (Pl. 39, Fig. 4), showing as a ridge on the internal moulds, and continuing anteriorly as a slight mid-glabellar depression. The same depression is seen on *C. sibiricus*, and as a median smooth line on *C. rugosus* (Pl. 34, Fig. 8). The thorax is of unusual convexity, and the lateral aspect shows that the free cheek hung well below the level of the rest of the exoskeleton.

As discussed above this species is intermediate morphologically and stratigraphically between *C. genacinaca* and *C. rugosus*, and there seems no reason to doubt that *C. genacinaca* — *C. ekphymosus* — *C. rugosus* form a phyletic series.

Carolinites sibiricus Chugaeva 1964
(Pl. 40, Figs. 1–10, 12, 13)

1964 *Carolinites sibiricus* Chugaeva in Chugaeva, Rozman and Ivanova; p. 45, Pl. 1, Figs. 4, 5.
1967 *Carolinites angustagena* Ross; p. D10, Pl. 3, Figs. 29–39.
1968 *Carolinites sibiricus* Chugaeva; Chugaeva in Balashov et al., p. 110, Pl. 21, Figs. 6, 7.
1974 *Carolinites angustagena* Ross; Shaw, p. 10, Pl. 1, Figs. 29–34; Pl. 2, Figs. 1–4, 7, 8.

Stratigraphic range. — Profilbekken Member, 40–80 m from base, associated with typical Whiterock (*Orthidiella* zone) trilobite and brachiopod fauna.

Material. — Cranidia numerous throughout the range of the species, including SMA 84219–21, PMO NF 1228, 1398; pygidia: PMO NF 3153, SMA 84223. Free cheeks are abundant in some beds, but borders must be prepared to be sure of distinction from those of *C. killaryensis*: PMO NF 3153, 34, SMA 84222.

Diagnosis. — A *Carolinites* species with fixed cheeks narrower than those of other species of the genus, almost the whole fixigenal area occupied by large bacculae. Dorsal surface without surface sculpture. Free cheek with genal spine reduced to a stub on larger specimens. Pygidium with three axial rings, each equally well-defined by transverse ring furrows, gently tapering, posterior margin transversely truncate.

Description. — The following remarks supplement the descriptions given by Ross (1967), Chugaeva (1964) and Shaw (1974). All parts of the exoskeleton are smooth externally. The front margin of the glabella is slightly indented on larger cranidia, and this is more apparent on internal moulds. The indentation is not seen on smaller cranidia, the glabella of which is more nearly square. These ontogenetic and internal/external differences account for some of the apparent differences between the cranidia figured by Chugaeva (1964) and Ross (1967). The anterior border expands very slightly towards the mid-line.

The fixed cheeks are very narrow (narrower than those of *C. rugosus* and *C. ekphymosus*), the bacculae are inflated and occupy almost all their width. The low intrapalpebral ridge outlining the inner side of the palpebral furrow runs outwards-backwards at a low angle (20 degrees to the sag. line), almost straight to the posterior border furrow (compare the sinuous outward swing of this feature in *C. ekphymosus* and *C. rugosus*). The free cheek lacks the stout genal spine of other *Carolinites* species, a very short and slender genal spine is present on stratigraphically early specimens, but on higher specimens the spine is reduced to a stub as on the larger free cheeks illustrated by Ross (1967, Pl. 3, Fig. 34). The pygidium tapers very slightly, with four axial rings, and the pleural and interpleural furrows very faint, external surface smooth.

Discussion. — The present material agrees very closely with that figured by Chugaeva (1964) and Ross (1967 as *C. angustagena*). As pointed out above the apparent differences between the Siberian and Basin Range material are due to differences in size and preservation of specimens figured, and I therefore regard *C. angustagena* as a junior subjective synonym of *C. sibiricus*. The differences between the two specimens of *C. sibiricus* figured by Chugaeva (1964) are greater than those between *C. angustagena* and the type of *C. sibiricus*. *C. macrophthalmus* (Harrington and Leanza 1957), recorded from the Llanvirn of Argentina (according to the authors' list of localities, although described as Caradocian in the systematic description) is also closely similar to *C. sibiricus* but comparison with the flattened South American material is difficult.

Carolinites genacinaca genacinaca Ross 1951
(Pl. 37, Figs. 1–15; Pl. 38, Figs. 1–3; Fig. 15)

1951 *Carolinites genacinaca* Ross; p. 84, Pl. 18, Figs. 25, 26, 28–36.
1953 *Carolinites genacinaca* Ross: Hintze, p. 145, Pl. XX, Figs. 7-9.
1964 *Carolinites genacinaca* Ross; Chugaeva in Chugaeva, Rozman and Ivanova; p. 44, Pl. 1, Figs. 1–3.

1968 *Carolinites genacinaca* Ross; Chugaeva in Balashov et al., p. 109, Pl. 7, Figs. 6–8.
1973 *Carolinites genacinaca* Ross; Chugaeva in Chugaeva et al., p. 44–45, Pl. 1, Figs. 6.

Stratigraphic range. — Olenidsletta Member 15 m to 102 m from base

Material. — One of the commonest fossils of the Olenidsletta Member, abundant material includes 8 more or less complete specimens.

Diagnosis. — A *Carolinites* species with fixed cheeks of transverse width only less than those of *C. killaryensis killaryensis* of species described here. Bacculae of moderate size, slightly indenting base of glabella. Genal spines very long, outward curved at base. Pygidium with two anterior axial rings defined by deep ring furrows, third axial ring faintly defined. Stratigraphically high specimens carry small mid-axial tubercles (indentical to Ross' type population) lacking on stratigraphically early material.

Description. — The following remarks supplement the descriptions of Ross (1951) and Hintze (1953). Compared with the species described above the bacculae are small and indent the base of the glabella less noticeably, in this respect resembling the early growth stages of the stratigraphically younger species. The relatively wide fixed cheeks are characteristic of the species, and on some large specimens may show an indistinct sculpture of low ridges. The anterior border is not expanded medially. Free cheek with an enormous globular eye, the largest of which has a long diameter of 6 mm with some 4000 lenses. As with other species the free cheek hangs below the level of the fixed cheeks and thorax, with the proximal, outward directed part of the genal spine pointing downwards. The spine in this species is quite strongly curved (contrast *C. genacinaca nevadensis*), with a broad base, distally tapering.

Hypostoma (Pl. 38, Figs. 2, 3) of length 1.2 times maximum width, greater part occupied by broad, oval middle body of low convexity, which is narrowest at the anterior margin, widest at about half hypostomal length. Middle body cut by a pair of shallow middle furrows at three-quarters hypostomal length which delimit the narrow (sag., exsag.) posterior lobe of the middle body. Lateral borders narrow and steep; posterior border nearly horizontal; both carry sculpture of raised lines parallel to perimeter. Border furrows deep anteriorly, shallowing abruptly behind middle furrows. Anterior margin of hypostoma curves forwards medially, laterally continued downwards into narrow (trans.), steeply downsloping anterior wings.

Thorax of 10 segments, with an extremely convex axis wider than the pleurae, and which hardly tapers posteriorly. Each segment of same structure as that described for *C. rugosus*, with broad pleural furrow dying out abaxially. The articulation appears to be simple boss-and-socket type near the axial furrow. The pygidium characteristically tapers at about 20 degrees to the sagittal line, and possesses only three distinct axial rings, of which the first two

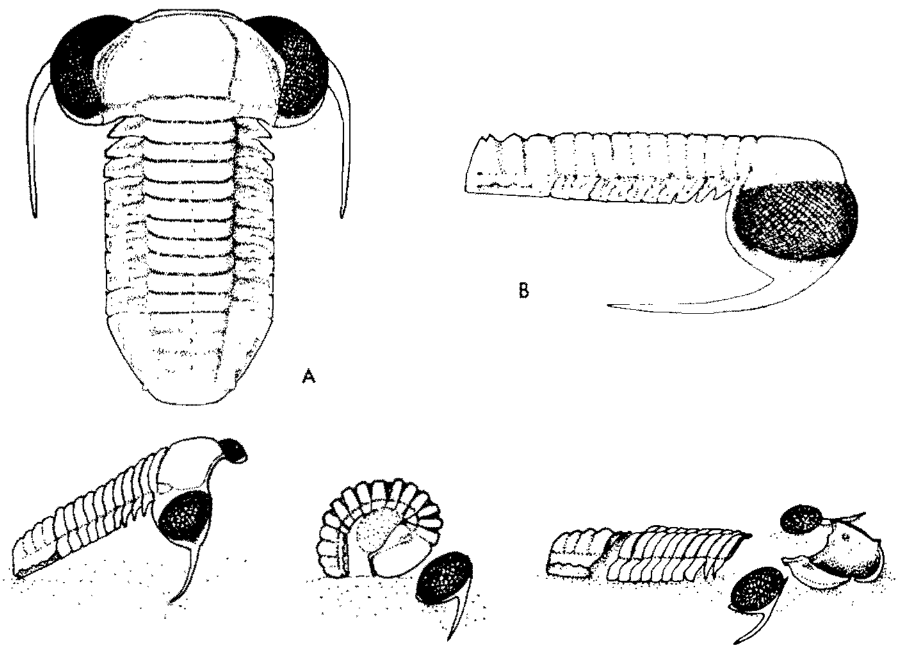

Fig. 15. Reconstruction of *Carolinites genacinaca genacinaca* in dorsal (A) and lateral (B) views, × 2.5. C–E. Inferred sequence of actions involved in moulting of *Carolinites*, based on specimens such as Pl. 37, Fig. 6, Pl. 36, Fig. 19. *Carolinites* is presumed to have temporarily forsaken its actively swimming mode of life, settled to the bottom, and used its long, downward-directed genal spines as levers (C) to prise off the free cheeks. This done the cephalic region was inverted (D) and the cranidium and hypostoma sloughed, enabling the animal to wriggle free of thorax and pygidium (E).

are defined by deep ring furrows, the third by a fainter furrow which curves backwards medially. In dorsal view the tips of the pleurae on the pygidium do not completely overhang the border anteriorly. The axial rings typically bear small median tubercles.

Several dorsal exoskeletons are preserved in a way that suggests a moulting arrangement of the parts (Pl. 37, Fig. 6), comparing with that described by Fischer (1946) for *Telephina*. The cranidium is inverted, with the free cheek, right way up, lying at some small distance from it. It is possible that the downward pointing genal spines (see Fig. 15C–E) may have been used as levers to ease off the "old" eyes, this being accomplished by a backward pull, which would at the same time detach and reverse the hypostoma (Pl. 36, Fig. 17). The trilobite then crawled forwards out of the thorax and pygidium, which remain right way up. Finally the cranidium is shed by inverting the head region. This motion is independent of the others, and may have occurred at some distance away from the rest of the exoskeleton in some examples where the cranidium is missing.

Small growth stages (Pl. 37, Fig. 11) resemble those of other *Carolinites*, but an "*indentus*" stage has not been found of this species.

A reconstruction of the dorsal exoskeleton is given in Fig. 15.

Discussion. — The characteristic features of the Spitsbergen material agree so well with those of the type material (Ross 1951) that, although the present specimens are mostly considerably larger, their specific identity to *C. genacinaca genacinaca* is not in doubt. The species is recorded also outside N. America from Siberia (CHUGAEVA 1964), and I have examined material from East Greenland (Cap Weber Formation) and can confirm the identification of *C. genacinaca* given by COWIE and ADAMS (1957). Its range through the greater part of the Olenidsletta Member represents a considerable time span, but I do not feel justified in recognising further subspecies on the basis of the present material. Stratigraphically early material shows features transitional with *C. genacinaca nevadensis* as discussed above (p. 103). In particular, pygidia lack median tubercles although the third ring furrow is visible (Pl. 38, Fig. 11). Bacculae increase in size upwards through the range of the species. High specimens of *C. genacinaca genacinaca* may show relatively large bacculae and the intra-palpebral ridge may bear fine granules. These late forms are transitional in these respects with the succeeding species *C. ekphymosus* to which *C. genacinaca* gave rise in the highest part of the Olenidsletta Member. *C. genacinaca* is a widespread species indicative of the early part of the Arenig (pre *hirundo* age, = zone J of ROSS–HINTZE, zone 6–7 of BERRY 1960) which in other localities is found in non-graptolitic faunas. It is obviously an extremely important species for correlation.

Carolinites minor (SUN 1931) (see LU et al. 1965, Pl. 64, Fig. 32) bears a closer resemblance to a small cranidium of *C. genacinaca genacinaca* than other species from Spitsbergen, but the material of *C. minor* is inadequate for unequivocal specific comparisons. Dr. D. LEGG informs me that the poorly known type species of *Carolinites*, *C. bulbosus* KOBAYASHI 1940, from the Arenig of Tasmania, resembles *C. genacinaca genacinaca* closely; it is important that the type species be redescribed to clarify the synonymy.

Carolinites genacinaca nevadensis HINTZE 1953
(Pl. 38, Figs. 4–13)

1953 *Carolinites genacinaca nevadensis* n. subsp.; HINTZE, p. 146, Pl. XX, Figs. 3–6.

1970 *Carolinites* ex. gr. *genacinaca* ROSS; BURSKY in BONDAREV (ed.), p. 103, Pl. 6, Fig. 10.

Stratigraphic range. — Basal part of the Olenidsletta Member, lowest 6 m only, early Arenig (*fruticosus* zone).

Material. — Cranidia: PMO NF 793, 2592, 786, 785, 811, 814, 781; free cheeks: PMO NF 804, 800, 808; pygidium: PMO NF 785.

Diagnosis. — A *Carolinites* species with bacculae smaller than those of other species. Glabella broadly rounded anteriorly, fixed cheeks narrow to moderate width intergrading with *C. genacinaca genacinaca.* Free cheek with strongly inflated band subparallel to base of eye, long, almost straight genal spine which originates relatively posteriorly compared with other species of the genus. Pygidium with only two (traces of a third) axial rings deeply defined.

Discussion. — The following remarks supplement the description of HINTZE (1953, p. 146, Pl. XX, Fig. 3–6) of type material from zone H (Pogonip Group, Utah). Attention is drawn particularly to the following diagnostic characters: the glabella of this subspecies differs from that of *C. genacinaca genacinaca* in having more rounded anterolateral corners; the bacculae are small and slightly inflated. The width of the fixed cheeks appears to be somewhat variable; some specimens, like HINTZE's type, having fixed cheeks narrower than *C. genacinaca genacinaca*, others (Pl. 38, Fig. 4) not greatly different in this proportion (especially smaller cranidia). The palpebral lobe shows a rapid contraction from maximum width posteriorly. Most diagnostic of all characters of the subspecies is the presence below the eye of an inflated crescentic band (Pl. 38, Fig. 10) which is not present on *C. genacinaca genacinaca forma typica* (cf. Ross 1951, Pl. 18, Fig. 34). The genal spine is not strongly curved like that of *C. genacinaca genacinaca*, is less broad-based and originates further back, so that the posterior border of the free cheek curves forwards only slightly to the base of the genal spine. Pygidia from Spitsbergen also agree with HINTZE's type material: gently tapering posteriorly, with a low sub-pleural "wall", axis with only two axial rings distinctly defined, the third indicated only by incomplete furrows on sides of posterior part of axis.

It has been emphasised above that there is an intergradational series between this subspecies and *C. genacinaca genacinaca* (p. 103), stratigraphically early material of the latter in the Olenidsletta Member retaining a "ghost" of the subocular inflated band and lacking median tubercles on the pygidial axial rings. Through the guidance of Drs. HINTZE and Ross I was able to collect material of *C. genacinaca genacinaca* from zone I of the Ibex area, Utah, and this material also has the transitional characters between *C. genacinaca nevadensis* and *C. genacinaca genacinaca forma typica* from zone J faunules. *Carolinites parma* OGIENKO 1972 (OGIENKO in ZANINA 1970, p. 239–240, Pl. 56, Figs. 1–3) resembles *C. genacinaca nevadensis* more closely than other *Carolinites* species discussed here, but appears to have distinct 1P glabellar furrows and a highly vaulted anterior profile.

Carolinites killaryensis killaryensis (STUBBLEFIELD 1950)
(Pl. 40, Figs. 11, 14–19)

1950 *Dimastocephalus killaryensis* STUBBLEFIELD; p. 345, Pl. II, Figs. 1–7.
1950a *Carolinites killaryensis* (STUBBLEFIELD); STUBBLEFIELD, p. 451.

Stratigraphic range. — Throughout lower 80 m of Profilbekken Member, earliest part of range corresponding to *Isograptus* zone (probably equivalent to late Arenig, *hirundo* zone) and extending upwards into typical Whiterock assemblage.

Material. — Numerous cranidia in Profilbekken Member include PMO NF 1251, 528, 357 (pygidium on same bedding plane), 354, 237, 1329, 187, 2372, SMA 84234, 84236; pygidia: PMO NF 254, 357 (cranidium on same bedding plane), 3002, 1252, SMA 84237; free cheek: 84235.

Diagnosis. — A *Carolinites* species with fixed cheeks wider than those of other species of the genus described here; bacculae of moderate size comparable with *C. genacinaca genacinaca*. Free cheek with broad, curved genal spine. Pygidium tapering, axial rings bearing short median spines, that on terminal piece produced backwards into a long, blade-like spine.

Discussion. — The material of this species from Spitsbergen agrees completely with that described from Western Ireland by STUBBLEFIELD (1950); further detailed description is therefore unnecessary. Particularly characteristic of this species are the wide (trans.) fixed cheeks, and the tapering pygidium with long, backward-curving posterior spine. This spine was derived from the small median tubercle of stratigraphically high *C. genacinaca genacinaca*. Stratigraphically early *C. killaryensis* have a relatively slender terminal spine, but no specimen has been found in which the spine is intermediate between the *genacinaca genacinaca* and *killaryensis* condition. Well-preserved specimens show the impressions of caeca on the internal moulds of fixed cheeks and border of free cheek.

The species makes its first appearance in beds low in the Profilbekken Member, late *hirundo* zone, and continues relatively high in the same Member into beds of early Llanvirn (*Orthidiella* zone, and equivalent to European *bifidus* zone) age. The species is stratigraphically important as it is very widespread, apart from its occurrences in Spitsbergen and Western Ireland it is reported from the Basin Ranges, Western U.S.A. (Ross 1967, p. D11), and a species close and possibly identical to *C. killaryensis* from Meiklejohn Peak, Nevada (Ross 1972, Pl. 11, Figs. 11–14; Pl. 12, Figs. 1–6).

Glossary of new names — Origin of names

arcticus — (Latin) found in northerly regions
catillus — (Latin) a small plate
clavaria — (Latin) a club, referring to club-shaped glabella of *Endymionia clavaria*
costatus — (Latin) ribbed
delicatulus — (Latin) very delicate
disputa — (Latin) subject to argument
diodyx — (Greek) a pestle, referring to glabella of *Mendolaspis diodyx*
ekphymosa — (Greek) an eructation of pimples
extensa — (Latin) wide, extended
fistulosus — (Latin) full of holes
flabellifera — (Latin) a fan, referring to the shape of the pygidium of *Niobe flabellifera*

glaber — (Latin) smooth
Globampyx — (Greek) swollen *Ampyx*
Gog — Giant of English mythology, applied to *Gog catillus* — the largest of the Valhallfonna trilobites. Masculine.
graia — (Greek) an old woman, referring to wrinkled appearance of cranidium of *Pytine graia*
inermis — (Latin) unarmed
isoteloides — referring to general similarity of *Poronileus isoteloides* to the asaphid genus *Isotelus*
jugatus — (Latin) linking, referring to the intermediate characters of *Poronileus jugatus*
occulta — (Latin) hidden
omega — greek letter, with outline similar to that of facial suture of *Peraspis omega*
Oopsites — (Greek) egg-like (+ *-ites*). Masculine
porcus — (Latin) a pig, referring to shape of glabella of *Ampyx porcus*
Poronileus — (Latin) punctate *Nileus*
porosus — (Latin) filled with holes
Pytine — (Greek) a flask covered with wattles, describing glabella of *Pytine graia*
Rhombampyx — (Greek) rhomb-shaped *Ampyx*
rugosus — (Latin) rough-surfaced
spongiosus — (Latin) spongy, referring to surface sculpture of *Ampyx spongiosus*
squamosus — (Latin) with a scaly surface
striatellus — (Latin) covered with fine lines
svalbardensis — from Svalbard, group name for the islands of which Spitsbergen is the largest
toxotis — (Latin) an archer, referring to the bowed form of the border furrows of *Ampyx toxotis*
tragula — (Latin) a javelin, referring to form of glabella of *Rhombampyx tragula*
trinucleoides — describing the superficially *Trinucleus*-like appearance of *Globampyx trinucleoides*
vallancei — named after G. Vallance, who shared the original discovery of the trilobites described here with the author

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Plates 1–41

Specimens blackened with photographic opaque and sprayed with ammonium chloride sublimate before photography. Except where stated otherwise, illumination is with 30 cm diameter ring light. Dorsal orientation follows the convention used in the previous part of this monograph (FORTEY 1974b, p. 81). The derivation of palpebral and fossular views is explained on p. 15.

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

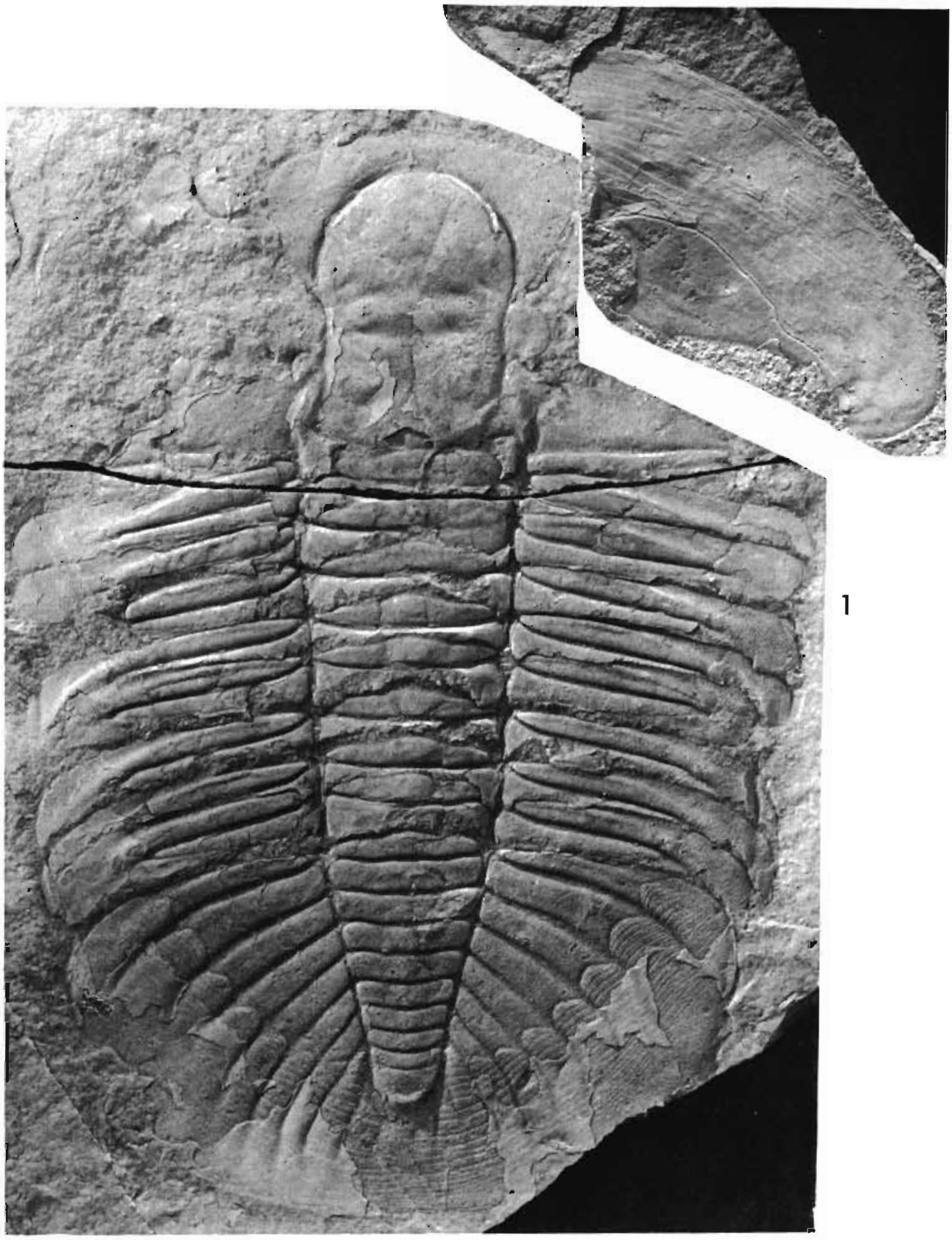
PLATE 1

Fig. 1, 2. *Gog catillus* n. gen., n. sp. .... (p. 23)

Fig. 1. Holotype, large dorsal exoskeleton lacking free cheeks, PMO NF 1679, × 1.25. Specimen largely exfoliated, revealing para-doublural line. Note pathologically deformed third thoracic segment on left side. Melt stream E on Olenidsletta, probably 80–90 m from base of Olenidsletta Member.

Fig. 2. Exfoliated free cheek, PMO NF 439, × 1.5. Olenidsletta Member, shore section along Profilstranda, 85 m from base.

PLATE 1



2

1

PLATE 2

Fig. 1–6. *Gog catillus* n. gen., n. sp. .... (p. 23)

Fig. 1. Latex cast of well-preserved dorsal exoskeleton lacking free cheeks, × 3, PMO NF 1673. Melt stream E on Olenidsletta, from same beds as holotype Pl. 1, Fig. 1.

Fig. 2. Hypostoma preserved in relief, ventral view, × 2, and lateral view, × 3, showing upward arch in lateral border and anterior wing. PMO NF 1726, isolated limestone block derived from Olenidsletta Member.

Fig. 3–5. Latex cast of internal mould of hypostoma, PMO NF 459. Fig. 5 dorsal view, × 2; Fig. 4 anterior view in strong oblique light to emphasise anterior median inflated area, × 2; Fig. 3 detail of macula to show smooth exterior surface, × 4. Olenidsletta Member, shore section on Profilstranda, 86 m from base of Member.

Fig. 6. Mould of hypostoma and cephalic doublure, largely internal, to show mode of attachment, × 2. PMO NF 426, locality as previous specimen, 92 m from base of Member.

PLATE 2

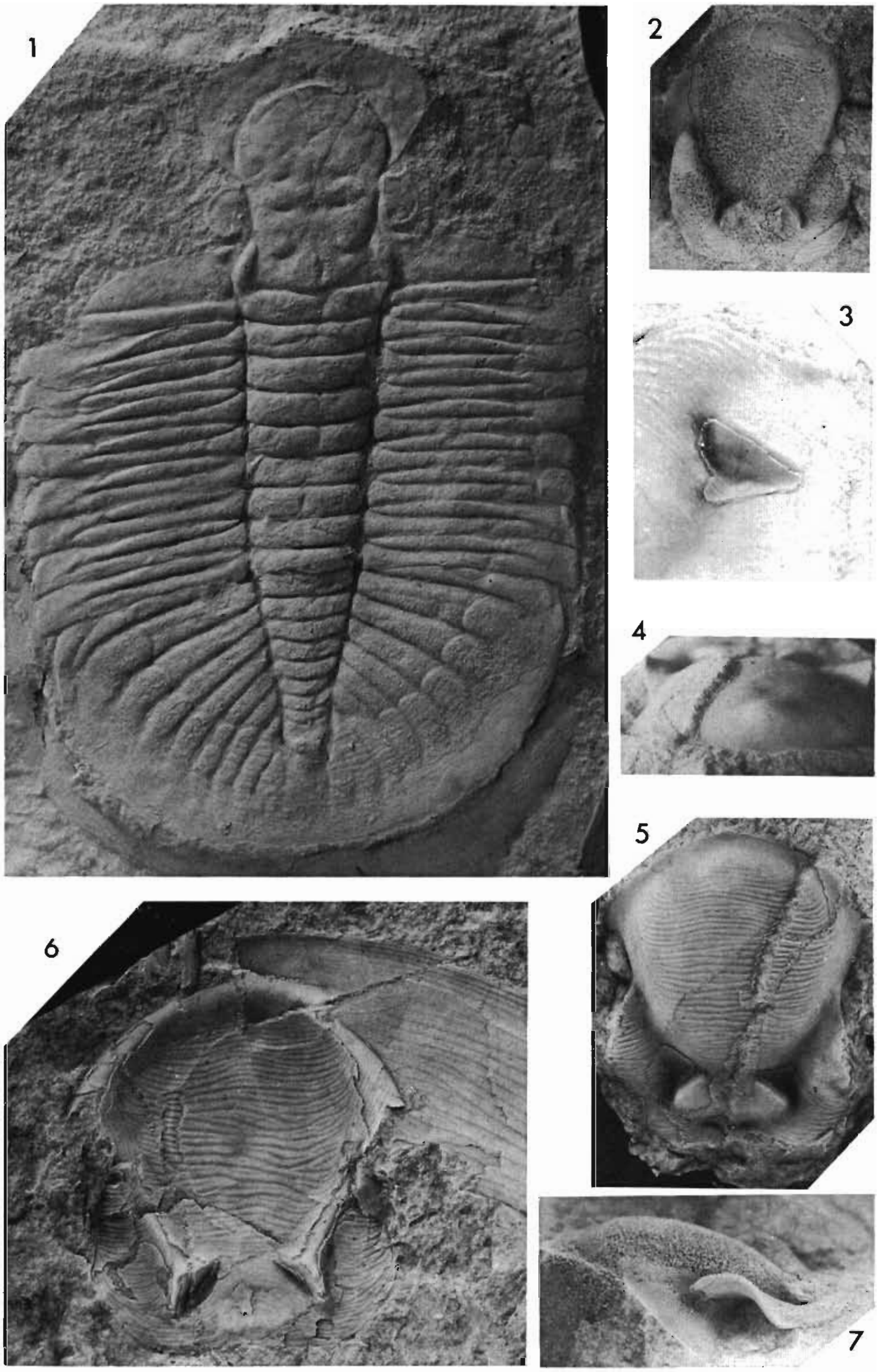


PLATE 3

Figs. 1–7. *Gog catillus* n. gen., n. sp. .... (p. 23)

Figs. 1, 2. Cranidium preserved in full relief, PMO NF 421, in dorsal and lateral views, × 1. Olenidsletta Member, shore section on Profilstranda, 92 m from base.

Fig. 3. Detail of doublure of thoracic segment, showing terrace lines and panderian opening, (× 6) PMO NF 450. Locality as previous, 89 m from base of Olenidsletta Member.

Figs. 4, 5, 6. Incomplete pygidium preserved in relief and showing details of dorsal surface. Fig. 4, dorsal view, × 2; Fig. 5, lateral view, natural size; Fig. 6, detail of left lateral part of pygidial axis and adjacent pleural field showing muscle impressions on axial rings, and sculpture of raised lines. PMO NF 444, horizon and locality as Fig. 3.

Fig. 7. Latex cast of external mould of cranidium, × 2, PMO NF 423. Olenidsletta Member, shore section on Profilstranda, 92 m from base of Member.

PLATE 3

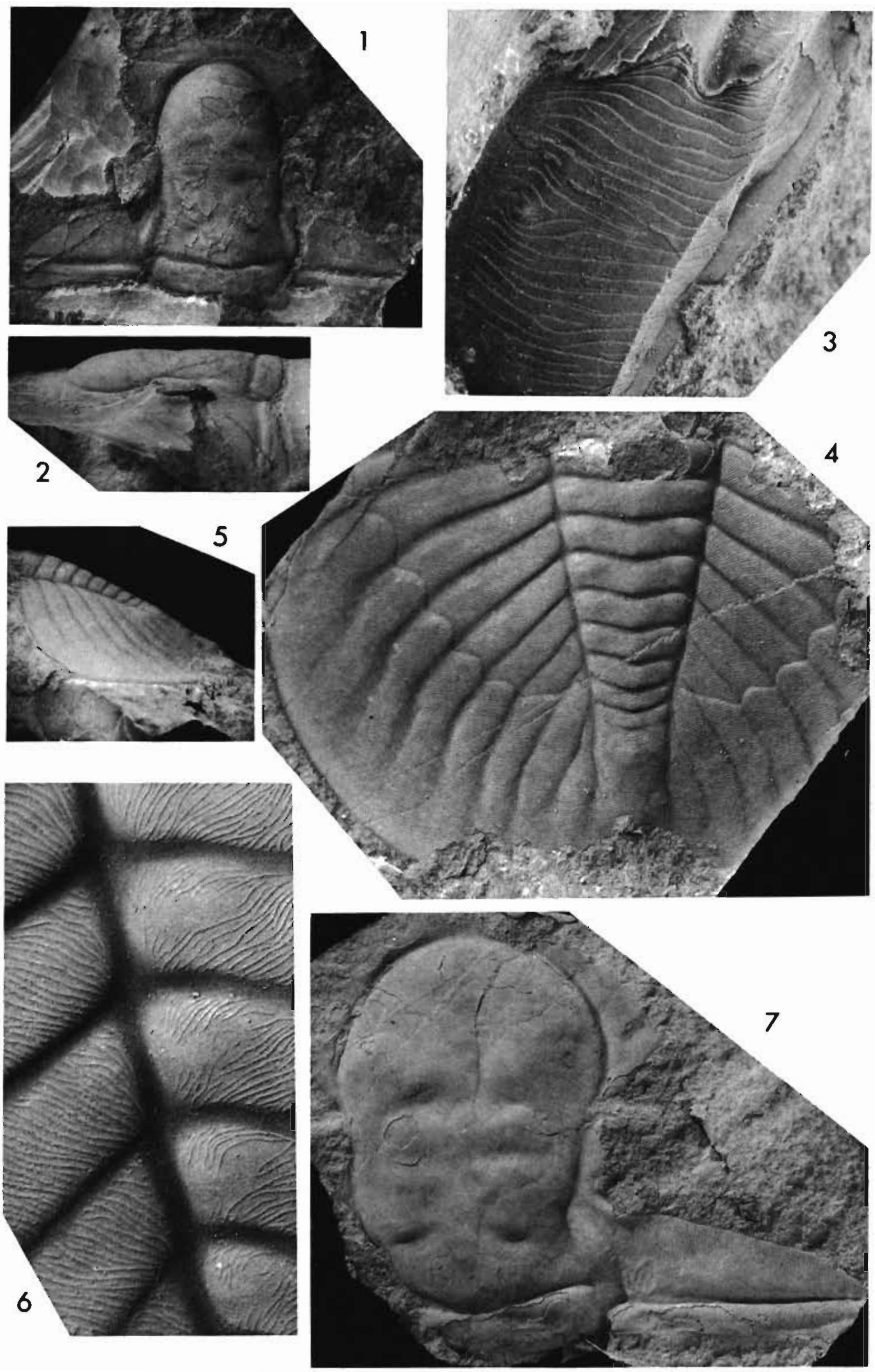


PLATE 4

Figs. 1, 2. *Gog explanatus* (ANGELIN 1851) .... (p. 27)

Fig. 1. Lectotype (here selected) cranidium incomplete on right side, and largely exfoliated, dorsal view × 1, Naturhistoriska Riksmuseet, Stockholm, no. Ar 24085. Probable original of ANGELIN (1851, Pl. XII, Fig. 2). Black limestones of Skåne, Fågelsång, Sweden, probably of late Arenig age (see p. 27).

Fig. 2. Pygidium, dorsal view × 1. Original of ANGELIN (1851, Pl. 11, Fig. 4). Horizon and locality as previous. Naturhistoriska Riksmuseet, Stockholm, no. 24088.

Fig. 3. *Gog* n. sp. .... (p. 27)

Fig. 3. Cast of incomplete pygidium, × 2, showing doublure on left side. Uppsala Palaeontological Institute no. J. 97-b. Planilimbata limestone Anderson, Jämtland, Sweden. Recorded as *Niobe*? sp. by TJERNVIK (1956, p. 173).

Fig. 4. *Niobe occulta* n. sp. .... (p. 30)

Fig. 4. Detail of anterior part of glabella and preglabellar field of cranidium figured on Pl. 6, Fig. 6, × 7.

Figs. 5, 6. *Ptyocephalus* cf. *P. vigilans* WHITTINGTON 1948 .... (p. 21)

Fig. 5. Latex cast of cranidium, dorsal view, × 5, PMO NF 1629. Olenidsletta Member, shore section on Olenidsletta, 103 m from base of Member.

Fig. 6. Latex cast of hypostoma, ventral view, × 6, PMO NF 1619. Same bed as cranidium, Fig. 5.

PLATE 4

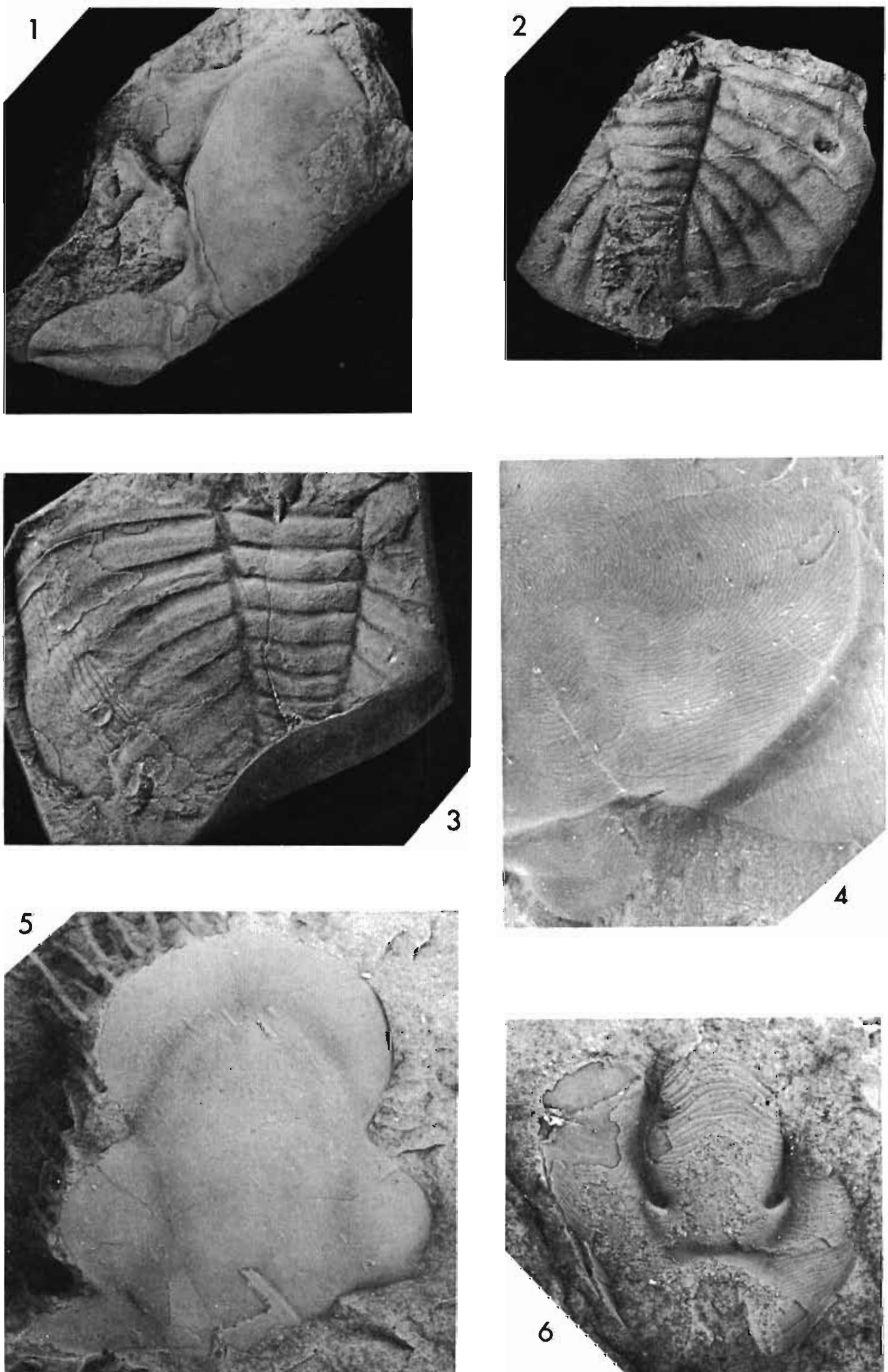


PLATE 5

Figs. 1–5. *Niobe flabellifera* n. sp. .... (p. 28)

Fig. 1. Left free cheek, × 3, showing doublure and median suture anteriorly, dorsal surface and sculpture posteriorly. PMO NF 420, Olenidsletta Member, shore section on Profilstranda, 92 m from base of Member.

Figs. 2, 5. Well-preserved cranidium, slightly flattened, Fig. 2, × 3; Fig. 5, detail of minute glabellar tubercle (T) to show presence of four, symmetrically disposed pits, × 30. PMO NF 460, Olenidsletta Member, shore section on Profilstranda, 86 m from base of Member.

Fig. 3. Holotype, well-preserved dorsal exoskeleton lacking free cheeks, × 3, PMO NF 457. Olenidsletta Member, shore section on Profilbekken, 86 m from base of Member.

Fig. 4. Pygidium, slightly flattened, × 2, PMO NF 535, locality, horizon as holotype, Fig. 3.

PLATE 5

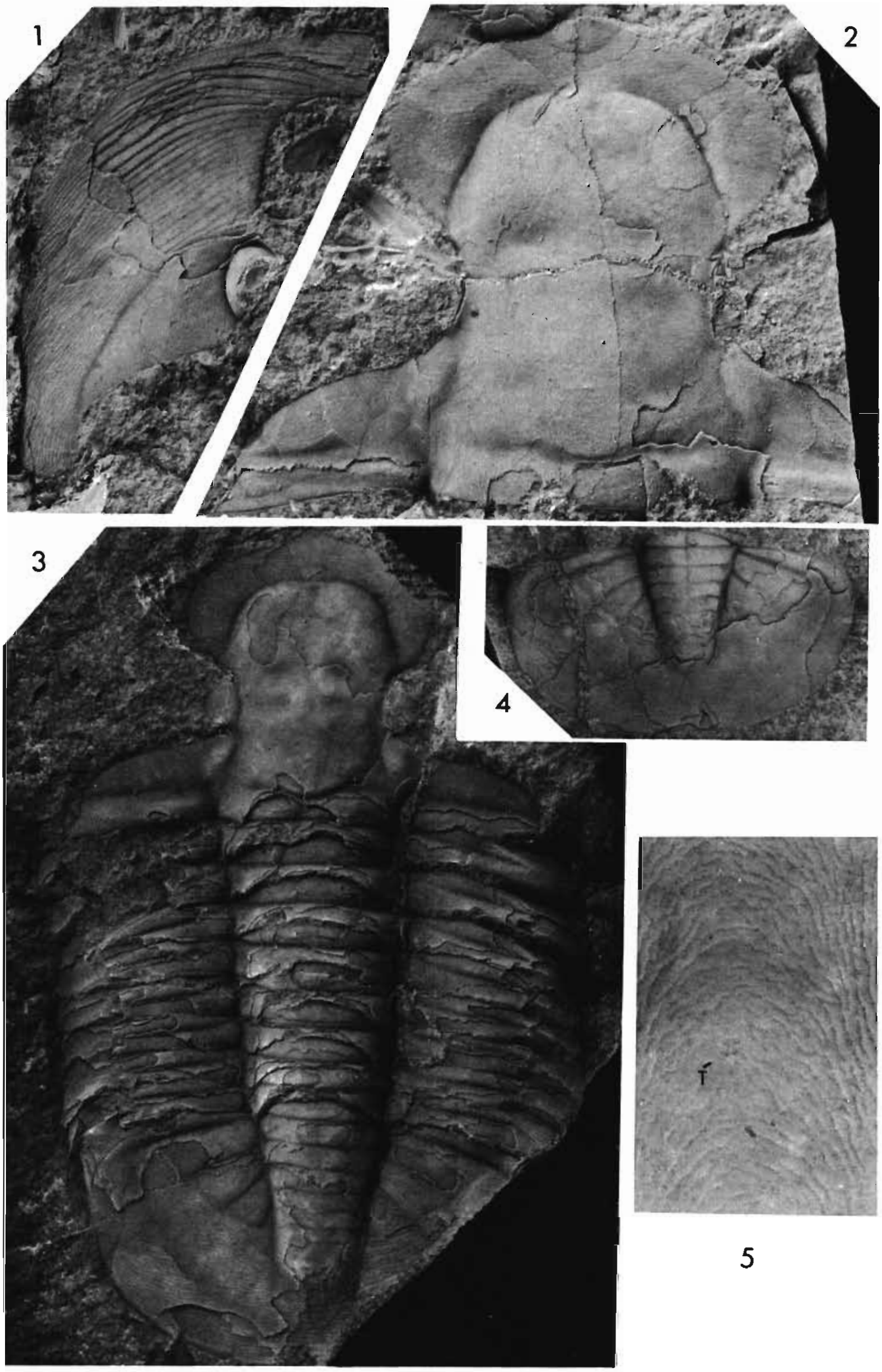


PLATE 6

Figs. 1, 2, 4–6. *Niobe occulta* n. sp. .... (p. 30)

Figs. 1, 4. Holotype, incomplete dorsal exoskeleton, PMO NF 106. Displacement of the cranidium relative to the thorax, and the thorax relative to the pygidium has occurred along joint planes in the limestone. Fig. 1 dorsal view, × 2; Fig. 4, lateral view × 1. Olenidsletta Member, shore section along Profilstranda, 102 m from base of Member.

Fig. 2. Flattened pygidium, × 2, PMO NF 1623. Locality as holotype, 103 m from base of Olenidsletta Member.

Fig. 5. Latex cast of free cheek, showing sculpture, × 5, PMO NF 10. Horizon and locality as holotype, Fig. 1.

Fig. 6. Cranidium, anterior border incompletely preserved, × 2. PMO NF 47. Horizon and locality as previous specimen and holotype, Fig. 1.

Fig. 3. *Niobe ornata* (REED 1945) .... (p. 31)

Fig. 3. Holotype, fragmentary pygidium, × 2.5, SMA 10418a. Tourmakeady Limestone (Arenig), western Ireland.

PLATE 6

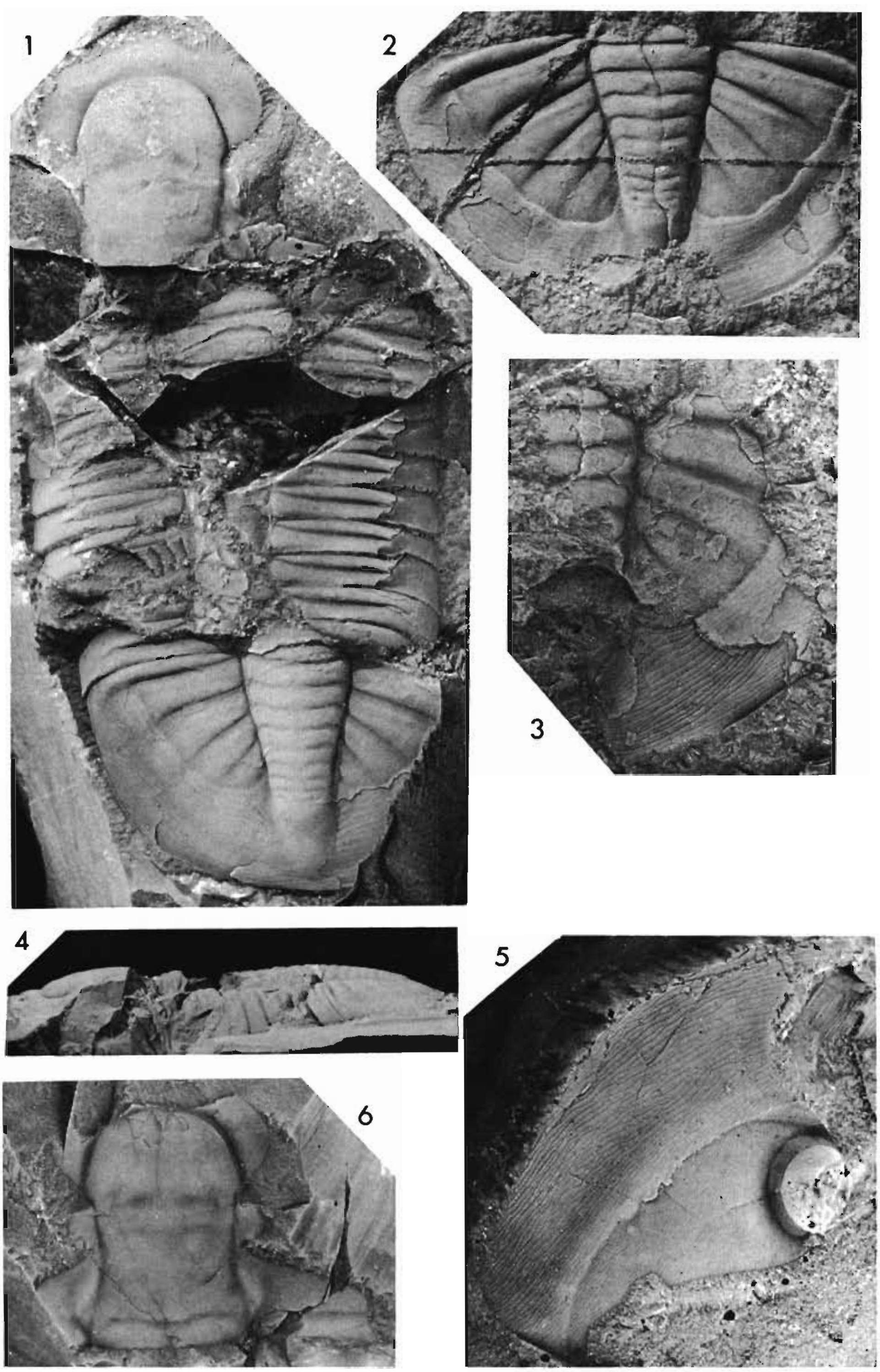


PLATE 7

Figs. 1–7. *Megalaspides striatellus* n. sp. .... (p. 16)

Fig. 1. Cast of almost complete dorsal exoskeleton, natural size, PMO NF 1718. Olenidsletta Member, shore section along Profilstranda, about 80 m from base of Member.

Fig. 2. Incomplete cranidium, preserved in full relief, × 3.5, and photographed in oblique light to emphasise muscle impressions, PMO NF 520. Olenidsletta Member, locality as exoskeleton, Fig. 1, 85 m from base of Member.

Figs. 3, 7. Holotype, cranidium and right free cheek, well-preserved but slightly flattened, PMO NF 425. Fig. 3, dorsal view, × 2; Fig. 7, detail of right hand side of preglabellar field, suture on right, showing surface sculpture of fine terrace lines, × 8. Olenidsletta Member, shore section on Profilstranda, 92 m from base of Member.

Fig. 4. Latex cast of external mould of pygidium, × 2, PMO NF 1856. Locality as Fig. 3, about 85 m from base of Member.

Fig. 5. Incomplete pygidium, × 2, flattened, sculpture shown on right, doublure and pygidial pleural ribs on left, PMO NF 1727. Locality and horizon as Fig. 4.

Fig. 6. Hypostoma, left hand side concealed beneath anterior border of *Niobe flabellifera* cranidium shown on Pl. 5, Fig. 2, × 3, PMO NF 460a. Locality as holotype, Fig. 3, 86 m from base of Olenidsletta Member.

PLATE 7

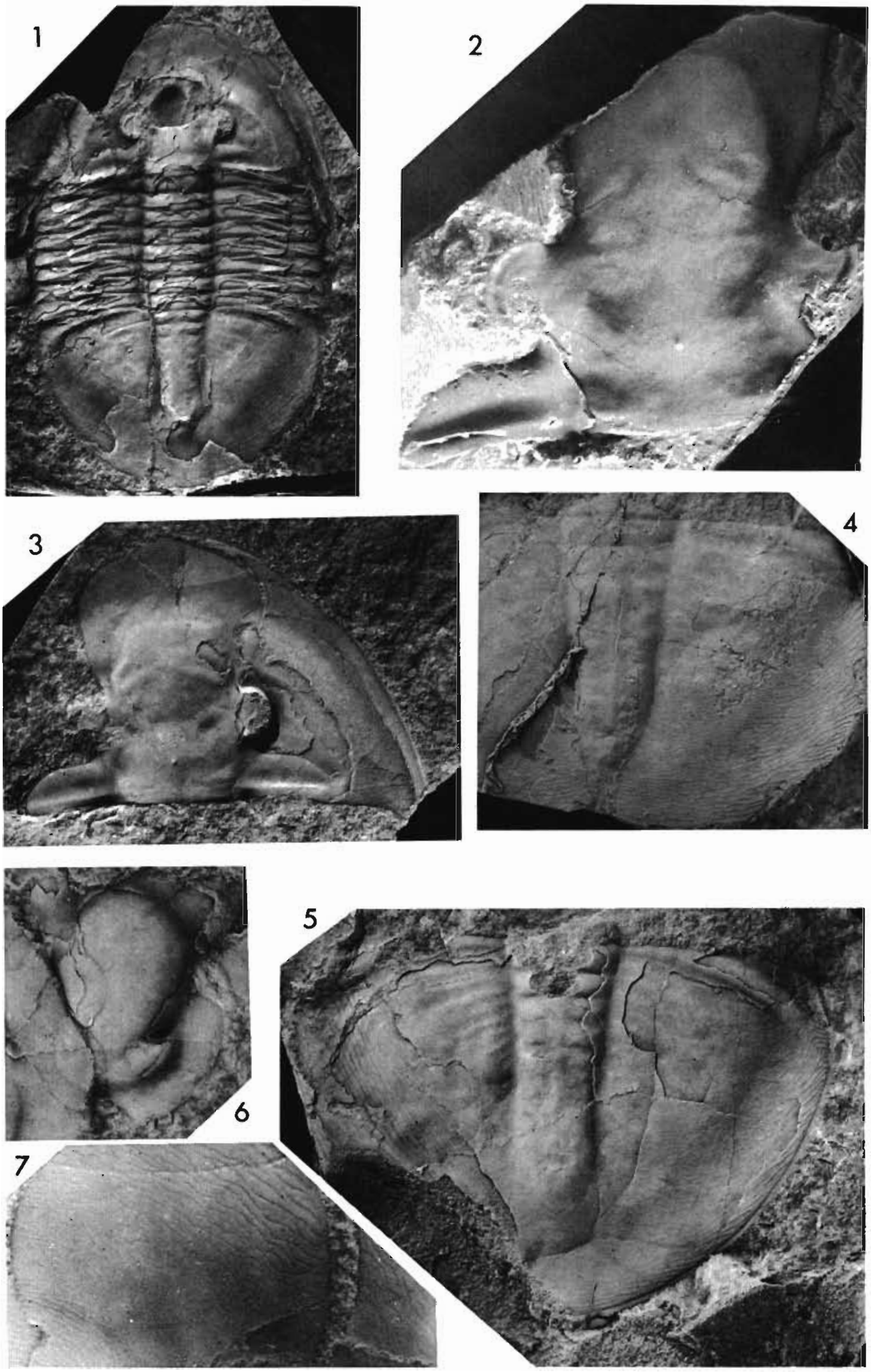


PLATE 8

Figs. 1–9. *Paraptychopyge disputa* n. sp. .... (p. 32)

Figs. 1, 4, 6. Holotype, cranidium retaining cuticle, PMO NF 2488. Figs. 1, 4, dorsal, right lateral views, × 2; Fig. 6, detail of anterior part of cranidium, showing sculpture, × 8. Basal black limestone of Olenidsletta Member, melt stream C on Olenidsletta Member, in beds underlying those with *Psilocara comma* FORTEY 1974.

Fig. 2. Latex cast of external mould of free cheek, not complete, but showing narrow border and fine terrace lines, × 4, PMO NF 778 Low Olenidsletta Member, shore section on Profilstranda, 2–3 m above base of Member.

Fig. 3. Pygidium, dorsal exoskeleton removed to show wide doublure, × 4, PMO NF 796. Same bed as previous specimen, Fig. 2.

Fig. 5. Free cheek, showing doublure and panderian opening, × 6, PMO NF 1291, locality as free cheek, Fig. 2, 8 m from base of Member.

Fig. 7. Small pygidium, × 6, PMO NF 3166, same bed as holotype, Fig. 1.

Figs. 8, 9. Incomplete large pygidium retaining cuticle; internal mould on right hand side also shows faint reflexion of sculpture. Fig. 8, dorsal view, × 2; Fig. 9, lateral view × 1.5. PMO NF 1766, basal Olenidsletta Member, melt stream D on Olenidsletta.

PLATE 8

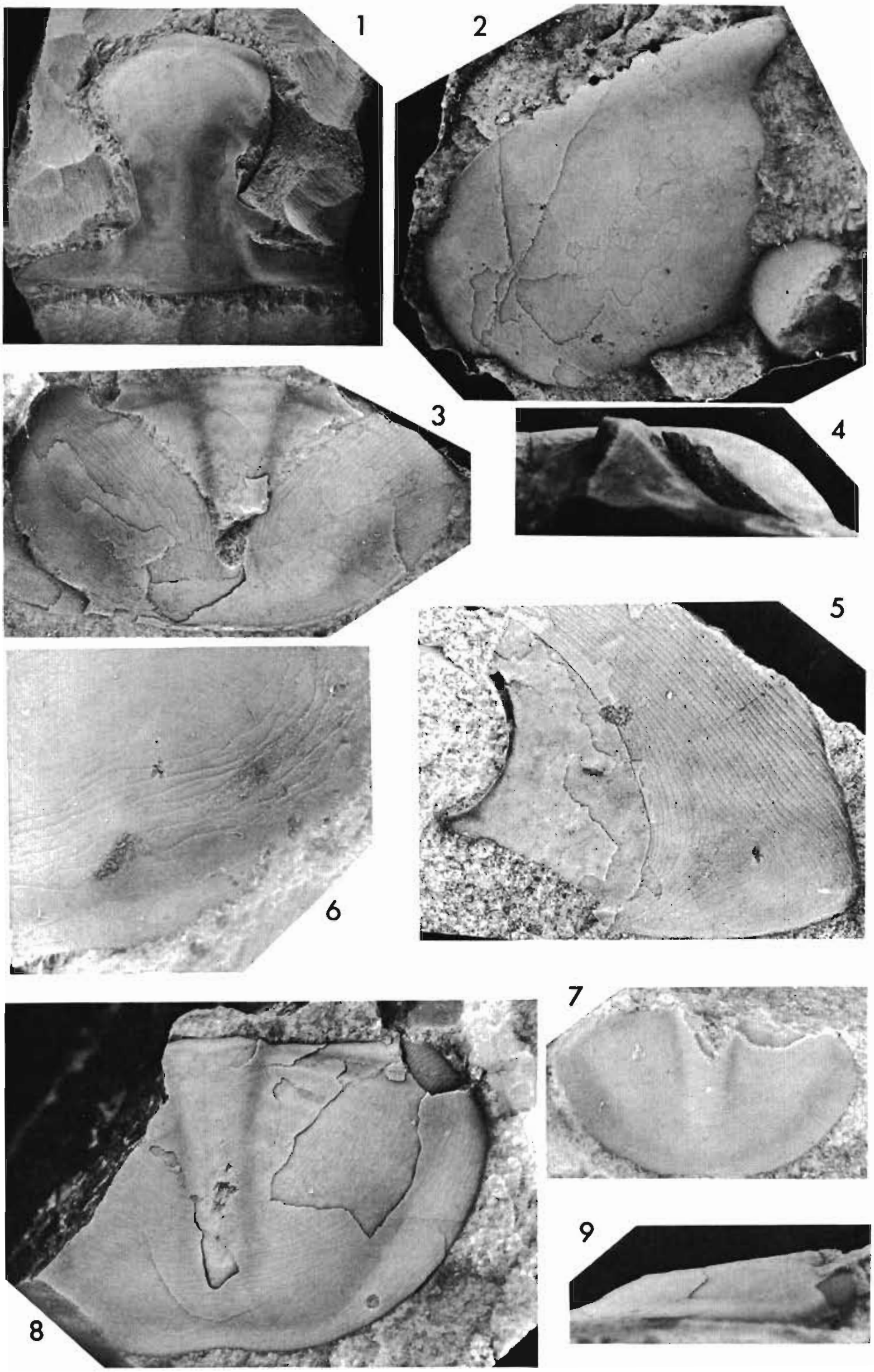


PLATE 9

Figs. 1–6. *Presbynileus* (*Protopresbynileus*?) *glaber* n. sp. .... (p. 19)

Figs. 1, 4. Cranidium, holotype, preserving cuticle, in dorsal and lateral views, × 2, PMO NF 41.

Fig. 2. Latex cast of external mould of incomplete cranidium, PMO NF 109 (counterpart PMO NF 79), × 2, showing terrace lines on anterior part of glabella not extending to anterior margin.

Fig. 3. Pygidium, dorsal surface removed to show broad doublure and terrace lines, × 2, PMO NF 93.

Figs. 5, 6. Pygidium with six thoracic segments, PMO NF 38. Fig. 5, dorsal view, × 1.5, note terrace lines around posterior margin of pygidium only; Fig. 6, detail showing thoracic doublure and panderian openings, × 4.

All specimens from a single bed, Olenidsletta Member, 102 m from base, shore section on Profilstranda.

PLATE 9

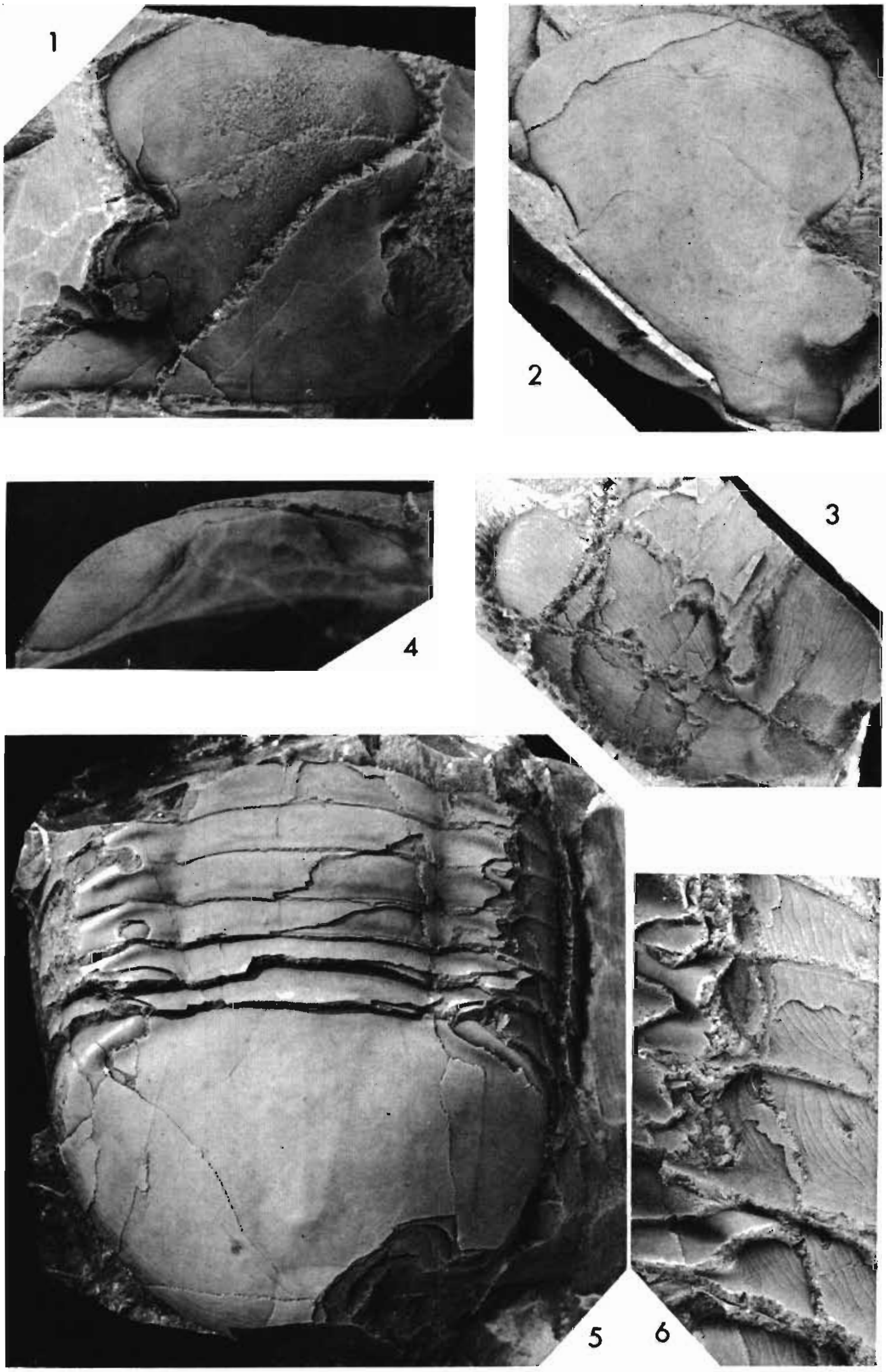


PLATE 10

Figs. 1–16, 18. *Nileus glazialis costatus* n. subsp. .... (p. 41)

Figs. 1–3. Cranidium, largely exfoliated, in palpebral, anterior and lateral views, × 5. PMO NF 432, Olenidsletta Member, shore section on Profilstranda, 91 m from base of Member.

Fig. 4. Free cheek, internal mould, × 6, PMO NF 1661, horizon and locality as holotype, Fig. 5.

Figs. 5, 8, 10. Holotype, pygidium retaining cuticle except in axial region, in dorsal, lateral and posterior views, × 7, PMO NF 1651. Olenidsletta Member, shore section on Profilstranda, 97 m from base of Member.

Fig. 6. Cranidium, largely exfoliated, palpebral view, × 5, PMO NF 1657. Horizon and locality as holotype, Fig. 5.

Fig. 7. Cephalic doublure, × 4, partly exfoliated, SMA 84283. Locality as holotype, Fig. 5, about 98 m from base of Olenidsletta Member.

Figs. 9, 11, 13. Internal mould of pygidium. Figs. 11, 12 in dorsal, lateral views, × 3; Fig. 9, detail of pygidial axis to show muscle impressions, photographed in oblique light, × 7. PMO NF 1577, shore section on Profilstranda, 97 m from base of Olenidsletta Member.

Figs. 12, 14. Pygidium, right hand side showing doublure, in dorsal, lateral views, × 4, SMA 84272. Same bed as cephalic doublure, Fig. 7.

Fig. 15. Latex cast of external mould of pygidium showing distinctive surface sculpture, × 3, SMA 84270. Horizon as cephalic doublure, Fig. 7.

Fig. 16. Exfoliated transitory pygidium, × 24, SMA 84277. Horizon and locality as pygidium, Fig. 12.

Fig. 18. Exfoliated pygidium, showing gently undulating inner margin of doublure, × 4. PMO NF 1664, from same locality and horizon as holotype pygidium, Fig. 5.

Fig. 17. Pygidium, the only possible example of that of *N. glazialis glazialis* from Spitsbergen, showing indication of posterior border on left, different outline of doublure from that of *N. glazialis costatus*, × 5. PMO NF 112, locality as other material of *N. glazialis costatus*, but 103 m from base of Olenidsletta Member.

PLATE 10

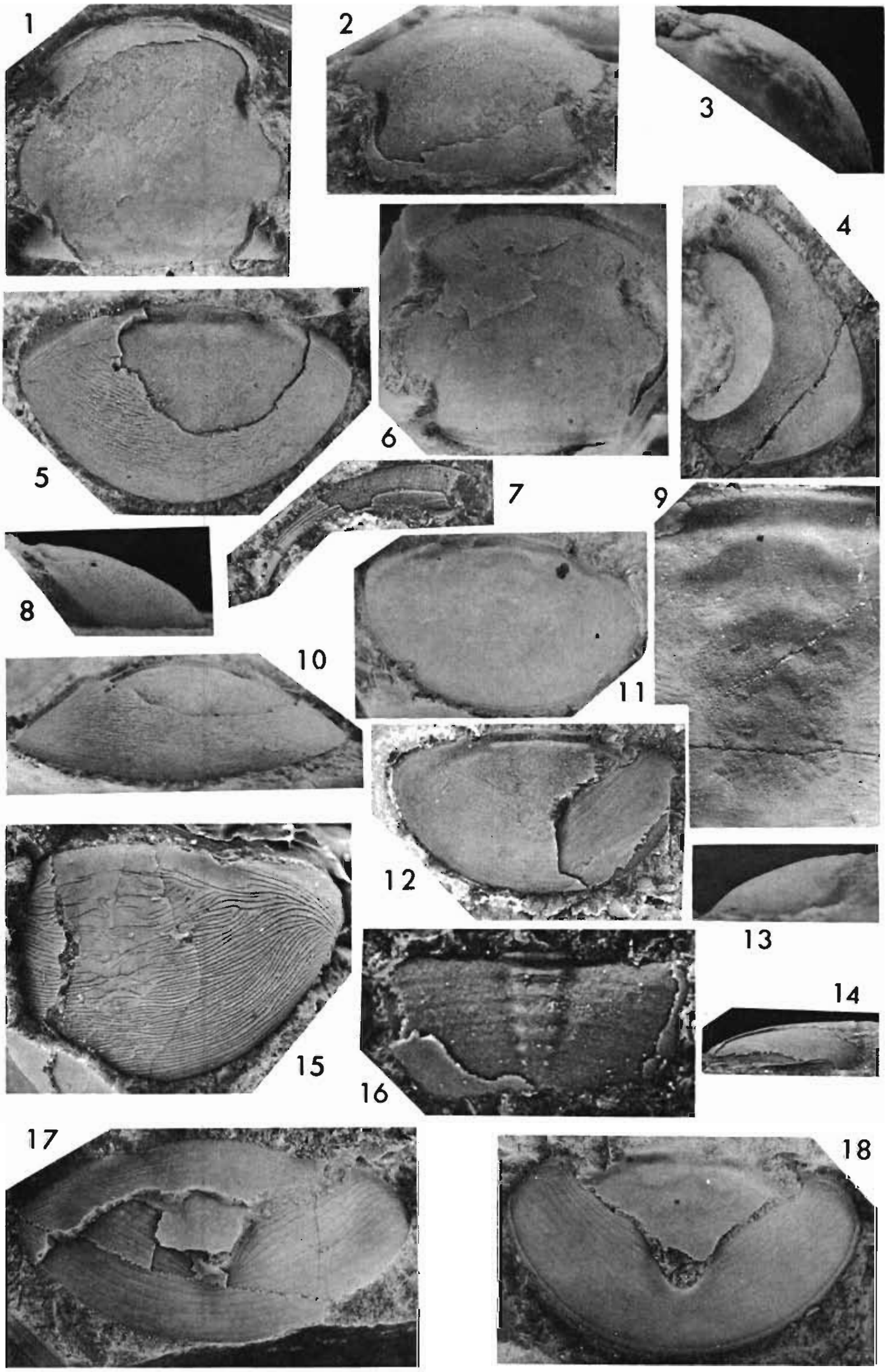


PLATE 11

Figs. 1–13. *Nileus orbiculatoides svalbardensis* n. subsp. .... (p. 43)

Figs. 1, 2, 9. Incomplete small cephalon, PMO NF 2407. Figs. 1, 2, specimen showing minute genal spines, in palpebral, anterior oblique views, cuticle missing from cranidium, × 10; Fig. 9, latex cast of counterpart, external mould showing punctate sculpture on cranidium. Lower part of Profilbekken Member, melt stream A on Olenidsletta, 23 m from base of Member.

Fig. 3. Hypostoma, ventral view, × 6, PMO NF 2417. Lower part of Profilbekken Member, locality as cephalon, Fig. 1, 23 m from base of Member.

Figs. 4, 7. Left free cheek and cephalic doublure, × 5, dorsal and lateral views. Note lack of genal spine present on small cephalon, Fig. 1. PMO NF 2477, horizon and locality as cephalon, Fig. 1.

Figs. 5, 14. Small cranidium retaining exoskeleton, in palpebral and lateral views, × 10, PMO NF 3155. Horizon and locality as cephalon, Fig. 1.

Fig. 6. Holotype, internal mould of cranidium, palpebral view, × 10. PMO NF 2412. Lower part of Profilbekken Member, melt stream A on Olenidsletta, 23 m from base of Member, same bed as specimens on Figs. 1, 4, 5 above.

Fig. 8. Latex cast of external mould of pygidium, × 8, specimen close to SCHRANK's (1972) type of *N. orbiculatoides orbiculatoides*. PMO NF 342, locality as pygidium, Figs. 11, 13, near base of Profilbekken Member.

Figs. 10, 12. Pygidium, dorsal surface removed to show doublure, in dorsal and posterior views, × 5, PMO NF 2460. Profilbekken Member, locality as holotype, Fig. 6, 23 m from base of Member.

Figs. 11, 13. Pygidium, exfoliated over axis, in dorsal and right lateral views, × 8, PMO NF 344. Near base of Profilbekken Member, south of melt stream A on Olenidsletta.

PLATE 11

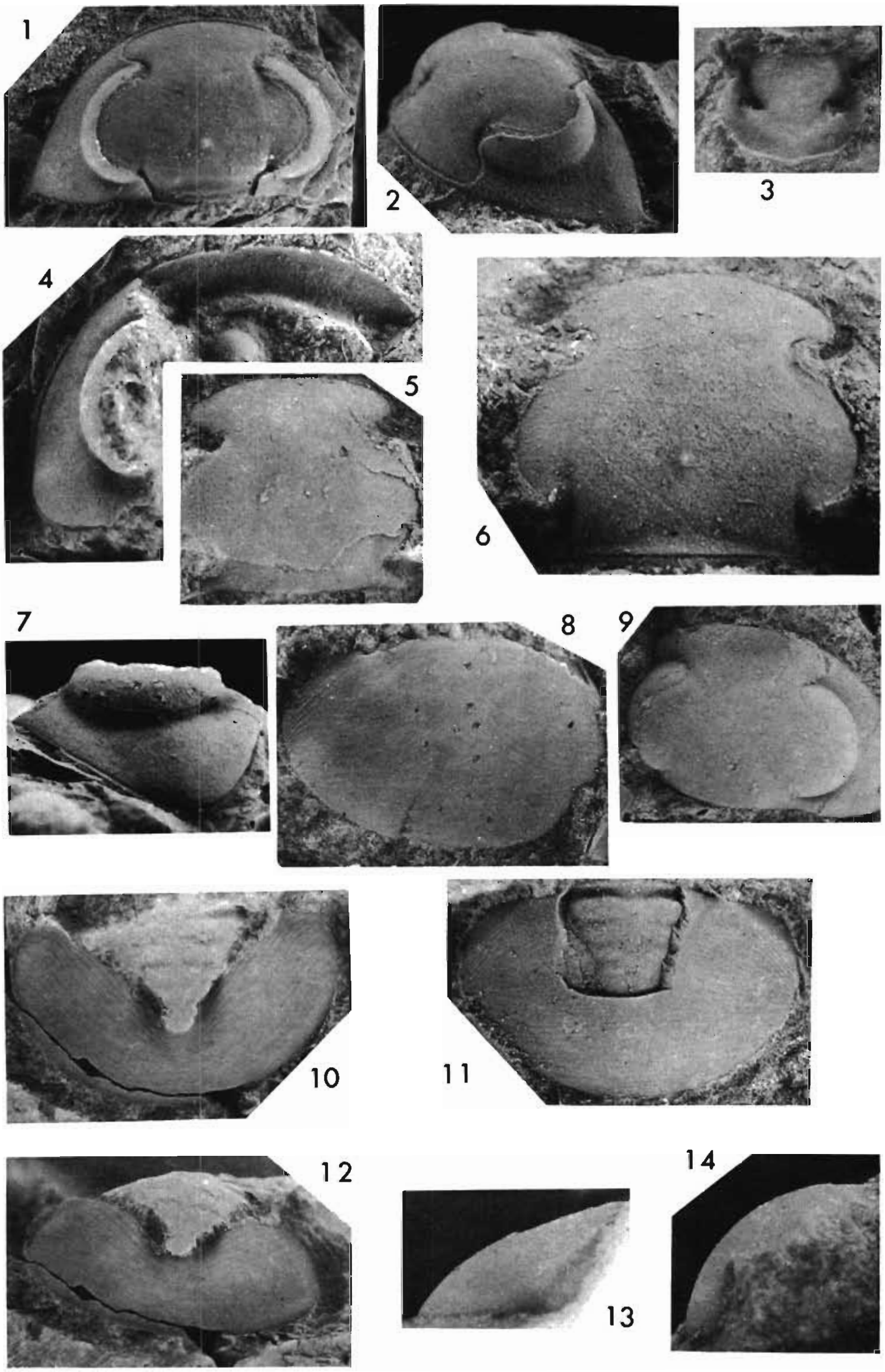


PLATE 12

Figs. 1–14. *Nileus porosus* n. sp. .... (p. 44)

Figs. 1–3. Holotype, incomplete cranidium exfoliated on right in palpebral, lateral and anterior views, × 6. Higher part of Profilbekken Member, shore section immediately south of Profilbekken, estimated 67 m from base of Member. PMO NF 1357.

Fig. 4. Free cheek, internal mould, × 6, PMO NF 3160, locality as holotype, Fig. 1, about 67 m from base of Profilbekken Member.

Fig. 5. Cranidium, palpebral view of internal mould, × 4, PMO NF 328, 47 m from base of Profilbekken Member, on Profilbekken.

Fig. 6. Internal mould of hypostoma PMO NF 322, × 6. Profilbekken Member, section on Profilbekken, 47 m from base of Member.

Fig. 7. Transitory pygidium, × 6, showing presence of two unreleased thoracic segments, SMA 84288. Locality as holotype, Fig. 1, 80 m from base of Profilbekken Member.

Figs. 8, 9. Large pygidium, × 3, in dorsal and lateral views. PMO NF 1344, immediately south of Profilbekken on shore about 67 m from base of Profilbekken Member.

Figs. 10, 11. Pygidium retaining cuticle, incomplete on right side, in dorsal and posterior views, showing surface sculpture and indistinct, flattened border, × 5. PMO NF 333, locality as holotype, Fig. 1, 54 m from base of Profilbekken Member.

Fig. 12. Incomplete cephalic doublure, largely internal mould, × 5. SMA 84290, 80 m from base of Profilbekken Member.

Fig. 13. Pygidium, × 4, showing internal mould of axis, dorsal surface of doublure. Note post-axial furrow on doublure. PMO NF 1361, locality and horizon as holotype, Fig. 1.

Fig. 14. Stratigraphically high pygidium, × 3. PMO NF 1304. Profilbekken Member, shore section on Profilstranda south of Profilbekken about 100 m from base of Member.

PLATE 12

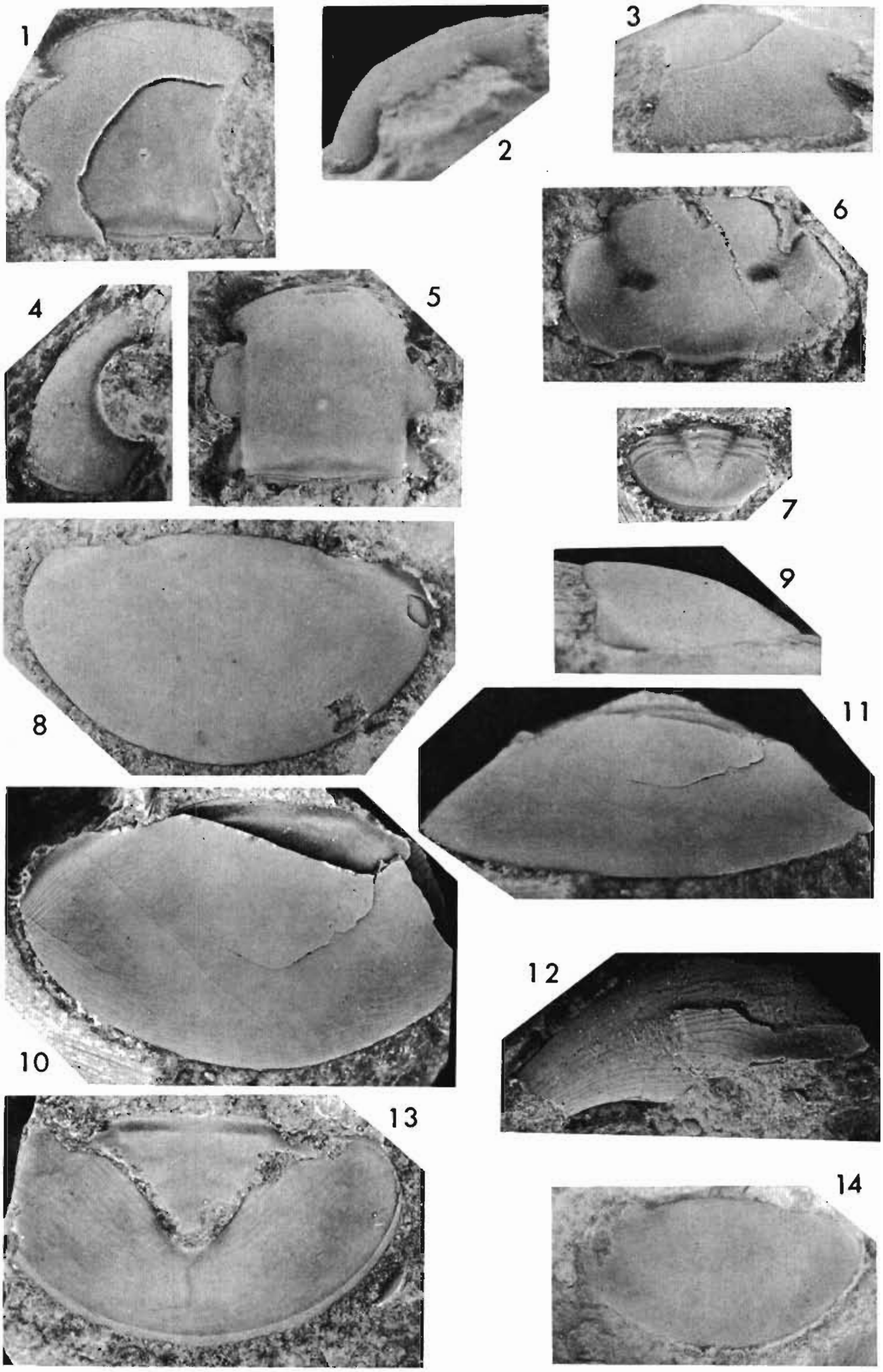


PLATE 13

Figs. 1–9. *Poronileus fistulosus* n. gen., n. sp. .... (p. 51)

Figs. 1–3. Holotype, cranidium, largely exfoliated, palpebral, anterior and lateral views, × 3. PMO NF 2440, lower part of Profilbekken Member, melt stream A on Olenidsletta, 21 m from base of Member.

Figs. 4, 6. Latex cast of cephalon, largely external mould, × 2.5, in palpebral, anterior views. SMA 84238, lower part of Profilbekken Member, shore section on Profilstranda north of Profilbekken, about 20 m from base of Member.

Figs. 5, 9. Pygidium and six thoracic segments, PMO NF 123, × 3, in dorsal and left lateral views. Note outline of inner margin of doublure on left. Lower part of Profilbekken Member, immediately south of melt stream A on Olenidsletta.

Fig 7. Internal mould of small cranidium showing median ridge and glabellar "tubercle" more prominent than on holotype, Fig. 1, × 5. PMO NF 3156, locality as holotype, Fig. 1, 20 m from base of Profilbekken Member.

Fig. 8. Hypostoma, latex cast of largely external mould, × 10, PMO NF 2420, melt stream A on Olenidsletta, 23 m from base of Profilbekken Member.

PLATE 13

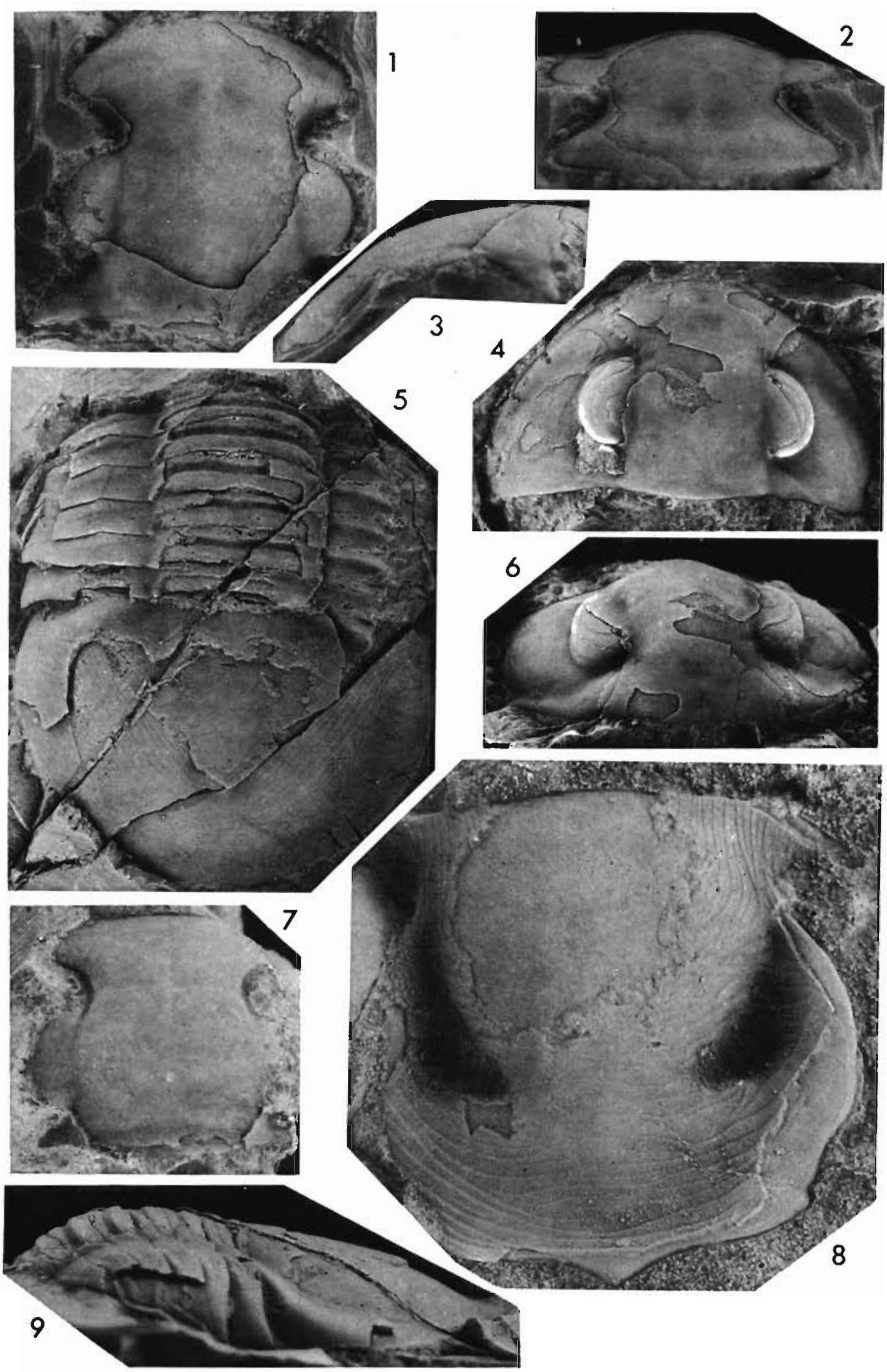


PLATE 14

Figs. 1–5. *Poronileus fistulosus* n. gen., n. sp. .... (p. 51)

Figs. 1, 3. Large pygidium, × 3, exfoliated to show gently tapering axis and shallow axial furrows, in dorsal, left lateral views. PMO NF 355. Low Profilbekken Member, locality just south of melt stream A on Olenidsletta, about 2 m from base of Member, same bed as pygidium, Fig. 5.

Fig. 2. Exfoliated pygidium showing doublure, × 1.5. PMO NF 2439. Low Profilbekken Member, same bed as holotype, Pl. 13, Fig. 1.

Fig. 4. Small, incomplete pygidium, × 5. PMO NF 1091, Profilbekken Member, lower part, melt stream A on Olenidsletta.

Fig. 5. Well preserved pygidium showing crowded terrace lines, × 6. PMO NF 343, locality immediately south of melt stream A on Olenidsletta, low (about 2 m from base) Profilbekken Member.

Figs. 6–8. *Poronileus isoteloides* n. gen., n. sp. .... (p. 55)

Figs. 6–8. Small pygidium showing close resemblance to larger pygidia of the stratigraphically older *P. fistulosus*. Fig. 6, dorsal view, × 5; Fig. 7 left lateral view, × 4; Fig. 8, detail showing sculpture, × 15. PMO NF 23, higher part of Profilbekken Member, section on Profilbekken, 47 m from base of Member.

PLATE 14

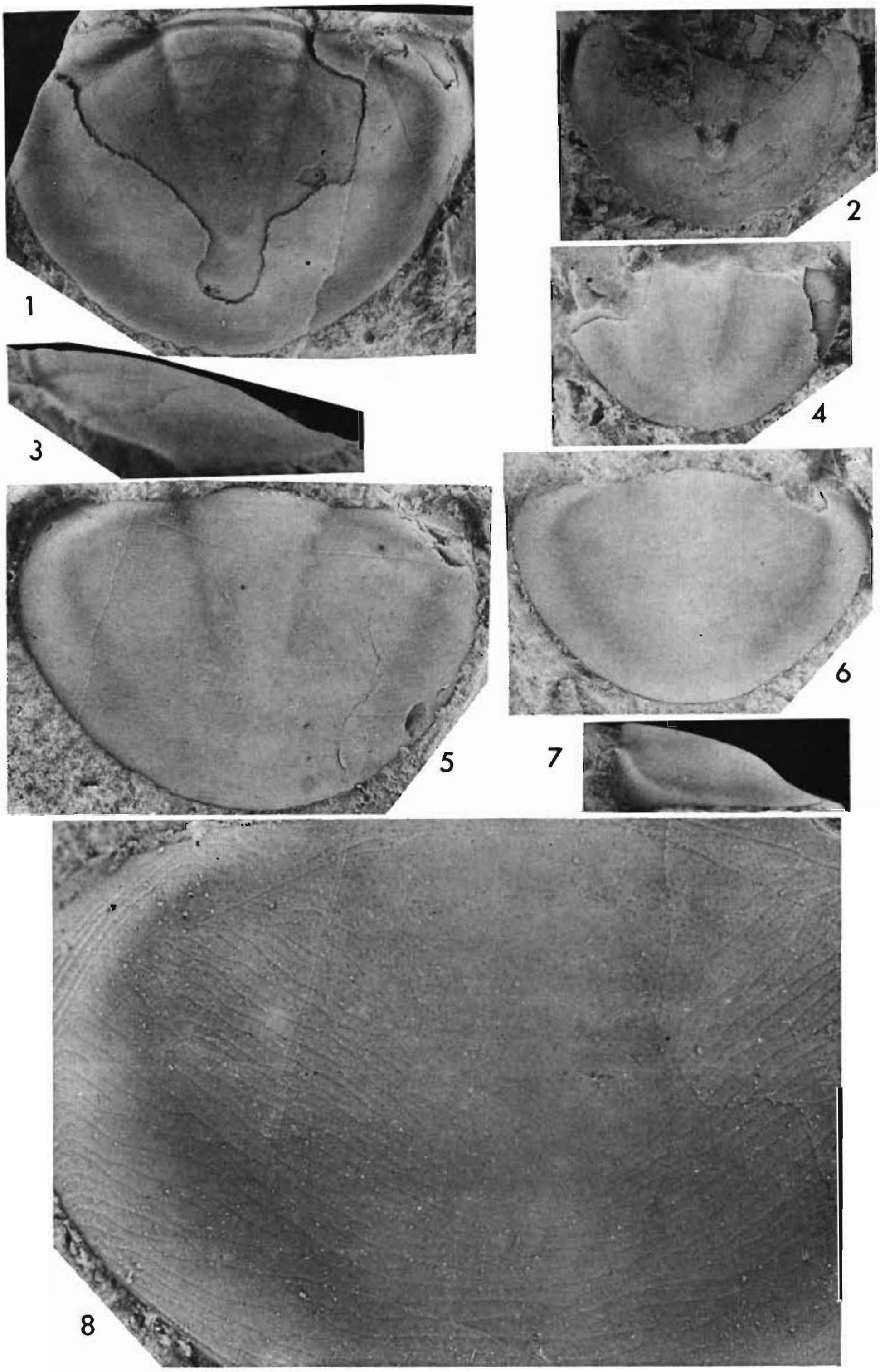


PLATE 15

Figs. 1–9, 11. *Poronileus isoteloides* n. gen., n. sp. .... (p. 55)

Figs. 1, 2, 4. Holotype, large, almost complete cranidium in palpebral, left lateral and anterior views, × 2. PMO NF 24, Profilbekken Member, section on Profilbekken, 61 m from base of Member.

Fig. 3. Pair of fused free cheeks of an immature specimen showing small genal spines, × 8. SMA 84253, locality as holotype, Fig. 1, 44 m from base of Profilbekken Member.

Figs. 5, 6, 8, 9. Pair of fused free cheeks in lateral, palpebral, anterior and ventral views. Note particularly absence of median or connective sutures on ventral view, Fig. 9. SMA 84259, Profilbekken Member of Profilbekken, limestone block derived from about 50 m from base of Member.

Fig. 7. Hypostoma, incomplete, but showing well the sculpture of terrace lines with scattered punctae, × 9. PMO NF 337, 50 m from base of Profilbekken Member, on Profilbekken.

Fig. 11. Incomplete small cranidium, × 10.5, palpebral view. Largely exfoliated, but showing typical sculpture of the species on right. PMO NF 1365, locality as holotype, Fig. 1, 52 m from base.

Fig. 10. *P. fistulosus* — *P. isoteloides* transient cranidium, flattened, × 7.5. PMO NF 1387. Note mixture of terrace lines and fine punctae near front of anterior border only. Profilbekken member, 30–31 m from base of Member on Profilbekken.

PLATE 15

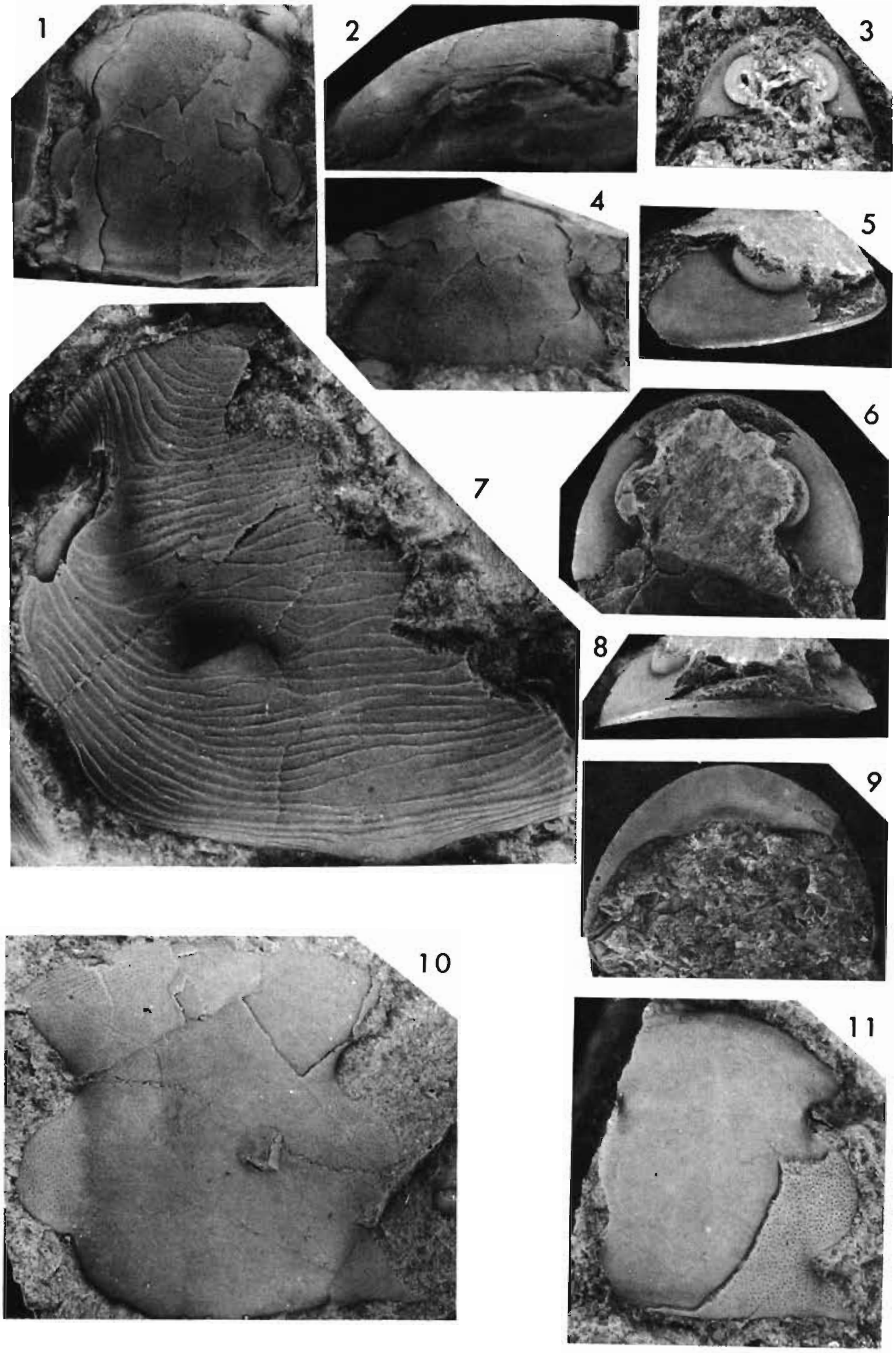


PLATE 16

Figs. 1–5, 7, 9, 10. *Poronileus isoteloides* n. gen., n. sp. .... (p. 55)

Fig. 1. Large pygidium, × $2\frac{1}{2}$, PMO NF 130, Profilbekken Member, higher part, 66 m from base of Member on Profilbekken. Note faint impression of pygidial axis on dorsal surface and contrast pygidium of *P. vallancei*, Pl. 18, Fig. 15.

Fig. 2. Pygidium, dorsal surface removed to show straight inner margin of doublure, × 3. SMA 84260, locality as pygidium, Fig. 1, 50 m from base of Member.

Figs. 3, 4. Small pygidium in posterior, × 3.5, and dorsal, × 6, views, PMO NF 339. Locality as previous specimen, 50 m from base of Profilbekken Member.

Fig. 5. Small pygidium showing presence of one unreleased thoracic segment, × 10. SMA 84255. Profilbekken Member, 54 m from base on Profilbekken.

Fig. 7. Large pygidium at natural size, exfoliated over a median area to show axis. SMA 84256, locality as last, 41 m from base of Profilbekken Member.

Fig. 9. Small pygidium, × 5, partly exfoliated to show muscle impressions on narrow axis, contrasting with *Nileus* species. SMA 84254, Profilbekken Member, 46 m from Base of Member on Profilbekken.

Fig. 10. Smallest pygidium, × 24. SMA 84258, 57 m from base of Profilbekken Member on Profilbekken.

Fig. 6. *Poronileus fistulosus* n. gen., n. sp. .... (p. 51)

Fig. 6. Flattened cranidium, preserved in a way that emphasises cephalic muscle impressions. PMO NF 2357. Profilbekken Member, upper part of range of species, 30 m from base on melt stream A on Olenidsletta.

Fig. 8. *Nileus glazialis costatus* n. subsp. .... (p. 41)

Fig. 8. Cranidium, palpebral view, to show pitted surface sculpture, × 10. PMO NF 1481 Olenidsletta Member, section on Profilstranda, 98 m from base of Member.

PLATE 16

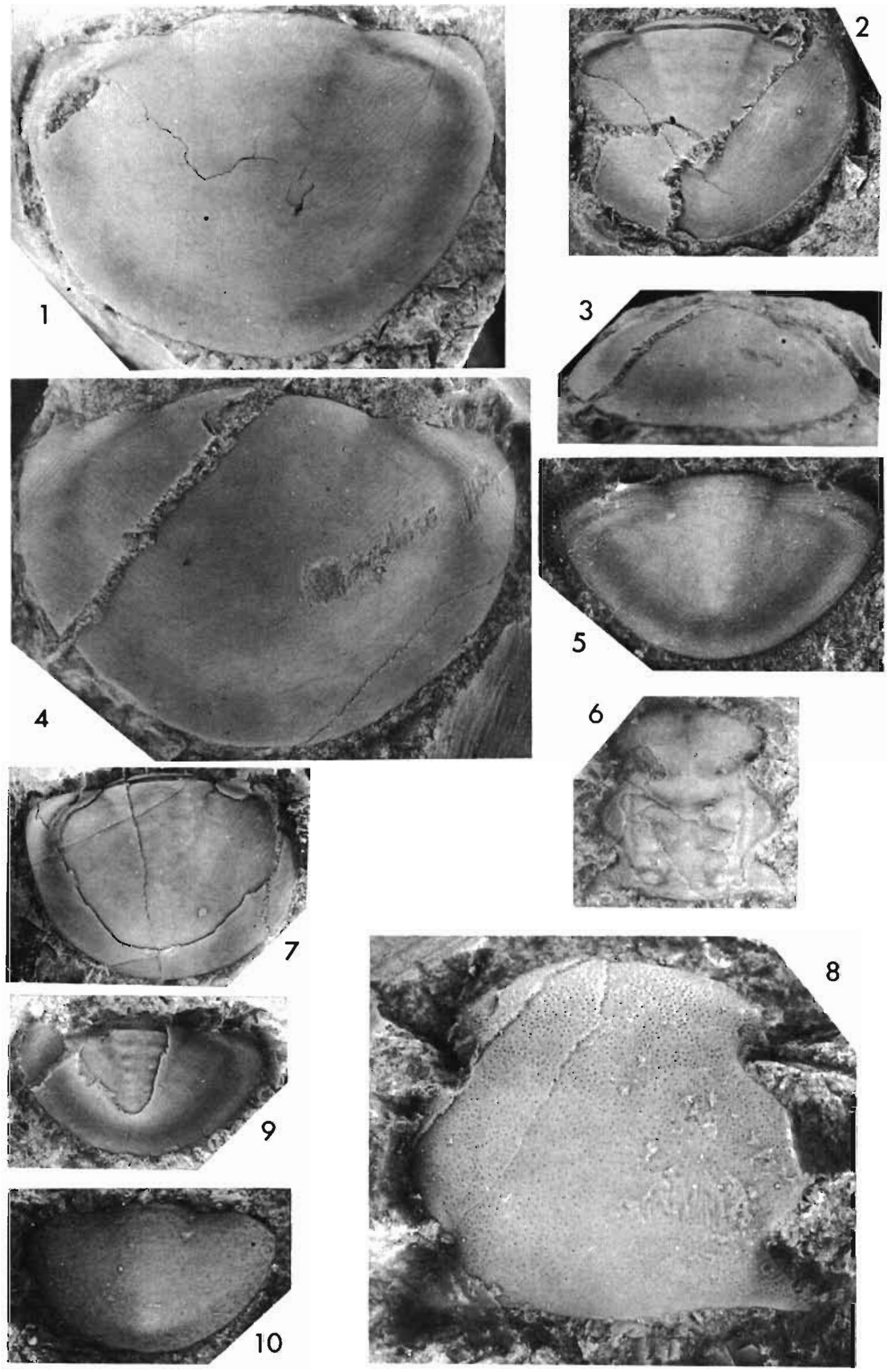


PLATE 17

Figs. 1–9. *Poronileus jugatus* n. gen., n. sp. .... (p. 59)

Figs. 1, 9. Cranidium partly preserving cuticle, and hardly flattened, palpebral view, × 3, detail of left anterior part of cranidium showing fine and scattered pits, × 10. PMO NF 2979, Olenidsletta Member, upper part, shore section on Olenidsletta, just south of stream A, about 130 m from base of Member.

Fig. 2. Latex cast of free cheek, × 3. PMO NF 2966, horizon and locality as holotype, Fig. 1.

Figs. 3, 7. Imperfectly preserved cranidium preserving natural convexity, in dorsal and lateral views, × 3. PMO NF 2977, area between melt streams A and B on Olenidsletta on shore, about 130 m from base of Olenidsletta Member.

Fig. 4. Detail of ocular region on free cheek, × 10, showing arrangement of lenses on eye, minutely pitted subocular "sensory zone" and scattered pits on dorsal surface of cheek. PMO NF 2967, from the same bed as holotype, Fig. 1.

Fig. 5. Internal mould of pygidium, × 3, showing axis and doublure. PMO NF 2955. Locality and horizon as cranidium, Fig. 1.

Figs. 6, 8. Latex cast of external mould of holotype pygidium in dorsal, lateral views, × 3. PMO NF 2964, horizon and locality as cranidium, Fig. 1.

PLATE 17

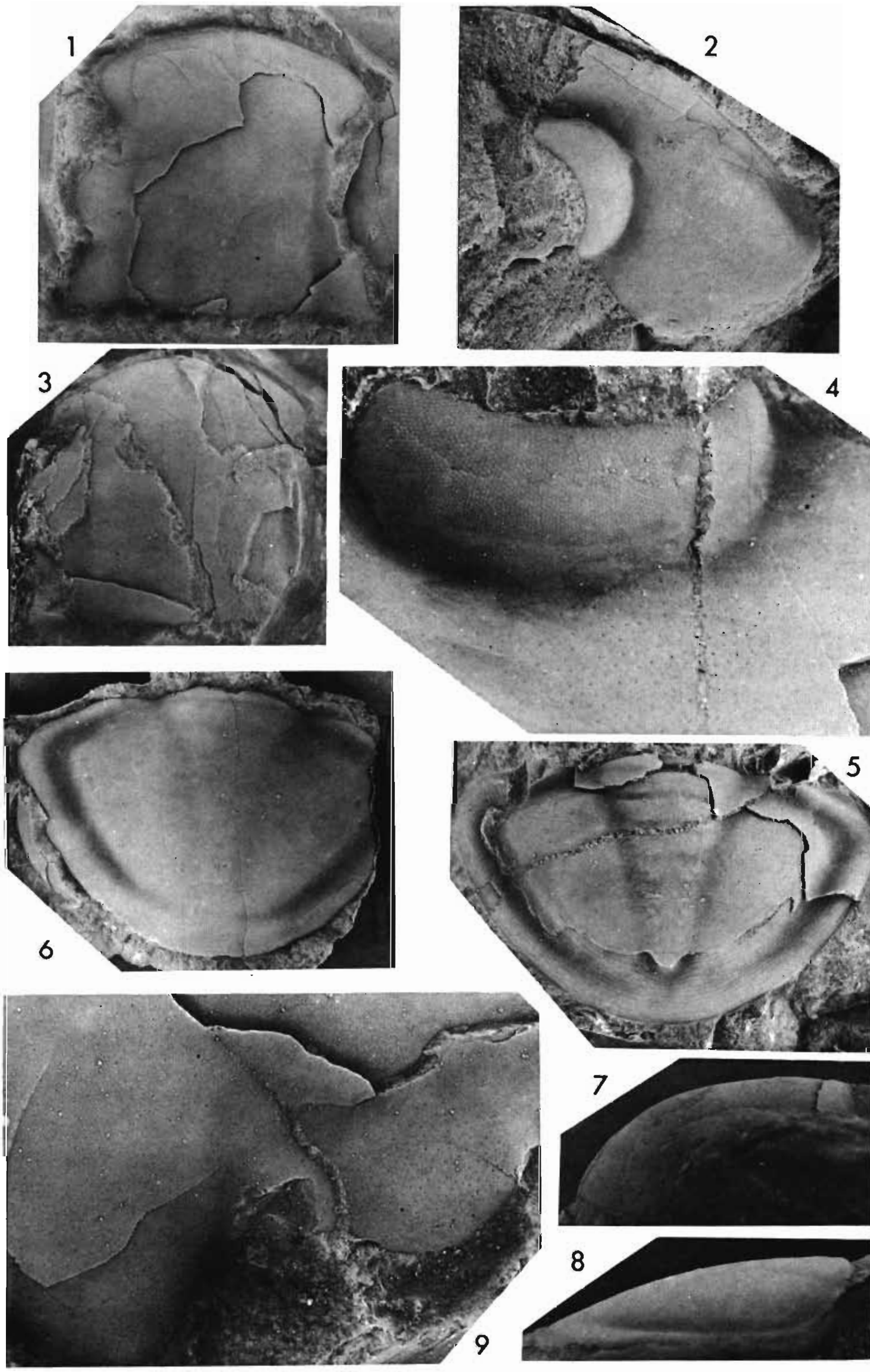


PLATE 18

Figs. 1–16. *Poronileus vallancei* n. gen., n. sp. .... (p. 57)

Figs. 1–3. Holotype, cranidium largely preserving cuticle, in palpebral anterior and lateral views, × 3. Outline of posterior section of facial suture well displayed on left. SMA 84263, Profilbekken Member, higher part, section on Profilbekken, 77 m from base.

Figs. 4–6. Small cranidium, in dorsal, palpebral and lateral views, × 4. SMA 84264, Profilbekken Member, locality as holotype, Fig. 1, 75 m from base.

Figs. 7–9. Fused pair of free cheeks, cuticle preserved on right side, dorsal, lateral and ventral views, showing lack of median sutures, × 3. See also Pl. 41, Fig. 4 for sculptural detail. SMA 84266, Profilbekken Member, locality as holotype, Fig. 1, 85 m from base.

Fig. 10. Detail of right palpebral lobe of holotype, Fig. 1, × 15, showing minute, scattered punctae characteristic of species.

Fig. 11. Internal mould of pygidium, × 4, showing faint outline of axis with muscle impressions and paradoublural line. Locality as pygidium, Fig. 14, about 67 m from base of Profilbekken Member, PMO NF 1350.

Figs. 12–13. Cranidium, internal mould, Fig. 13 palpebral view, × 4, Fig. 12 mid-posterior part, × 8, showing glabellar "tubercle", median ridge running forwards from it, and transversely directed depressions (thickened bars on internal surface of cuticle) on either side of ridge. SMA 84267, horizon and locality as small cranidium, Fig. 2.

Figs. 14, 15. Latex cast of external mould of pygidium, × 2.5, right lateral and dorsal views, showing smooth exterior. PMO NF 1355, Profilbekken Member, section immediately south of Profilbekken, about 67 m from base of Member.

Fig. 16. Pygidium with dorsal exoskeleton removed to show details of doublure, × 2.5. PMO NF 1345, locality as previous specimen.

PLATE 18

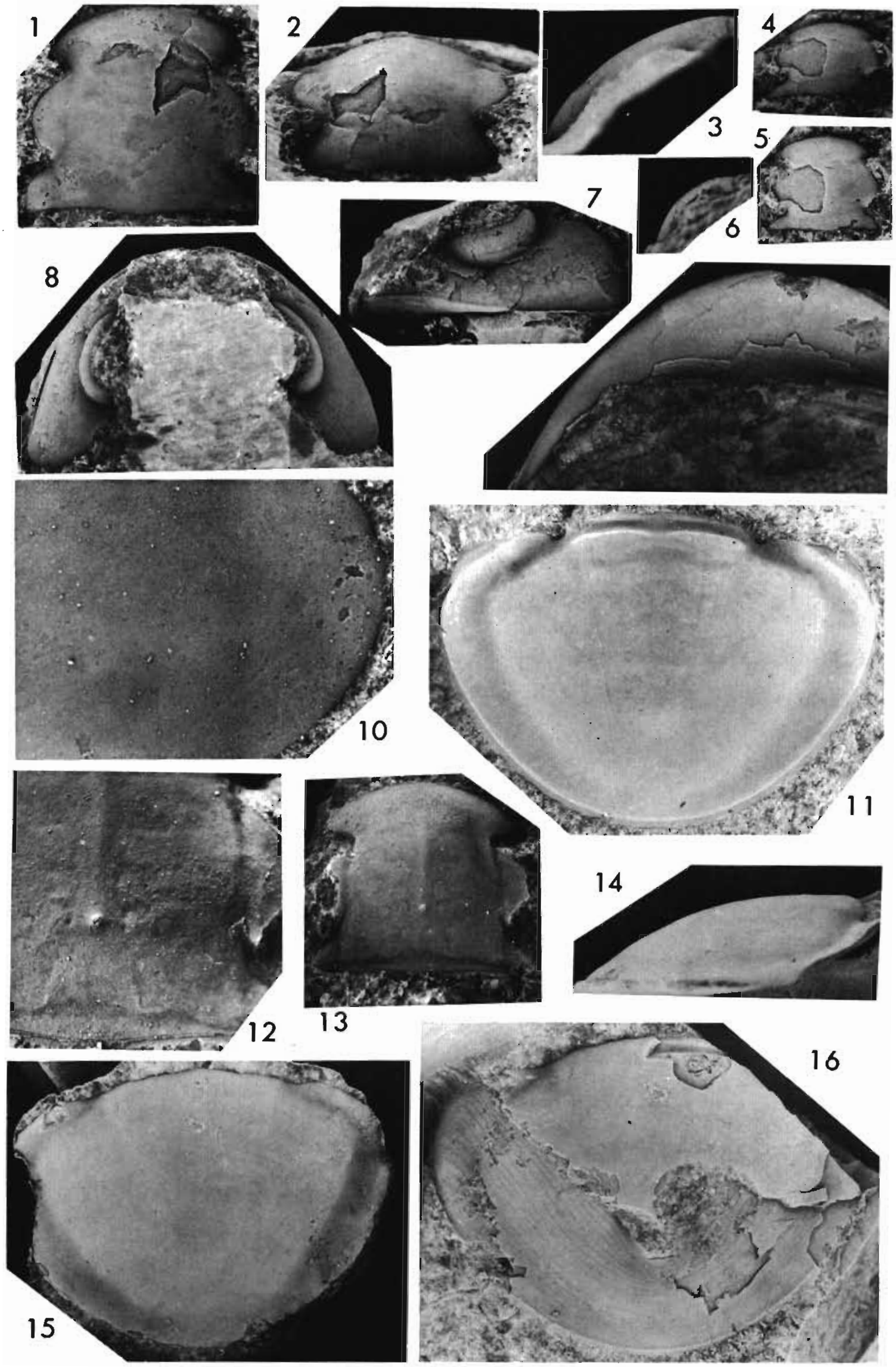


PLATE 19

Figs. 1–9, 11. *Peraspis erugata* Ross 1970 .... (p. 47)

Fig. 1. Almost complete dorsal exoskeleton, slightly crushed, × 4. SMA 84304, Profilbekken Member, section on Profilbekken 39 m from base of Member.

Fig. 2. Pygidium showing doublure and faint pleural ribbing, × 2. SMA 84305. Locality as exoskeleton, Fig. 1, 50 m from base of Member.

Fig. 3. Latex cast of external mould of fused free cheeks, × 3. SMA 84306, lower part of Profilbekken Member, shore section on Profilstranda south of Profilbekken, about 20 m from base of Member.

Figs. 4, 8. Fused free cheeks with hypostoma almost in place, part and counterpart, × 6. Note relation of anterior wing of hypostoma to cephalic doublure. SMA 84307, horizon and locality as previous specimen.

Figs. 5–7. Pygidium, preserving cuticle, dorsal, lateral, posterior views, × 4. SMA 84308, Profilbekken Member, 43 m from base of Member on Profilbekken.

Fig. 9. Incomplete cranidium showing faint outward-bowed axial furrows, × 6. SMA 84309, Profilbekken Member, horizon and locality as free cheeks, Fig. 3.

Fig. 11. Pygidium showing surface sculpture of fine terrace lines, × 6. PMO NF 332a, higher part of Profilbekken Member, 54 m from base of Member on Profilbekken.

Fig. 10. *Symphysurus* (*Kodymaspis*) *puer* (BARRANDE 1872). .... (p. 51)

Fig. 10. Cephalon and first thoracic segment, × 2.5. Cast of specimen illustrated by PRANTL and PŘIBYL 1949, Pl. II, Fig. 1.

PLATE 19

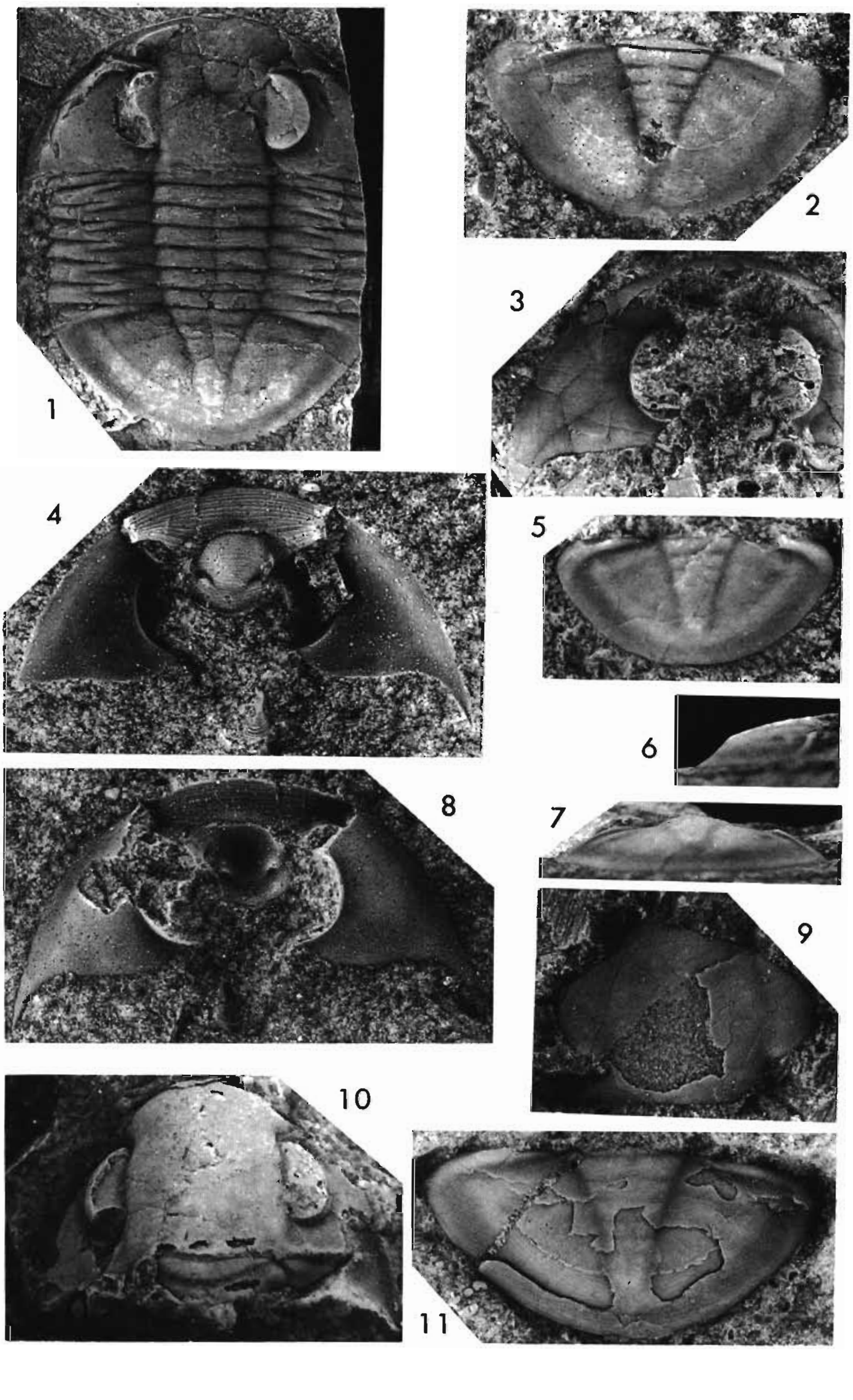


PLATE 20

Figs. 1–11. *Peraspis omega* n. sp. .... (p. 49)

Fig. 1. Holotype, cranidium preserving cuticle, left anterior slightly distorted, × 4. PMO NF 374, Olenidsletta Member, upper part, section on Olenidsletta between melt streams A and B, about 115 m from base of Member.

Fig. 2. Free cheek, preserving cuticle showing fine terrace lines, × 4. PMO NF 365, from the same bed as holotype cranidium, Fig. 1.

Figs. 3, 5. Internal mould of cranidium, showing "tubercle" and internal impressions, palpebral, × 3, and lateral, × 2, views. PMO NF 3150, Olenidsletta Member, upper part, shore section on Profilstranda, about 130 m from base of Member.

Fig. 4. Small free cheek, which still retains genal spine, × 2. PMO NF 3151, horizon and locality as cranidium on previous figure.

Fig. 6. Hypostoma, × 10, PMO NF 364, horizon and locality as holotype, Fig. 1.

Figs. 7, 8. Pygidium, exfoliated, in dorsal and lateral views, × 2.5. SMA 84313, upper part of Olenidsletta Member from shore section on Profilstranda, about 140 m from base of Member.

Fig. 9. Latex cast of external mould of pygidium, showing fine terrace lines, × 3. PMO NF 2978, upper part of Olenidsletta Member, shore section between melt streams A and B about 130 m from base of Member.

Fig. 10. Exfoliated pygidium showing outline of doublure, × 1.5. PMO NF 376, Olenidsletta Member, upper part, exposed on shore between melt streams A and B on Olenidsletta, about 115 m from base of Member.

Fig. 11. Latex cast of pygidium and five incomplete thoracic segments, × 3.5. PMO NF 2969, same bed as pygidium, Fig. 9.

PLATE 20

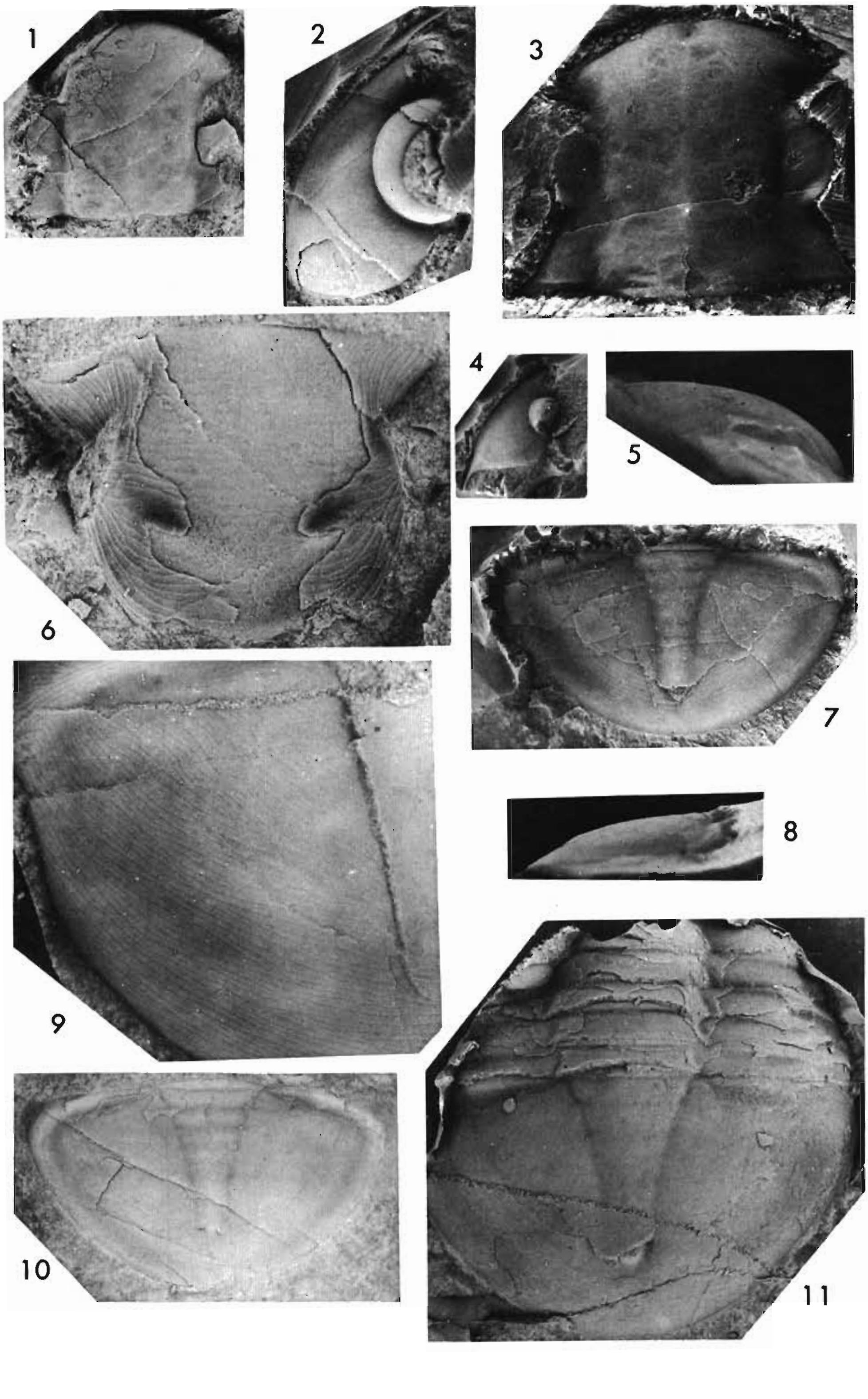


PLATE 21

Figs. 1–16. *Symphysurus arcticus* n. sp. .... (p. 60)

Figs. 1–3. Cranidium preserving cuticle, × 7, in palpebral, anterior and lateral views. PMO NF 3165, Olenidsletta Member, shore section on Profilstranda, 86 m from base of Member.

Fig. 4. Free cheeks preserving external mould of hypostoma in life position, × 5. PMO NF 2118, Olenidsletta Member, melt stream B on Olenidsletta, about 96 m from base of Member.

Fig. 5. Detail of internal mould of pygidium from internal mould of dorsal exoskeleton lacking free cheeks, showing caeca, × 10. PMO NF 2642, melt stream B on Olenidsletta, about 86 m from base of Olenidsletta Member.

Fig. 6. Holotype, dorsal exoskeleton lacking free cheeks, largely exfoliated, × 3. Note how pygidium is slightly detached from thorax suggesting moult arrangement (compare FORTEY 1975, Fig. 8). PMO NF 538, Olenidsletta Member, shore section on Profilstranda, 90 m from base of Member.

Fig. 7. Complete but flattened dorsal exoskeleton, × 3. PMO NF 2014, melt stream E on Olenidsletta, exact horizon in Olenidsletta Member unknown.

Fig. 8. Pygidium preserving cuticle, relative length and extent of posterior border furrow suggests transitional form between *S. arcticus* and *Poronileus jugatus* n. gen., n. sp., × 3. PMO NF 1670, Olenidsletta Member, shore section on Profilstranda, 97 m from base of Member.

Fig. 9. Hypostoma, PMO NF 3161, × 10. Horizon and locality as cranidium, Fig. 13.

Figs. 10, 12. Pygidium, immature, in posterior (× 10) and dorsal view, × 16. Note well-defined posterior border. PMO NF 3164, Olenidsletta Member, shore section on Profilstranda, 86 m from base of Member.

Fig. 11. Hypostoma, immature, × 10. PMO NF 3161a, locality and horizon as previous two, and following two specimens, on same rock fragment as the larger hypostoma, Fig. 9.

Fig. 13. Small cranidium retaining cuticle, palpebral view, × 25. Note the retention of the characteristic sigmoidal outline of posterior section of facial suture even at this size. Olenidsletta Member, shore section on Profilstranda, with the other small growth stages illustrated here (except Fig. 16) from a single bed, 86 m from base of Member. PMO NF 3162.

Figs. 14, 15. Smallest cranidium showing weakly defined axial furrows, in palpebral and lateral views, × 12.5. PMO NF 3163, locality see cranidium, Fig. 13.

Fig. 16. Degree 6 meraspide, × 6. Like the holotype, Fig. 6, this specimen lacks free cheeks and may represent a moulted exoskeleton. Indications of seventh segment in anterior part of pygidium. SMA 84293, Olenidsletta Member, locality as holotype, Fig. 6, about 80 m from base.

PLATE 21

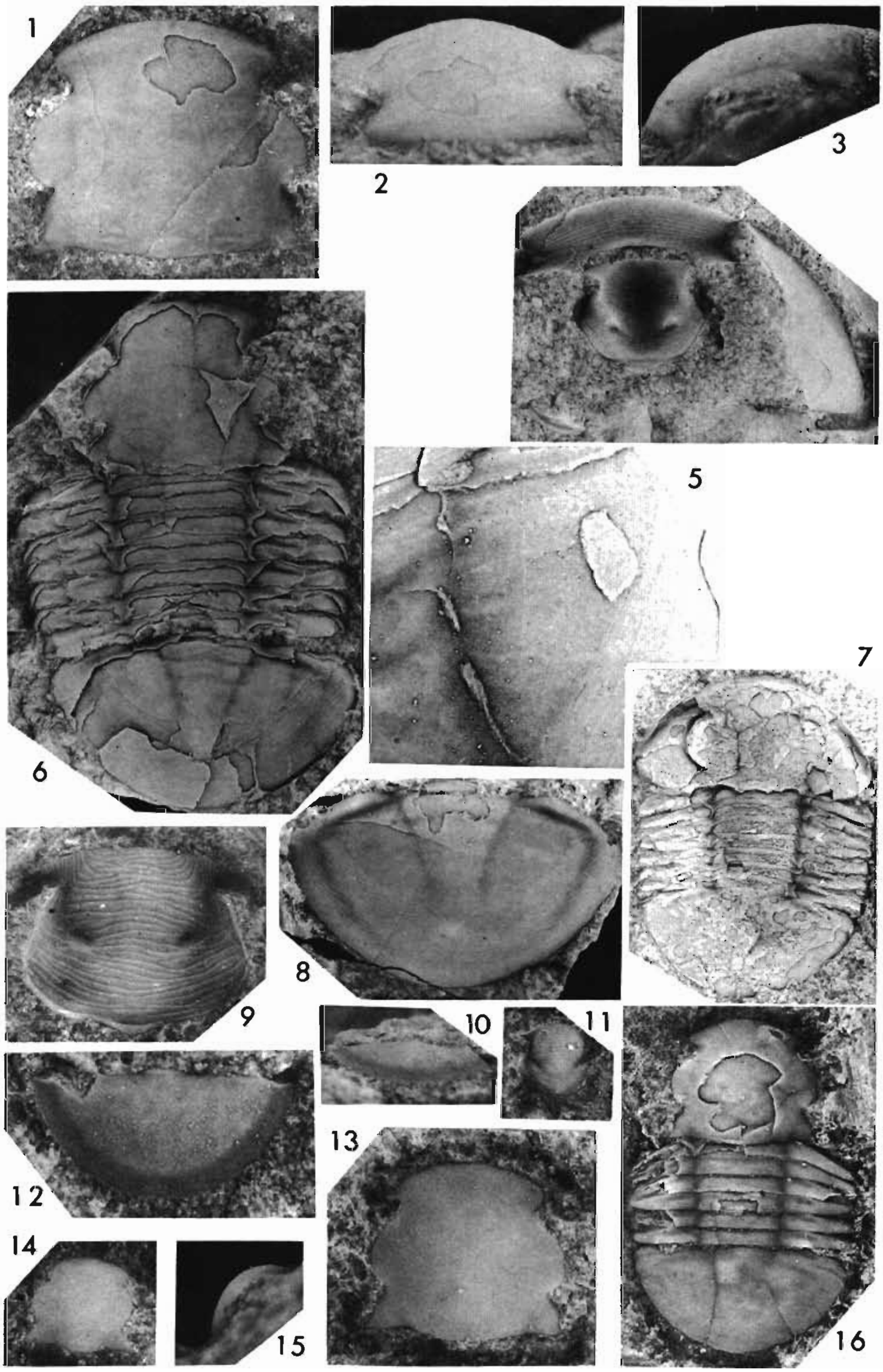


PLATE 22

Figs. 1–10. *Ampyx spongiosus* n. sp. .... (p. 67)

Figs. 1, 2, 7. Incomplete cranidium, preserving cuticle, in anterior, × 4, and fossular, × 6, views. Note pair of genal ridges reflected as relatively smooth areas on dorsal surface. Fig. 7, detail of left lateral side of glabella, occipital ring uppermost. 1, 2, 3 muscle impressions preserved as smooth areas on exoskeleton (3 may be bicomposite), BACC — baccula, PAR — Paraglabellar area of fine pitting, possibly an additional muscle impression, FOS — anterior fossula. PMO NF 436, Olenidsletta Member, shore section on Profilstranda, 90 m from base of Member.

Fig. 3. Hypostoma preserving cuticle, × 7. PMO NF 406, locality as cranidium Figs. 1, 2, 90 m from base of Olenidsletta Member.

Fig. 4. Hypostoma, internal mould, × 6. PMO NF 408, horizon and locality as previous specimen.

Figs. 5, 8. Internal mould of cranidium, in lateral and fossular views, × 3. Declined anterior spine, and 1P and 2P muscle impressions shown. SMA 84139, Olenidsletta Member, locality as previous specimens, 85 m from base of Member.

Fig. 6. Free cheek, × 1.5. PMO NF 1768, isolated limestone block on Olenidsletta derived from interval 80–90 m from base of Olenidsletta Member.

Figs. 9, 10. Internal mould of pygidium preserving muscle impressions, dorsal, posterior views, × 3. Note small furrow running from posterior limit of axis to border on mid-line. SMA 84140, locality as cranidium, Figs. 1, 2, about 78 m from base of Olenidsletta Member.

PLATE 22

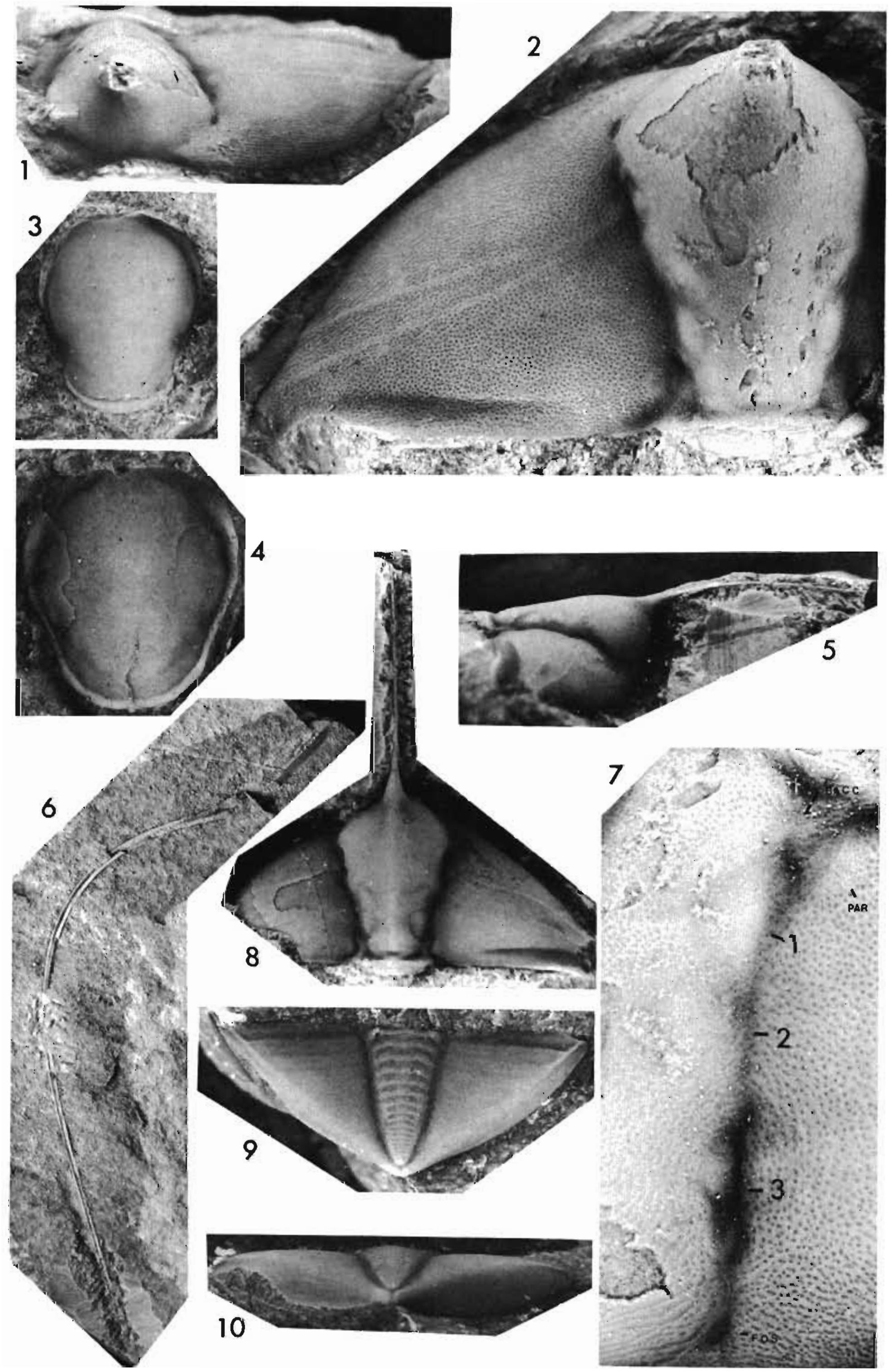


PLATE 23

Figs. 1, 3, 4, 5. *Ampyx spongiosus* n. sp. .... (p. 67)

Figs. 1, 3, 5. Pygidium preserving cuticle in dorsal, posterior views, × 7. Fig. 5, detail of axis, × 14, showing muscle impressions developed as smooth areas on axis. PMO NF 440, from same bed as cranidium, Pl. 22, Figs. 1, 2.

Fig. 4. Latex cast of holotype, dorsal exoskeleton lacking free cheeks, × 2. Details of dorsal surface not well preserved. PMO NF 2021, Olenidsletta Member, melt stream E on Olenidsletta, precise horizon not known, probably 80–90 m from base of Member.

Fig. 2. *Ampyx volborthi* SCHMIDT. .... (p. 69)

Fig. 2. Detail of part of the pygidium figured by SKJESETH 1952, Pl. V, Fig. 11, × 8, for comparing surface sculpture with that of *A. spongiosus* n. sp. PMO 6631.

Fig. 7. *Pytine graia* n. gen., n. sp. .... (p. 89)

Fig. 7. Flattened dorsal exoskeleton lacking free cheeks and largely preserved as an internal mould, × 8. PMO NF 2638, melt stream B on Olenidsletta, 86 m from base of Olenidsletta Member.

Fig. 8. *Niobe occulta* n. sp. .... (p. 30)

Fig. 8. Incomplete hypostoma, ventral view, × 5. PMO NF 107, shore section on Profilstranda, 103 m from base of Olenidsletta Member.

PLATE 23

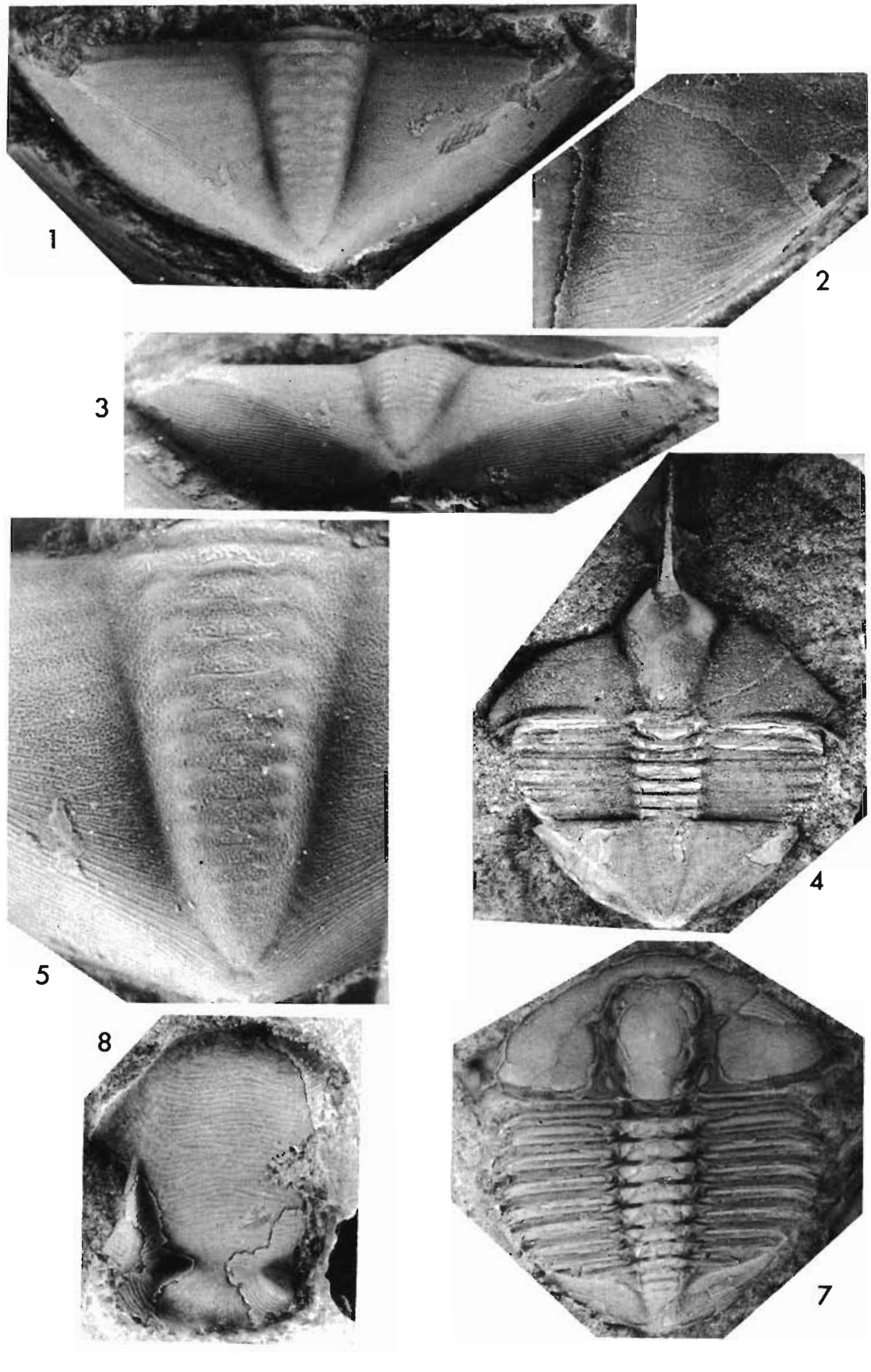


PLATE 24

Figs. 1–8. *Ampyx porcus* n. sp. .... (p. 70)

Figs. 1, 2. Holotope, dorsal exoskeleton lacking free cheeks, exfoliated over cranidium, × 10, anterior view × 5. PMO NF 502, Olenidsletta Member, shore section on Profilstranda, 86 m from base of Member.

Fig. 3. Latex cast of (largely) external mould of exoskeleton lacking free cheeks, × 6. PMO NF 2745, Olenidsletta Member, melt stream B on Olenidsletta, about 80 m from base of Member.

Figs. 4, 5, 8. Cranidium preserving exoskeleton except for small area on mid-part of glabella. Fig. 4, fossular view, × 11; Fig. 5 lateral (slightly oblique) view, × 18, showing depressed area on side of glabella representing confluent 1P and 2P glabellar furrows, surface sculpture and attitude of anterior spine; Fig. 8, × 10, posterior view showing lack of inflation of glabella in occipital region. PMO NF 511, horizon and locality as holotype, Fig. 1.

Figs. 6, 7. Pygidium retaining cuticle in dorsal and posterior views, × 10. PMO NF 1659, locality as holotype, 97 m from base of Olenidsletta Member.

PLATE 24

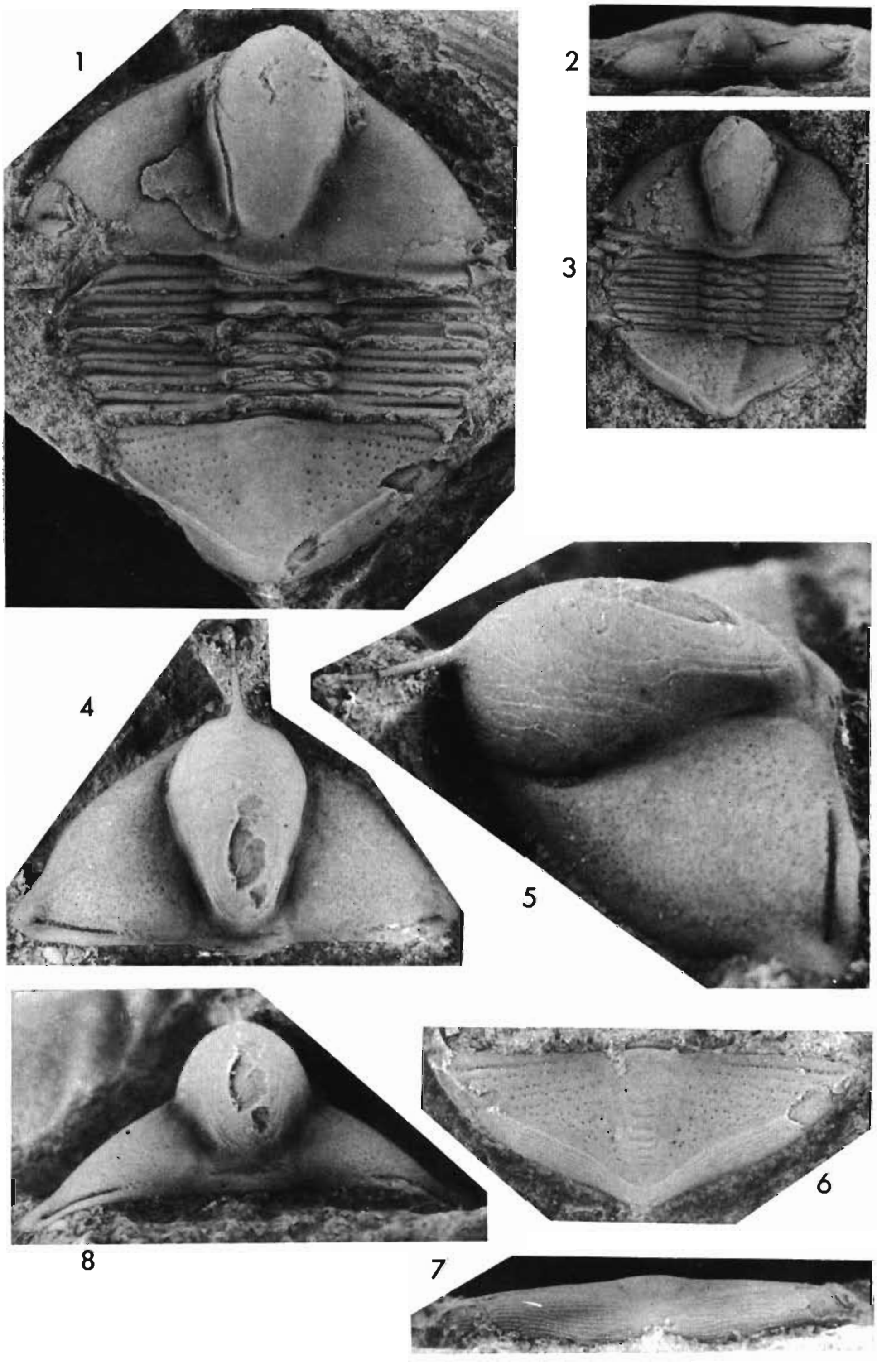


PLATE 25

Figs. 1–7. *Ampyx delicatulus* n. sp. .... (p. 72)

Fig. 1. Imperfectly preserved dorsal exoskeleton, exfoliated, × 5. Olenidsletta Member, upper part, shore section on Profilstranda, 102 m from base of Member, PMO NF 80.

Figs. 2, 3. Holotype, cranidium with three thoracic segments, Fig. 2, fossular view × 5, Fig. 3, details of left fixed cheek showing distinctive sculpture, × 20. PMO NF 1, horizon and locality as exoskeleton, Fig. 1.

Figs. 4, 7. Cranidium, largely exfoliated, in fossular, lateral views, × 8. Note upward-curving anterior spine contrasting with those of *A. spongiosus* and *A. porcus* above. PMO NF 77, locality as exoskeleton, Fig. 1, 103 m from base of Olenidsletta Member.

Figs. 5, 6. Latex cast of internal mould of pygidium in dorsal and posterior views, × 10. PMO NF 2234, Olenidsletta Member, upper part, melt stream B on Olenidsletta, about 101 m from base of Member.

PLATE 25

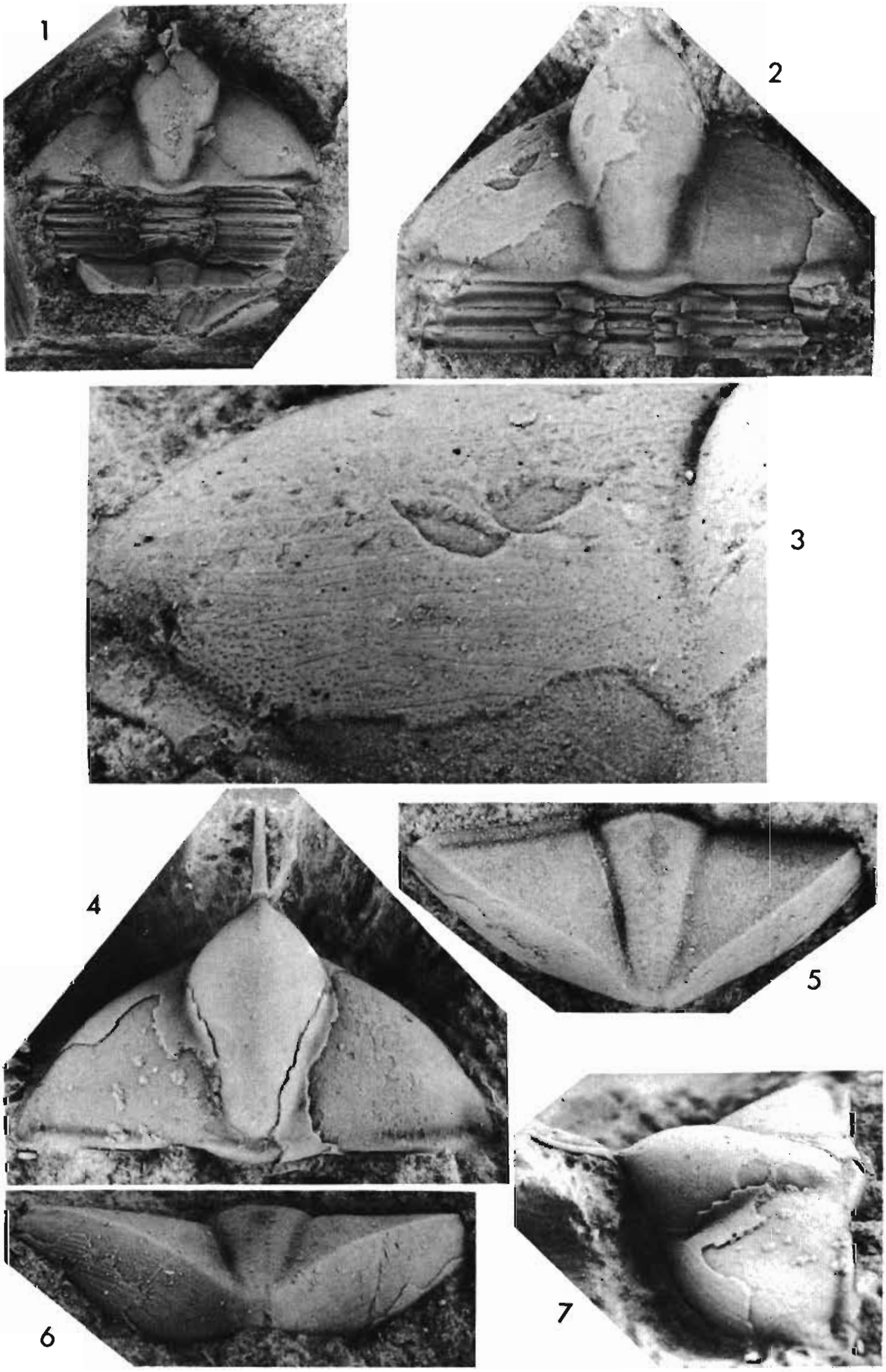


PLATE 26

Figs. 1–11. *Ampyx toxotis* n. sp. .... (p. 73)

Figs. 1, 2, 5. Holotype, exfoliated cranidium, in dorsal, right lateral and fossular views, × 12.5. PMO NF 261, lower part of Profilbekken Member, shore section on Profilstranda, about 20 m from base of Member.

Figs. 3, 4. Incomplete cranidium preserving frontal spine, fossular, lateral views, × 9. PMO NF 189, horizon and locality as holotype cranidium, Fig. 1.

Figs. 6, 7. Pygidium, internal mould, dorsal and posterior views, × 10. PMO NF 281, horizon and locality as holotype cranidium, Fig. 1.

Figs. 8, 10. Cranidium preserving cuticle, Fig. 10, dorsal view, × 12; Fig. 8, × 24, detail of left fixed cheek showing sculpture of very fine terrace lines. PMO NF 1330. Limestones from lower part of Profilbekken Member, isolated outcrop adjacent to Profilbekken, exact horizon undetermined.

Figs. 9, 11. Exfoliated cranidium, fossular and anterior views, × 10. PMO NF 1321, locality as previous specimen. Anterior border shown by narrow, median horizontal part adaxial to sutures.

PLATE 26

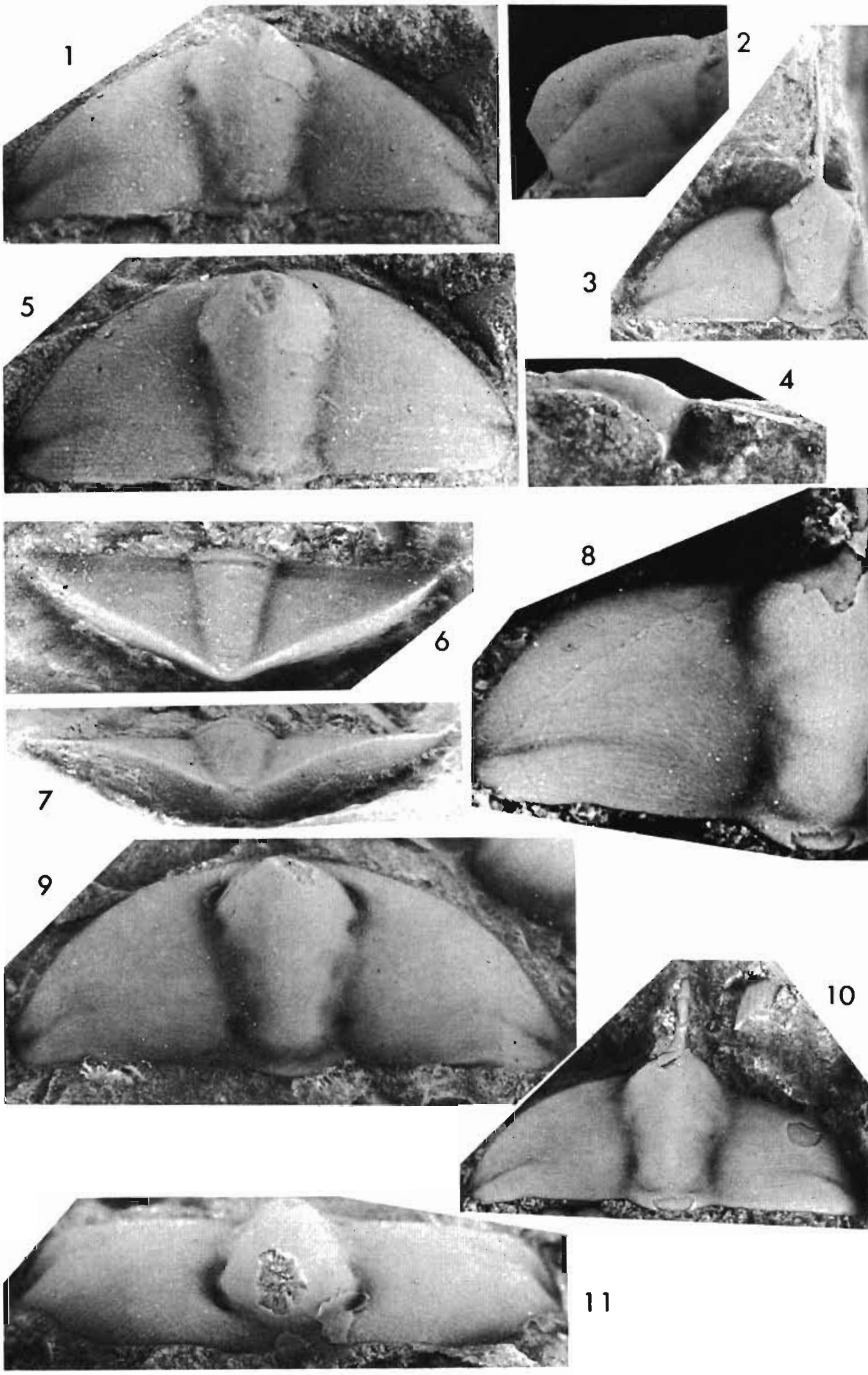


PLATE 27

Figs. 1–10. ***Rhombampyx rhombos*** n. gen., n. sp. .... (p. 83)

Fig. 1. Holotype, dorsal exoskeleton lacking free cheeks, × 10. SMA 84143, Profilbekken Member, 32 m from base of Member on Profilbekken.

Figs. 2, 6, 7. Small exfoliated cranidium, dorsal, lateral, anterior views, × 12. SMA 84144, Profilbekken Member, 30 m from base on Profilbekken.

Figs. 3, 4. Large cranidium retaining patch of cuticle on right hand side. Fig. 3, palpebral view, × 10; Fig. 4, lateral view, × 5. SMA 84145, locality and horizon as cranidium, Fig. 2.

Fig. 5. Large pygidium in dorsal view, cuticle preserved on left hand side, muscle impressions well shown on axis, × 14. PMO NF 1192. Locality as holotype, Fig. 1.

Figs. 8, 9. Small pygidium preserving cuticle, dorsal, posterior views, × 15, SMA 84146. Same bed as holotype, Fig. 1.

Fig. 10. Slightly flattened cranidium, × 10. PMO NF 1378, 40 m from base of Profilbekken Member on Profilbekken.

PLATE 27

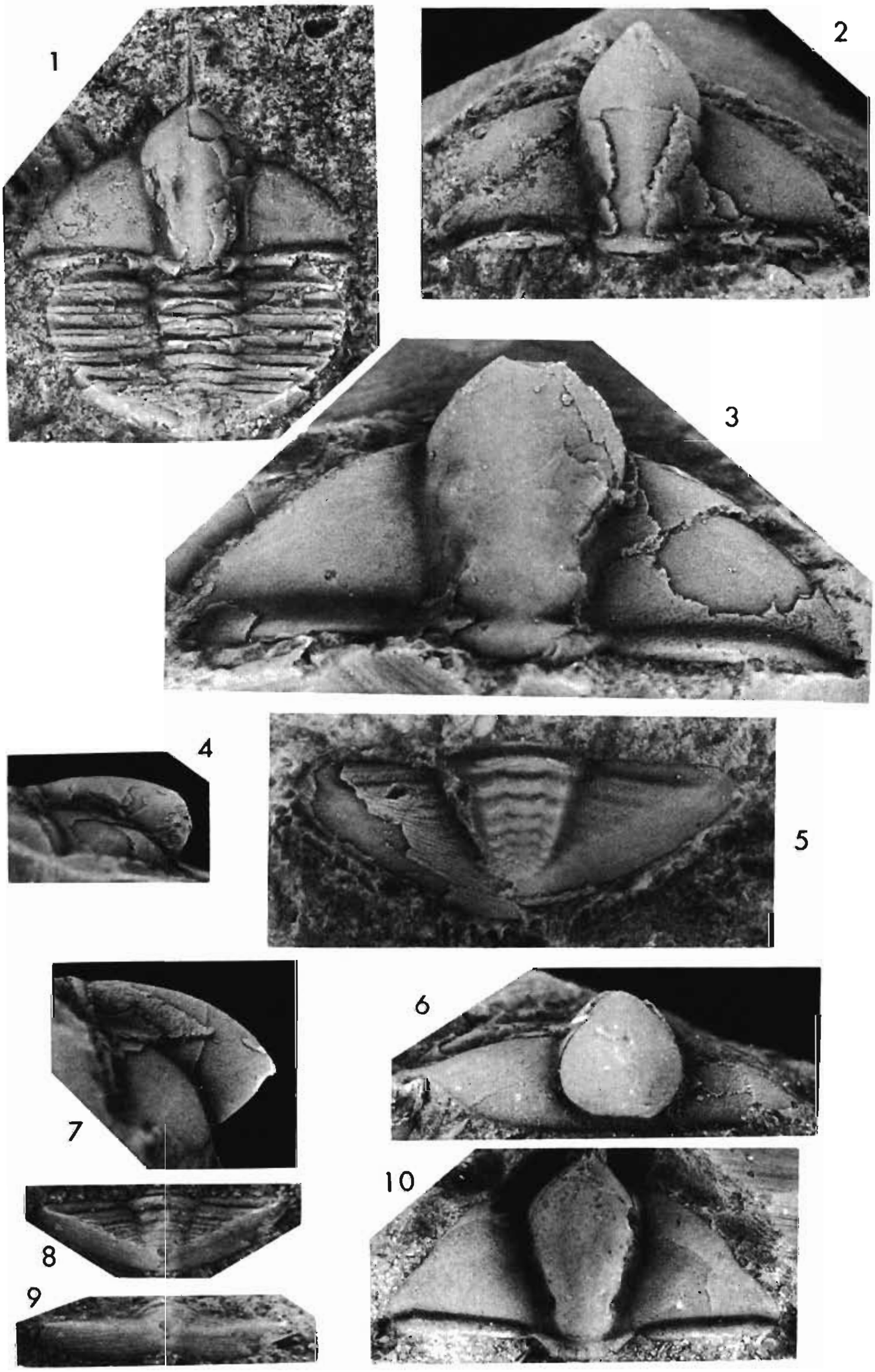


PLATE 28

Figs. 1–9. ***Rhombampyx*** *tragula* n. gen., n. sp. . . . . (p. 85)

Figs. 1–5. Holotype, large incomplete cranidium. Figs. 2–5, internal mould, fossular, anterior and lateral views, × 8. Fig. 5 side of glabella to show muscle impressions and fine pitting, × 12. PMO NF 2476. Fig. 1, latex cast from counterpart, PMO NF 2459, to show frontal spine. Lower part of Profilbekken Member, melt stream A on Olenidsletta, 23 m from base of Profilbekken Member.

Fig. 6. Hypostoma, internal mould, × 12. PMO NF 2427, same bed as holotype, Figs. 1–5.

Fig. 7. Internal mould of cranidium, × 10. PMO NF 2412a. Same bed as holotype, Fig. 1.

Figs. 8, 9. Incomplete internal mould of cranidium, fossular, lateral views, × 6. PMO NF 3154, same bed as holotype, Figs. 1–5.

PLATE 28

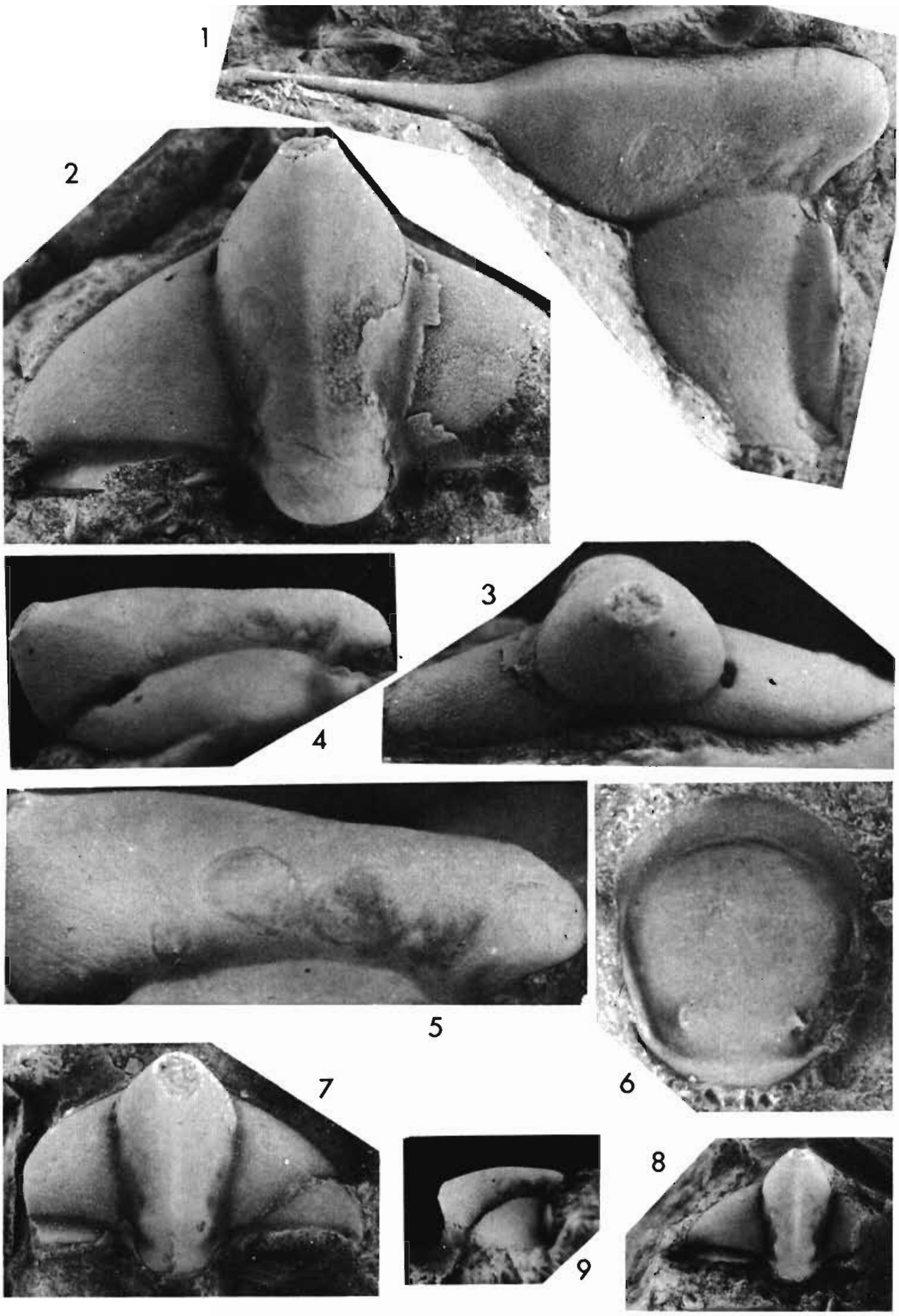


PLATE 29

Figs. 1–21. *Globampyx trinucleoides* n. gen., n. sp. .... (p. 76)

Figs. 1–3. Well preserved cranidium showing pitting, fossular, anterior and lateral views, × 15. PMO NF 334, Profilbekken Member, 50 m from base of Member on Profilbekken.

Figs. 4, 5, 7, 10. Holotype, internal mould of dorsal exoskeleton lacking free cheeks, dorsal, × 6, oblique and lateral views, × 5; Fig. 10 detail of lateral view, showing muscle impressions, minute scattered pits on the internal mould of the glabella and apparent horizontal "rim" around the margin of the cheek (see p. 77). SMA 84152, Profilbekken Member, 33 m from base on Profilbekken.

Figs. 6, 8. Internal mould of cranidium, fossular, anterior views. PMO NF 314. Lower 20 m of Profilbekken Member, shore section on Profilstranda.

Fig. 9. Transitory pygidium, × 20, SMA 84159. Locality as holotype, Fig. 4, 50 m from base of Profilbekken Member.

Fig. 11. Poorly preserved complete exoskeleton, showing free cheeks, × 5. Isolated limestone block on Olenidsletta, originally from Profilbekken Member, PMO NF 1762.

Figs. 12, 15. Small pygidium, dorsal, posterior views, × 10, PMO NF 3157, locality as holotype, Fig. 4, 40 m from base of Profilbekken Member.

Figs. 13, 14. Pygidium, dorsal, posterior views, × 10. PMO NF 3158, same bed as preceding specimen.

Fig. 16. Latex cast of fused free cheeks, × 6. Note posterior band carrying fine terrace lines. PMO NF 3326, Profilbekken Member, 54 m from base on Profilbekken.

Figs. 17, 18. Internal mould of pygidium, dorsal, posterior views, × 12. PMO NF 1369, locality as holotype, Fig. 4, 51 m from base of Profilbekken Member.

Fig. 19. Stratigraphically earliest cranidium, internal mould, × 10. Olenidsletta Member, shore section on Profilstranda 135 m from base of Member, SMA 84153.

Figs. 20, 21. Immature cranidium in fossular, anterior views, × 20. Note presence of small eye ridges. SMA 84160, locality as holotype, Fig. 4, 53 m from base of Profilbekken Member.

PLATE 29

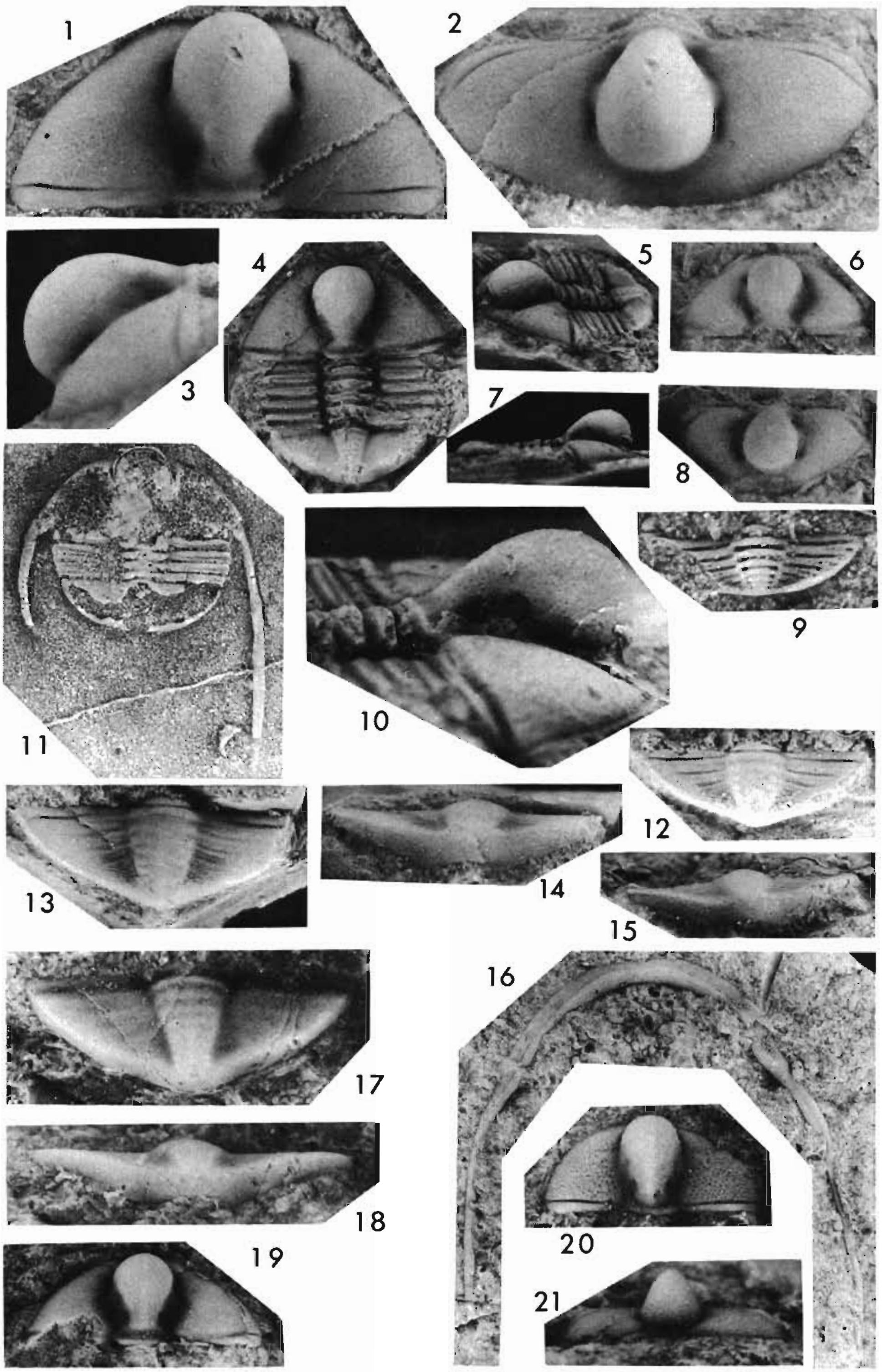


PLATE 30

Figs. 1–9. *Mendolaspis doidyx* n. sp. .... (p. 80)

Fig. 1. Holotype, dorsal exoskeleton lacking free cheeks, slightly crushed, × 4. PMO NF 1283, Olenidsletta Member, shore section on Profilstranda, about 85 m from base of Member.

Figs. 2, 3, 5, 8. Cranidium preserved in full relief, internal mould showing glabellar furrows, fossular, lateral and anterior views, × 6; Fig. 8, detail of anterior part of glabella showing minute tubercle (t) in position homologous to that of anterior spine in other Raphiophorinae, beneath which there is a triangular area of ? muscle scars, × 24. PMO NF 505, locality as holotype, Fig. 1, 86 m from base of Olenidsletta Member.

Fig. 4. Internal mould of cranidium and four incomplete thoracic segments; oblique light to emphasise glabellar furrows, × 10. PMO NF 504, locality as holotype, Fig. 1, 86 m from base of Olenidsletta Member.

Figs. 6, 7. Internal mould of pygidium in full relief, dorsal and posterior views, PMO NF 3152, Olenidsletta Member, locality as holotype Fig. 1, 80 m from base of Olenidsletta Member.

Fig. 9. Detail of right anterior fixed cheek taken from a flattened dorsal exoskeleton lacking free cheeks, SMA 84162, preserving very thin cuticle and caeca anteriorly, × 9. Locality as holotype, Fig. 1, about 85 m from base of Olenidsletta Member.

Figs. 10–15. *Ampyxoides inermis* n. sp. .... (p. 74)

Figs. 10–12. Holotype, small internal mould of a cranidium, in anterior, fossular and oblique lateral views, × 15. Lowest bed of Profilbekken Member on melt stream A, Olenidsletta. PMO NF 1825.

Figs. 13, 14. Cranidium, internal mould, imperfectly preserved on left side, in lateral and fossular views, × 10. PMO NF 1870, locality and horizon as holotype, Figs. 10–12.

Fig. 15. Pygidium, internal mould, × 10. PMO NF 1826, same bedding plane as preceding cranidium.

PLATE 30

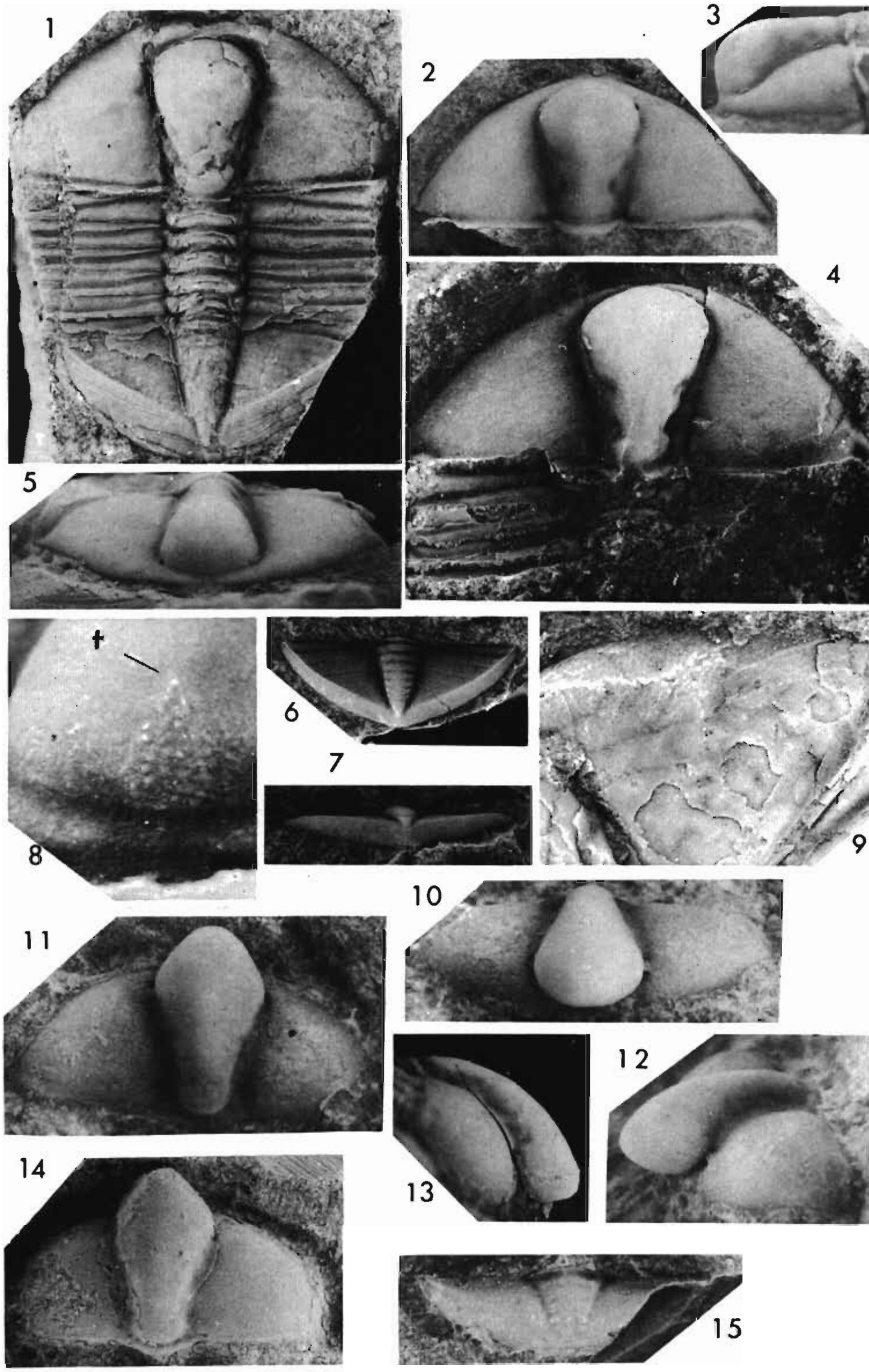


PLATE 31

Figs. 1–11. *Pytine graia* n. gen., n. sp. .... (p. 89)

Figs. 1–4. Holotype, dorsal exoskeleton preserved in relief but lacking free cheeks, PMO NF 40, dorsal, × 13, oblique lateral and anterior views, × 6.5. Fig. 4, posterior view of pygidium, × 20. Olenidsletta Member, shore section on Profilstranda, 102 m from base of Member.

Figs. 5–7. Internal mould of cranidium in fossular, lateral and anterior views × 10, PMO NF 2639, Olenidsletta Member, melt stream B on Olenidsletta, 86 m from base of Olenidsletta Member.

Fig. 8. Two incomplete dorsal exoskeletons, the upper of the two preserving the genal spine on the right hand side, × 2, PMO NF 1936, isolated limestone block derived from the Olenidsletta Member.

Figs. 9–11. Well-preserved cranidium, preserving cuticle, in fossular and anterior views, × 10. Note narrow (trans.) anterior border. Fig. 11, detail of mid-part of glabella showing tubercle, × 40. PMO NF 2153, Olenidsletta Member, melt stream B on Olenidsletta, about 96 m from base of Member.

PLATE 31

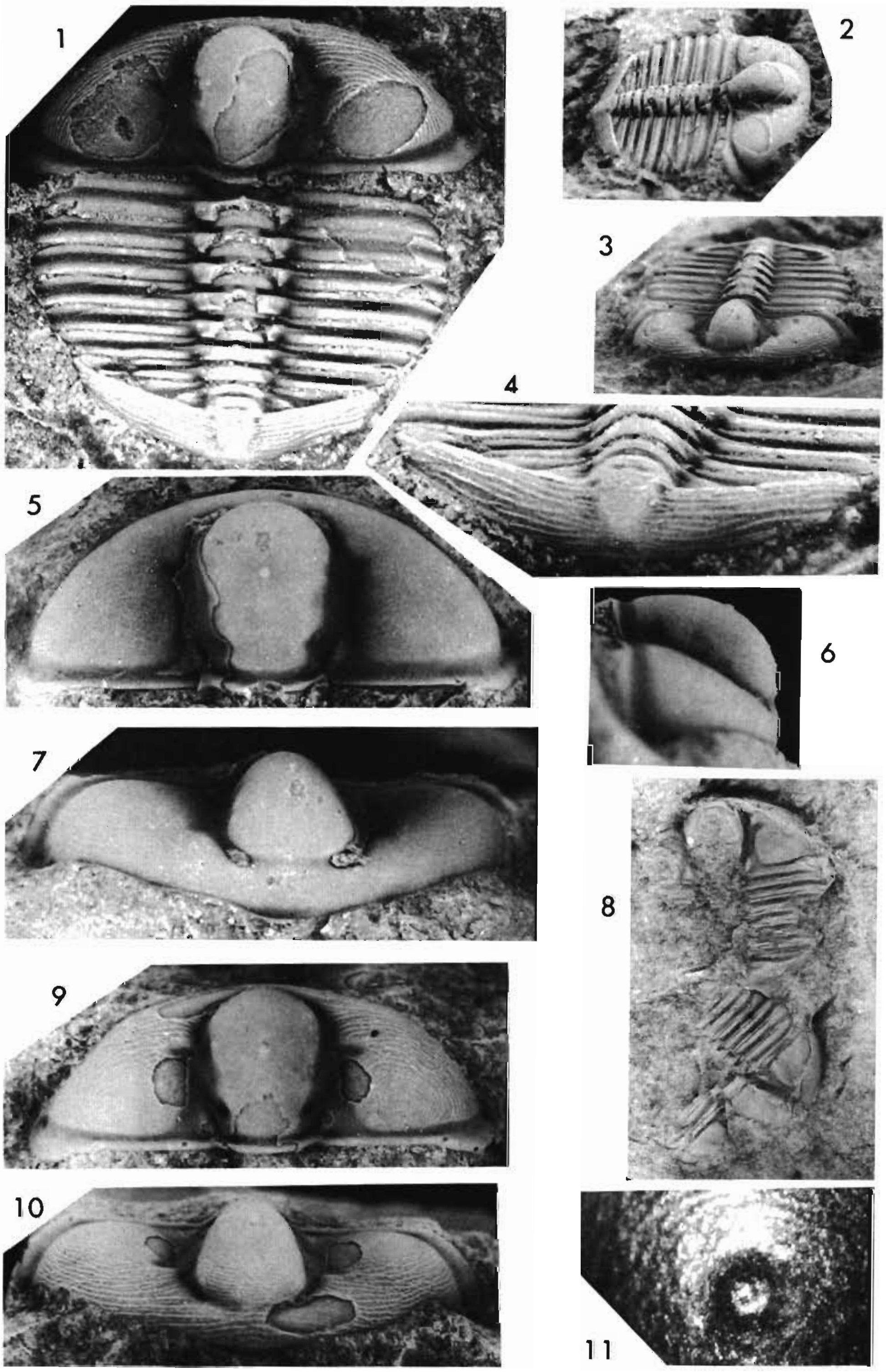


PLATE 32

Figs. 1–4. *Endymionia raymondi* WHITTINGTON 1965 .... (p. 88)

Figs. 1–4. Cranidium, largely exfoliated, lateral, dorsal and anterior views, × 9. Fig. 4, detail of anterior border, showing tubercles and narrow band of fine terrace lines (cf. WHITTINGTON 1965, Pl. 15, Fig. 22), × 25. PMO NF 319, Profilbekken Member, 42 m from base on Profilbekken.

Figs. 5–15. *Endymionia clavaria* n. sp. .... (p. 87)

Fig. 5. Holotype, dorsal exoskeleton lacking free cheeks, flattened, × 5. PMO NF 1735, upper part of Olenidsletta Member, area between melt streams A and B on Olenidsletta, estimated 130 m from base of Member.

Fig. 6. Small exfoliated cranidium, × 8, showing faint "eye ridges". Lateral lobes doubtfully present. SMA 84173, upper part of Olenidsletta Member, along shore of Profilstranda, 133 m from base of Member.

Figs. 7, 8, 10. Cranidium, preserving cuticle on left side, fossular, lateral and anterior views, × 8, SMA 84174, upper part of Olenidsletta Member, shore section on Profilstranda, 136 m from base of Member.

Fig. 9. Smallest cranidium, × 8. SMA 84175, locality as cranidium, Fig. 7, 132 m from base of Olenidsletta Member.

Fig. 11. Exfoliated cranidium, most close in the population to *E. raymondi*, × 8. SMA 84176, horizon and locality as cranidium, Fig. 7.

Figs. 12, 13. Cranidium preserving exoskeleton, × 5, palpebral, anterior views. SMA 84177. Locality as cranidium, Fig. 7, 132 m from base of Olenidsletta Member.

Figs. 14–16. Pygidium, posterior, dorsal, oblique views, × 15. SMA 84178, horizon and locality as previous specimen.

PLATE 32

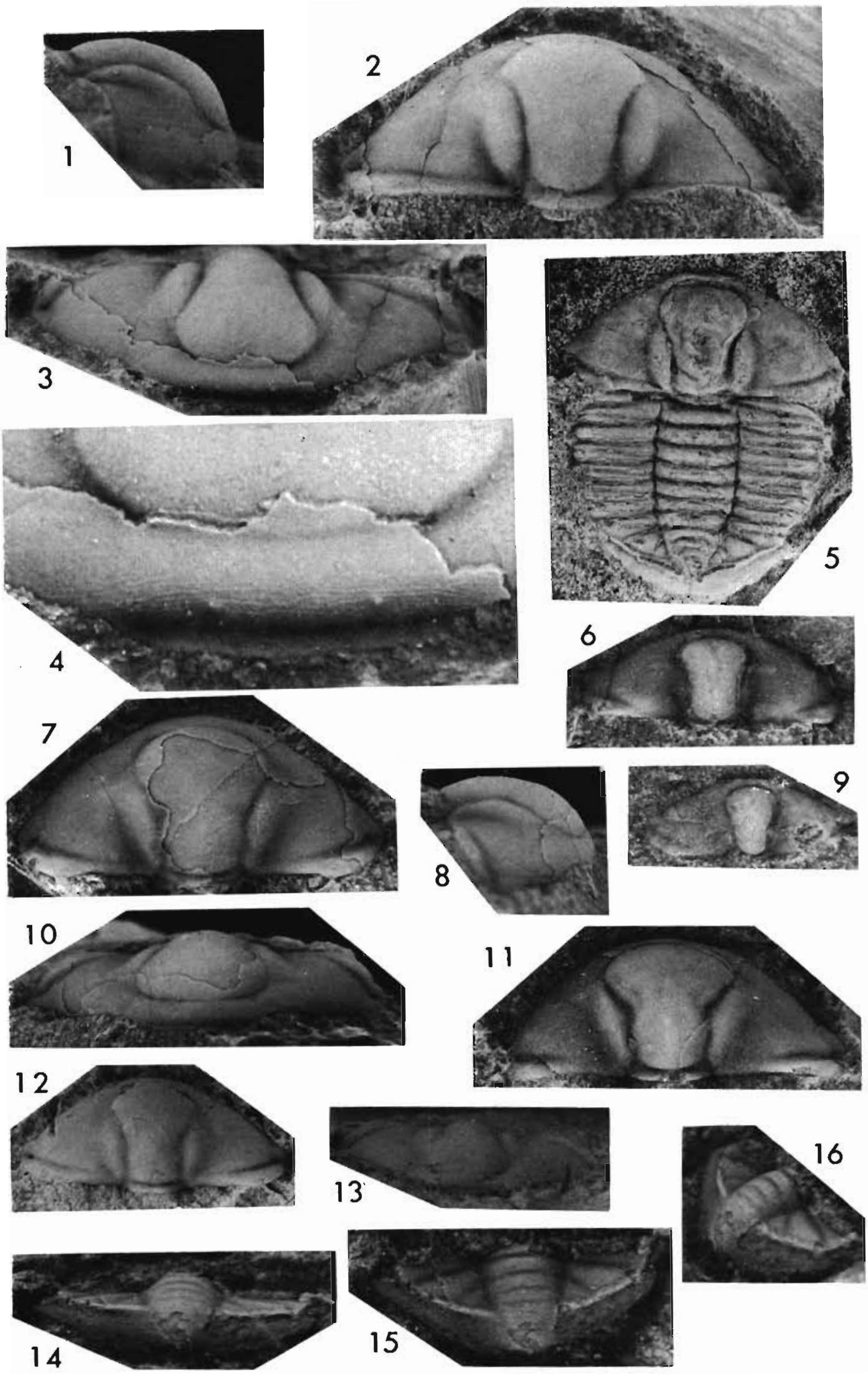


PLATE 33

Figs. 1-3. *Falanaspis extensa* n. sp. .... (p. 93)

Figs. 1, 2. Holotype, internal mould of cranidium, × 10. PMO NF 2255, Olenidsletta Member, melt stream B on Olenidsletta, 101 m from base of Member.

Fig. 3. Poorly preserved cranidium, × 11. PMO NF 850, Olenidsletta Member, shore section on Profilstranda, 60 m from base of Member.

Figs. 4-7. Endymioniinid gen. and sp. indet. .... (p. 91)

Figs. 4-6. Cranidium, incomplete on left side, fossular, lateral and anterior views, × 10. PMO NF 1880, Olenidsletta Member, melt stream B on Olenidsletta, about 90 m from base of member.

Fig. 7. Internal mould of cranidium, fossular view, × 10. PMO NF 2121, Olenidsletta Member, melt stream B on Olenidsletta, about 96 m from base of Member.

Figs. 8-19. *Oopsites hibernicus* (Reed 1909) .... (p. 97)

Fig. 8. Incomplete cranidium, original of Reed 1909, Pl. 6, Fig. 10, here selected as lectotype, × 8. SMA 10398, Tourmakeady Limestone (Arenig), 100 yds. west of Gortbunacullin Farm, Tourmakeady district, Eire. Note typical arched anterior border of *Oopsites* on second fragmentary specimen lower right of photograph.

Figs. 9, 10. Cranidium of similar size to lectotype, Fig. 8, dorsal, lateral views, × 8. PMO NF 773, Olenidsletta Member, shore section on Profilstranda, 75 m from base of Member.

Figs. 11, 12. Incomplete, large cranidium, showing occipital and well-developed 1P muscle impressions, dorsal, anterior views, × 10. PMO NF 737. Horizon and locality as cranidium, Fig. 9.

Figs. 13, 17. Small cranidium, dorsal, anterior views, × 6, showing anterior border. PMO NF 635. Horizon and locality as cranidium, Fig. 9.

Fig. 14. Small cranidium with glabellar furrows present, × 6. SMA 84187. Olenidsletta Member, shore section on Profilstranda, 40 m from base of Member.

Figs. 15, 16, 19. Incomplete pygidium, × 10, dorsal, lateral, posterior views. SMA 84183. Same bed as cranidium, Fig. 9.

Fig. 18. Smallest cranidium, × 6, SMA 84188, same bed as cranidium, Fig. 14.

PLATE 33

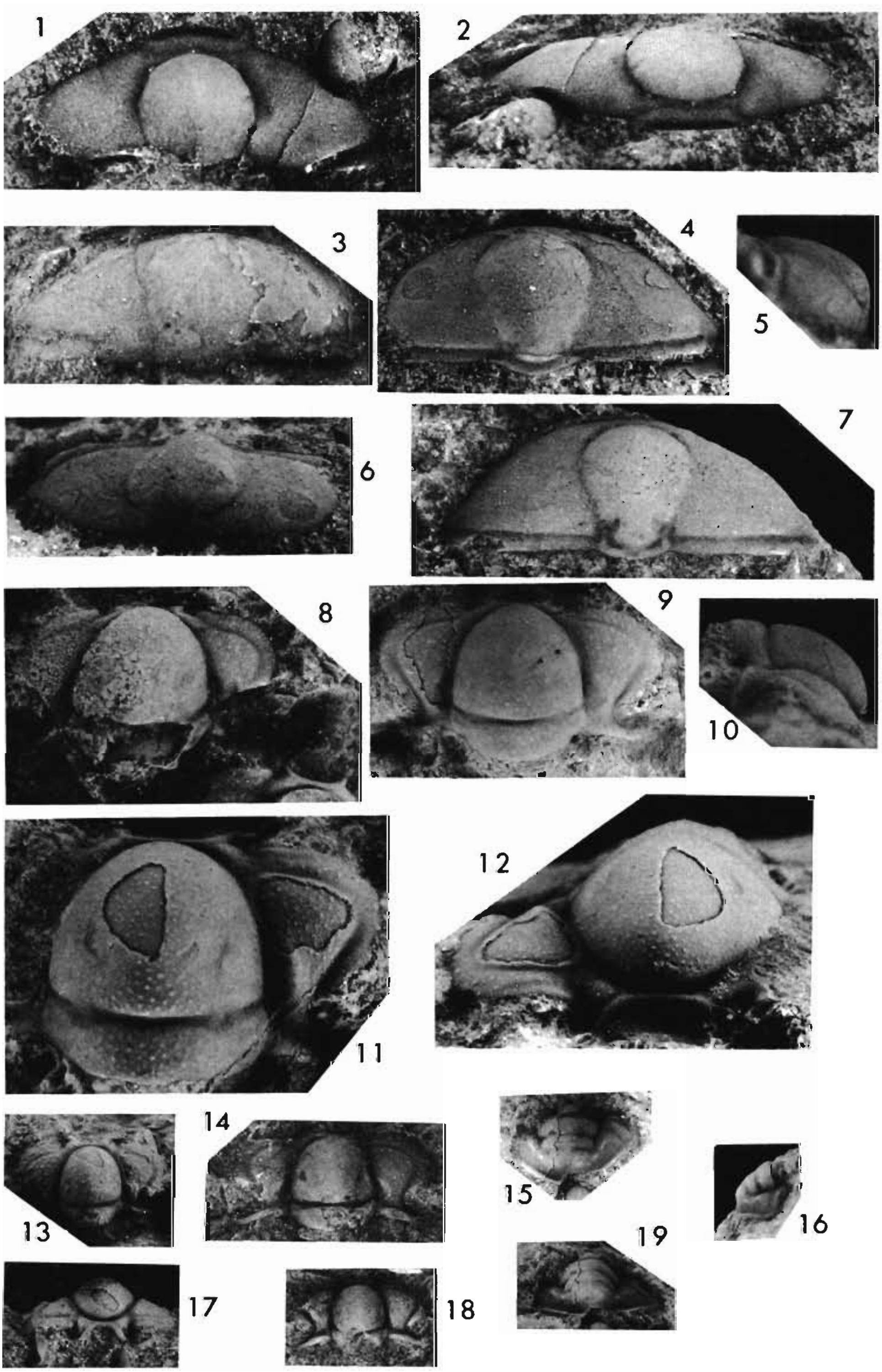


PLATE 34

Figs. 1–7. *Oopsites hibernicus* (REED 1909) .... (p. 97)

Figs. 1, 3, 4, 6. Well preserved cranidium, dorsal, lateral and anterior views, × 10. Fig. 4, detail of righthand side of glabella showing surface sculpture, × 20. PMO NF 689, Olenidsletta Member, shore section on Profilstranda, 60 m from base of Member.

Figs. 2, 5. Free cheek, dorsal and lateral views, × 6, SMA 84181, locality as cranidium, Fig. 1, 75 m from base of Olenidsletta Member.

Fig. 7. Incomplete dorsal exoskeleton, × 10, showing presence of eight thoracic segments. SMA 84180, locality as cranidium, Fig. 1, about 50 m from base of Olenidsletta Member.

Figs. 8–10. *Carolinites rugosus* n. sp. .... (p. 105)

Figs. 8–10. Sculptural details of holotype, Pl. 36, Fig. 1, × 25. Fig. 8, anterior border and front of glabella showing anterior (4) muscle impression and medial smooth line (ML); Fig. 9, posterior mid part of glabella showing break-up of raised lines sagittally; Fig. 10, lateral aspect of glabella showing complex muscle impressions, mid-occipital depression, raised lines on intra-palpebral ridge.

PLATE 34

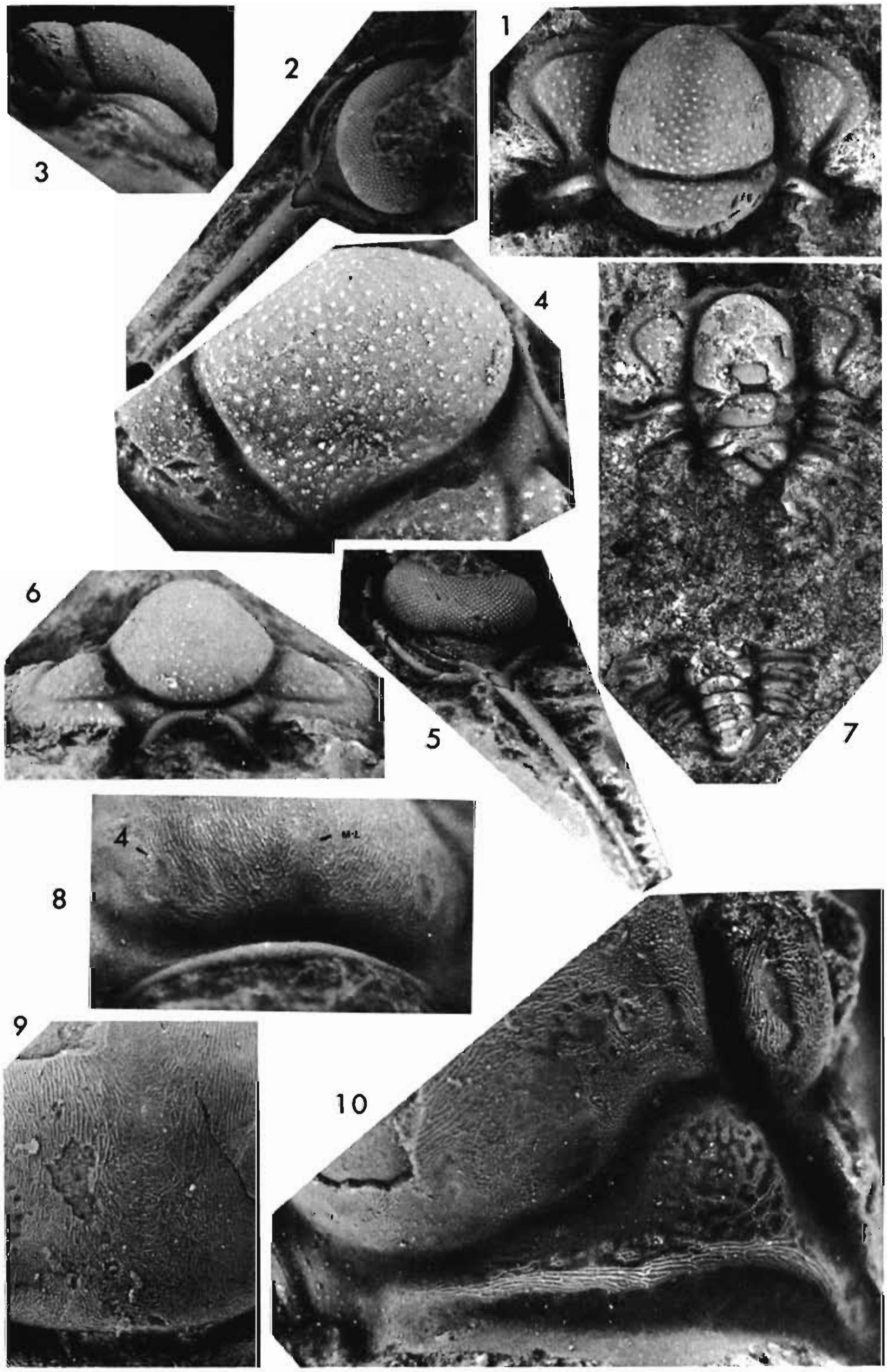


PLATE 35

Figs. 1–11. *Oopsites squamosus* n. gen., n. sp. .... (p. 100)

Figs. 1, 4. Holotype, cranidium, dorsal and anterior views, × 10. Olenidsletta Member, melt stream B on Olenidsletta, about 82 m from base of Member. PMO NF 2879.

Figs. 2, 3. Pygidium, dorsal and lateral views, × 10. PMO NF 1576, Olenidsletta Member, 97 m from base on Profilstranda.

Fig. 5. Free cheek, × 5, showing rapidly tapering genal spine. SMA 84192, Olenidsletta Member, about 95 m from base on Profilstranda.

Fig. 6. Stratigraphically low cranidium, right free cheek slightly displaced, × 10. This is the earliest specimen with *squamosus* sculpture on the fixed cheeks, although in proportions resembling *O. hibernicus* more closely. PMO NF 2748, melt stream B on Olenidsletta, about 80 m from base of Olenidsletta Member.

Figs. 7, 8. Incomplete cranidium, Fig. 7, dorsal view, × 6, Fig. 8, lateral view showing muscle impressions, × 14. SMA 84189, Olenidsletta Member, 92 m from base on Profilstranda.

Fig. 9. Large cranidium, with muscle impression 1P visible on internal mould of glabella, × 5.5. PMO NF 416, Olenidsletta Member, 90 m from base of Member on Profilstranda.

Figs. 10, 11. Free cheek, genal spine incomplete, dorsal, lateral views, × 10. PMO NF 2876, Olenidsletta Member, horizon and locality as holotype, Fig. 1.

PLATE 35

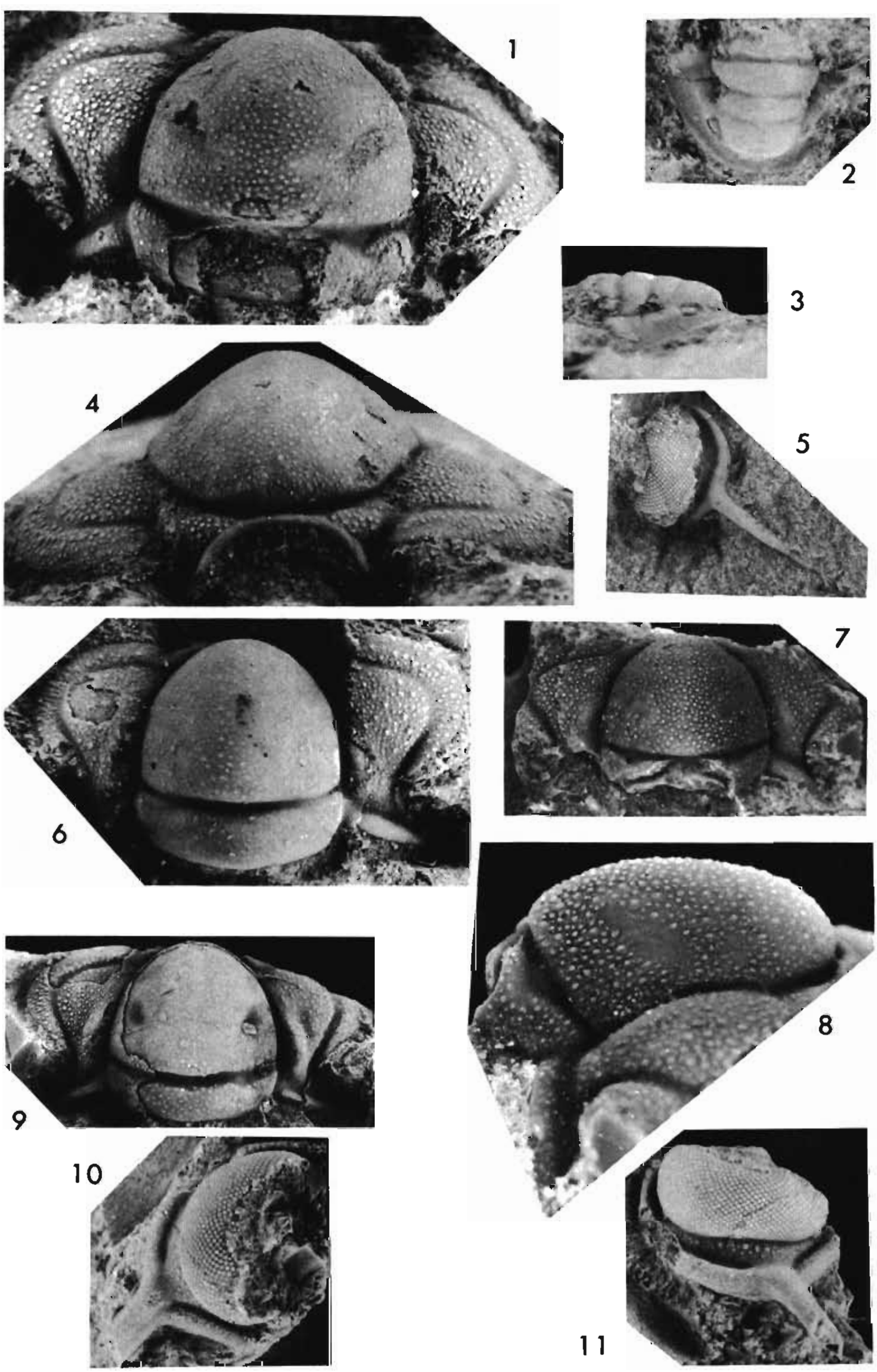


PLATE 36

Figs. 1–19. *Carolinites rugosus* n. sp. .... (p. 105)

Figs. 1, 7. Free cheek, dorsal, lateral views, × 4. SMA 84196, Profilbekken Member, 36 m from base on Profilbekken.

Figs. 2, 3, 5. Holotype, cranidium preserving cuticle, dorsal, lateral and oblique anterior views, × 6. SMA 84195, Profilbekken Member, 34 m from base on Profilbekken.

Figs. 4, 8. Pygidium, dorsal, posterior views, × 3. Same bed as free cheek, Fig. 1. SMA 84200.

Figs. 6, 11. Pygidium, dorsal, lateral views, × 4. SMA 84198. Same bed as holotype, Fig. 2.

Figs. 9, 10. Cranidium, dorsal, lateral views, × 8. SMA 84197. Horizon as holotype, Fig. 2.

Figs. 12–16. Small growth stages all from a single thin limestone from the same horizon and locality as holotype: Fig. 12, cranidium, × 15, SMA 84203; Fig. 13, small cranidium, "indentus" stage, × 15, SMA 84204; Fig. 14, very small cranidium, × 40, SMA 84202; Fig. 15, smallest cranidium, × 30, SMA 84205; Fig. 16, incomplete transitory pygidium, × 30, SMA 84208.

Figs. 17–19. Incomplete dorsal exoskeleton with the various parts in presumed moult arrangement. Fig. 19, dorsal view, × 6. Fig. 18, detail of left side of thorax, × 12, showing minute anterior projections on pleurae (arrowed); note also middle furrows on axial rings. Fig. 17, latex cast prepared from the counterpart of Fig. 19, to show the posterior part of the hypostoma, and the doublure of the free cheek on left. Note that the orientation of this Fig. is reversed compared with Fig. 19. PMO NF 1374, locality as holotype, Fig. 2.

PLATE 36

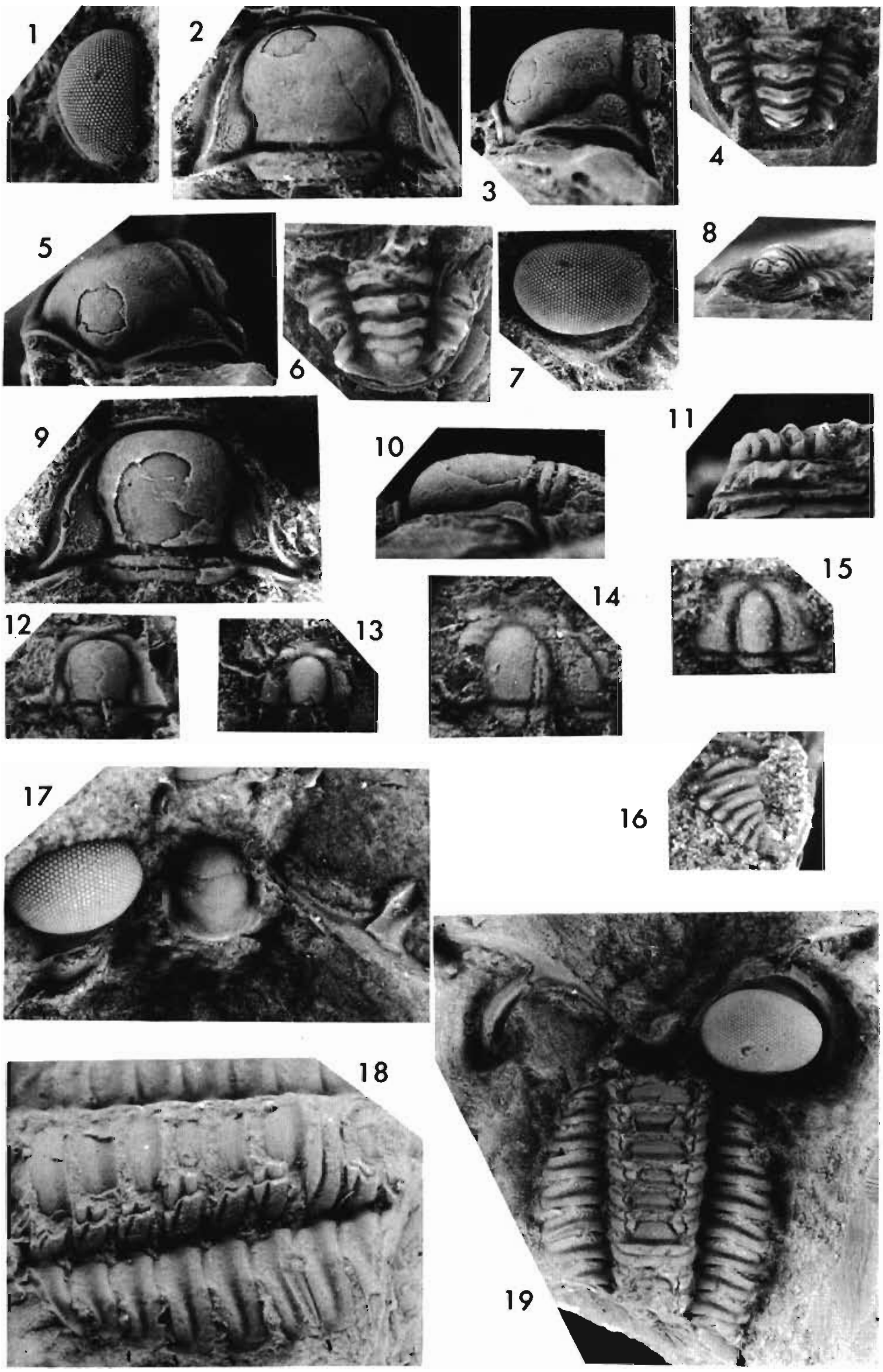


PLATE 37

Figs. 1–15. *Carolinites genacinaca genacinaca* Ross 1951 .... (p. 112)

Figs. 1–3. Cranidium preserving cuticle, dorsal, anterior and lateral views, × 8. Specimen close to the type of Ross 1951, Pl. 18, Figs. 29, 33, 36. PMO NF 1563, Olenidsletta Member, shore section on Profilbekken, 97 m from base of Member.

Figs. 4, 5. Pygidia orientated such that the smaller of the pair and the larger are in dorsal view, × 8. PMO NF 1578, same bed as previous specimen.

Fig. 6. Incomplete dorsal exoskeleton in presumed moult arrangement of parts × 1.5. SMA 84229, Olenidsletta Member on Olenidsletta, exact horizon uncertain but within lower 30 m and above range of *C. genacinaca nevadensis*.

Figs. 7, 12. Free cheek in dorsal and lateral views, × 4. Same bedding plane as previous specimen, Fig. 6.

Fig. 8. Mould, largely internal, of incomplete dorsal exoskeleton, × 1.5. SMA 84228, about 20 m from base of Olenidsletta Member on Olenidsletta.

Fig. 9. Internal mould of cranidium, narrow form, × 4. PMO NF 743, Olenidsletta Member, shore section on Profilstranda, 75 m from base of Member.

Fig. 10. Free cheek, lateral view, showing lenses, × 10. PMO NF 2871, Olenidsletta Member, melt stream B on Olenidsletta, 82 m from base.

Fig. 11. Immature cranidium, × 25, SMA 84220, locality as cranidium, Fig. 1, 70 m from base of Olenidsletta Member.

Fig. 13. Pygidium, exfoliated on right side, × 7.5. PMO NF 2759, Olenidsletta Member, melt stream B on Olenidsletta, about 80 m from base of Member.

Fig. 14. Stratigraphically high cranidium, × 2, SMA 84227, Olenidsletta Member, shore section on Profilstranda, 100 m from base of Member.

Fig. 15. Well preserved cranidium, × 7, PMO NF 694. Olenidsletta Member, 60 m from base on Profilstranda.

PLATE 37

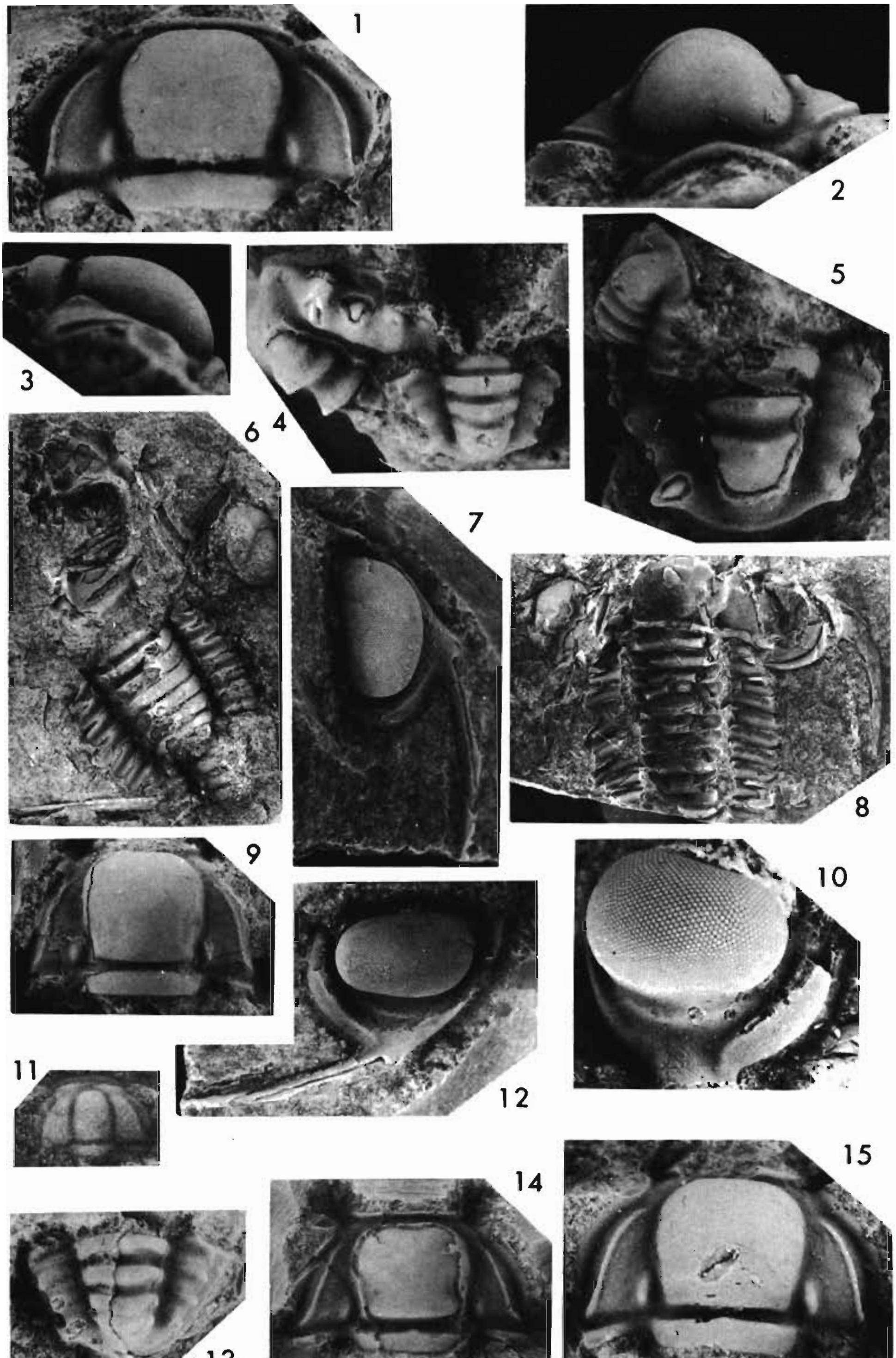


PLATE 38

Figs. 1–3. *Carolinites genacinaca genacinaca* Ross 1951 .... (p. 112)

Fig. 1. Stratigraphically low specimen, dissociated exoskeleton, × 3. Pygidium lacks median tubercles characteristic of higher specimens. PMO NF 2801, Olenidsletta Member, shore section on Olenidsletta, 25 m from base of Member.

Figs. 2, 3. Hypostoma, ventral and posterior views, × 10. PMO NF 679, Olinedsletta Member, shore section on Profilstranda, 60 m from base of Member.

Figs. 4–13. *Carolinites genacinaca nevadensis* HINTZE 1953 .... (p. 115)

Figs. 4, 5, 8. Cranidium retaining cuticle, dorsal, anterior and lateral views, × 10. PMO NF 793, Olenidsletta Member, lowest part, 3 m from base on Profilstranda. Compare size of bacculae here with those of *C. genacinaca genacinaca*.

Fig. 6. Cranidium, incomplete on right hand side, comparing in proportions with the type of HINTZE 1953, dorsal view, × 4. PMO NF 2592, from basal bed of Olenidsletta Member on melt stream C on Olenidsletta.

Figs. 7, 10. Free cheek in dorsal and lateral views, × 10. Note subocular ridge characteristic of, and restricted to, this sub-species. PMO NF 804, from same bed as cranidium, Fig. 4.

Figs. 9, 11. Pygidium, dorsal and lateral views, × 10. Two axial rings only completely defined across axis, third visible in lateral aspect. PMO NF 785, from the same bed as the cranidium, Fig. 4.

Figs. 12, 13. Small cranidium in dorsal and anterior views, × 20. Note faint eye ridges. PMO NF 786, same bed as cranidium, Fig. 4, pygidium, Fig. 9 and free cheek, Fig. 7.

PLATE 38

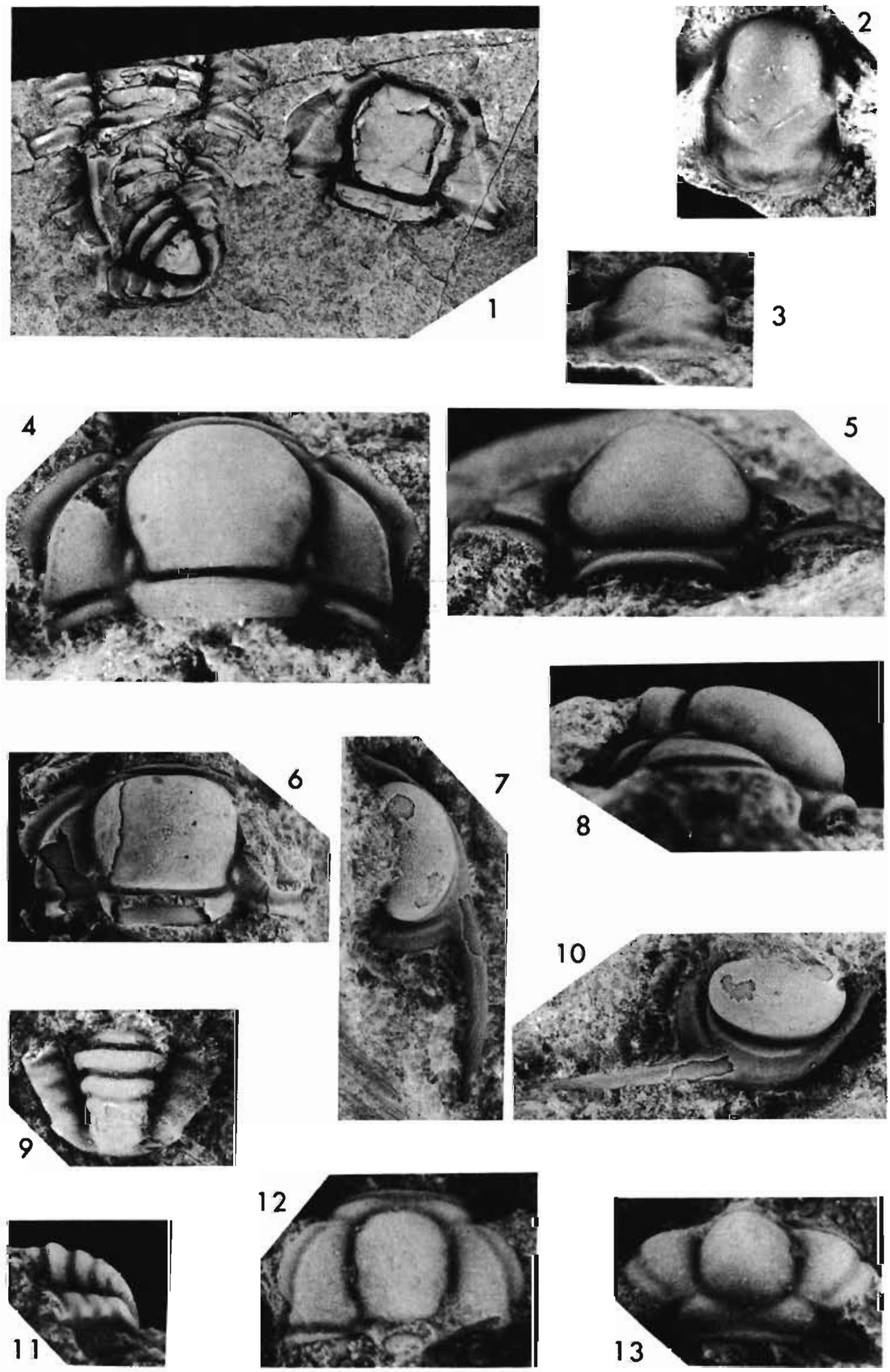


PLATE 39

Figs. 1–13. *Carolinites ekphymosus* n. sp. .... (p. 110)

Figs. 1–7. Holotype, cranidium, partly exfoliated, with five thoracic segments incomplete on lefthand side, dorsal, × 8, and lateral, × 4, views. Right free cheek shows rugulose sculpture. SMA 84212, Olenidsletta Member, higher part, 140 m from base on Profilstranda.

Fig. 2. Free cheek, × 8, view orientated to show genal spine shorter than that of *C. genacinaca genacinaca*. SMA 84213, locality and horizon as holotype, Fig. 1.

Figs. 3, 5, 6. Well preserved, small cranidium retaining cuticle, dorsal and lateral views, × 8. Fig. 6, detail of right lateral part of glabella showing fine granulation, × 35. SMA 84210, Olenidsletta Member, within upper 10 m of that Member on Profilbekken.

Fig. 4. Cranidium, exfoliated over glabella, showing median sagittal ridge, × 5. SMA 84217, same bedding plane as free cheek, Fig. 2.

Fig. 8. Small cranidium, × 15. SMA 84214, locality and horizon as holotype, Fig. 1.

Fig. 9. Small cranidium, × 15, at "indentus" stage of development. SMA 84215, same bedding plane as previous specimen.

Fig. 10. Stratigraphically early cranidium, × 4, close to narrow cheek form of *C. genacinaca genacinaca* (Pl. 37, Fig. 15). SMA 84211, locality as holotype, Fig. 1, 105 m from base of Olenidsletta Member.

Fig. 11. Detail of righthand side of glabella of holotype, Fig. 1, showing fine pitting on internal mould, × 25.

Fig. 12. Internal mould of incomplete pygidium, showing the four axial rings, × 5. PMO NF 1320, lowest part of Profilbekken Member, on Profilbekken, exact horizon unknown.

Fig. 13. Incomplete pygidium, preserving exoskeleton, × 6. SMA 84218, locality as holotype, Fig. 1, 130 m from base of Olenidsletta Member.

PLATE 39

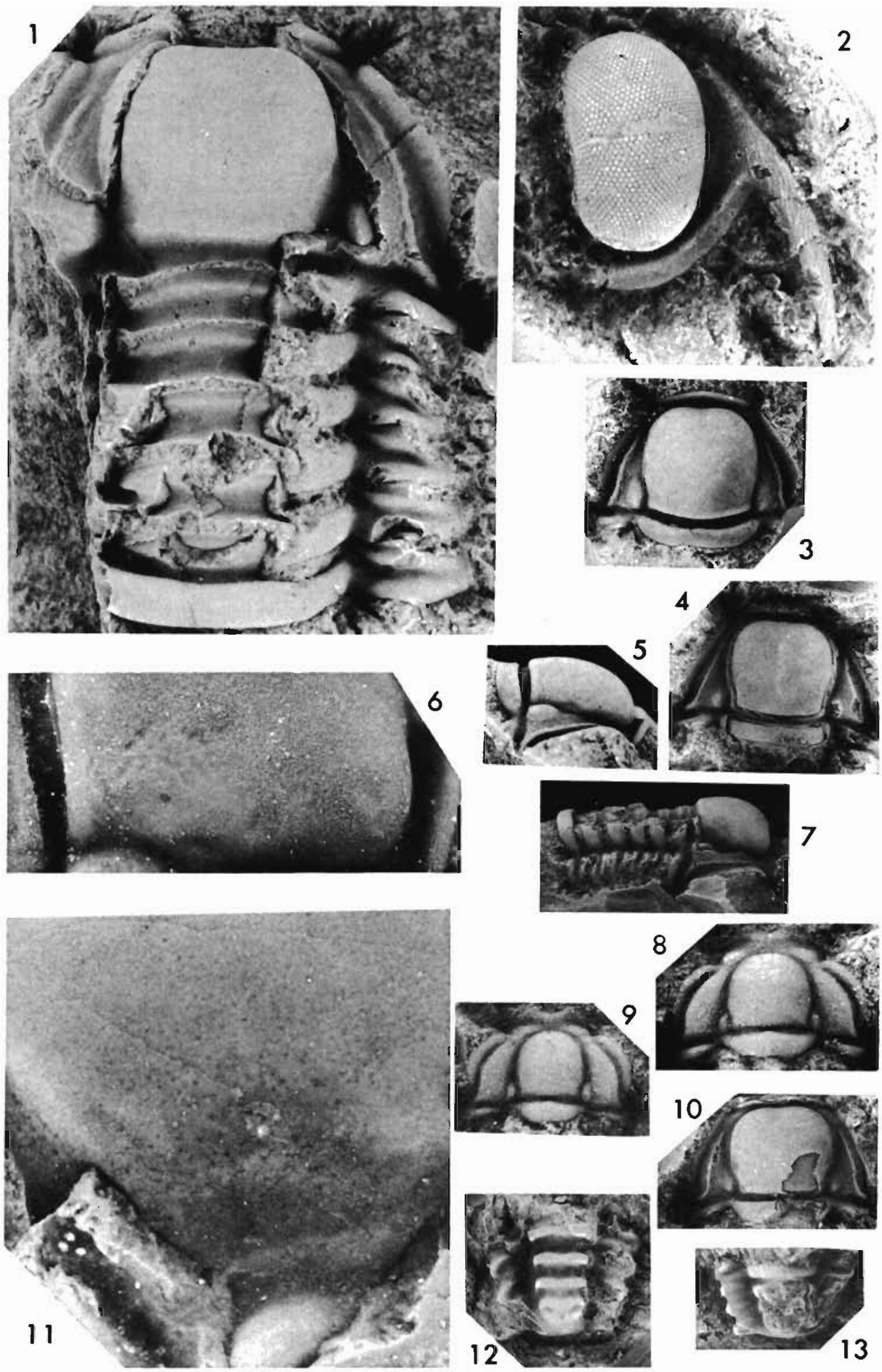


PLATE 40

Figs. 1–10, 12, 13. *Carolinites sibiricus* Chugaeva 1964 .... (p. 116)

Figs. 1, 2, 6. Cranidium retaining cuticle in dorsal, × 8, left lateral and anterior views, × 5. SMA 84219, Profilbekken Member, 75 m from the base of the Member on Profilbekken.

Figs. 3, 4. Cranidium, dorsal, left lateral views, × 5. SMA 84220, locality as cranidium, Fig. 1, 66 m from base of Profilbekken Member.

Fig. 5. Internal mould of cranidium, × 5, specimen comparing closely with the holotype of Chugaeva (1964). SMA 84221, locality and horizon as cranidium, Fig. 1.

Fig. 7. Dorsal exoskeleton lacking free cheeks, × 4. Rosroc Peninsula Co., Galway, western Eire, 1 mile northwest of boat quay, in graptolitic shales (coll. J. B. Archer). British Museum, reg. BM It 13284.

Figs. 8, 9. Pygidium and one thoracic segment, in oblique anterior and dorsal views, × 11. PMO NF 3153, locality as cranidium, Fig. 1, 66 m from base of Profilbekken Member.

Figs. 10, 12. Free eheek, lateral view showing genal spine reduced to a stub (as in *C. angustagena* Ross) and dorsal view, × 10. PMO NF 3159. Profilbekken Member, 70 m from base on Profilbekken.

Fig. 13. Cranidium with bacculae relatively uninflated, PMO NF 1228, × 10, locality as previous specimen but 68 m from base of Profilbekken Member.

Figs. 11, 14–19. *Carolinites killaryensis killaryensis* (Stubblefield 1950) .... (p. 116)

Figs. 11, 16. Free cheek, dorsal, lateral views, × 3. Profilbekken Member, upper part, 64 m from base on Profilbekken, SMA 84235.

Fig. 15. Cranidium and pygidium on same bedding plane, × 5, the former in oblique posterior, the latter in oblique anterior aspect. Lower part of the range of the species, low Profilbekken Member, south of melt stream A on Olenidsletta about 2 m from base of Member. PMO NF 357.

Figs. 17, 18. Cranidium, anterior and dorsal views, × 5. PMO NF 1251, locality as free cheek, Fig. 11, 68 m from base of Profilbekken Member.

Fig. 14. Cranidium, dorsal view, × 3.5. PMO NF 528. Profilbekken Member, 68 m from base of Profilbekken.

Fig. 19. Pygidium, showing long terminal spine in lateral view, × 6. PMO NF 3002, same bed as cranidium, Fig. 18.

PLATE 40

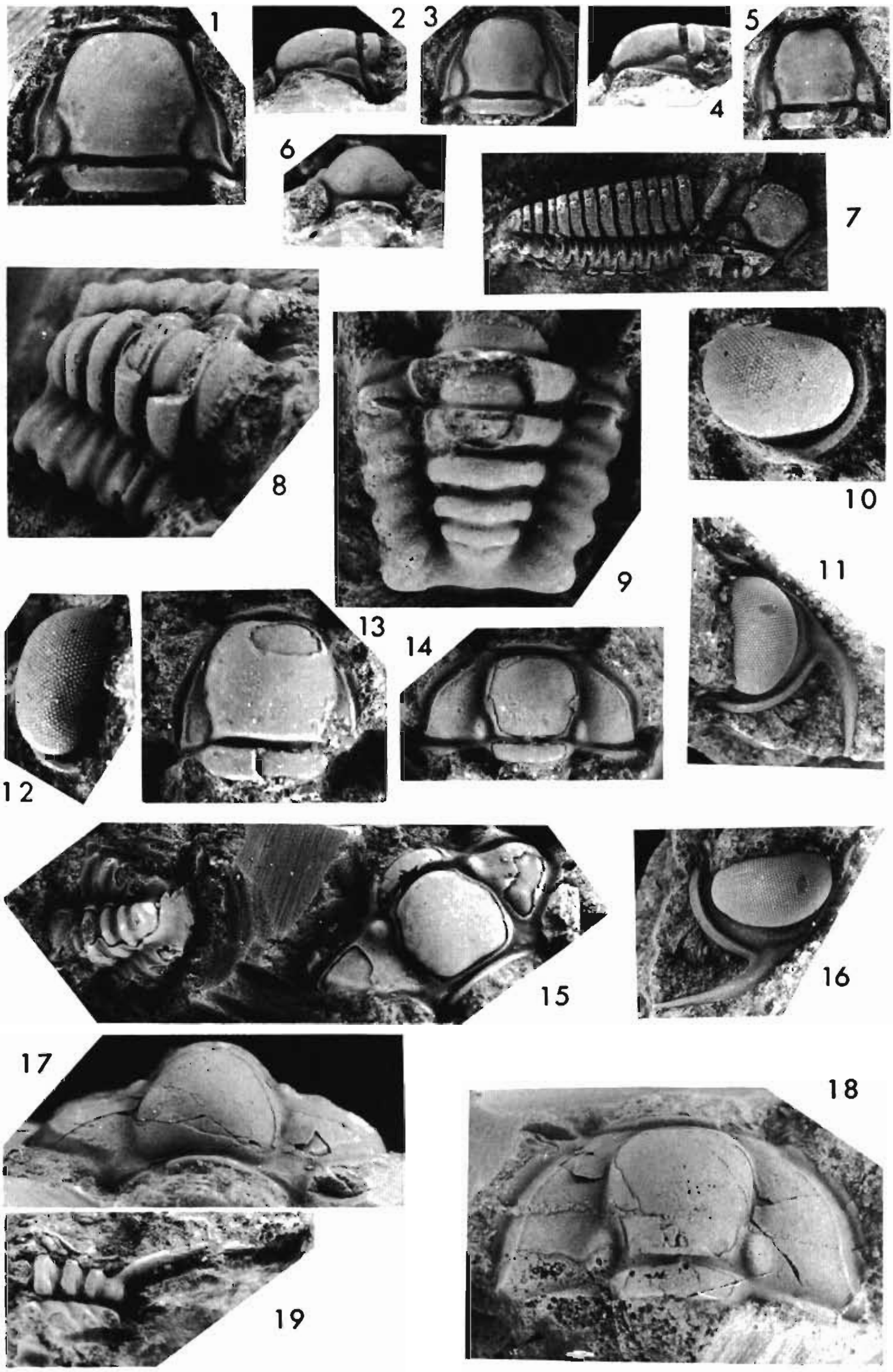


PLATE 41

Nileidae — sculptural details.

Figs. 1, 2, 5, 7. *Poronileus isoteloides* n. gen., n. sp. . . . . (p. 55)

Figs. 1, 2. Incomplete cranidium, palpebral view × 1.5, and detail of mid-part of glabella, × 8, showing punctate surface sculpture, median smooth line, smooth internal mould on right. SMA 84247, upper part of Profilbekken Member, 37 m from base on Profilbekken.

Figs. 5, 7. Internal mould of free cheek, × 2, doublure on right, and detail of lefthand part photographed in strong, oblique light to emphasise the faint genal caeca (running left–right), × 15. SMA 84260, locality as preceding cranidium, 50 m from base of Profilbekken Member.

Figs. 3, 6. *Poronileus fistulosus* n. gen., n. sp. . . . . (p. 51)

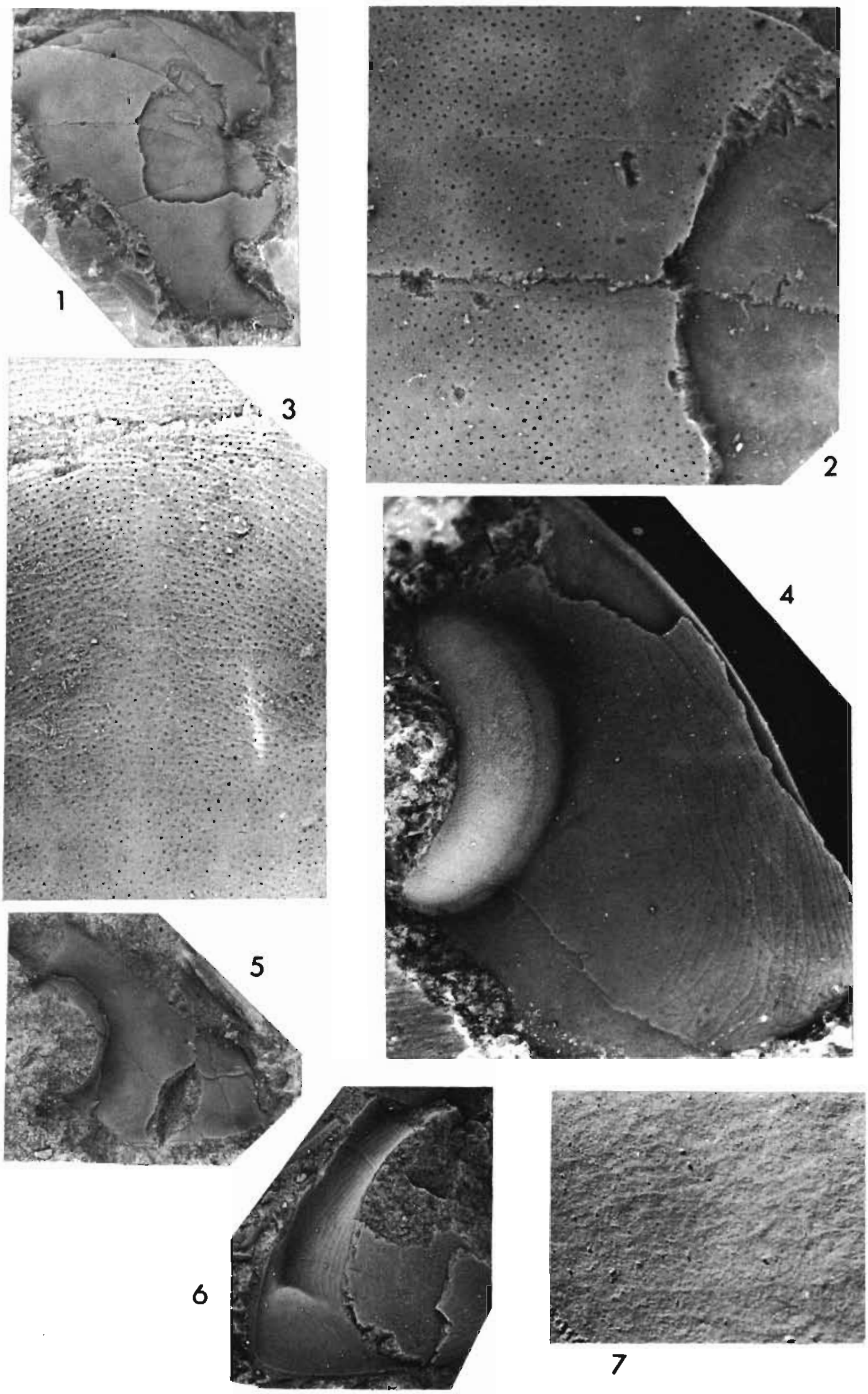
Fig. 3. Detail of mid-anterior part of glabella of incomplete cephalon, at same scale as sculpture of *P. isoteloides*, Fig. 2, to show admixture of fine scale terrace lines and pits. SMA 84239, low Profilbekken Member, locality and horizon as cephalon, Pl. 13, Fig. 4.

Fig. 6. Free cheek, dorsal exoskeleton removed to show upper surface of doublure, and vincular furrow, × 4. SMA 84262, locality and horizon as previous.

Fig. 4. *Poronileus vallancei* n. gen., n. sp. . . . . (p. 57)

Fig. 4. Free cheek showing sculpture of scattered, fine pits and terrace lines, minute and crowded lenses on eye, × 20. Detail of right free cheek of specimen shown on Pl. 18, Fig. 7.

PLATE 41



A.s John Griegs Boktrykkeri, Bergen