

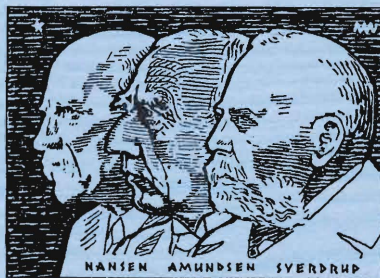


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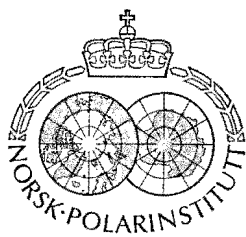
R. A. FORTEY

The Ordovician Trilobites of Spitsbergen

III. Remaining trilobites of the Valhallfonna Formation



NORSK POLARINSTITUTT
OSLO 1980

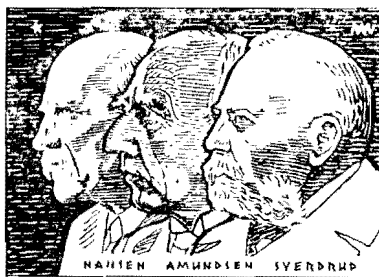


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Manuscript received September 1979

Printed February 1980

ISBN 82-90307-07-1

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Abstract

This paper completes the description of Arenig—Llanvirn trilobites from the Valhallfonna Formation, northern Ny Friesland, Spitsbergen. The fauna includes more than a hundred species and subspecies. Forty-eight species are described in this part, of which fifteen are under open nomenclature.

The following families and genera are described herein: Agnostidae: *Micragnostus* (2 species); Metagnostidae: *Arthrorhachis* (2 subspecies); Shumardiidae: *Shumardia* (3 species); Catillicephalidae: *Buttsia* (1 species); Remopleurididae: *Lacorsalina* (1 species), *Eorobergia* (1 species), *Remopleurides* (1 species), *Robergiella* (2 species) and gen. et sp. indet.; Opipeuteridae: *Opipeuter* (2 species); Scutelluidae: *Raymondaspis* (1 species), *Turgicephalus* n. gen. (2 species), *Protostygina* (1 species), *Theamataspis* (1 species); Illaenidae: *Illaeus* (1 species); Aulacopleuridae: *Oenonella* n. gen. (1 species); Dimeropygidae: *Ischyrotoma* (1 species), *Ischyrophyma* (1 species); Bathyruridae: *Acidiphorus* (2 species), *Punka* (1 species), 2 gen. et sp. indet.; Harpedidae: *Scotoharpes* (1 species); Cheiruridae: *Sycophantia* n. gen. (1 species), *Parapilekia* (1 species), *Kawina* (4 species), *Cydonoccephalus* (1 species), *Kolymella*? (1 species); Pliomeridae: *Europeites* (1 species), *Pliomerops* (1 species), *Ectenonotus* (1 species), *Strotactinus* (1 species); Encrinuridae: *Cybelurus* (3 species), *Lyrapyge* n. gen. (1 species); Odontopleuridae: *Ceratocephala* (1 species), *Diacanthaspis* (1 species).

The stratigraphic distribution of the trilobites is summarised. The Valhallfonna Formation is divided into four major faunas (V_1 to V_4 upwards), the boundaries between which represent a facies shift between community types of FORTEY (1975a). Faunal subdivisions within these major units (V_1a , V_1b , etc.) are biostratigraphic units within any one facies type. It is concluded that there is a stratigraphic gap between the Canadian and Whiterock, from which shelly faunas of North American provincial aspect have not been described from outside Spitsbergen. The term "Valhallan Stage" is introduced for this interval. The Whiterock is defined by the *Orthidiella* Zone at its base. The Valhallan Stage includes three successive faunas in Spitsbergen — V_3a , V_3b and V_4a . The overlying V_4b fauna is early Whiterock. The top of the Canadian Series, as defined by the base of the Valhallan, does not extend beyond zone J of the Ross zonal scheme.

General consideration of Ordovician agnostids shows that some species referred to *Geragnostus* should be referred to *Micragnostus* and the Agnostidae. The genus *Arthrorhachis* is revived for Ordovician Metagnostidae (= Geragnostidae) often referred to *Trinodus*. The homology of muscle insertion areas in Scutelluidae and Illaenidae is demonstrated.

I. Introduction and acknowledgements

This paper completes the description of the Ordovician trilobites of the Valhallfonna Formation, and includes all families except Asaphidae, Nileidae, Olenidae, Raphiophoridae and Telephinidae described in previous parts. With the exception of the agnostids and a few other species the forms described here are from the upper part of the sequence in the Profilbekken Member. Some of these are known from allochthonous material, often fragmentary, particularly those of the illaenid-cheirurid community (FORTEY 1975a). Taxonomic difficulties with such material are considerable, and proportionately more taxa are accordingly left in open nomenclature in this part of the monograph. The total number of species from the Formation now number over a hundred, making the fauna of the Valhallfonna Formation possibly the richest of any known in the Arenig-Llanvirn interval. This is partly due to the unique mixture of faunas of different community types (FORTEY 1975a) within the restricted area of outcrop. The first part of the monograph dealt with the trilobites of the Olenid community, the second part with forms adapted to the Nileid and pelagic communities, while this part includes species with a wide spread of adaptations, with a bias towards those of the Nileid and illaenid-cheirurid communities.

Stratigraphic and biogeographic notes have been given in the introductory sections of the previous parts. Here the information is summarised. Because of the richness of the faunas, and their association with abundant remains of other groups such as graptolites, nautiloids and conodonts, an informal "lumping" of the faunas has been adopted here, which is a useful way of summarising co-incident stratigraphic ranges of species for ready comparison with faunas elsewhere. These are *not* intended as formally-named zones, because they are hybrid concepts with both time and facies significance. In some cases (change within one community type) a boundary between such faunas has an absolute time meaning in that facies; in others a change merely marks the transition from one community type to another. A new stage — the Valhallan — is erected, however, as a bridge between the Canadian and the Whiterock of the North American shelly environmental suite. This is justified (apart from its value as a solution to a problem) because the Spitsbergen faunas are the richest of this age around the North American—Greenland—Spitsbergen plate in the earlier part of the Ordovician.

I thank Dr. D. L. Bruton for his continued help in the curation of the material, and Dr. R. M. Owens, Dr. P. D. Lane, Dr. A. W. A. Rushton and Mr. R. P. Tripp for useful discussions on some details of the taxonomy.

II. Stratigraphy

A. Summary of succession of faunas in the Valhallfonna Formation

A summary of the stratigraphic ranges of the trilobites described from the Valhallfonna Formation is presented in Fig. 1,* incorporating the species named in the previous parts of this monograph as well as those described herein. I have indicated before (FORTEY 1974a, p. 7) that these ranges tend to clump together (though not precisely) to form a succession of faunas that replace one another. The major faunal changes are caused by facies shifts between the olenid and nileid communities, and this at once divides the Valhallfonna Formation into four — here termed V_1 to V_4 in ascending order. Within all four primary divisions there are replacements of the fauna by another in the *same* facies. These are denoted by the small letter suffixes — V_1a , V_1b , V_1c etc.

These changes in the same biological facies are of direct time significance, and the confacial faunas have the status of Assemblage Zones within that facies. This is *not* the case with the shifts from one environmental/faunal suite to another (V_1 to V_2 , V_2 to V_3 etc.) as it is not known in many cases to what extent the time ranges of the species above and below such junctions would have extended in their own facies outside Spitsbergen. In short, it is not known precisely to what extent V_1 and V_2 , V_2 and V_3 , V_3 and V_4 overlap in time at their junctions. So the faunal assemblage nomenclature used here is a hybrid concept, involving notions of both time and facies. For this reasons the units are not to be regarded as formally erected zones. They are convenient units of comparison with faunas elsewhere, and a way of summarising the complex interplay between facies, time, and individual ranges of taxa in the Ordovician of the Valhallfonna Formation. Finally, it is noted that there is nothing absolute about the ranges from which they are compiled, doubtless further collections will alter the details of many of them. I believe that the general order of succession will remain largely unchanged.

Starting with the earliest assemblages and working to the top of the Formation:

V_1 Lower olenid sequence, sharply transitional with Nordporten Member below, and gradual transition with V_2 above. Lower-Middle Arenig. Partly contemporary olenid faunas occur in Wales (FORTEY and OWENS 1978).

V_1a <i>Carolinites genacinaca nevadensis</i>	<i>Svalbardites hamus</i> (early forms)
<i>Hypermecaspis venulosa</i>	<i>Tropidopyge alveus</i>
<i>Paraptychopyge disputa</i>	<i>Balnibarbi scimitar</i>
<i>Psilocara comma</i>	<i>Opipeuter angularis</i>

V_1a correlates with zone H of the Utah/Nevada sections (FORTEY 1976 p. 270) and with the early Arenig *D. deflexus* Zone of the European sequence.

V_1b <i>Balnibarbi ceryx ceryx</i>	<i>Plicatolina</i> sp.
<i>Balnibarbi ceryx anataphra</i>	<i>Anaximander clavatus</i>
<i>Balnibarbi sombrero</i>	<i>Carolinites genacinaca</i>
<i>Psilocara patagiatum</i>	<i>genacinaca</i> (early forms)

* See inside cover.

V _{1c} <i>Balnibarbi pulvurea</i>	<i>Opsites hibernicus</i>
<i>Balnibarbi erugata</i>	<i>Carolinites genacinaca</i>
<i>Bienvillia stikta</i>	<i>genacinaca</i>
<i>Svalbardites hamus</i> (.forma typica)	<i>Opipeuter inconnivus</i>
<i>Micragnostus</i> sp. A	

V_{1b-c} includes the *D. protobifidus* Zone of West Texas (BERRY 1960), and extends into the basal *D. bifidus* Zone, on the basis of the included graptolites, and probably equates with zone I of Utah/Nevada. It is succeeded by an olenid fauna with *Balnibarbi tholia*, the range of which overlaps with V₂.

V₂ Lower nileid sequence, transitional upwards into V₃ (FORTEY 1975a, p. 342). Middle Arenig, including equivalents of the *D. bifidus* zone of Texas (but not of south Wales), zone J of Utah and Nevada. Extending to the top of the Canadian and the base of the Valhallan (see following section).

V _{2a} <i>Ampyx porcus</i>	<i>Megalaspides striatellus</i>
<i>Ampyx spongiosus</i>	<i>Niobe flabellifera</i>
Endymioniid gen. et sp. indet.	<i>Nileus glazialis costatus</i>
<i>Arthrorhachis danica proxima</i>	<i>Mendolaspis doidyx</i>
<i>Gog catillus</i>	<i>Pytine graia</i>
<i>Lyrapyge ebrius</i>	<i>Shumardia minaretta</i>
<i>Opsites squamosus</i>	<i>Carolinites genacinaca</i>
<i>Theamataspis tuber</i>	<i>genacinaca</i> (.forma typica)
<i>Symphysurus arcticus</i>	<i>Opipeuter inconnivus</i>
V _{2b} <i>Ampyx delicatulus</i>	<i>Micragnostus serus</i> (late forms)
<i>Presbynileus</i> (<i>Protopresbynileus</i> ?) <i>glaber</i>	<i>Arthrorhachis danica brevis</i>
<i>Opipeuter</i> sp.	<i>Strotactinus</i> sp. A.
<i>Ptyocephalus</i> cf. <i>vigilans</i>	<i>Bienvillia stikta</i> (Late, ornamented forms)
<i>Lacorsalina bellatula</i>	<i>Niobe occulta</i> (upper range)
<i>Svalbardites hebaxis</i>	
<i>Symphysurus arcticus</i> (transitional with later nileids see FORTEY 1975, p. 38)	

V₃ Upper olenid sequence, merging with V₂ below and, less gradually, with V₄ above. Upper Arenig, including part of the *Isograptus* Zone of North America, and probably European *D. hirundo* Zone. Lower part of the Valhallan Stage herein.

V _{3a} <i>Cloacaspis ekphymosa</i>	<i>Triarthrus papulosus</i>
<i>Hypermeaspis latigena</i>	
<i>Carolinites ekphymosus</i>	
V _{3b} <i>Cloacaspis senilis</i>	<i>Endymionia clavaria</i>
<i>Hypermeaspis brevifrons</i>	<i>Peraspis omega</i>
<i>Triarthrus thor</i>	<i>Poronileus jugatus</i>
	<i>Carolinites ekphymosus</i>

V₄ Upper nileid sequence of the Profilbekken Member, leading up into allochthonous illaenid-cheirurid assemblages, progressively less fossiliferous at top. The Arenig-Llanvirn boundary lies within Profilbekken Member, exact horizon not known, but possibly near V_{4a}-V_{4b} boundary. V_{4a} comprises the upper part of Valhallan stage.

V _{4a} <i>Ampyxoides inermis</i>	<i>Parapilekia jacquelini</i>
<i>Ampyx toxotis</i>	<i>Peraspis erugata</i>
<i>Cybelurus brutoni</i>	<i>Rhombampyx tragula</i>
<i>Oenonella paulula</i>	<i>Robergiella lundehukensis</i>
<i>Evropeites hyperboreus</i> (early forms)	<i>Shumardia acuticaudata</i>
<i>Nileus orbiculatoides svalbardensis</i>	<i>Turgicephalus falcatus</i>
<i>Poronileus fistulosus</i>	<i>Carolinities killaryensis</i>
<i>Globampyx trinucleoides</i> continues	<i>killaryensis</i>
upwards into V _{4b}	<i>Carolinities ekphymosus</i>

V_{4b} Whiterockian (*Orthidiella* zone) for the richer, lower part, possibly extending upwards into zone M equivalents in the upper part (e.g. *Cybelurus* cf. *mirus* is present there). Total faunal list includes mixed illaenid-cheirurid and nileid community elements.

<i>Ischyrophyma borealis</i>	<i>Triarthrus parapunctatus</i>
<i>Cybelurus halo</i>	<i>Nileus porosus</i>
<i>Cybelurus</i> cf. <i>mirus</i> (upper part)	<i>Poronileus isoteloides</i>
<i>Evropeites hyperboreus</i> (late forms)	<i>Poronileus vallancei</i>
<i>Globampyx trinucleoides</i>	<i>Raymondaspis vespertina</i>
<i>Carolinities rugosus</i> (lower part)	<i>Turgicephalus hinloppensis</i>
<i>Carolinities killaryensis killaryensis</i>	<i>Ectenonotus connemarcus</i>
<i>Carolinities sibiricus</i>	<i>Pliomerops praematura</i>
<i>Ischyrotoma twenhofeli</i>	<i>Acidiphorus? ligo</i>
<i>Illaenus oscitatus</i>	<i>Acidiphorus brevispicatus</i>
<i>Kawina</i> sp. A, B	<i>Shumardia phalloides</i>
<i>Kawina wilsoni</i>	<i>Robergiella brevilingua</i>
<i>Sycophantia seminosa</i>	<i>Remopleurides</i> sp. A.
<i>Scotoharpes aduncus</i>	<i>Rhombampyx rhombos</i>
<i>Punka caecata</i>	<i>Peraspis erugata</i> (late forms)

B. The Valhallan Stage

I have commented in the previous part of this monograph (FORTEY 1975, p. 10) and in a discussion of early Ordovician correlation in general (FORTEY 1976, p. 273) on the problems of correlating the later part of the Canadian and the early part of the Whiterock. This centres on the fact that there is an interval of time here that has not been adequately characterised by North American shelly faunas. It is included within the unconformity below the "Middle Ordovician" which is general over platform North America (FÄHRÅEUS 1977; VAIL et al. 1977). In the classic areas of Utah and Nevada (ROSS

		DIVISIONS		FACIES TYPE	DOMINANT FAUNAL TYPE	SELECTED TYPICAL TRILOBITES	BENTHIC
VALHALLFONNA FORMATION	PROFILBEKKEN MEMBER	V ₄	V ₄ b	Allochthonous Illaenid - Cheirurid Nileid	Trilobites Brachiopods Nautiloids	Turgicephalus hintopenius Cybelurus holo Paranileus vollonci Paranileus isoteloides Raymondaspis vespertina Punka coecata Rhombampyx rhombos	
			V ₄ a	Nileid transition	Trilobites Brachiopods	Turgicephalus falcatus Paranileus fistulosus Cybelurus brutoni Robergiella lundehukensis Shumardia acuticaudata Ampyx taxalis Rhombampyx traquila	
	OLENIDSLETTA MEMBER	V ₃	V ₃ b	Olenid	Graptolites Trilobites	Cloacaspis senilis Paranileus jugatus Perapix omega	
			V ₃ a	transition		Cloacaspis ekphymosa Triarthrus populatus	
		V ₂	V ₂ b	Nileid	Trilobites Nautiloids	Ampyx delicatula Micrognostus serus	
			V ₂ a			Gag catillus Niobe flabellifera Symphysurus arcticus	Ampyx spongiosus Lyrpyge ebrius
		V ₁	V ₁ c	Olenid	Graptolites Trilobites	Balnibarbi pulvurea B. erugata	
			V ₁ b			Cloacaspis dejecta Anaximander clavatus	Balnibarbi sombrero
			V ₁ a			Hypermeacaspis venulosa Balnibarbi ceryx	Trapidopyge alveus

Fig. 2. Summary of letter divisions of the Valhallfonna Formation, with a few of the characteristic benthic trilobite species.

1951; HINTZE 1953) this time interval was one of temporary stillstand over much of that region, represented by the brachiopod coquina of zone K. In western Newfoundland the disconformity below the Table Head Group includes the same interval. In Spitsbergen the interval is spanned by prolific trilobite faunas, developed in the olenid and nileid community types, V₃ and V₄a in the terminology introduced in this paper. The fauna represented in the lower Profilbekken Member I had previously characterised as a "pre-*Orthidiella* Whiterock zone" (FORTEY 1975, p. 10). The top of the Olenidsletta Member might equally well have been termed a post-zone J (*Carolinites genacinaca genacinaca*) Canadian interval.

A better solution seems to be to introduce an additional stage between the Canadian and the basal Whiterock *Orthidiella* zone. The latter has a wide distribution around the North American craton (McKEE, NORFORD and ROSS 1972), and taking the top of the Canadian at zone J (WHITTINGTON 1968; ROSS 1975) also has the prospect of wide correlation on the basis of the pelagic trilobites *Carolinites genacinaca genacinaca* and *Opikopter inconnivus*, and conodonts of the *Prioniodus* (*Opikodus*) *evae* assemblage. This intermediate stage is termed the Valhallan (after Valhallfonna - the glacier giving its name to

the Valhallfonna Formation). The base of the Whiterock is thereby defined at the base of the *Orthidiella* zone.

In Spitsbergen three faunal subdivisions may be recognised within the Valhallan – V_{3a}, V_{3b} and V_{4a}. There is a major facies change from olenid to nileid at the base of the Profilbekken Member, which introduces the possibility of some overlap in time between the olenid V_{3b} and nileid V_{4a} faunas. However, the fact that nileids of the same genera as those in the lower part of the Profilbekken Member, but of different species (*Poronileus jugatus*, *Peraspis omega*), occur at certain horizons in the upper part of the Olenidsletta Member, shows that there is a minimum division in either facies into two. We are dealing with several successive faunas in any benthic community type. The stage seems the appropriate level to recognise such a division.

Important restricted species are:

V _{4a} <i>Cybelurus brutoni</i>	<i>Robergiella lundehukensis</i>
<i>Poronileus fistulosus</i>	<i>Turgicephalus falcatus</i>
<i>Nileus orbiculatoides svalbardensis</i>	<i>Parapilekia jacquelini</i>
<i>Shumardia acuticaudata</i>	<i>Ampyxoides inermis</i>
	<i>Ampyx toxotis</i>

Globampyx trinucleoides and *Peraspis erugata* extend up into the *Orthidiella* zone.

V _{3b} <i>Triarthrus thor</i>	<i>Endymionia clavaria</i>
<i>Hypermecaspis brevifrons</i>	<i>Poronileus jugatus</i>
<i>Cloacaspis senilis</i>	<i>Peraspis omega</i>
V _{3a} <i>Cloacaspis ekphymosa</i>	<i>Hypermecaspis latigena</i>
<i>Triarthrus papulosus</i>	nileids transient from
	<i>Symphysurus arcticus</i> to
	succeeding <i>Poronileus</i> and
	<i>Peraspis</i> spp.

In graptolitic terms the lower fauna of the Valhallan stage is widely correlatable, as the rocks including the V_{3a} trilobites also yielded graptolites described by FORTEY (1971), ARCHER and FORTEY (1974) and *Isograptus victoriae victoriae* (see FORTEY 1976, p. 276). The Castlemainian stage of the Australian succession is indicated, and this is correlated with the upper part of the Arenig series (*D. hirundo* zone) of the British sequence. The highest stratigraphically important graptolite is *Isograptus victoriae maximus* in the basal bed of the Profilbekken Member (*ibid.*, p. 277), which, in COOPER's (1974) revision, indicates the upper Castlemainian Ca 3. The Arenig–Llanvirn boundary is difficult to place, as the graptolitic facies is replaced by the nileid-bearing rocks in the Profilbekken Member, and the trilobites do not provide species level correlation with Europe. The wide acceptance of the Whiterock as early Llanvirnian, especially by comparison with the Kundan of the Baltic region, is followed here, and the boundary placed at the base of the *Orthidiella* zone. This means that at present the whole of the Valhallan is regarded as upper Arenig, although further refinement is necessary. FLOWER (pers. comm.

1976) states that the nautiloids from the lower part of the *Orthidiella* zone in the Profilbekken Member are of Baltic aspect, and include forms consistent with a Llanvirnian age. The conodonts may provide some of the evidence towards more precise correlation into the Scandinavian succession. BARNES (in FORTEY and BARNES 1977) has indicated that a new *Prioniodus* assemblage occurs in V_3 at the top of the Olenidsletta Member, and within the Valhallan.

Two choices are available for the type section for the Valhallan Stage: along Profilstranda, or the area around stream A on Olenidsletta. The former includes the contact at the upper limit with the *Orthidiella* zone on Profilbekken; the lower boundary is exposed also, but poorly along Profilstranda. Exposure of rocks representing the whole of the stage is excellent in the southern outcrop area, and for this reason the area centred on melt stream A is preferred as a type section, the base of the Valhallan being exposed just north of melt stream B, V_3 occupying much of the area between streams B and A, and an excellent section through V_{4a} along stream A. The contact with the *Orthidiella* zone is not well-exposed there however.

A boundary problem remains with the lower contact with V_2 . V_{2b} may overlie the Canadian as defined by zone J and the presence of *Carolinites genacinaca genacinaca*, containing a different fauna from that of the underlying V_{2a} (including *Ampyx delicatula*, *Lacorsalina*, *Arthrorhachis danica brevis*, *Micragnostus serus* (late form), *Presbynileus* (*Protopresbynileus*?) *glaber*). The presence of *Ptyocephalus* cf. *vigilans*, however, invites comparison with Canadian faunas of zone J or earlier age, and therefore the boundary is defined above this fauna as it appears in the Spitsbergen sections.

C. Comparison of the upper Profilbekken Fauna, V_{4b} , with other Whiterock faunas

The upper Profilbekken Member fauna is considered to correlate with the early zone of the Whiterock Stage (*Orthidiella* zone). All available lines of evidence lead to this conclusion:

1. The fauna overlies the Valhallan without stratigraphic break.
2. L. R. M. Cocks, who is studying the brachiopods, reports the presence of *Orthidiella* probably identical with *O. longwelli* COOPER, from silicified residues from this interval.
3. Where trilobite species are identical with those outside Spitsbergen they are from the *Orthidiella* zone in Nevada, described in the various papers of Ross (1967, 1970, 1972). Identical species include: *Peraspis egugata* Ross, *Raymondaspis vespertina* Ross, *Kawina wilsoni* Ross, *Cybelurus halo* n. sp. (= *Miracybele* spp. of Ross 1967, 1972), *Punka caecata* n. sp. (= *Bathyurellus* sp. 4 Ross 1972) and *Carolinites sibiricus* CHUGAEVA (= *C. angustagena* Ross). Additional species with closely related species in Nevada, which may prove to be identical when further material from Nevada is described, include *Acidiphorus?* *ligo* n. sp., *Iliaenus oscitatus* n. sp. and various nileids (discussed

in FORTEY 1975). The weight of these similarities seems to put correlation with the *Orthidiella* zone beyond doubt. Faunas of this age are widely distributed, and have been recognised particularly along the western side of the North American continent (McKEE, NORFORD and ROSS 1972). Additionally, I note here that the fauna of the Shangort Grits, Co. Mayo, western Eire, includes one species (*Ectenonotus connemarius*) in common with the Profilbekken Member, and has several other genera with similar species, but too poorly preserved for comparison with the Spitsbergen fauna. It is likely to be of similar age.

4. Conodonts, which occur prolifically in the Valhallfonna Formation, are being studied by C. R. BARNES and S. M. BERGSTRÖM. Preliminary determinations consistent with the trilobite evidence (FORTEY and BARNES 1976).

The uppermost part of the Profilbekken Member is poorly fossiliferous, and it is possible that there is an extension there into a higher zone. The occurrence near the top of *Punka caecata* n. sp. shows that this upper part lies within the range zone of one species, and is unlikely, therefore, to be very much younger.

The Table Head Group (Lower, Middle and Upper Table Head Formations) of western Newfoundland, includes Whiterock trilobites in the Lower and Middle divisions. None of the species from the Profilbekken Member are in common with the Middle Table Head, although the large number of genera in common prove the similarity in facies that I have discussed elsewhere (FORTEY 1975a): *Ampyx*, *Endymionia*, *Shumardia*, *Triarthrus*, *Ischyrophyma*, *Nileus*, *Peraspis*, *Remopleurides*, *Illaenus*, *Raymondaspis*, *Turgicephalus* n. gen., *Cybelurus*, *Scotoharpes* and *Carolinites*, all of related but distinct species from those in the upper part of the Profilbekken Member. Evidence from graptolites from the Middle Table Head, conodonts (FÄHRÆUS 1970) and nautiloids (FLOWER 1978) point to the Middle Table Head being "younger" Whiterock, i.e. younger than *Orthidiella* zone (including at least the equivalent of zone M of Utah/Nevada, and above the base of the Llanvirn). There is nothing in the trilobite faunas from Spitsbergen inconsistent with this, and the younger age of the Middle Table Head is no doubt reflected in a different suite of species. The Lower Table Head is in a shallow water facies in Newfoundland, with a sparse fauna, and it is not perhaps surprising to find that it, too, has different species from those in Spitsbergen. Several species range through both Lower and Middle Table Head Formations, however, and it is possible that *both* are younger than *Orthidiella* zone in their type sections. Recent work in Northeast Newfoundland of the Northern Peninsula, in the region around Hare Bay, has revealed the presence there (in "Table Head" lithologies) of a fauna including *Carolinites sibiricus*, which may possibly be indicative of an age as old as *Orthidiella* zone.

The fauna of the allochthonous boulder in the Cow Head Breccia at Lower Head (WHITTINGTON 1963) includes only one species in common with the Valhallfonna Formation, *Ischyrotoma twenhofeli* RAYMOND, although all the

Pelagic trilobites	Carolinites sibiricus	Carolinites ekphymosa	Carolinites ekphymosa	Oppeuter inconnivus	Carolinites genacinoca inconnivus genacinoca				
	C. killaryensis	C. killaryensis							
Approx. British Zones	European "bifidus"	hirundo		gibberulus	nitidus	deflexus			
Australian Stages	? Darrwillian	? Yapeenian	Costlemainian	Chewtonian		Top Bendigo			
North American Graptolite Zones	"etheridgei"	Isograptus		bifidus	protobifidus	Top fruticosus			
Rose/Hintze Trilobite Zones	≅ Orthidiella	"K"		3	4	5			
North American "Shelly" Stages	Whiterockian	VALHALLAN		Cassinian					
Concurrent Range Zones	V ₄ ^b	V ₄ ^a	V ₃ ^b	V ₃ ^a	V ₂ ^b	V ₂ ^a	V ₁ ^c	V ₁ ^b	V ₁ ^a
Main Environment Divisions	V ₄		V ₃		V ₂		V ₁		
	Member	Profilbekken	Member	Olenidsletta		Member			
Formation	Valhallfonna Formation								

Fig. 3. Summary of the correlation of the Valhallfonna Formation, and the position of the Valhallan Stage.

genera of the Illaenid-cheirurid assemblages in the Profilbekken Member are present there. This single species is not enough to prove correlation of the Lower Head boulder with the *Orthidiella* zone rather than the Table Head, but it is enough to suggest that the possibility of a pre-Table Head age for the upper breccias of the Cow Head Group should be considered. FÅHRÆUS and NOWLAN (1978) obtained conodonts no younger than ? earliest Llanvirn from the Cow Head, which may be consistent with such a suggestion.

D. Genera with long stratigraphical ranges, and stratigraphical method

The fauna of the Valhallfonna Formation includes some genera with long stratigraphic ranges extending upwards into the Arenig from the Tremadoc or even Upper Cambrian (*Buttsia*, *Micragnostus*, *Bienvillia*, *Plicatolina*, *Hypermeccaspis*, *Parapilekia*, *Shumardia* and *Europeites*). These are associated with the nileid or the olenid environments. Conversely, some other genera are more usually associated with "Middle" Ordovician or younger faunas — *Illaenus*, *Scotoharpes*, *Plimerops* and *Robergiella* are examples. Similarly *Oopsites* and *Gog* are Arenig forms with closest relatives in Middle Ordovician rocks (*Telephina* and *Ogygiocaris* respectively). To the extent that the Valhallfonna fauna contains a mixture of such forms it does represent a transition between typical Cambrian and Ordovician faunas, but the dangers of using the generic assemblages alone for comparison and correlation with other faunas are now obvious. Thus the Simpson Index (e.g. WHITTINGTON and HUGHES 1972),

which provides a method of measuring generic similarity, should not be used to assess the age of a trilobite fauna in any but the most general way. Specific identities are more compelling evidence of similar age. But here one runs across the reluctance of trilobite workers in general to identify a species as identical to one described from an area far removed from the type area (which often coincides with the present day physiographic barriers). When starting to describe the Spitsbergen faunas, which are far removed from any area with described faunas, the evidence of morphology alone was used in the determinations. Although most of the species are new (as are a number of the genera) a number of forms, particularly from the Profilbekken Member, have been identified specifically with species originally described from very distant localities. This is on the basis of significant shared similarities in characters which are *known to be variable within the genus concerned*. For example, concerning *Cybelurus halo*, to which several specimens from Nevada are also assigned, the anterior cranidial border is known to be variable in a series of related species, and the broad border of *C. halo* is regarded as a reliable specific determinant. The specific identity achieves added stratigraphic significance if there are a series of species of the same genus in the sections, so, for example, the appearance of *C. halo* above *C. brutoni* in the Profilbekken Member is a reliable way of discriminating the Whiterock fauna from the Valhallan fauna below it.

E. Marker horizons

In the systematics, range charts and stratigraphic discussions the distribution of trilobites has been given calibrated against metres of section. This is the most convenient way of summarising stratigraphic information, but has one or two disadvantages. In the first place measurements of section are never exactly repeatable, and cumulative small differences may lead in sum to differences of several metres. Secondly, the stream sections change from season to season according to the distribution of superficial gravel, and the same applies to a lesser degree to some parts of the shore sections, particularly the upper part of the Olenidsletta and lower Profilbekken Member on Profilstranda. Fixed points in the sections are provided by a few, distinctive beds that are marker horizons, and these are listed following to enable future workers to repeat, and more importantly to refine the stratigraphic data given in this monograph. From the base of the Valhallfonna Formation upwards these are:

1. Basal nautiloid beds. In the lowest few metres of the Olenidsletta Member (V_1a) crystalline grey or black limestones with a profusion of orthoconic nautiloids in current lamination with extensiform didymograptids in the same beds. The succeeding black limestones of the olenid facies are monotonous and without distinctive marker horizons.

2. Coarse-grained olenid limestones. At the top of the black, flaggy olenid limestones, as V_2 is approached, centering on about 75 m from base of the Olenidsletta Member, the beds take on a "rhythmic" character with shale

and limestone — shales capped by thicker (up to 50 cm) beds of relatively pure limestone. These are peculiarly distinctive, containing a mass of beautifully preserved olenids (particularly *Balnibarbi* and *Svalbardites*) at 75 m.

3. *Gog* beds. Typical V_2 assemblages occur especially between 80–90 m from the base of the Olenidsletta Member, on dark, thin-bedded, slabby limestones. Conspicuous among the trilobites are large specimens of *Gog catillus*, sometimes articulated. Complete specimens of trilobites are more numerous here than in any other part of the section.

4. Basal Profilbekken Member phosphatised bed. Above the monotonous black limestones of the upper part of the Olenidsletta Member (V_3) a conspicuous marker horizon is formed by the basal phosphatic horizon of the Profilbekken Member, particularly well seen on melt stream A on Olenidsletta. This can be remarked in the field by shiny, black phosphatic brachiopods, the globular, phosphatised eyes of *Carolinites*, and small molluscs. Other phosphatised surfaces occur above this in V_{4a} , but none with the profusion of fossils of the basal horizon.

5. Green Beds. At about 30 m from the base of the Profilbekken Member, and with the introduction of the V_{4b} fauna, there are a series of highly glauconitic beds, containing drifts and pockets of bright green glauconitic minerals. Nautiloids are numerous here, often enveloped *post mortem* in algal laminates. Some silicification occurs in these beds. The pygidia of the pliomerid trilobite *Europeites* are particularly numerous here.

6. Basal algal microconglomerate. This is not the first appearance of allochthonous material in the Profilbekken sections, which appear as thin lenses of fossil-rich material within the darker, bedded limestones, but it is the first prominent feature (70 m from base). It forms a conspicuous rib near the seaward end of Profilbekken. Algal and other nodules are visible on weathered surface and can even be picked out by hand.

Phosphatised horizons. These are important for obtaining small growth stages of trilobites by solution of the limestones in acetic acid, and for other phosphatic (or secondarily phosphatised) microfossils, such as *Anatolepis* and *Janospira*. Small grains of phosphate are usually visible on the surfaces of the weathered rock. Such horizons seem to be found especially at the junction between the olenid and nileid facies (as between V_3 and V_4 , or V_2 and V_3), but also sporadically through V_2 and V_4 . It is presumed that these horizons are the product of former upwelling producing excess phosphate enrichment in the oceanic environment. Radiolaria are often associated with these horizons, and their unusual abundance at some horizons may also record the former existence of plankton “blooms”.

III. Summary in Russian

Свита Валхаллфонна и ее трилобиты

Из этой на севере Шпицбергена хорошо обнаженной свиты получены первые изобильные трилобитные фауны ордовика этого острова. По возрасту фауны распространяются по всему аренигу, переходя в лланвирн. Автором (FORTEY 1974, 1974a, 1975) описано больше 100 видов, составляющих, возможно, наиболее разнообразную фауну своего возраста во всем мире. Новыми являются большинство видов и ряд родов.

Трилобиты объединяются в три крупных бентических, частично связанных с глубиной (FORTEY 1975a) типа сообществ. Самым глубоководным является сообщество оленид, продолжающих развиваться здесь и после тремадока и составляющих преимущественно новые формы, в том числе и новое подсемейство *Balnibarbiinae* (FORTEY 1974). На промежуточных глубинах сообщество нилеид вмещает особенное обилие *Nileidae*, *Asaphidae*, *Raphiophoridae*, наряду с *Shumardia*, несколькими *Pliomeridae*, *Scutelluidae* и *Cybelinae*. Мелководное сообщество иллаенид - хейрурид представлено только в верхней части свиты Валхаллфонна, где преобладают *Illaenidae*, *Bathyruridae* и *Cheiruridae*, вместе с другими родами, как *Selenoharpes* и *Ischyrotoma*. В низах свиты Валхаллфонна (подсвита Оленидслетта: ранний - поздний арениг) чередуются сообщества оленид и нилеид, а в верхах свиты (подсвита Профилбеккен: позднейший арениг - лланвирн) сообщество нилеид поднимается в сообщество иллаенид - хейрурид.

Глубоководные роды бывают наиболее космополитскими, тогда как мелководные относятся к типу, ограниченному Северной Америкой и северо-востоком Сибири.

Четвертый тип сообщества состоит из не связанных фациями пелагических трилобитов. Это роды *Carolinites*, *Opireuter* и *Ooprites*, которые особенно широко распространены, обладая исключительным стратиграфическим значением (FORTEY 1976).

Самостоятельное доказательство возраста представляют многочисленные граптолиты, наутилоиды и конодонты тех же пород.

Последовательные фауны указаны буквами на рис. 1 этой статьи. Детальное сравнение проведено с видами, описанными из северо-восточной Сибири, Казахстана, с Пай-Хоя и Новой Земли, также как из Скандинавии, Северной и Южной Америки. Шпицбергенские фауны представляют собой с биогеографической точки зрения исключительную смесь, что объясняется смесью прежних сред, присутствующих в разрезах.

Представляющие интерес особенно для советских специалистов систематические детали сводятся к следующим:

1. Предками подсемейства оленид Balnibarbiinae могут быть представители рода Agalatus LISOGOR из тремадока Казахстана.
2. Те же виды рода Carolinites встречаются и в Сибири и на Шпицбергене. Семейство Telephrinidae расширено с целью включения в него и рода Carolinites и родственных ему родов, вызванного обнаружением рода Oopsites (FORTEY 1975), устанавливающего связь между родами Goniophrys и Telephina.
3. Многие шпицбергенские роды соответствуют родам Русской платформы. Это относится особенно к Europeites, Paraptychopurges и Parapilekia. Europeites и Parapilekia встречаются на несколько более молодом горизонте на Шпицбергене. Такие же виды родов Амрух, Nileus и агностид также встречаются в обеих областях.
4. Многие формы также подобны видам, описанным с Пай-Хоя Бурским (1970); при этом надо особенно отметить Lacorsalina и Cybelurus.
5. Фауна части подсвиты Оленидслетта (V_2^b и V_3^a) похожа на фауну Копалинской свиты Казахстана в отношении содержащих ее Asaphidae и Nileidae.

IV. Systematic descriptions

Systematic order. Rather more families are dealt with in this part of the monograph than in the previous parts. Because of the problems concerning the satisfactory definition of trilobite orders they are not given here, with the exception of the Agnostida, which has general acceptance. Families appear in the order used in the *Treatise on Invertebrate Palaeontology* (MOORE 1959), with the exception that the Scharyiinae are included in the Aulacopleuridae following THOMAS and OWENS (1978), Celmidae is now regarded as a subfamily of the Dimeropygidae, and both precede the Bathyruridae, to which they are probably related (FORTEY and OWENS 1975). Where more than one species is present in a given genus only the first is generally described in full, subsequent ones discriminated by a comparative discussion. Several forms are known from only a small amount of material and for these open nomenclature is generally employed, even when they are obviously new species. The remarkable *Theamataspis tuber* n. sp. is an exception to this.

Morphological terms. Terminology follows that of previous parts. 'Ala' (pl. alae) is restricted to the structures alongside the base of the glabella in harpids, as described in FORTEY (1975, p. 15).

Preservation. Most of the species are illustrated using testate material on the rock. Some supplementary information is gathered from silicified or phosphatised material. This consists of rather small specimens, and the species obtained from phosphatic horizons may include some that are not readily found on the surface, such as odontopleurids. Again, their small size has limited the formal naming of new species. Many phosphatised larval trilobites remain to be described, and this will be the subject of a future paper.

ORDER AGNOSTIDA SALTER 1864

Discussion. — The classification of agnostoid trilobites above the generic level is one of the more contentious issues in trilobite taxonomy. Little attempt has been made to relate Ordovician agnostoids to their Cambrian precursors. Recently, particularly due to the work of ÖPIK (1967), PALMER (1962), SHERGOLD (1977), and ROBISON (1964), the morphology of this group has become the subject of more critical appraisal. Here an attempt is made to discuss the affinities of the Ordovician agnostoids using a combination of internal and external features, which places them in families known in the Upper Cambrian. If this classification is correct it indicates that the Cambro-Ordovician boundary is not the major taxonomic barrier for the agnostoids as for many other trilobite groups, a view in accordance with ROBISON's (1972, p. 35) observation that agnostoid trilobites "have longer stratigraphic ranges than non-agnostoid trilobites" and might, therefore, be expected to have a relatively slow speciation rate. Such conservatism is not unique to this group out of the Valhallfonna trilobites, for the fauna also includes *Plicatolina* and a catillicephalid, related to Upper Cambrian species, as well as a number of genera persisting from the Tremadoc (p. 15). The discussion here centres on those species which have been referred to *Geragnostus*; other Ordovician agnostoids are discussed by PEK (1977), and CAPERA et. al. (1978).

Family AGNOSTIDAE M'COY 1849

Subfamily AGNOSTINAE M'COY 1849

Genus *Micragnostus* HOWELL 1935

Type species. — *Agnostus calvus* LAKE 1906.

Discussion. — Two species attributed to *Micragnostus* occur in the Arenig of the Valhallfonna Formation. They closely resemble the type species, *M. calvus* (LAKE), except that the posterior lobe of the pygidial axis is transversely wider than the preceding axial ring. In the past *Micragnostus* has been much confused with *Geragnostus*; here they are regarded as sufficiently distinct to be placed in separate families, a view contrary to that of WOLFART (1970), SDZUY (1955) and PEK (1977). The deep glabellar furrow defining the anterior

lobe in *Micragnostus* is straight and transverse. The glabellar tubercle is placed well behind this furrow. In *Geragnostus* glabellar furrows are best displayed on internal moulds, which show a short, transverse anterior furrow, the outer ends of which are deflected forward as a pair of shallow, outward-curving furrows which are convex-forwards. These furrows are the traces of the anterior margins of the prominent 6P muscle impressions, described in detail below. They are well displayed on the cephalon of the type species, *Geragnostus sidenbladhi*, as described and illustrated by TJERNVIK (1956, p. 188–9, Pl. 1, Figs 5, 6). The glabellar tubercle lies *immediately* behind the transverse part of the anterior furrow (Pl. 2, Fig. 2). Thus glabellar structure of *Micragnostus* and *Geragnostus* is radically different; indeed development of a *Micragnostus*-type transglabellar furrow on a *Geragnostus* cephalon is not possible without transecting the anterior two pairs of lateral glabellar muscle impressions. The tightly “rolled” posterolateral borders of *Micragnostus* is quite different from the broad, flattened borders of geragnostids.

In view of the distinctions used here a number of species previously referred to *Geragnostus* may be re-assigned to *Micragnostus*: viz. *M. intermedius* (PALMER (1968), *M. curvatus* (ROBISON and PANTOJA-ALOR 1968), *M. elongatus* (CHIEN 1961), *M. spinosus* (CHIEN 1961), and also probably “*Homagnostus*” *reductus* WINSTON and NICHOLLS 1967.

Micragnostus is closely related to *Homagnostus*, and may have been derived from it, the latter genus being distinguished from *Micragnostus* by a median longitudinal furrow wholly or partly bisecting the preglabellar field. ROBISON and PANTOJA-ALOR (1968, p. 776) indicate that transitional populations can exist between the *Homagnostus* and *Micragnostus* condition, a few members of the population retaining a vestige of the preglabellar furrow. Once lost, however, the median furrow does not seem to have re-appeared; on the Spitsbergen species no trace of such a furrow is visible on any specimen, even on small growth stages.

Homagnostus is a close relative of *Agnostus* itself (PALMER 1962, p. 11) and for this reason *Homagnostus*, *Agnostus* and *Micragnostus* are regarded as belonging within the same subfamily of the Agnostidae. They constitute a conservative plexus of species, persisting from the Upper Cambrian to the Arenig with only relatively minor morphological changes.

Micragnostus serus n. sp.
(Pl. 1, Figs. 1–14, 16)

Stratigraphic range. — Olenidsletta Member almost throughout lower part, 20 m to 106 m from base, commonest in limestones underlying earliest *Isograptus* fauna.

Material. — Holotype, pygidium, PMO NF 404. One poorly preserved exoskeleton PMO NF 2024; numerous cephalae include: PMO NF 2755, 2758, 677, 2893, 2671, 3142, 3135, 2927, 3134, 2918, 2921 pygidia: PMO NF 402, 3140, 1456, 1747, 2930, 2919, 2618, 672.

Diagnosis. — A *Micragnostus* species with surface sculpture of fine raised lines. Pygidial axis (excluding half-ring) 0.63–0.68 total pygidial length. First axial ring tapers backwards; lateral parts of first ring furrow longer (exsag.) than mid-part. Terminal piece of greater transverse width than preceding axial ring, which is parallel sided. Axial node on second axial ring tumid over posterior half of ring. Pygidial marginal spines minute.

Description. — One poorly preserved external mould of a complete specimen indicates that the species attained a length of at least twice its width. Cephalon of maximum transverse width equal to, or slightly exceeding sagittal length; width increases slightly from the posterior margin to reach a maximum at about half cephalic length. Highest point of cephalon at posterior part of glabella, where the height is about half cephalic width. Glabella extends to 0.70–0.75 cephalic length, anterior half parallel sided, posterior half (pre-occipital) tapering slightly forwards, axial furrows narrow. Transverse glabellar furrow at about two-thirds glabellar length, deeply dividing convex anterior lobe from posterior lobe of glabella, not quite reaching axial furrows on external surface of larger cephalia, passing completely across on internal moulds and small specimens. There is an indication of a faint pair of furrows slightly constricting the sides of the glabella just anterior to the glabellar tubercle, which is small and (sag.) elongate, just posterior to half glabellar length. Posterior margin of pre-occipital glabella obtusely rounded about mid-line, steeply downsloping; occipital furrow deep. Occipital ring developed as two broadly triangular basal lobes connected by a narrow (sag.), downsloping median band which bulges slightly backwards about mid-line. Axial furrows defining lateral edges of occipital ring run inwards and forwards at about 45 degrees to sag. line. Cheeks convex, especially posteriorly where they just overhang the borders. Pre-glabellar field shows no sign of a median furrow, even on small cranidia (Pl. I, Fig. 8). Posterior border furrow passes behind lateral extremity of occipital ring, passing without a break into lateral border furrow. The short posterior border expands rapidly to a rather blunt genal spine, thence curving downwards and abaxially into the narrow lateral borders. The borders are narrow posteriorly where they are partly tucked beneath the cheeks, expanding gradually in width to about mid-length of cephalon, thereafter of constant width around front margin of cephalon.

Thorax not preserved well enough to permit description.

Pygidia of maximum width at about mid-length equal to or slightly exceeding sagittal length (including half ring); pygidial axis slightly variable in length, between 0.63 and 0.68 pygidial length (excluding half ring). Axis of maximum width across first axial ring, which is slightly less than half maximum width of pygidium. Axial furrows converge posteriorly adjacent to first axial ring, become subparallel adjacent to the second axial ring, and diverge at the anterior part of the terminal piece, although the divergence here is less than the initial convergence. The furrows curve around the terminal piece, the posterior half of which has a semicircular outline. The furrow defining the first ring consists of a short (less than one-third) shallow, transverse median

part, flanked by slightly deeper, outward and backward-sloping sections. The first ring is trisected by a pair of shallow furrows running forwards (exsag.) from the tips of the transverse median part of the ring furrow. The second axial ring is defined by a transverse or slightly backward-bowed furrow of uniform depth.

Because of the direction of curvature of the ring furrows the second axial ring is twice as long (sag.) as the first. Mid part of the second axial ring carries a prominent globular node which forms the highest point on the pygidium; the furrows flanking this node do not extend further forward than about the mid-length of the axial ring. The length of the terminal piece is a variable character in this species: in some specimens (Pl. 1, Fig. 16) it just exceeds the length of the previous two axial rings, in others it is somewhat shorter. Every intermediate between these extremes can be found, and no taxonomic importance is attached to this axial variation. The tip of the terminal piece carries a minute tubercle. Pleural fields convex, downward slope terminating abruptly at deep border furrow. The posterior border has an almost circular cross-section, widening backwards from the anterior margin as far as pair of minute, blunt-tipped marginal spines, thereafter of constant width around posterior margin of pygidium. Articulating device of agnostoid type (ÖRİK 1967, p. 72) fulcrum close to axis. Anterior border furrow widening abaxially, confluent with posterior border furrow, which it meets at an obtuse angle. Articulating half ring less than half length (sag.) of first axial ring.

Dorsal surface of cuticle covered with fine, anastomosing raised lines, which are arranged in ranks generally parallel to the cephalic and pygidial margins; internal moulds smooth.

Discussion. — This species is associated with trilobites of the olenid community, and, like some of the olenids themselves, has its close relatives in rocks of Tremadoc or even upper Cambrian age. The persistence of *Micragnostus* is probably due to the persistence of the peculiar olenid environment. I regard it as unlikely that *Micragnostus* was planktonic as its occurrence in any abundance is limited to a particular lithofacies and faunal association; furthermore it seems to have a mutually exclusive relationship to *Arthrorhachis*, the abundance of which falls off rapidly in the olenid environment and which is commonest in Spitsbergen in beds containing the nileid community.

M. serus differs from the type species of *Micragnostus*, *M. calvus* (LAKE 1906), the lectotype of which species is illustrated on Pl. 1, Fig. 15, as the transverse width of the pygidial terminal piece exceeds that of the preceding ring, the length (sag.) of that ring itself greatly exceeding the length of the first axial ring. The elevation of the median node only on the posterior half of the second pygidial ring is another distinguishing feature of *M. serus*. Of other species of *Micragnostus* the closest is *M. vilonii* from the Tremadoc rocks of Argentina (HARRINGTON and LEANZA 1957, p. 68–9, Figs. 12, 13: 7–8) which has an expanded terminal piece and similarly positioned pygidial node to *M. serus*. The pygidium of *M. vilonii* differs from that of *M. serus* in two features: the median, horizontal part of the first ring furrow is effaced; and the pygidial

axis extends to 0.8 pygidial length. Of cephalic differences the deeper transglabellar furrow of *M. vilonii*, and the fact that this furrow is described as curving slightly backwards may be due to crushing of the Argentine material. Some specimens of *Micragnostus bisectus* (MATTHEW) from the Trempealeau of Vermont (SHAW 1951, Pl. 23, Figs. 15, 17) have an expanded terminal piece, but the whole axis is much more tumid than that of *M. serus*, the posterior taper of the first axial ring is much less, and the marginal spines (*ibid.* Pl. 23, Fig. 15) are longer. The resemblance between an Argentine and Spitsbergen species is of interest as it has already been noted in trilobites of other families, *Mendolaspis* and *Rhombampyx* in the Raphiophoridae (FORTEY 1975) and *Bienvillia stikta*, and *Hypermecaspis* spp. in the Olenidae (FORTEY 1974a).

In spite of its long stratigraphic range, stratigraphically early specimens of *M. serus* display few differences from later ones; pygidia are identical (Pl. 1, Fig. 11), but the cephalae of the earlier specimens have borders which expand rather rapidly in width anterolaterally and attain a greater width than the borders of the later specimens (Pl. 1, Fig. 8). Since few well preserved early specimens are available the variability is not sufficiently known to formally designate these early specimens as a distinct subspecies.

Micragnostus sp. A.

(Pl. 1, Figs. 17, 18)

Stratigraphic range. — Lower part of Olenidsletta Member, 70 m to 75 m.

Material. — Two incomplete pygidia, PMO NF 3133, 601.

Discussion. — This second species of *Micragnostus* is represented by sparse, fragmentary material insufficient to permit naming formally as a new species. The pygidia are relatively longer than those of *M. serus*, and the posterior margins with more truncate outline. The outer parts of the first ring furrow are concave-forwards, and the (exsag.) furrows trisecting the first axial ring are deep. In other respects *M. sp. A.* differs from other *Micragnostus* in the same features as *M. serus*. Although border spines are apparently not present, the only specimen with border preserved is a poor internal mould, and it is not possible to be certain on this point.

Family METAGNOSTIDAE JAEKEL 1909

Subfamily METAGNOSTINAE JAEKEL 1909

(= Trinodidae HOWELL, 1935; Geragnostidae HOWELL 1935; Arthrorhachidae RAYMOND, 1913).

Family name. — The family name Metagnostidae JAEKEL, 1909 is revived here to embrace some of the genera usually referred to the family Geragnostidae HOWELL, 1935. The holotype of the type species of *Metagnostus*, *M. erraticus* JAEKEL, 1909, is a well-preserved, entire, enrolled exoskeleton from *geschiebe*

material originating from the Asaphus-Kalk of Scandinavia. This specimen has been reillustrated by NEBEN and KRUEGER (1971, Pl. 11, Figs. 34–36). As RAYMOND (1913, p. 139) noted, *M. erraticus* shares many points of similarity with *Arthrorhachis tarda* (BARRANDE), and *Metagnostus* is best regarded as a junior subjective synonym of *Arthrorhachis*. This does not, however, affect the validity of the family name Metagnostidae, which (ICZN Art. 40) takes precedence over the later names proposed by RAYMOND and HOWELL listed above.

Discussion. — There are interesting problems in the definition and affinities of the genera included here in the Metagnostidae which well-preserved material from Spitsbergen help to clarify.

A distinctive arrangement of muscle impressions in the *Arthrorhachis* glabella is described below (Fig. 4A). Internal moulds of some species attributed to *Geragnostus*, including the type species *G. sidenbladhi* (LINNARSSON) (TJERNVIK 1956, Pl. 1, Fig. 5) have a short transverse furrow or depression immediately in front of the glabellar tubercle. The outer ends of this furrow are continued into forward- and outward-curving furrows, which are the traces of large, anterior muscle impressions on the glabella (SHERGOLD 1977). This cephalic pattern on the parietal (internal mould) surface is regarded as an important unifying character of the *Geragnostus*/*Trinodus*/*Arthrorhachis* group regardless of the ways in which these genera may be further distinguished. The axial characters are considered of special importance in the following notes on the classification of metagnostines:

(1) Some species hitherto assigned to *Geragnostus* are transferred to *Micragnostus*, and to a different family. These species are discussed above, under *Micragnostus*.

(2) The genus *Galbagnostus* WHITTINGTON 1965, type species *G. galba* (BILLINGS 1865) has glabellar musculature homologous with that of *Arthrorhachis* (Fig. 4B). In *Galbagnostus* the anterior glabellar lobe has contracted so that the musculature extends almost to the front of the glabella, and the glabellar tubercle is concomitantly found in an anterior position. The pygidium also shows some differences from most *Arthrorhachis* and *Geragnostus* species, notably a deep depression behind the axis, but the caecate internal mould can now be matched by the *Arthrorhachis* species from Spitsbergen described below. *Galbagnostus* species may be more widespread than WHITTINGTON's (1965, p. 308–9) original discussion indicates, for example, *Trinodus? saltaensis* HARRINGTON and LEANZA 1957, from the Tremadocian of Argentina, shows the diagnostic combination of cephalic and pygidial features of *Galbagnostus*, and *Geragnostus?* sp. no. 2 of TJERNVIK (1956, p. 194, Pl. 1, Fig. 15), from the early Arenig of Sweden, is a cephalon showing an advanced position of the glabellar tubercle typical of *Galbagnostus*. *Granuloagnostus* PEK 1970, from the Llanvirn of Bohemia may be a scrobiculate *Galbagnostus*.

(3) The difference or otherwise between *Geragnostus* and *Trinodus* has been the subject of much discussion in the literature (DEAN 1973, p. 290; HUGHES 1969, p. 55–56; DEAN 1966, p. 274; WHITTARD 1966, p. 265; WHITTINGTON

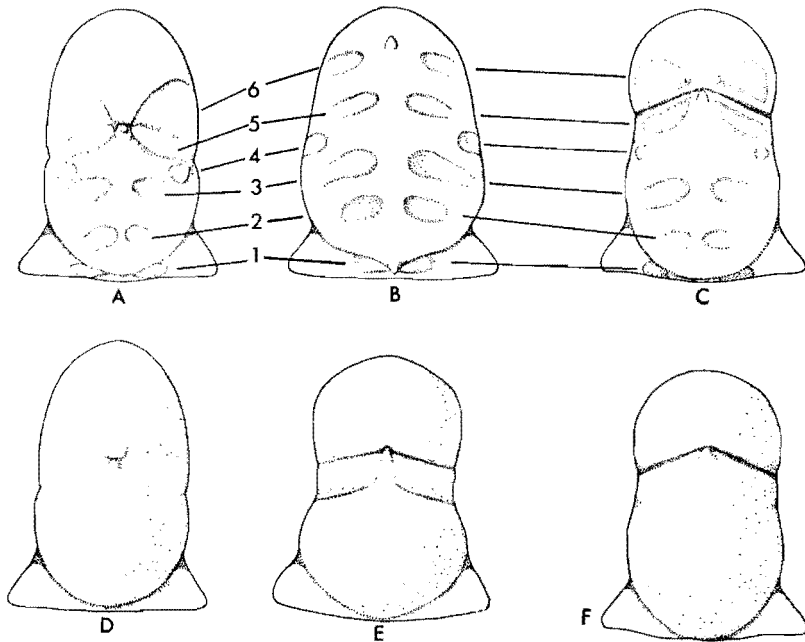


Fig. 4. Glabellar structure in metagnostid genera. A-C: parietal (internal mould) surfaces showing homology of muscle insertion areas 1-6. A. *Geragnostus* and *Arthrorhachis* groundplan; B. *Galbagnostus*; C. *Segmentagnostus*, showing how glabellar furrow relates to insertion areas. D-F: diagrams of external glabellar surfaces. D. *Arthrorhachis*/*Geragnostus*; E. *Corrugatagnostus*; F. *Segmentagnostus*.

1963, p. 28; Ross 1958, p. 563-4). The type species of *Trinodus*, *T. agnostiformis* M'COY, is known from a single, poorly preserved and distorted cephalon. For most comparative purposes *Trinodus* is based upon *T. tardus* (BARRANDE), a widespread species of the upper Ordovician. Of the differences between this species and those of *Geragnostus*, the most consistently cited is the relatively greater length of the pygidial axis of the latter. This feature is variable in many agnostids, and in the species from Spitsbergen the axis varies in length at a subspecific level (Pl. 2, Fig. 13). As a generic determinant it is not entirely adequate. Similarly the dorsal expression of both glabellar tubercle and median, transverse glabellar furrow is variable within a single species (DEAN 1966, p. 275-6), and, although effaced on the dorsal surface, may be prominent on internal moulds (see *Geragnostus fabius* (BILLINGS) WHITTINGTON 1965, Pl. 2, Figs. 4, 20). Add to this the fact that on KIELAN's (1960, Pl. 1, Figs. 7, 8) illustrations of *Trinodus tardus* there are indications of the faint, forward curving anterolateral cephalic furrows characteristic of internal moulds of *Geragnostus*, and the differences between the cephalon of two genera become extremely difficult to define (cf. DEAN 1966, p. 274). However it is equally difficult to suppose that two species as different in pygidial proportions as, say, *Trinodus tardus* and *Geragnostus crassus* TJERNVIK 1956 should be placed in the same genus. It is furthermore unlikely that "long pygidial axis" forms have the intranotular axis developed posteromedially, as discussed below for the shorter

forms. While recognising the arbitrariness of such a division, a distinction between *Geragnostus* and short axis ("Trinodus") forms might be made if the former genus is taken to include species with the terminal lobe on the pygidial axis exceeding the length of the postaxial region (sag.) inside the border. However, since the pygidium of the type species of *Trinodus* is unknown it is not possible to evaluate its most critical characters. For this reason, and because attempts to recover topotype material of *T. agnostiformis* have met with no success, it seems preferable to restrict the use of *Trinodus* to the type specimen, and to use instead the generic name *Arthrorhachis* HAWLE and CORDA 1847, type species *A. tarda* (BARRANDE), for the species with a short terminal piece on the pygidial axis. The loss of the much-used name *Trinodus* may seem unfortunate, but at least *Arthrorhachis* has a completely known type species, and one which has for a long time been the "effective" type of *Trinodus*. The holotype of *Arthrorhachis tarda* has been refigured by PEK (1977, Pl. 8, Fig. 2).

(4) Even after removing species properly assigned to *Micragnostus* from *Geragnostus* there remain a number of species formerly assigned to *Geragnostus* which differ fundamentally from both *Geragnostus* and *Arthrorhachis* as here defined. I refer to those species with a complete transglabellar furrow, but one which has the form of an inverted 'V'; the glabellar tubercle lies just behind the apex of the inverted 'V'. This position of the tubercle, together with the flattened rather than "rolled" borders, indicates that these agnostids have affinities with the metagnostines rather than with the agnostines. The form of the transglabellar furrow is explained by its incision along the *posterior* margin of the 6P glabellar muscle impression rather than the anterior margin as in *Arthrorhachis* (Fig. 4C, D). These species should now probably be referred to *Segmentagnostus* PEK 1977 (type species *Agnostus caducus* BARRANDE 1872). Besides the type species the following should be included in *Segmentagnostus*: *Agnostus mccoyi* SALTER 1854 (see WHITTARD 1955, p. 8, Pl. 1, Figs. 5, 6; WHITTARD 1966, p. 265-6, Pl. 46, Fig. 2; HUGHES 1969, p. 56-60, Pl. 1, Figs. 1-12), *Agnostus hirundo* HICKS (Whittard 1955, p. 7, Pl. 1, Figs. 1-4), *Geragnostus neumanni* (HARRINGTON and LEANZA 1957, p. 69, Fig. 13: 9-11), *Anglagnostus? pradesensis* CAPERA et al. (1978, Pl. 5, Fig. 9) and also that specimen incorrectly identified by LAKE (1906, p. 22, Pl. 2, Fig. 17) as *Geragnostus sidenbladhi* (and used in error in the 1959 *Treatise* by HOWELL to illustrate the type characteristics of *Geragnostus*).

Corrugatagnostus (type species *C. morea* (SALTER) — WHITTARD 1955, p. 10-12, text-Fig. 2b, c) also has an "inverted V" anterior glabellar furrow, but with a second furrow of similar form behind the first. It is tempting to speculate that this second furrow represents a deepening of the posterior margins of the 5P glabellar furrows on the metagnostine groundplan, and that *Corrugatagnostus* is a scrobiculate metagnostine rather than a glyptagnostid (●PIK 1967, opp. p. 66).

The type species of *Girvanagnostus* KOMAYASHI 1936, *G. girvanensis* (REED 1903) is a normal *Arthrorhachis*; *Girvanagnostus* is considered to be a junior synonym of *Arthrorhachis*.

KOBAYASHI and HAMADA (1978) have recently proposed the genus *Geratrinodus*, based on *G. perconvexus* from the Upper Ordovician of the Langkawi Islands, Malaysia. The genus is discriminated on the effacement of the cephalic and pygidial furrows within the axis: on the pygidium only the median node is clearly visible. However, effacement is one of the most variable features in this group of agnostids, even within a single species (DEAN 1966), and it seems to me unwise to found a genus on these sort of characters. *Geratrinodus* is accordingly regarded as a subjective synonym of *Geragnostus*. *Neptunagnostella* PEK 1977, is probably a senior synonym of *Geratrinodus*.

(5) The Ordovician metagnostines discussed above are considered to be related to the Pseudagnostinae. This conclusion is reached from a number of lines of evidence.

- (a) Both *Galbagnostus* and *Arthrorhachis* (Pl. 2, Fig. 8) show a series of "post-axial" muscle scars on the pygidium. This means, as WHITTINGTON (1965, p. 308) observed, that the true axis extends backwards beyond its obvious surface expression. This median series of paired muscle impressions constitute an intranotular axis (ÖPIK 1967) which are found on many upper Cambrian pseudagnostids.
- (b) *Neoagnostus bilobus* (SHAW 1951, p. 112-3, Pl. 24, Figs. 17-22; SHERGOLD 1977, pl. 16, Figs. 7, 8) shows a number of particularly relevant features: the cephalon shows a combination of the furrows typical of *Segmentagnostus* on the one hand and *Arthrorhachis* on the other, indicating that both the anterior and posterior margins of the 6P muscle are incised, forming a cruciform pattern on the forward part of the glabella; the anterior part of the pygidial axis is divided transversely into three lobes (rather than two, as is normal for *Pseudagnostus*), furthermore accessory furrows are absent and the axial furrows are defined around the tip of the (pseudo) axis. The presence of the intranotular axis is not obvious from the figures but apparent from SHAW's (p. 112) description. *N. bilobus* closely resembles *Machairagnostus tmetus* HARRINGTON and LEANZA (1957, p. 64, Figs. 6, 7) on which the intranotular axis is especially prominent.
- (c) A curious cobweb-like surface sculpture is developed sporadically on species of Metagnostidae: *Galbagnostus galba* WHITTINGTON 1965 and *Arthrorhachis elspethi* (COOPER 1953) (see also HUNT 1967). The same sort of sculpture is present on *Pseudagnostus* (or *Neoagnostus*) *araneavelatus* SHAW (1951, p. 113, Pl. 24, Figs. 12-16), which, in addition, shows a *Segmentagnostus*-like glabellar furrow pattern.
- (d) The cephalic and pygidial borders of pseudagnostids have the low profile and broad border furrow found on metagnostines, and different from the "rolled" border of the Agnostinae.
- (e) The furrow defining the articulating half ring deepens laterally into a pair of apodemes on our *Arthrorhachis* (e.g. Pl. 2, Fig. 4) as it does on *Pseudagnostus* and related genera (compare agnosteid articulation of *Micragnostus*).

While it is not suggested that the pseudagnostids listed above are the direct ancestors of the metagnostines reviewed here, they are considered

to show a plexus of common characters sufficient to suggest that they may eventually need to be included within the same higher taxon. Since *Galbagnostus*, *Arthrorhachis* and *Segmentagnostus* are found as early as the Tremadoc, it is possible that they have separate pseudagnostid origins, in which case the Metagnostidae will take precedence over Pseudagnostidae as family name. More knowledge of the early forms is needed before this can be justified. For example, it is possible that some of the metagnostines with a long pygidial axis may have evolved from species of *Oxyagnostus* (ÖPIK 1967, p. 159–161, Pl. 63, Figs. 5–7).

Genus *Arthrorhachis* HAWLE and CORDA 1847

Girvanagnostus KOBAYASHI 1936.

Type species. — *Arthrorhachis tarda* HAWLE and CORDA 1847.

Arthrorhachis danica danica (POULSEN 1965).

Remarks. — Although this species does not occur in Spitsbergen the highly variable *Arthrorhachis* there include forms so close to *A. danica danica* that they are regarded as different only at a subspecific level. *A. danica danica* is from a limestone on the island of Bornholm, of similar Arenig age to that part of the Olenidsletta Member containing *Arthrorhachis* in Spitsbergen.

Arthrorhachis danica proxima n. subsp.
(Pl. 2, Figs. 1–9, 11, 12)

Stratigraphic range. — Middle part of Olenidsletta Member, ?75, 80–92 m from base, intergrading with *A. danica brevis* n. subsp. Confined to nileid community type.

Material. — Holotype, pygidium PMO NF 401a. Other material includes one imperfectly preserved dorsal exoskeleton PMO NF 2044; pygidia: PMO NF 3111, 3141, 527; cephalae: PMO NF 401b, 3138, 501.

Diagnosis. — Subspecies of *A. danica* with gently tapering pygidial axis (excluding half ring) between 0.48 and 0.57 total pygidial length; terminal piece with rounded posterior margin, axis tapering less than that of *A. danica brevis*. Pygidial node tumid over posterior part of second axial ring.

Description. — The only complete specimen is incompletely preserved and crushed, but it does show that the surface of the cuticle is without surface sculpture, and that the border furrows and axial furrows are narrower and fainter on the dorsal surface than the internal moulds. Most of the other material is exfoliated, and the description which follows is based on uncrushed internal moulds.

Cephalon of length 0.8–0.9 maximum width, which is at about half cephalic length. Glabella extends to two-thirds cephalic length, tapering gently forwards in front of occipital ring; broadly rounded anteriorly. Prominent glabellar tubercle at, or slightly anterior to glabellar mid-length. Glabellar musculature best developed on the cephalon attributed to *A. danica brevis* (Pl. 2, Fig. 10), but with identical form in this subspecies. 1P on lateral occipital lobes; 2P and 3P small, transversely elongate, within glabella behind tubercle; 4P circular, often elevated as a small prominence, adjacent to axial furrows; 5P immediately in front of 4P and adjacent to glabellar tubercle, transversely elliptical and sloping slightly outwards-backwards. Glabella shows a slight constriction at the outer ends of 5P. 6P largest, adjacent to axial furrows in front of glabellar tubercle. Margins of muscle impressions deepened on internal moulds representing linear cuticle thickening on the internal surface of the exoskeleton. The development of these thickened rims is variable, but the anterior margins of the 6P muscle impressions are always visible as a pair of forward and outward curving furrows, their inner and posterior ends connected by a short transverse furrow immediately in front of glabellar tubercle. Occipital ring with triangular lateral lobes, narrow, slightly depressed median band below posterior part of pre-occipital glabella, which although rounded in dorsal view, has a slight median carination when viewed posteriorly. Axial furrows converge strongly forwards adjacent to lateral occipital lobes, thereafter converging only gently; furrows are deep and broad on most specimens, but the transverse width of the furrows seems to be another rather variable feature. Cheeks slope steeply downwards, but without bulging convex-outwards. Posterior border produced into a blunt spine. Posterior margin of cephalon steeply upward-arched on mid-line. Cephalic border furrow wide, defining borders which are almost flat adaxially, downward-turned sharply at periphery of cephalon. Borders are widest anterolaterally, expanding in width from posterior margin where they merge with posterior border, and narrowing adaxially again towards mid-line.

Thorax known only from the one imperfect complete specimen, of similar form to that of *A. clusa* (WHITTINGTON 1963, Fig. 3A, B).

Pygidium of dimensions similar to those of cephalon (excluding half ring) with short axis occupying between 0.48 and 0.57 pygidial length, excluding half ring. Axis tapers backwards gently, axial furrows including an angle of as little as five and no more than thirty degrees, terminal piece rounded posteriorly. Much of the axial variability in pygidia of this species is due to the variation in the axial taper — those specimens with relatively convergent axial furrows have a narrower (trans.) and therefore smaller terminal piece. The first axial ring is narrower (exsag.) than the second; outer parts of first ring furrow slope backwards, and are not continued across the mid-part of the axis. They curve forwards in gentle arcs, converging to where they meet the furrow defining the half ring, and thereby trisecting the first axial ring. Some specimens show traces of the mid-part of the first ring furrow on the flanks of the middle lobe of the first axial ring (Pl. 2, Fig. 7); the second ring furrow is complete and transverse. Posterior half or two-thirds of mid-part of second ring

consists of a prominent tubercle, forming the highest point of the pygidium. The tip of the tubercle is broken off on available material; it is likely to have been similar to that of *A. danica brevis* (Pl. 2, Fig. 14), which is not produced into a spine. The terminal piece occupies between 0.35–0.45 length of axis; mid-part, behind pygidial tubercle, slightly inflated on some specimens. Tip of the axis marked by a minute tubercle which is present also on the dorsal surface. Ring furrow deep, and deepest in its lateral portions. Pleural fields steeply downsloping except behind axis. On this area one specimen (Pl. 2, Fig. 8) shows faint intranotular axis extending to about third length of post-axial pleural field. Posterior border like that of cephalon, widest postero-laterally where there is a minute pair of spines; these are present wherever the border is well-preserved and are probably invariable for this subspecies. Anterior border a narrow (exsag.) ridge, easily destroyed in preparation, adaxial part horizontal, terminating in a small articular process; abaxial part downsloping, with steeply downward-sloping facet widening to anterolateral margin.

Internal moulds are caecate on a fine scale — the degree to which the caeca are developed is highly variable — on the specimen displaying them best (Pl. 2, Fig. 5) they appear to be approximately radially arranged on the flanks of the cephalon, more irregularly pitted anteriorly. Internal moulds are also densely pitted, especially on the borders, indicating that the internal surface of the cuticle was granulate.

Discussion. — This subspecies intergrades with *A. danica brevis* which occurs above it in the Olenidsletta Member. The specimens with the larger, rounded terminal piece on the pygidium and axial furrows more nearly subparallel are the stratigraphically earlier, successively younger specimens having smaller terminal pieces and more tapering furrows. The line between *A. danica proxima* and *A. danica brevis* is therefore an arbitrary one, the latter name being applied to those pygidia with axial taper (angle enclosed by axial furrows in dorsal view) greater than thirty degrees, small terminal piece with a faintly tripartite posterior margin. Pygidial border of one specimen (Pl. 2, Fig. 15) is conspicuously wider than that of *A. danica proxima*. There are no convincing differences between the cephalae of the subspecies. The subspecific differences here span the differences between *Geragnostus* and *Trinodus* of authors, but both lie within *Arthrorhachis* using the arbitrary division on pygidial proportions given above.

A. danica proxima includes some pygidia remarkably close to the nominate subspecies (compare Pl. 2, Fig. 7 with POULSEN 1965, Pl. 1, Fig. 1); although POULSEN's figured material does not display marginal spines, he mentions (*ibid.* p. 62) their presence on one specimen and this cannot be used as a distinction. A more compelling difference is that on POULSEN's material the mid-part of the two pygidial rings is inflated and continuous with the pygidial tubercle; this single character merits subspecific distinction, but hardly more. Cephalae are difficult to compare because of the incompleteness of POULSEN's material; it is possible that the glabellar taper anteriorly is greater on the Bornholm subspecies.

A. danica brevis more closely approaches the type species *A. tarda* (BARRANDE) (KIELAN 1960, p. 59–62, Pl. 1, Fig. 6–13; DEAN 1971, p. 8, Pl. 1, Figs. 1, 2;

РЕК 1977, Pl. 8, Figs. 1–4) in the proportions of the pygidial axis; however the latter species has a reticulate sculpture, prominent marginal spines more posteriorly positioned, and cephalic musculature less impressed.

Other species which have comparable specimens in the Spitsbergen populations are: “*Trinodus*” *hebetatus* DEAN (1973a, p. 289–90, Pl. 1, Figs. 6, 13, 15) from the Arenig of Turkey, which compares most closely with the pygidium of *A. danica brevis* on Pl. 2, Fig. 13, but has a median inflated area on the pygidial axis like that of *A. danica danica*; “*Geragnostus*” *brevirhachis* BURSKEY (1970, p. 98–9, Pl. 1, Figs. 1–3) from the late Tremadoc of north Arctic Urals, which compares with stratigraphically early *A. danica proxima*, but for the terminal piece on the pygidial axis slightly exceeding in width the preceding axial ring, and the axis being slightly longer (sag.); “*Trinodus*” *mobergi* TJERNVIK (1956, p. 195–6, Pl. 1, Figs. 18, 19) from the late Tremadoc of Sweden resembles *A. danica brevis* of Pl. 2, Fig. 15 but for the terminal piece of the pygidial axis tapering backwards more markedly than the axial furrows, and the glabella being shorter. All three species just named are known from a few specimens (in the case of “*T*”. *hebetatus* DEAN a single specimen). In view of the great variation exhibited within populations of *A. danica* illustrated here, the few specimens of these species scarcely presents a sufficient sample for comparative purposes. *Trinodus* ? *valmyensis* ROSS (1958, p. 562–564, Pl. 83, Figs. 1–4, 7, 14–16) has a pygidium similar to that of *A. danica proxima* in its general proportions, but the glabellar tubercle is in the advanced, *Galbagnostus* position. A specimen attributed to *Geragnostus mediterraneus* HOWELL 1935, and figured by CAPERA et al. (1978, Pl. 7, Fig. 18) is not unlike earlier pygidia from Spitsbergen, but for a longer terminal piece and ? tumid marginal spines.

Arthrorhachis danica brevis n. subsp.

(Pl. 2, Figs. 10, 13–15)

Stratigraphic range. — Upper part of Olenidsletta Member 102 m to 106 m from base.

Material. — Holotype, pygidium, PMO NF 2664. Pygidium, PMO NF 70; cephalae: PMO NF 3137, 1625.

Diagnosis. — A subspecies of *A. danica* with pygidial axis (excluding half ring) 0.45–0.50 total pygidial length; axis tapers more rapidly than that of *A. danica proxima* thereby defining a smaller terminal piece, the posterior margin of which is truncate, tripartite.

Discussion. — Because this subspecies intergrades with *A. danica proxima* it is fully discussed in relation to that subspecies in the preceding paragraphs. Further comment is unnecessary here, except to note that it is represented by few specimens in that part of the Olenidsletta Member transitional between the nileid and upper olenid communities; scarcity of *Arthrorhachis* is there associated with an abundance of *Micragnostus*.

POLYMERID TRILOBITES

Family SHUMARDIIDAE LAKE 1907

Genus *Shumardia* BILLINGS 1862*Type species.* — *Shumardia granulosa* BILLINGS 1862.

Discussion. — DEAN (1973, p. 8) has suggested that the concept of *Shumardia* is rather broad, and that there may be reasons to revive CALLAWAY's (1877) genus *Conophrys*. Certainly a comparison of the type species of *Conophrys* (*C. salopiensis* CALLAWAY) with that of *Shumardia* (redescribed by WHITTINGTON 1965) shows several important differences. *Shumardia* has large anterior glabellar lobes compared with *Conophrys*, and the pygidium is elongate rather than transverse, with a flattened postaxial border. Other described *Shumardia* species have elongate pygidia like *S. granulosa*, for example *S. dicksoni* MOBERG and SEGERBERG 1906. On the other hand considering species attributed to *Shumardia* as a whole the differences between these extremes are straddled by several intermediate forms. Both *S. acuticaudata* and *S. minaretta*, described below, and *S. exophthalmus* ROSS 1967 have large anterior glabellar lobes, but the pygidia of these species are more transverse, like *Conophrys*. *S. acuticaudata* shows a postaxial extension which may be homologous with the posterior border of *S. granulosa*. While it is generally true that Tremadocian *Shumardia* species have small anterior glabellar lobes compared with those later in the Ordovician this is not invariably so; for example, *S. pentagonalis* LU (see LU, 1975, Pl. 1, Figs. 21, 22) has prominent lobes, while the late Ordovician species *S. bohémica* MAREK 1964 has relatively small ones. Some species of *Shumardia* have broad anterior glabellar tongues: *S. lacrimosa* DEAN 1973 and *S. acuticaudata* are examples; there is a tendency in these same species (also *S. exophthalmus* ROSS 1967) towards effacement of the forward part of the axial furrows. Considerable pygidial variation is also noted. The type species, and *S. matchensis* LEGG 1976 lack pygidial borders laterally; many species with transverse pygidia seem to have a narrow, flat or slightly convex pygidial border, but *S. alata* ROBISON and PANTOJA-ALOR 1968, has an elevated crest-like rim. This great variation within *Shumardia* does not seem to "clump" in any systematic way. Critical appraisal of the whole group may well result in several generic groups, but at the moment the criteria appropriate for such subdivision are not obvious. For this reason a broad view of *Shumardia* is adopted in this work.

Species assigned to *Shumardia* which have been considered in determining the Spitsbergen forms are: *S. granulosa* BILLINGS 1862, *S. pusilla* (SARS 1835), *S. miqueli* POMPECKJ 1902, *S. bottnica* WIMAN 1905, *S. nericiensis* WIMAN, 1905, *S. salopiensis* (CALLAWAY 1877), *S. oelandica* MOBERG 1901, *S. dicksoni* MOBERG and SEGERBERG 1906, *S. scotica* REED 1903, *S. curta* STUBBLEFIELD and BULMAN 1927, *S. erquensis* KOBAYASHI 1937, *S. minutula* HARRINGTON 1938, *S. pellizzarii* KOBAYASHI 1934, *S. pusillina* POLETAEVA (in POLETAEVA and PETRUNINA 1960), *S. optima* PETRUNINA (in POLETAEVA and PETRUNINA 1960), *S. extensa* WEIR 1959, *S. pentangularis* LU 1962, *S. lacrima* KOROLEVA 1964, *S. secunda* KOROLEVA 1964, *S. cylindrica* CHANG and FAN 1960, *S. transversa* CHANG and FAN 1960,

S. semicirculata CHANG and FAN 1960, *S. polonica* KIELAN 1960, *S. bohémica* MAREK 1964, *S. agnosta* KOROLEVA 1964, *S. sagittula* WHITTINGTON 1965, *S. exophthalmus* ROSS 1967, *S. alata* ROBISON and PANTOJA-ALOR 1968, *S. ctenata* ROBISON and PANTOJA-ALOR 1968, *S. lacrimosa* DEAN 1973, *S. gonioloba* LU 1975, *S. lata* LU 1975, *S. matchensis* LEGG 1976, *S. changshanensis* LU (in LU et al. 1976), *S. zotzeshanensis* LU (in LU et al. 1976) and *S. tenacis* ZHOU (in LU et al. 1976).

This is a long list, and some of the forms are known from very few specimens, or are not completely described. Relatively few of the species listed come from rocks of Arenigian or Llanvirnian age, and the Spitsbergen species all appear to be new. They are known from well preserved material in relief, and comparison with some of the species listed above, which are described from flattened and often somewhat distorted material in shales, is correspondingly difficult.

Shumardia acuticaudata n. sp.

(Pl. 3, Figs. 12–18, Pl. 25, Figs. 3, 4)

Stratigraphic range. — Lower part of Profilbekken Member, base to 25 m, V_{4a}, Valhallan.

Material. — Holotype, pygidium, PMO NF 311. Other material includes numerous cranidia: PMO NF 300a, b, 241, 225, 196, 211, 271, 301, 303, 3106, pygidia: PMO NF 240, 300c, 3107.

Diagnosis. — *Shumardia* species with cranidium with smooth exoskeleton, axial furrows almost effaced anteriorly. Pygidium with marginal rim and terminal spine, scattered tubercles on pleural fields.

Description. — The first appearance of this beautiful *Shumardia* characterises the basal phosphatic bed of the Profilbekken Member. It is known only from dissociated parts. Maximum width of cranidium in the range 1.6 to 1.8 times length in dorsal view. Lateral lobes on the glabella prominent, serving to double the glabellar width compared with that in front of the occipital ring (tr.). Posterior part of the glabella tapers forwards into deep furrows at the base of the lobes. Axial furrows are deep and wide here, (the adjacent parts of the cheeks slope down towards them) becoming narrower but still deep around the shoulders of the glabellar lobes, and then shallowing abruptly at about two-thirds (sag.) glabellar length. The very faint anterior course of the axial furrows indicates that the glabella runs far forwards to the anterior cranial margin as an anterior tongue (Pl. 3, Fig. 15), of transverse width comparable to that of the pre-occipital glabella. Occipital ring highly convex transversely, more so than the glabella, posterior margin bowed backwards, carrying a small, posteriorly placed occipital tubercle, more prominent on small specimens and internal moulds. Occipital furrow narrow, transverse. Posterior cranial borders on a level below cheeks, extremely narrow (exsag.), extending to two-thirds width of cheeks, presumably functioned to articulate with the forward margin of the anterior thoracic segment.

Pygidium about twice as wide as long, pleural fields nearly flat, axis transversely convex. Axis tapers gently backwards and is rounded posteriorly. Five or six axial rings are defined by transverse ring furrows deeper laterally; internal mould (Pl. 25, Fig. 3) shows prominent apodemal pits. Crescentic half-ring longer (sag.) than first axial ring. Axis extends far back, but is set off by a distinct furrow from postaxial spine, which is short, triangular and tilted upwards. Anterior pygidial border adaxially transverse, distally curving sharply posteriorly, divided by a shallow furrow (tr.). Up to three pairs of pleural furrows, of which the first is relatively deep, and widening laterally. Narrow posterior border runs around the posterior margin of the pygidium and into the postaxial spine. Surface sculpture of scattered tubercles, no more than four on the anterior pygidial pleurae, two or three on the pygidial axial rings.

The low population of this species consists of phosphatised internal moulds (Pl. 25, Figs. 3, 4). On these the postaxial spine is not so prominent as on the type and the pygidial border is broader. Important cephalic characters, the surface sculpture and proportions are the same as on the stratigraphically higher material, and it is considered that the pygidial differences are primarily due to preservation.

Discussion. — *S. acuticaudata* is a particularly distinctive *Shumardia* species, with its short, stubby spine-like projection at the rear of the pygidium. It resembles the type species, *S. granulosa* BILLINGS (WHITTINGTON 1965, pl. 16), more closely than do any of the other species from Spitsbergen. In particular the post-axial flattening in *S. granulosa* may be homologous with the pygidial spine of *S. acuticaudata*. However, the anterior effacement of the cephalic axial furrows of the new species, its lack of dense granulation on the cranidium, and the transverse pygidium are obvious differences. Of other species listed above *S. acuticaudata* is closely similar to *S. lacrimosa* DEAN 1973, from the Llanvirnian of the Yukon, which has a broad anterior glabellar 'tongue' effaced in a similar way to that of *S. acuticaudata*. The only significant differences are pygidial; DEAN (1973, p. 7) states that the pygidium of *S. lacrimosa* is "blunted posteriorly", and so lacks the spine characteristic of *S. acuticaudata*, and the tubercles on the pygidial pleural fields are twice as densely spaced in *S. lacrimosa*. Both *S. exophthalmus* ROSS 1967 and *S. matchensis* LEGG 1976 tend to effacement at the forward part of the glabella. The cranidium figured by ROSS (1967, Pl. 10, Fig. 24) shows that the glabella of *S. exophthalmus* runs to a point well inside the cranidial margin. In *S. matchensis* effacement has developed to a point beyond that in *S. acuticaudata* so that the axial furrows around the anterior glabellar lobes are poorly defined. Neither *S. matchensis* nor *S. exophthalmus* have posterior spines on their pygidia.

Shumardia minaretta n. sp.

(Pl. 3, Figs. 1–10, Pl. 25, Figs. 5, 6)

Stratigraphic range. — Olenidsletta Member, 80 m to 93 m from base, V_{2a}, middle Arenig.

Material. — Holotype, cranidium, PMO NF 3126; cranidia: PMO NF 1874, 3123, 3124a, 3144, 3260; pygidia: PMO NF 1244, 3125, 3124b, 3146.

Diagnosis. — *Shumardia* species with arrow-shaped glabella extending almost to cranial margin; axial furrows shallow anteriorly; fixed cheeks punctate. Pygidium finely tuberculate along pleural ribs; postaxial flattening, but no true spine.

Discussion. — This species is best discussed in relation to *S. acuticaudata*, which it resembles in general proportions. It is at once distinguished from that species by the narrower forward part of the frontal lobe of the glabella, which is defined by distinct, but shallow furrows. Well-preserved specimens show scattered punctae on the dorsal surface of the fixed cheeks, especially prominent alongside the axial furrows. The glabella is smooth, however. The pygidium lacks a postaxial spine, although there is a flattened, and slightly backward-bowed area in the same region.

Of Arenigian species of *Shumardia*, *S. minaretta* most resembles *S. exophthalmus* Ross 1967. The glabellar proportions of both species are similar although larger specimens of the latter are constricted in front of the occipital ring. The most important cephalic difference between the two species is that in *S. minaretta* the anterior, arrow-shaped portion of the glabella always extends forwards almost to the anterior cranial margin; this is true only of the smallest *S. exophthalmus* (Ross 1967, Pl. 10, Fig. 28). In specimens of comparable size to those from Spitsbergen the front of the glabella is obtusely pointed and does not extend far forward. Punctate surface sculpture is also a peculiar feature of the new species (although internal moulds may carry granules), but silicification could have obliterated this feature in *S. exophthalmus*. Pygidia of *S. exophthalmus* are longer than those of *S. minaretta*, more strongly furrowed, and consistently emarginate rather than transverse at the posterior mid line.

This species represents the morphological half way stage between *Conophrys* and *Shumardia sensu stricto* (discussed above). The definition of the glabella and the full development of the anterior glabellar lobes is very like that of the type species of *Shumardia*, *S. granulosa*. On the other hand the transverse pygidium is like that of Tremadocian species like *Shumardia* (= *Conophrys*) *salopiensis*.

Shumardia phalloides n. sp.

(Pl. 3, Figs. 19–24)

Stratigraphic range. — Profilbekken Member 40 m to 50 m from base, V₄b, Whiterock, *Orthidiella* zone (early Llanvirn).

Material. — Holotype, cranidium, PMO NF 3128; other cranidia: PMO NF 3127, 1363.

Diagnosis. — *Shumardia* with fixed cheeks much narrower (tr.) than glabella in front of occipital ring. Glabella transversely convex. Glabellar lobes narrower (tr.) than other species described herein. Axial furrows running forwards

to anterior margin of cranium, defining narrow anterior glabellar tongue, except where interrupted by buttresses connecting frontal lobe of glabella with fixed cheeks.

Discussion. — This small species of *Shumardia* is the stratigraphically youngest in the Spitsbergen sections. Its specific characters are summarised above, and it differs from all other species of the genus in the extreme narrowness of the fixed cheeks, which form a steeply sloping wall around the highly convex glabella. Two other characters serve to distinguish this species from all others of the genus: the glabella is continued to the anterior cranial margin as a narrow tongue (narrower than that of *S. acuticaudata*), and, even on the smallest specimen (Pl. 3, Fig. 24), the axial furrows are interrupted anterolaterally by narrow strips of exoskeleton connecting the forward of the frontal glabellar lobe with the adjacent fixed cheeks. It is noteworthy that the position of these buttresses corresponds to the anterior shallowing of the axial furrows in other species of the genus. There are several points of resemblance between this species and *Leioshumardia minima* WHITTINGTON 1965, notably the narrow fixed cheeks and wide, convex glabella (WHITTINGTON 1965, Pl. 17, Fig. 10). In *Leioshumardia* the glabellar lobes are obsolete, and it is possible that the genus was derived from a species like *S. phalloides*, in which the lateral lobes are already narrow compared with the median glabellar lobe (on the holotype, Pl. 3, Fig. 19).

S. phalloides occurs with numerous ostracodes of similar transverse dimensions. One might speculate that this reflects the exploitation of a similar food resource, as the size of the cephalic appendages of our species and the ostracodes were presumably similar.

Family CATILLICEPHALIDAE RAYMOND 1938

Genus *Buttsia* WILSON 1951

Type species. — *Buttsia drabensis* WILSON 1951.

Buttsia inexpectata n. sp.

(Pl. 3, Figs. 25–28)

Stratigraphic range. — One bed in the Olenidsletta Member, about 75 m from base (middle Arenig), associated with *Balnibarbi erugata*, *Bienvillia stikta*, *Carolinites genacinaca genacinaca* and *Svalbardites hamus*.

Material. — Holotype, cranium, PMO NF 2879. Other cranidia: PMO NF 1700, 1703–4, 1711, 1772.

Diagnosis. — *Buttsia* species with shallow, hooked 1P glabellar furrows, strongly curved palpebral lobes closely approaching glabella anteriorly.

Description. — In spite of the fact that cranidia are numerous in the bed in which this species occurs, no pygidia or free cheeks have been found. Glabella tumid, rising to mid-line, steeply downsloping anteriorly, length (including

occipital ring) equal to maximum transverse width at anterolateral corners. Glabella expands in width forwards from occipital ring more rapidly than in other species of the genus, such that its transverse width in front of the occipital ring is two-thirds maximum width anteriorly. Anterior margin convex forwards with slight median indentation. Sides of glabella slightly bowed outwards. Two pairs of glabellar furrows extend less than one-third across glabella, shallow (especially on internal mould), curved forwards medially. 1P does not quite reach the axial furrow, deeper at outer end: 2P very faint, apparently of similar form to 1P, outer end opposite anterior limit of palpebral lobe. Occipital furrow deep, transverse. Occipital ring occupying about one-sixth total glabellar length, widening slightly medially, transverse profile matching that of glabella. Axial and preglabellar furrows deep. Palpebral lobes placed at cranial mid-length, length (cxsag.) about one-third that of glabella, forward ends closely approaching axial furrows, with strongly curved outline and weakly-defined palpebral rims. Postocular cheek triangular, width (tr.) two-thirds that of occipital ring, the greater part occupied by convex posterior border raised well above genal field. Point of articulation near occipital ring. Preocular cheek narrow (tr.), forming a narrow band around anterolateral corner of glabella and running without a break into anterior cranial border. This border is tightly rolled, slightly wider and more convex medially, not upward-arched about mid-line. Posterior branches of facial suture diverge at 20–30 degrees behind the palpebral lobes to cut posterior margin at a high acute angle. Anterior branches slightly convergent before curving adaxially anteriorly. Surface sculpture lacking. This species has a thick cuticle, but there are few differences between the external surface and internal mould, except that the glabellar furrows are, if anything, fainter on the latter.

Discussion. — This trilobite is a most extraordinary discovery from the middle Arenig. The type species of *Buttsia*, *B. drabensis*, is from the Franconian of the central Appalachians (WILSON 1951, Pl. 89, Figs. 12, 19–24), and the genus is widespread in the Franconian of North America, and also occurs in the Upper Cambrian of Siberia (LAZARENKO 1966). *Buttsia* has not yet been recorded from the Trempealeauan, where other catillicephalids such as *Theodenisia*, *Triarthropsis* and *Acheilops* are characteristic. Nonetheless the resemblance of the Spitsbergen specimens to the type species of *Buttsia*, and particularly a specimen figured by STITT (1977, Pl. 1, Fig. 7) from Oklahoma is such that inclusion in this genus is probably well-founded. Strongly curved palpebral lobes that closely approach the glabella anteriorly distinguish *B. inexpectata* from the type species, but this scarcely qualifies as a generic distinction. Nor can it be convincingly argued that the morphology of *B. inexpectata* is so “generalised” that the Ordovician form is an independently derived homeomorph of *Buttsia*: in fact, the tumid, forward-expanding glabella, and ledge-like anterior border are rather unusual features, and most unlikely to have been independently derived in the Ordovician form.

The long survival of *Buttsia* is of particular interest because it shows that not all genera were extinguished at the biomere boundaries that affected

the Upper Cambrian trilobite faunas of the North American craton (STITT 1975). The assumption is usually made that at the end of each biomere the shallow water genera were extinguished, to be replaced in the following biomere by different genera that radiated into niches vacated by trilobites of the underlying biomere. *Buttsia* has been considered characteristic of the Pteroccephaliid biomere, which is separated from the Middle Arenig by the Ptychaspid biomere and what STITT (1977, p. 11) informally terms the "hystricurid" biomere, that is, by at least two major extinction events. If *Buttsia* survived, one may ask why apparently none of the genera accompanying it succeeded in doing so. There are, of course, some other survivors from the Cambrian in the Spitsbergen Arenig: *Plicatolina*, *Micragnostus* and *Bienvillia* are examples. But these were probably deep water forms from the start, and immune to the processes that exterminated the shelf species. *Buttsia*, on the other hand, seems to have accompanied a typical cratonic assemblage.

Family REMOPLURIDIDAE HAWLE and CORDA 1847

Remarks. — Various proposals have been made for the division of the Remopleurididae into subfamilies (WHITTINGTON 1959; PRIBYL and VANEK 1972; SHERGOLD 1975). None is satisfactory. For example, *Robergiella* spp. discussed below, show similarities both to *Remopleurides* and *Robergia*. SHERGOLD (1975) omitted both *Robergiella* and *Lacorsalina* from his summary of classification, which genera include the named Spitsbergen species. For this reason subfamilies are not used in this paper.

Genus *Lacorsalina* BURSLEY 1970

Type species. — *Lacorsalina sokoliensis* BURSLEY 1970.

Lacorsalina ? *bellatula* n. sp.
(Pl. 4, Figs. 1–5, 7, 8)

Stratigraphic range. — Olenidsletta Member 92 m to 102 m from base Arenig, V₂b.

Material. — Holotype, external mould of cranidium, PMO NF 96; Cranidia: PMO NF 97, 83, 75; pygidia: PMO NF 1596, 499; free cheek: PMO NF 75.

Diagnosis. — A ? *Lacorsalina* species with a wide anterior cranial border, preglabellar field narrower (sag.) than type species. Pygidium with two large pairs lateral spines, at least ten pairs of progressively smaller spines medially. Surface sculpture of exceedingly fine, dense terrace lines.

Description. — This beautiful species occurs rather rarely in the dark limestones at the top of V₂. The cranidium is on two planes: the posterior part of the glabella and the palpebral lobes form one plane, preglabellar field and anterior

border the other, lower plane, while the steep downward turn of the glabellar tongue connects the two. Width of glabella in front of occipital ring about half its maximum width, which is reached at one-third sagittal cranial length. Forward expansion of the glabella is gentle at first, adjacent to posterior parts of palpebral lobes, rapid in front of this; anterior taper as far as forward limits of palpebral lobes is more gentle. Transverse cranial width at this point is at a minimum, about 0.8 that in front of occipital ring. Three pairs of glabellar furrows are short and shallow, posterior pair deeper and longer on the smallest specimen (Pl. 4, Fig. 7), nearly equal in length on large crania. Outer end of 1P opposite max. cranial width; 3P runs into the axial furrow just behind point of maximum constriction of the glabella; 2P is equidistant from 1P and 3P. Furrows slope inwards at an angle of about 60 degrees to sagittal line. Glabellar tongue occupying about one quarter cranial length (sag.), expanding gently in width forwards, broadly rounded about mid-line at abrupt junction with preglabellar field.

Palpebral lobes with semicircular outline, broad (tr.), length (exsag.) slightly under half total cranial length. Small cranium shows that adjacent to the expanded part of the glabella there is a small area of intraocular cheek. On the larger specimen this is included within the extremely wide palpebral/axial furrow, and is not visible as a distinct lobe. Axial furrows become narrower and deeper forwards where they pass into the downsloping anterior gutter adjacent to the glabellar tongue. Occipital ring widest medially, where there is a small, anteriorly placed occipital tubercle. Postocular fixed cheek downturned, exceedingly narrow adaxially, widening laterally. Posterior border furrow not present adaxially, widening rapidly laterally. Preglabellar field narrowest medially, length (sag.) there less than that of anterior border; transverse width exceeds that across cranium at palpebral lobes. Anterior border wide, slightly raised, and becoming wider medially. Anterior branch of facial suture sigmoidal, running outwards transversely at anteriolateral corners of glabella, distally curving gently forward to curve round the front margin of the cranial border at an acute angle. Surface sculpture of extremely fine, raised lines on glabella which run transversely, medially arched forwards. Similar raised lines are slightly scalloped on the posterior part of the occipital ring, and are also present on the preglabellar field. Fine terrace lines on anterior border parallel to cranial margin.

Free cheek wide (tr.), genal spine not preserved. Shallow lateral border furrow dies out near genal angle. Broad lateral border slightly raised like cranial border. Shallow posterior border furrow bounded anteriorly by raised ridge; flattened posterior border not curving forwards to genal angle. Eye socle an extremely narrow protruding ridge around base of eye; eye lenses minute, with more than 100 dorso-ventral files. Surface sculpture of fine raised lines interspersed with minute pits, running approximately parallel to sag. line. On lateral border about five more prominent raised ridges run parallel to cranial margin. There is a smooth area forming a band parallel to the eye and adjacent to the eye socle. Fragment of cephalic doublure (Pl. 4, Fig. 2) narrow, concave, forming a peripheral tube with the cephalic border.

Doublure with four prominent terrace lines parallel to cephalic margin (steep slopes of terraces face outwards).

Thoracic segment (Pl. 4, Fig. 5) shows articulating half ring about half sag. length of axial ring, the latter bearing transversely sinuous terrace lines. Shallow pleural furrow bounded by a narrow ridge anteriorly. Tip imperfectly preserved, but probably a spinose termination.

Pygidium about twice as wide as long, pleural fields almost flat. Axis of about the same width anteriorly as front pygidial margin, tapering gently backwards, axial furrows enclosing an angle of about 30 degrees. Three axial rings are defined by narrow ring furrows that arch slightly forward and stop short of the deeper axial furrows. Terminal piece merges with narrower post-axial ridge, which does not reach the posterior pygidial margin. Front margin of pygidium subtends a right angle with the lateral margin. Four pleural furrows of decreasing length and prominence posteriorly: the first is distinct and approaches close to the pygidial margin. Like those of the thoracic segment it is bounded anteriorly by a ridge, which is present only adaxially by the second pleural furrow, absent on the third and fourth. Interpleural boundaries obscure, although indicated at the pygidial margin by distinct acute notches between the first and second, and second and third pairs of pygidial spines. The first two pairs of these are much the largest and are prolonged distally into long and delicate needle-like tips. The third to the twelfth pairs are progressively minute, arranged comb-like along the gentle posterior median emargination of the pygidium. Fine raised lines undulate gently over the dorsal surface. A single, stronger raised line follows the inner margin of the larger spines. Flat doublure underlies the entire pleural field (Pl. 4, Fig. 8), carrying about 15 widely spaced terrace lines (exsag.)

Discussion. — The only other described species of *Lacorsalina* is the type species, *L. sokoliensis*, from the upper Tremadoc of Pay Khoya, north arctic Urals (BURSKY 1970). The younger species from Spitsbergen is assigned with some reservation to this genus because its comb-like arrangement of pygidial spines is more reminiscent of *Apatokephalus*. However, the extremely wide preglabellar field, and the concave-forward anterior branches of the facial sutures are both matched by *L. sokoliensis*, and the new species is therefore probably better referred to *Lacorsalina*. Pits in the anterior border furrow, typical of many *Apatokephalus* species, are lacking both in *L. sokoliensis* and in *L. ? bellatula*.

Genus *Eorobergia* COOPER 1953

Type species. — *Roergia marginalis* RAYMOND 1925.

Eorobergia sp. A.

(Pl. 4, Figs. 9–11)

Stratigraphic range. — Olenidsletta Member, from one bed 75 m from base of Member, Arenig, V₁c.

Material. — One internal mould of cranium, PMO NF 3139.

Description. — The single specimen does not permit formal naming. The anterior border is partly broken off. Maximum transverse cranial width about equal to sag. length. Front glabellar margin broadly rounded in dorsal view. Glabella upward arched about mid-line, maximum width at about one-third glabellar length, and a little behind mid-length of palpebral lobes. Occipital ring and most posterior part of glabella of similar width (tr.), then expanding rapidly to maximum width, and anteriorly tapering more gently forwards. Three pairs of glabellar furrows all strongly impressed on the internal mould and all well removed from axial furrows. 1P transversely oval, outer ends at maximum cranial width; 2P narrower and longer than 1P, arched forwards medially; 3P smallest of the three, and more diffuse, opposite anterior end of palpebral lobes. Anterior tongue wide (tr.), about 0.8 max. cranial width (at anterior limits of palpebral lobes), downturned part expanding slightly in width forwards. Palpebral lobes about half (exsag.) cranial length, broad, and inward-sloping. Occipital furrow deep, medially constricted by forwardly placed occipital tubercle; occipital ring slightly wider medially. Anterior border narrow, convex, separated from front margin of glabella by a deep furrow. Large pits are developed in the border furrow at its extremities, although it is not known whether they were present medially. The internal mould shows the traces of coarse tuberculation, presumably developed on the dorsal surface; part of the occipital ring shows this sculpture.

Discussion. — This species is distinguished from the type species, *E. marginalis* (RAYMOND) (COOPER 1953, Pl. 8, Figs. 1–6), in the lesser curvature of the palpebral lobes, relatively short (sag.) frontal lobe of the glabella, and shallow glabellar furrows. In the subequal development of the glabellar furrows *Eorobergia* sp. A is more like *Robergia*, but the frontal glabellar lobe on that genus is greatly extended (sag.). No described species of *Robergia* or *Eorobergia* compares closely with the species from Spitsbergen. The most similar is *Eorobergia lata* CHUGAEVA (1973, p. 53–55; Pl. 3, Figs. 2–5) from the Llanvirn of the El'genchaksk Mountains, northeast Siberia, which has a similarly broad glabellar tongue. However the wide (sag.) anterior border and rapid median glabellar expansion of that species at once distinguish it from the earlier form from Spitsbergen. In the absence of a pygidium the formal naming of *Eorobergia* sp. A does not seem to be justified.

Genus *Remopleurides* PORTLOCK 1843

Type species. — *Remopleurides colbi* PORTLOCK 1843.

Discussion. — A cranium attributed to *Remopleurides* has been recovered from the Profilbekken Member, and is compared with *R. pilulus* WHITTINGTON 1965. Both these early species differ from later *Remopleurides* in the glabella being (both sag. and tr.) markedly convex and in having particularly narrow palpebral rims, which do not get wider posteriorly. The type species (WHITTINGTON 1950, p. 540–3; Pl. 70, Figs. 1, 2, 4, 5), and other Middle and Upper

Ordovician species assigned to the genus (well preserved examples described by WHITTINGTON 1959; SHAW 1964; WEBBY 1973; CHATTERTON and LUDVIGSEN 1976) have a flattened (tr.) glabella with a steeply downturned tongue, and flat palpebral rims widening backwards. These features are shared also with the species assigned below to *Robergiella*, which, however, retain a distinct cranial anterior border, and a broad genal area on the free cheek between borders and eye socle. I note that on *Remopleurides caphyroides* WHITTINGTON (1959, especially Pl. 8, Fig. 6) there remains a small triangular area between genal borders and eye socle. It does seem possible that *Remopleurides sensu stricto* was derived from a *Robergiella*-like form by progressive reduction of the genal area, and concomitant abbreviation of the anterior cranial border. If this proves to be the case then it is unlikely that the early species *Remopleurides pilulus* and *R. sp. A* (below) belong to this phyletic group.

Remopleurides sp. A
(Pl. 5, Figs. 15, 17, 18)

Stratigraphic range. — Profilbekken Member, Whiterock (*Orthidiella* zone), 60 m from base of Member, V₄b.

Material. — Cranium PMO NF 1295.

Description. — Cranium convex (sag., tr.), glabellar tongue protruding forwards, sagittal length in dorsal view equal to maximum transverse width at mid-point of palpebral lobes. Glabellar furrows not visible. Transverse width of occipital ring slightly more than half maximum cranial width, length (sag.) about one quarter cranial length in dorsal view. Palpebral rim outlined by deep furrow, very narrow, and not widening noticeably backwards. In anterior view the front margin of the cranium is not arched upwards about the mid-line, nor is there an anterior border. The dorsal surface of the cranium is covered with fine and evenly spaced granules.

Discussion. — This is probably a new species, but the single specimen is inadequate to establish it as such. As noted above the species from Spitsbergen compares with *R. pilulus* WHITTINGTON 1965, from the Middle Table Head Formation, and differs from other *Remopleurides* species, in the transverse convexity of the glabella, the long protruding glabellar tongue, and in the very narrow palpebral rims which do not widen backwards. *R. pilulus* shows a single pair of glabellar furrows which run into the palpebral furrows; this is more like the condition in *Opipeuter* than in other *Remopleurides*. *Remopleurides* sp. A differs from *R. pilulus* in the transverse, rather than upward-arched anterior cranial margin, and in the surface sculpture of scattered granules.

Remopleuridid gen. et sp. indet.
(Pl. 4, Fig. 6)

Stratigraphic range. — Olenidsletta Member 135 m from base, V₃a.

Material. — One cranium PMO NF 3138.

Discussion. — The single cranidium is imperfectly preserved and for this reason cannot be definitely assigned. Distinctive features are the broad palpebral rims (tr.), defined by shallow palpebral furrows, and the apparent lack of glabellar furrows, apart from a pair of shallow depressions that may represent 1P.

Genus *Robergiella* WHITTINGTON 1959

Type species. — *Robergiella sagittalis* WHITTINGTON 1959.

Discussion. — The type species was described from silicified material from the Lower Edinburg limestone (Middle Ordovician), and differs from the species assigned below to *Robergiella* in having a longer glabellar tongue. Both species share glabellar furrows of similar form, a narrow, horizontal rim in front of the tongue, and, most important, a relatively broad (tr.) area on the free cheek between the eye socle and borders. This area is reduced or absent on *Remopleurides*. The similarities are considered to outweigh the major point of difference, and the following species are included in a slightly expanded concept of *Robergiella*.

Robergiella brevilingua n. sp.

(Pl. 5, Figs. 1–8, 10, 11; Pl. 25, Figs. 7, 11, 13)

Stratigraphic range. — Profilbekken Member, V₄b, 35 m to 55 m.

Material. — Holotype, cranidium, PMO NF 3143; cranidia: PMO NF 320, 3131–2, 1401, 1370, 1366. free cheeks: PMO NF 3110, 3171; pygidium: PMO NF 3172.

Diagnosis. — *Robergiella* species with relatively short (sag.) glabellar tongue, posterior glabellar furrow broadest and best-defined, cranidial surface sculpture of scattered granules. Free cheek narrower (tr.) and genal spine more advanced than in *R. sagittalis*.

Description. — Cranidium of low transverse convexity, and with a relatively short, steeply downturned anterior tongue, which in dorsal view presents a convex profile about the mid-line. Total cranidial length in dorsal view is less than maximum cranidial width, width/length ratios being within the range 1.1 to 1.3; width of the tongue just in front of the palpebral lobes is about half maximum cranidial width, and here the convexity (tr.) increases so that the tongue bulges forwards slightly. Expression of the glabellar furrows varies; on the dorsal surface of small specimens they are faint, on internal moulds (Pl. 5, Fig. 2) they are deeply incised. Of the three pairs 1P is much the most deeply impressed, more than twice as wide (exsag.) as 2P. 1P is convex forwards, isolated within the glabella, outer end opposite maximum cranidial width; 2P is longer and straighter, inner end making an angle of about 75 degrees to sag. line, outer end almost touching the axial furrows;

3P a shallow pit, behind transverse line connecting anterior limits of palpebral lobes. Occipital ring about one sixth sag. length of cranidium, slightly narrower laterally, where it is downturned to meet the spine-like postocular fixed cheeks. Occipital furrow uniformly deep. There is a prominent occipital node anteriorly placed so as to constrict the occipital furrow medially. Palpebral/axial furrows similarly deep, narrowing anteriorly. Palpebral lobes of length (exsag.) between 0.6 and 0.7 cranial length, widening regularly backwards, maximum width approaching half that of occipital ring (sag.). Adjacent to the forward tongue the lobes pass into narrow gutters. Anterior border narrow (sag.), horizontal, widening laterally; at its widest point it is perforated by a single pit. Surface of cranidium (except furrows and palpebral lobes) carries a sculpture of scattered granules, interspersed in places with even smaller granules.

Free cheek with distinctly defined lateral and posterior borders. Anteriorly the lateral border is horizontal, rim-like where it abuts the cranial anterior border, posterolaterally widening, and sloping outwards and downwards, and running without a break into the sharply pointed genal spine; the latter is quite short, length slightly more than half length of eye, and carries fine raised lines running along its length which pass on to the adjacent parts of the lateral border. Posterior border without sculpture, adaxially transverse, near genal spine curving sharply forwards so that the genal spine lies in a slightly advanced position. Border furrows shallow, meeting at a large obtuse angle. Crescentic area inside borders widest posteriorly, carrying scattered granules like those on the glabella. Convex, rim-like eye socle as on other remopleurids. The long band of the eye, height about three times that of the eye socle, is composed of minute lenses smaller towards the base of the eye.

An incomplete silicified hypostoma (destroyed) was typically remopleuridid, with a prominent anteromedian boss, large striate maculae.

Pygidia known from silicified specimens (Pl. 25, Fig. 13), small, with short axis not reaching posterior pygidial margin. One axial ring is defined, which is narrower medially, and a short terminal piece. Two pairs of pygidial spines, of which the outside pair are the larger and extend further posteriorly, as in *R. sagittalis* (WHITTINGTON 1959, pl. 6, Figs. 25, 29, 32). Sculpture of raised lines running exsag. on outer pair.

Discussion. — The cranial difference in the glabellar tongue between *R. brevilingua* and the type species has been mentioned above. To this may be added the narrower free cheek of the Spitsbergen species, and the greater forward curvature of the posterior border on the free cheek, so that the genal spine is more advanced. On *R. sagittalis* lateral and posterior border furrows meet at about 90 degrees. The small free cheek of *R. sagittalis* figured by WHITTINGTON (1959, Pl. 6, Figs. 26, 28, 33) is more similar to that of the Spitsbergen species in the proportions of the notch behind the genal spine.

A *Robergiella* sp. described by TRIPP (1976, p. 379, Pl. 2, Figs. 21–23) from the *superstes* Mudstones, Girvan, Scotland, has a considerably broader (tr.) glabellar tongue than *R. brevilingua*. *R. correcta* REED (1903, Pl. 6, Figs. 1–3)

has a longer glabellar tongue, and the 1P and 2P glabellar furrows are equally incised.

Several species attributed to *Remopleurides*, based on cranidia alone, are sufficiently similar to the present species to require discussion here; when other parts are discovered they may prove referable to *Robergiella*. *Remopleurides* sp. ind. (WHITTINGTON 1965, Pl. 40, Figs. 1–4) from the Middle Table Head Formation has a cranidium very like that of *Robergiella brevilingua*, but with glabellar furrows scarcely visible, sculpture of granules around the perimeter of the glabella only. *Remopleurides shihtzupuensis* LU 1957 (see also LU 1975, p. 301–2, Pl. 4, Figs. 14, 15), from the Llanvirn of southwest China, is poorly preserved and apparently flattened, but has a distinct rim-like anterior border and protruding glabellar tongue, which, however, is much narrower (tr.) than in the Spitsbergen species. A similarly narrow tongue is present on *Remopleuridiella? khitica* CHUGAEVA 1973 (p. 48–9, Pl. 2, Figs. 1–3) from the Arenig (Khitinsk Formation) of Northeast Siberia; this species has glabellar furrows similarly distributed to *Robergiella brevilingua*, but 1P is long and narrow (like 2P) in this species, and the granulation is coarser and denser.

Robergiella lundehukensis n. sp.
(Pl. 5, Figs. 9, 12–14, 16)

Stratigraphic range. — Profilbekken Member 18 m to 23 m from base, V₄a, (Valhallan).

Material. — Holotype, cranidium, PMO NF 2405. Other material includes cranidia: PMO NF 2429, 2475, 2462b, 2455; free cheek: PMO NF 2466.

Diagnosis. — *Robergiella* species with glabellar furrows not impressed, anterior tongue narrow. Surface sculpture of low tubercles around posterior part of glabella, finer granules anteriorly.

Discussion. — This species occurs stratigraphically below *R. brevilingua* in the Profilbekken Member, and is closely similar to that species. It is perhaps more similar than *R. brevilingua* to the type species of *Robergiella* in its longer glabellar tongue, which expands forwards, but the glabellar furrows are not impressed. They are, however, represented by smooth areas on the dorsal exoskeletal surface, which show that they are identical in form to those of *R. brevilingua*. The principal points of difference between *R. lundehukensis* and *R. brevilingua* are as follows:

- (1) The glabellar tongue is narrower, such that its transverse width at the anterior limits of the palpebral lobes is less than half the maximum width of the glabella (greater than half on *R. brevilingua*).
- (2) The tongue is also longer (sag.) and expands in width forwards.
- (3) The anterior cranidial border is slightly wider.
- (4) The surface sculpture includes coarser, flattened tubercles posterior to the 1P muscle impressions. These become smaller and sparser progressively anteriorly.

Family OPIPEUTERIDAE FORTEY 1974

Genus *Opipeuter* FORTEY 1974

Type species. — *Opipeuter inconnivus* FORTEY 1974.

Discussion. — Since the type species and a second, unnamed *Opipeuter* sp. were described two more species can be added to the genus — *Opipeuter angularis* (YOUNG 1973) and *O. emanuelensis* LEGG 1976. The latter was discovered in northwestern Australia, and adds weight to the functional arguments given by FORTEY (1974) that *Opipeuter* led an actively swimming existence in the surface water layers of the open ocean, resulting in wide geographic dispersal. LEGG (1976) allied *Opipeuter* with *Carolinites*, a resemblance considered by FORTEY (1974) to be due to homeomorphy in response to a similar mode of life. I have not changed my opinion, and additional evidence is added below from the discovery of the hypostoma of the genus.

Opipeuter inconnivus FORTEY 1974

(Pl. 6, Figs. 12, 14, 15)

1974 *Opipeuter inconnivus* FORTEY (*pars.*), Pl. 13, Figs. 2–4, 9, 11, 12; Pl. 14, Figs. 1–3, 5, 8–10, 11–13.

Stratigraphic range. — Olenidsletta Member, V₁b–V₂, early to middle Arenig, coincident with the range of *Carolinites genacinaca genacinaca*.

Material. — Additional material described here includes a hypostoma: PMO NF 769; free cheek: PMO NF 648.

Diagnosis. — Diagnosis follows that of FORTEY (1974), with the exception that specimens with truncate anterior glabellar profile are assigned to *O. angularis* (below).

Discussion. — A full description of this species was given by FORTEY (1974) and repetition is not necessary here, except to note that the stratigraphically early material is here removed to *O. angularis*. A hypostoma is attributed to *O. inconnivus* (Pl. 6, Figs. 14, 15), and because it is important in the arguments on the familial affinities of the genus it is worth explaining the grounds on which the attribution has been made. The hypostoma was found in a bed 60 m from the base of the Olenidsletta Member on Profilstranda, where *O. inconnivus* is more than usually common. Occurring with *Opipeuter* in the same bed are the genera *Carolinites*, *Oopsites*, *Balnibarbi* and *Svalbardites*. The hypostoma of *Carolinites* has been established beyond doubt from an *in situ* occurrence (FORTEY 1975, p. 108). The telephinid hypostoma is also known (WHITTINGTON 1965), and that of *Balnibarbi* and related olenids was described by FORTEY (1974a). The hypostoma of *Svalbardites* is not known, but the hypostoma in question is too large for that small genus, and it is not similar to other pelturine hypostomata. The fauna of the olenid community is sparse, consisting of the

eponymous family and a few pelagic species; it therefore is improbable that the hypostoma belongs to some other species unrepresented in the fauna by other skeletal parts — nor can it be attributed to any described genus. So the probability that it belongs to *Opipeuter* is high. It has a pair of densely pitted maculae close together near the mid-line, and a distinct, transversely truncate posterior border, somewhat thickened and backward-deflexed at its lateral edges. Neither of these features can be matched on hypostomata of Telephinae (*sensu* FORTEY 1975). This may be added to the evidence given previously (FORTEY 1974, p. 119) that *Opipeuter* is not related to *Carolinites* or *Telephina*. On the other hand prominent maculae and truncate posterior borders (with posterolateral spines) can be matched with examples from the Remopleuridacea (e.g. WHITTINGTON 1959, Pl. 6, Fig. 14). However, proportional development of these features in *Remopleurides*, for example, is very different, and if the structures are homologous the morphological distance from described remopleuridids is considerable, which might be adduced as evidence for the familial separation of *Opipeuter*. In any case a close relationship to *Carolinites* and allied genera (LEGG 1976) is improbable.

The larger free cheeks used to illustrate the species by FORTEY (1974) are from the early stratigraphic occurrences, and now better referred to *O. angularis* (below). A free cheek from a stratigraphic horizon close to that of the holotype is illustrated here (Pl. 6, Fig. 12) and it is like the cheek attributed to *O. inconnivus* from Western Ireland (FORTEY 1974, Pl. 14, Figs. 12, 13). Another type of free cheek, undoubtedly opipeuterid, has been found from the same horizon (Pl. 6, Fig. 10), in which the border is wider, and the area between border and eye correspondingly reduced. It is not known whether this form is an extreme intraspecific variant of *O. inconnivus* (but it is perhaps unlikely) and for the present it is referred to *O. cf. inconnivus*.

The ancestors of *Opipeuter* must be sought in the Tremadoc. One suggestive species is *Remopleuridiella acuta* FLOWER 1968, from the Tremadoc of New Mexico, which appears to have an almost hexagonal glabella like the early *O. angularis*.

Opipeuter angularis (YOUNG 1973)
(Pl. 6, Figs. 9, 13)

1973 *Remopleuridiella angularis* YOUNG, p. 112, 114, Pl. 1, Figs. 21, 22, 26 non Figs. 25, 27.

1974 *Opipeuter inconnivus* FORTEY (pars.), Pl. 13, Figs. 1, 6–8, 10; Pl. 14, Figs. 4, 6, 7.

Stratigraphic range. — Lowest part of the Olenidsletta Member, V_{1a} (early Arenig).

Material. — Cranidia: PMO NF 2982, 2983, 2986; free cheeks PMO NF 2980, 2981; incomplete pygidium: PMO NF 3147.

Diagnosis. — *Opipeuter* species with glabella truncate anteriorly in dorsal view, due to broader anterior tongue than *O. inconnivus*.

Discussion. — In the original description of *O. inconnivus*, FORTEY (1974) included a wide morphological range of specimens, the species being proposed to include material from the greater part of the Olenidsletta Member. While *O. inconnivus* was in press YOUNG (1973) described a fauna from the early Arenig (zone H) of Utah, including *Remopleuridiella angularis*. This species is now better referred to *Opipeuter*. Furthermore it compares with the stratigraphically earliest *Opipeuter* specimens from Spitsbergen (FORTEY 1974, Pl. 13, Fig. 6, cf. YOUNG 1973 Pl. 1, Fig. 26) in having an hexagonal glabella and wider glabellar tongue than the type of *O. inconnivus*, differences already remarked by FORTEY (1974, p. 118). It seems beyond coincidence that the Spitsbergen and Utah specimens resemble one another in these features - furthermore they had been deduced to have been the same age independently on the presence in the same beds of a diagnostic *Carolinites* species with a subocular ridge, *C. genacinaca nevadensis* HINTZE (FORTEY 1976, p. 269). YOUNG's attribution of *Opipeuter* to *Remopleuridiella* is interesting because it shows a judgment compatible with FORTEY's derivation of *Opipeuter* from a remopleuridid, but different from LEGG's (1976) assignment to the same family as *Telephina* and *Carolinites* (Telephinidae *sensu* FORTEY 1975, p. 94). It should be added that the free cheek attributed to *O. angularis* by YOUNG (1973) is far more like small cheeks of *Carolinites genacinaca nevadensis* in the long, almost straight genal spine; a subocular ridge is also visible (*ibid.* Pl. 27, Fig. 1).

Family SCUTELLUIDAE RICHTER and RICHTER 1955

Subfamily STYGININAE VOGDES 1890

Genus *Raymondaspis* PŘIBYL in PRANTL and PŘIBYL 1949

Type species. — *Holometopus limbatus* ANGELIN 1854.

Discussion. — The type species of *Raymondaspis* has been fully redescribed by POULSEN (1969), who also gave a list of characters discriminating the genus from other styginines. Descriptions of *Raymondaspis* species by WHITTINGTON (1965), ROSS (1967), DEAN (1971) and TRIPP (1976), show that the genus can be extended to include forms with variable widths of the cranial anterior border, and pygidia with or without a concave border. When preservation is good enough all the species show a fine bertillon sculpture on the cephalon and terrace lines on the pygidium. Three species with greater cephalic convexity (sag.) than is usual in *Raymondaspis*, and with blunt genal angles, form a separate but closely-related group, and have been included in the new genus *Turgicephalus* below. *Raymondaspis vespertina* ROSS, from the Profilbekken Member, is in all respects a typical *Raymondaspis*. Since the name *Raymondaspis* is derived from the greek and Latin 'aspis' — shield, it should take the gender of that name, which is feminine.

Raymondaspis vespertina Ross 1967
(Pl. 6, Figs. 1–8, 11)

1967 *Raymondaspis vespertinus*, n. sp. Ross, p. 15–16, Pl. 4, Figs. 26–30.

Stratigraphic range. — Profilbekken Member, V₄b, (*Orthidiella* zone) 35 m to 55 m.

Material. — Figured material includes cranidia: PMO NF 3117, 3119; pygidia: PMO NF 3118, 3121; free cheek: PMO NF 3120. Also, cranidium, PMO NF 324, pygidium, PMO NF 331.

Diagnosis. — A *Raymondaspis* species with cranidial border in front of glabella narrower than that of all species except *R. hermaion* TRIPP and *R. arcuata* DEAN. Occipital organ minute. Bertillon pattern on glabella finer than on cheeks. Pygidium with narrow, flattened border.

Discussion. — Ross (1967, p. 15–16) has described this species from the *Orthidiella* zone of the Antelope Valley, Limestone Nevada, and the following remarks amplify his description. Ross' material is silicified and the holotype, a cranidium, is small and not as well-preserved as the Spitsbergen material. But the specimens, from the two widely-separated localities share features which are of unequivocal taxonomic importance. The narrow border on the cranidium, which produces a distinctive rim in anterior view (Pl. 6, Figs. 5, 8; Ross 1967, Pl. 4, Fig. 28) is a feature shared only by *R. vespertina* and *R. arcuata* DEAN (1971, Pl. 6, Fig. 2). The pygidium has a narrow, flattened border, of about half the relative width of that of the type species, *R. limbata* (ANGELIN 1854), which has been re-illustrated by POULSEN (1969, Fig. 2B). *R. arcuata* DEAN 1971 lacks a pygidial border, and a cranidium attributed to this species (DEAN 1971, Pl. 6, Fig. 10) has much coarser terrace lines than *R. vespertina*. The Spitsbergen and Nevada specimens have identical proportions in exactly those characters which are liable to variation in other species, and for this reason we regard them as conspecific. The pygidial axis of the type pygidium appears slightly more truncate, but since the silicification of the specimen is coarse (sufficient to obscure the sculpture) it is possible that this is a preservational feature. *R. hermaion* TRIPP (1962, p. 8, Pl. 2, Figs. 1–3) lacks a rim altogether in front of the glabella. *R. reticulata* WHITTINGTON (1965, p. 402–6, Pl. 55, Figs. 2, 3, 5–9; Pl. 56, Figs. 1–10; Pl. 57, Figs. 1–13; Pl. 58, Figs. 1, 7) and *R. angelini* BILLINGS (see WHITTINGTON 1965, Pl. 56, Figs. 11–13) both have wider preglabellar rims than *R. vespertina*, and the former lacks a concave border on the pygidium, as does *R. nitens* (WIMAN) (see SKJESETH 1955, Pl. 4, Fig. 3).

Raymondaspis reticulata has been given an exhaustive description by WHITTINGTON (1965), and most of the features he notes can be remarked also on the present species and do not require reiteration here. Among fine points of distinction attention is drawn to the occipital organ, which is minute in *R. vespertina*, but spans almost half the width (sag.) of the occipital ring of *R. reticulata* (ibid. Pl. 55, Fig. 9). The occipital tubercle is typical of FORTEY and

CLARKSON's (1975) morphological type D of cephalic organ. The scale of the bertillon pattern on the glabella of *R. vespertina* is much finer than that on *R. reticulata*; genal bertillon of the former is less crowded than that on the glabella. Muscle insertion areas show as smooth patches on the exterior of the glabella, with disposition much like that described by WHITTINGTON (1965, p. 402-3). The 1 P furrow appears to be bicomposite; 2 P is smaller than 3 P and both lie a little above the axial furrow, within the glabella. A shallow median cleft in the front of the glabella may represent the point of attachment of an anterior muscle.

A number of species with wide pygidia, which have been assigned to *Raymondaspis*, for example, *R. infundibularis* TJERNVIK (1956, p. 263, Pl. 10, Fig. 19) and a species identified with *R. limbata* (ANGELIN) by SKJESETH (1952, especially Pl. 4, Fig. 21), are probably to be referred to the genus *Turgicephalus* below.

Genus *Turgicephalus* n. gen.

Type species. — *Turgicephalus falcatus* n. gen., n. sp.

Diagnosis. — Styginine trilobites generally resembling *Raymondaspis*, but cephalon highly convex (sag.), genal borders inflated and genal angle not sharply spinose. Hypostoma with prominent middle body surrounded by narrow and convex borders. Pygidium about twice as wide as long, with or without concave border. Transverse width of articulating facets on pygidium occupies only a small part of total pygidial width (trans.). Surface sculpture of coarse bertillon pattern.

Discussion. — *Turgicephalus* is erected here to include three species of Arenig and Llanvirn age, and possibly some species from Scandinavia of which only the pygidia are so far described. The genus is close to *Raymondaspis*, but seems to form a morphologically distinct group contemporaneous with or older than the earlier representatives of that genus. Most obvious of these differences are a greater cephalic convexity, produced by a marked downward flexure in front of the eyes; this is not accompanied by an increase in pygidial convexity, pygidia being slightly less convex than those of *Raymondaspis*. The effect is to produce an illaenid-like morphology. The type species, with its peculiarly extended (trans.) cheeks, may be appropriately compared with a genus such as *Harpillaenus* WHITTINGTON 1963 (p. 77, Fig. 5) in its organisation, and differs from *Raymondaspis*, which has a more usual styginid morphology, like that of *Stygina* or *Bronteopsis*.

The general differences are accompanied by other small features which permit recognition of all parts of the exoskeleton. The hypostoma differs from that of *Raymondaspis* (WHITTINGTON 1965, Pl. 55, Figs. 2, 3, 5-8) in its convex and narrow borders, which surround an inflated middle body. Spot-like maculae are similar on the hypostomata of the two genera. The border of the free cheek in *Raymondaspis* species is co-planar with the cranial border; in *Turgicephalus* the border of the free cheek becomes gently inflated, convex

forwards rather than flat or concave, and in *T. falcatus* greatly extended laterally. The *Turgicephalus* pygidium tends to be relatively wider than that of *Raymondaspis*, the former with a maximum width about twice the sagittal length, the latter about one and a half times. More importantly, the articulating facets in *Turgicephalus* are much less wide (trans.) than the adjacent anterior margin of the pygidium up to the axis; in *Raymondaspis* facet width is approximately equal to the adjacent anterior pygidial margin. The occipital organ in *Turgicephalus* is developed as a minute tubercle. Four symmetrically disposed pits have been observed at the apex of the tubercle in *T. hinloppensis*.

PŘIBYL and VANEK (1971) have proposed the genus *Styginella*, type species *S. macrophthalma*, which was originally described by CHUGAEVA (1958, p. 109–112, Pl. 11, Figs. 5–9) under open nomenclature as “Gen. Indet. II”. As far as may be judged from available illustrations *Styginella* differs from *Turgicephalus* in having low convexity, large eyes, glabella greatly forward-expanded anteriorly, and pygidium generally more similar to that of *Raymondaspis*. Of other early styginines neither *Hallanta* POULSEN 1965 nor *Perischoclonus* RAYMOND (see WHITTINGTON 1963) are at all similar to *Turgicephalus*.

Included species. — *T. falcatus* n. sp., *T. hinloppensis* n. sp. and *T. turgidus* (WHITTINGTON 1965). Probably congeneric are a number of Arenig forms from Scandinavia described from pygidia which have the proportions of *Turgicephalus* rather than *Raymondaspis*, under which generic name they have been described: *R. brevicauda* TJERNVIK 1956, *R. infundibularis* TJERNVIK 1956 and material identified with *R. limbata* (ANGELIN), by SKJESETH (1952, p. 171–2), but differing in pygidial details from the type material of that species redescribed by POULSEN (1969).

Turgicephalus falcatus n. gen., n. sp.

(Pl. 7, Figs. 1–4, 6, Pl. 8, Figs. 1, 2, 4–6, 8, 10; Fig. 5)

Stratigraphic range. — Lower part of Profilbekken Member (V_{4a}), Valhallan, 7 m to 23 m.

Material. — Holotype, cranium, PMO NF 235. Other material includes crania: PMO NF 264, 272, 276, 289, 1092, 1100, 2437; pygidia: PMO NF 2423, 214, 230, 258, 293, 2363, 2433, 2370, 2449; free cheeks: PMO NF 1879, 284 (2 specimens), 1011; hypostoma: PMO NF 1840.

Diagnosis. — A *Turgicephalus* species with free cheeks greatly extended laterally. Cranial border wider (sag.) than other *Turgicephalus* species. Pygidium about twice as wide as long with distinct flattened or concave border.

Description. — This species is known from plentiful and well-preserved material in the Profilbekken Member. The cranium is highly convex (sag.) such that the sag. length on dorsal view is about three-quarters the cranial height (border to occipital) in anterior view. This convexity is produced by a downward-deflexion of the cranium across a line in front of the palpebral

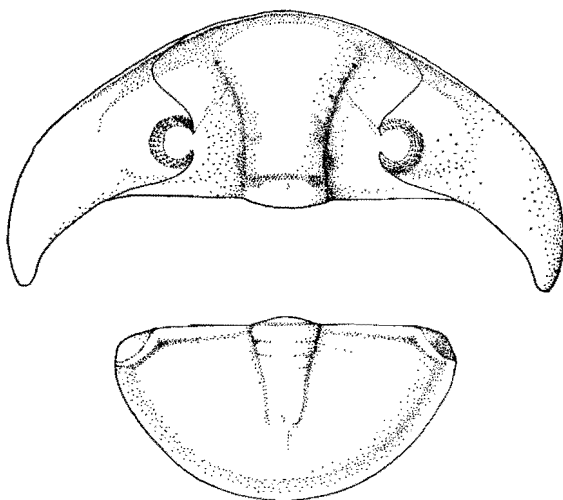


Fig. 5. Cephalon and pygidium of *Turgicephalus falcatus*, n. gen., n. sp., about three times natural size.

lobes. This may be contrasted with the condition in *Raymondaspis* where the forward and downward slope of the cranidium is on a line with the frontal lobe of the glabella. Maximum cranidial width is at the posterior margin, where the occipital ring occupies (trans.) between one third and one quarter this width.

Glabella pestle-shaped, expanding evenly forwards to maximum width at anterolateral corners, this being about 1.6 to 1.7 times the transverse width of the occipital ring. Front margin of glabella gently rounded about mid-line. Muscle impressions show as smooth patches on external surface. Occipital impression abuts the occipital furrow on the lateral parts of the occipital ring. 1P is bicomposite, and well impressed enough to show as a forked furrow extending beyond the level of the palpebral lobes, consisting of two oval (trans.) impressions extending less than one quarter across the glabella. 2P and 3P small, spaced at equal distances between 1P and the anterior fossula, just isolated within the glabella. Occipital furrow deep and straight. Minute occipital organ on forward part of occipital ring, more prominent on small cranidia. There does not seem to be a small median furrow at the anterior margin of the frontal lobe of the glabella, as is the case in *Raymondaspis* from Spitsbergen.

Fixed cheeks slope downwards towards the glabella inside the eyes, anteriorly are nearly vertical. Palpebral lobes forming almost three quarters of a circle, on a level with the highest part of the glabella, positioned relatively posteriorly, such that transverse line connecting anterior limits lies at about 0.4 cranidial length (in dorsal view). Eye ridges are quite prominent, but terrace lines pass over them without break. They slope backwards at about 45-50 degrees to sag. line. Anterior border of cranidium slightly concave, with narrow upturned rim, length (sag.) about one-third that of occipital ring. Facial sutures swing out almost at right angles to sag. line behind the eyes, cutting the posterior cranidial margin at a low acute angle, thereby defining long (trans.) and narrow (exsag.) postocular cheeks of transverse length ex-

ceeding that of occipital ring. Posterior border furrow hardly defined. Dorsal bertillon pattern of strong terrace lines, which are concentric about the posterior part of pre-occipital glabella (here they are raised lines rather than true cuesta-like terraces). Steep slopes of the terraces otherwise face upwards and backwards, except where deflected on fixed cheeks adjacent to the palpebral lobes. Smooth area in «alar» position probably represents another muscle insertion area. Preocular sutures diverge in front of palpebral lobes, and due to the strong downward deflexion of the cheeks at this point the anterior branch makes an angle of at least 45 degrees to the sag. line in dorsal aspect. In anterior view (Pl. 7, Fig. 3) the suture meets the anterior border at a right angle.

Wide, sickle-shaped free cheek with strongly forward-bowed anterior margin, back margin weakly so, not produced into a sharp spine as in *Raymondaspis*. Anterior border adaxially continues concavity of cranial border, with the same upturned rim. The great width of the cheek is produced by expansion of the lateral border, which is also inflated. The border furrow almost bisects the cheek, forming a gentle depression between the convex adaxial, and inflated border regions of the cheek. Doublure is also extended (trans.) beneath the border, but is concave upwards, so that the whole genal prolongation must have had the form of a curved, hollow cylinder. The strongly curved eye has its larger lenses concentrated dorsally; about 9–10 lenses per dorso-ventral file. Narrow strip beneath the eye with a few pits may represent a peripheral sensory zone. Terrace lines become faint near border furrow, and then absent on genal borders.

A small free cheek (Pl. 8, Fig. 10) has a genal spine, showing that at this size the cheek was like that of other styginines. The border is also flat, so that the peculiar genal inflation of this species was evidently acquired late in ontogeny.

Hypostoma (Pl. 7, Figs. 4, 6) with maximum width at anterior margin, this about one and a half times maximum posterior width. Middle body convex, slightly longer than broad; middle furrows deep, inclined inwards at a low acute angle to sag. line, and terminating in prominent spot-like maculae. Border furrows deep, converging backwards; posterior border furrow transverse. Middle body surrounded by narrow and convex borders carrying two or three raised lines. Anterior wings large, strongly dorsally directed, and excavated into prominent pits near anterolateral extremities, the sites of forward-directed apodemes. External hypostomal surface with relatively sparse terrace lines running approximately parallel with perimeter, but not extending far on to anterior wings or into border furrows.

Pygidium semicircular, slightly inflated adaxially, peripherally curving downwards quite sharply to flattened or slightly concave border, which extends to about one sixth (sag.) length of pygidium. Axis occupying one fifth max. pygidial width, and extending to just over half its length. Axial furrows well defined, converging backwards adjacent to first three rings, thereafter becoming almost parallel. First two ring furrows distinct; traces of four more shown by smooth muscle areas, and by repeated terrace line patterns. End of

axis not defined posteriorly, except on some specimens by a median dimple (Pl. 8, Fig. 1); postaxial ridge faint. Articulating facets occupy only a small part of the transverse pygidial width at anterior margin: — their width (trans.) about two-thirds that of axis, and a lesser part of the adjacent anterior pygidial border. No doubt this reflected form of posterior thoracic segments, which must have had long horizontal adaxial sections, sharply downturned and faceted pleural tips. Pygidial pleural furrows faint behind anterior furrow, two pairs can be seen on some specimens. Surface sculpture of faint terrace lines slightly oblique to posterior pygidial outline. Concave doublure which widens backwards with stronger terrace lines (about 30 sag.) parallel to posterior margin.

Discussion. — A second *Turgicephalus* species is discussed below, and differences from *T. falcatus* are summarised there. *T. turgidus* (WHITTINGTON 1965) from the Middle Table Head Formation, Newfoundland, resembles *T. falcatus* in many features of cranium and pygidium, but the pygidium lacks a concave border, and the cranium is virtually without an anterior border. The free cheek is narrower than that of *T. falcatus*, but like this species has a convex lateral border without a genal spine. WHITTINGTON (1965, p. 407–8) noted the many differences displayed by *T. turgidus* from *Raymondaspis* species (to which he assigned *T. turgidus*), and suggested that they might warrant generic recognition. Abundant material from Spitsbergen, particularly with the distinctive hypostoma, indicates that there are a cluster of species sharing such differences, which are probably closely related, and best united within a genus other than *Raymondaspis*.

Turgicephalus hinloppensis n. gen., n.sp.
(Pl. 7, Figs. 5, 7; Pl. 8, Figs. 3, 7, 9)

Stratigraphic range. — Profilbekken Member, upper part, V₄b (*Orthidiella* zone), ?35, 49 m to 80 m from base.

Material. — Holotype, cranium, PMO NF 3122; pygidia: PMO NF 1257, 1272, 1246.

Diagnosis. — A *Turgicephalus* species with distinct, but very narrow anterior cranial border; postocular fixed cheeks narrower (trans.), and anterior divergence of facial sutures less than in *T. falcatus*.

Discussion. — This species so closely resembles *T. falcatus*, which it follows stratigraphically in the Profilbekken Member, that it is best discussed in relation to that species, and detailed description is unnecessary. Cranidia of the two species are closely similar, but an obvious difference is in the relatively narrow cranial border of *T. hinloppensis*, which also has a deeper thickened rim medially (Pl. 7, Fig. 7). Anterior and posterior divergence of the facial sutures is less in *T. hinloppensis*, the latter resulting in a shorter (trans.) postocular cheek, which only just exceeds transverse width of the occipital ring. No free

cheek has been discovered for *T. hinloppensis*, but a small hypostoma, PMO NF 3190, is similar to that of *T. falcatus* and very likely belongs here. Terrace lines are denser on the middle body than in *T. falcatus*, but we do not know to what extent this may be a function of their difference in size. Pygidia are closely similar, the only difference being the relative length of the pygidial axis: in *T. falcatus* ratio of axial length to total pygidial length ranges between 0.58 to 0.61; in *T. hinloppensis* 0.54 to 0.55. The variability of these figures is diminished because of the difficulty in precisely defining the axial tip, and the few specimens of *T. hinloppensis* available. *T. hinloppensis* pygidia are preserved largely as internal moulds, which show additional details. Caeca are present on one specimen (Pl. 8, Fig. 7) but these are not as strong, nor so clearly related to segmentation, as those illustrated on *Raymondaspis reticulatus* by WHITTINGTON (1965, Pl. 57, Fig. 13). Another specimen from the same bed is not caecate, nor is the paradoublural line so clearly visible; this is regarded as purely a matter of preservation. Axis shows six (?seven) axial rings with traces of muscle impressions: the internal mould shows short elevated transverse ridges on the forward lateral edges of the ring furrows; inner ends of these are backed by subcircular depressed areas; lateral edges of rings themselves with oval (long axis. sag.) elevated area. The first and last of these are not unlike the muscle insertion areas described from *Eophacops musheni* by CAMPBELL (1975, Fig. 1, Pl. A, Fig. 6).

T. turgidus (WHITTINGTON 1965) has the anterior border on the cranium even further reduced than *T. hinloppensis*; the pygidium is wider, with narrower doublure (sag., exsag.), and lacking a concave border.

A few pygidia (Pl. 9, Figs. 6, 7) stratigraphically between *T. falcatus* and *T. hinloppensis* include large specimens with narrow, ill-defined borders and generally low convexity. Terrace lines are coarse and scalloped adaxially, and the caecal system is strong enough to appear on the dorsal surface. It is not certain whether these differences may be accounted for by continued growth of stratigraphically late *T. falcatus*, or early *T. hinloppensis*, or whether a third species is present. We designate these specimens as *Turgicephalus* cf. *hinloppensis*, because the proportions are closer to that species, although cephalic parts are needed to resolve the question of their identity.

Genus *Protostygina* PRANTL and PŘIBYL 1949

?*Protostygina* sp. ind.

(Pl. 9, Fig. 4)

Material. — A single incomplete cranium PMO NF 519a.

Stratigraphic occurrence. — Mid-part of Olenidsletta Member V_{2a}, about 90 m from base of that Member.

Discussion. — This species is represented by one fragmentary cranium, but is worth remarking as it shows several features unusual in styginines. The material available is inadequate to name it as a new species. Dorsal effacement

is considerable, and there are no glabellar furrows, although smooth patches adjacent to the axial furrows show sites of muscle attachment. The glabella itself is narrow (trans.) and parallel sided posteriorly, while anteriorly the axial furrows are completely effaced. There is a weakly defined occipital ring, and a very narrow (exsag.), concave anterior cranial border. Details of the sutures are not preserved although the fixigenal areas are wide (trans.) and the palpebral lobes therefore well-removed from the glabella. The dorsal surface is densely punctate — an exceptional surface sculpture among styginines.

This combination of characters sets this species apart from most other early scutelluid genera. With its low convexity and effacement it lies at the opposite morphological extreme to *Turgicephalus* (above), and may be compared in these characters with some later Ordovician and Silurian Goldillaeninae. Other cephalic characters, such as the cranial border and narrow, parallel-sided glabella, preclude a close relationship with this group. *Hallanta* POULSEN 1965, from the Arenig rocks of Bornholm, has a similarly narrow glabella, but one which is clearly defined anteriorly, and there are also distinct eye ridges in this genus. Only *Protostygina* PRANTL and PŘIBYL 1949, type species *P. bohémica* (BARRANDE 1872) from the Llanvirn Sárka Formation of Czechoslovakia (see (PŘIBYL in HORNÝ and BASTL 1970, Pl. 8, Fig. 3), compares in its low convexity, effacement, and posteriorly parallel-sided glabella, but other characters, for example of anterior border and facial sutures, are imperfectly preserved on the type material. Because of its incompleteness, the present specimen can only be tentatively referred to *Protostygina*.

Subfamily THEAMATASPIDINAE HUPÉ 1953

? Dulanaspinae PŘIBYL and VANEK 1971.

Discussion. — LANE (1972, p. 340) indicated that the subfamily Theamataspidae, assigned to the Illaenidae in the *Treatise* (JÄNNUSSON in MOORE 1959, p. 0–376), might better be referred to the Scutelluidae. The one genus in the subfamily, *Theamataspis* ÖRIK 1937, has been known hitherto with certainty only from the type species, *T. illaenoides* ÖRIK 1937. The discovery of a second species in the Arenig of Spitsbergen is therefore of considerable interest. It displays an odd amalgam of illaenid and scutelluid characters, and goes far to demonstrate the alliance between the two families, but on balance is perhaps closer to the Scutelluidae, particularly species of *Turgicephalus* described above.

PŘIBYL and VANEK (1971, p. 370) have erected a scutelluid subfamily Dulanaspinae to include the genus *Dulanaspis* CHUGAEVA 1958, type species *D. levis* CHUGAEVA 1958 from Caradocian of Kazakhstan. There are points of resemblance between *Dulanaspis* and *Theamataspis tuber* n. sp., notably the waisted glabella, which is anteriorly rounded, “alar” muscle impressions similarly placed, cranial border of comparable proportions, and palpebral lobes of similar form and in the same position. These similarities suggest that the subfamily Dulanaspinae may prove superfluous.

Genus *Theamataspis* ÖRIK 1937

Type species. — *T. illaenoides* ÖRIK 1937.

Theamataspis tuber n. sp.
(Pl. 9, Figs. 1–3, 5; Fig. 6)

Stratigraphic range. — The type specimen is from the mid part of the Olenid-sletta (M. Arenig) Member, V₂a, 89 m from base.

Material. — Holotype, cranidium retaining cuticle, PMO NF 510.

Diagnosis. — A *Theamataspis* species with concave cranidial border; palpebral lobes shorter than in *T. illaenoides*, not extending as far posteriorly. Surface sculpture of irregular and convoluted ridges.

Description. — Only one cranidium is known of this species, but this shows many distinctive features, and is so obviously new, that naming the species based on little material seems justified in this case.

Cranidium highly convex (sag.), flexed downwards especially in front of palpebral lobes; maximum width at posterior margin, this being about one and a half times sag. length in dorsal view. Anterior cranidial margin rounded gently about mid-line. Glabella gently convex (trans.), only slightly elevated above fixed cheeks. Glabella initially tapers forwards to about one quarter cranidial length (dorsal view), then expands gently forwards at a lesser angle, such that the axial furrows enclose an angle of about 27 degrees. Front margin of glabella rounded, more acutely so than front margin of cranidium. There is a total of six pairs of muscle impressions preserved as smooth areas on the dorsal surface of the exoskeleton: 1P serves to define the forward (exsag.) limit of the occipital ring; 3P is the largest impression, at glabellar mid-length (dorsal view), subcircular, touching the axial furrow; 2P immediately behind inner end of 3P and less than half its diameter; 4P and 5P equidistant from each other, 3P and the front of the glabella, 5P smaller than 4P; 6P is a very small, circular impression opposite the inner end of 5P. All impressions except 3P are isolated within the glabella; because 2P and 3P, and 5P and 6P are closely set together, and by comparison with styginids and illaenids (below), they might have been associated with the functioning of single appendages, indicating a total of four pairs, rather than six pairs of cephalic limbs. Major additional pair of muscle impressions in axial furrows adjacent to the narrowest, waisted part of the glabella. Occipital ring transversely fusiform, inclined forwards, width slightly exceeding that of glabella at frontal lobe; occipital furrow shallow. Faint, median occipital tubercle present. Axial furrows similarly shallow, slightly deepened into pits at anterolateral corners of glabella.

Fixed cheeks of transverse width about one-third that of adjacent glabella at frontal lobe, posteriorly relatively wider. Palpebral lobes gently arcuate frontal limits at about half cranidial length in dorsal view, length (exsag.) about one-third that of glabella in same view. Palpebral rims are not defined.

Strong eye ridges, running inwards to meet the axial furrows opposite muscle impression 4P. Postocular fixed cheeks narrow (exsag.), triangular, without border furrows, defined by strongly forward-converging postocular sutures. Preocular sutures subparallel in front of palpebral lobes, anteriorly converging slightly to cut anterior margin at obtuse angle. Concave cranial anterior border, about one-tenth length of glabella in dorsal view. External surface of cranium covered with coarse, irregular ridges, between which there are finer granules. The ridges, but not the granules, are reflected on the internal mould.

Discussion. — *T. tuber* n. sp. is distinguished from the type species, *T. illaenoides* ÖRIK 1937, from the Middle Ordovician of Estonia, in its smaller palpebral lobes, distinctive surface sculpture, concave anterior border, and wider postocular cheeks. ?*Theamataspis* sp., described by Lu (1975, p. 390, Pl. 34, Figs. 1–3) from a similar horizon to *T. illaenoides* in China, also lacks a concave border, and has a relatively narrow and convex glabella.

Comparison of cranial morphology of *T. tuber* with that of an early styginine (*Turgicephalus*) and early illaenid (*Illaenus gelasinus* WHITTINGTON 1965) demonstrates the intermediate position of *Theamataspis* (Fig. 6). General glabella form, presence of a concave border and transversely extended postocular cheeks, and the conspicuous eye ridges are features shared with *Turgicephalus*. Effacement of the occipital ring, isolation of muscle impressions from the axial furrows and the gently curved palpebral lobes are generally illaenid features. Comparison of the homology of muscle impressions is particularly informative. The constriction of the glabella in *Theamataspis* is homologous with the lunettes of *Illaenus*, being caused by extra-axial muscle impressions; the same are present also on *Turgicephalus* but do not constrict the glabella. Occipital impressions are similar on *Turgicephalus* and *Theamataspis*; they are not obvious on *I. gelasinus*, where the occipital ring is effaced, but they have been remarked on *I. dalmani* (JAANUSSON 1954). The first pre-occipital muscle impression of *Turgicephalus* is large and bicomposite, as it is on *Theamataspis* (termed 2P and 3P above); on *Illaenus* it seems to be a single impression, although the tendency of the impressions to become isolated from the axial furrows is matched in *Theamataspis*.

It is concluded that the inclusion of the Illaenidae and Scutelluidae within a single larger taxon (Superfamily Illaenacea HAWLE and CORDA 1847) is justified. What does not seem justified is bracketing this group with the

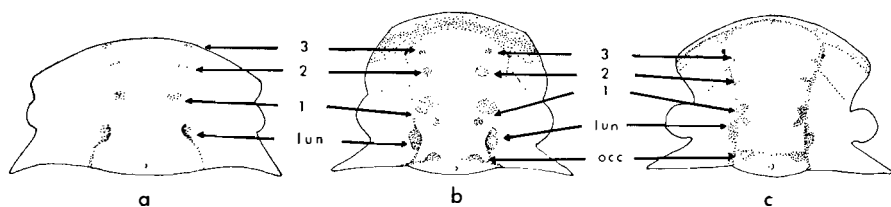


Fig. 6. Diagram demonstrating homology of muscle insertion areas in illaenids (a) *Theamataspis tuber* n. sp. (b), and scutelluids (*Turgicephalus*, c).

Proetacea in a single Order Illaenida, as advocated by BERGSTRÖM (1973, p. 41), since the muscle insertion areas and cephalic furrow patterns of this group are radically different. There is not, for example, an equivalent of the extraglabellar impression that produces the lunettes of the illaenids, and the homologous ("alar") impression of the scutelluids.

Family ILLAENIDAE HAWLE and CORDA 1847

Genus *Illaeus* DALMAN 1827

Type species. — *Illaeus crassicauda* (WAHLENBERG 1821)

Illaeus oscitatus n. sp.

(Pl. 10, Figs. 1–13)

?1972 *Illaeus* sp. c ROSS, 1972, p. 33.

1975 *Illaeus* sp. FORTEY, Fig. 7F.

Stratigraphic range. — Upper part of Profilbekken Member (V₄b) 38 m to 100 m from base, Whiterock, (*Orthidiella* zone, early Llanvirn).

Material. — Holotype, cranidium, PMO NF 282; cranidia: PMO NF 226, 1347, SMA 84351–5; pygidia: PMO NF 283, 228, SMA 84356–8; free cheek: PMO NF 317; hypostomata: PMO NF 227, 327a, 1246a, 3198.

Diagnosis. — *Illaeus* species with surface sculpture of dense terrace ridges interspersed with punctae. Glabella half cranidial width at posterior margin, slightly tapering to prominent lunettes; other cephalic muscle insertion areas not visible. Pygidium less than twice as wide as long, axis well-defined anteriorly only; pygidial doublure cusped.

Description. — One of the common species of the upper part of the Profilbekken Member, where it is represented by allochthonous material, in some cases broken (FORTEY 1975a, Fig. 7F). Cranidium of width at posterior margin in palpebral view between 1.5 and 1.6 times sag. length, anterior downward deflexion considerable, such that the cranidial height (seen in lateral view) is one and a half times sag. length. Glabella gently convex (tr.) posteriorly, occupying half total cranidial width at posterior margin. Axial furrow shallow, initially parallel or slightly converging inwards about the prominent lunettes which are the only smooth patches on the dorsal exoskeleton. On internal moulds the lunettes are also prominent, crescentic, and a minute, posteriorly placed glabellar tubercle is also visible. Palpebral lobes of length (exsag.) about 0.4 sag. cranidial length in palpebral view, gently arcuate. Facial sutures diverge behind palpebral lobes to define narrow, triangular postocular cheeks. Anterior branches subparallel in front of palpebral lobes, anteriorly converging slightly and more so near the anterior cranidial margin. Very narrow rim separates dorsal surface from narrow strip of doublure on cranidium, which curves slightly upwards to be visible in anterior view (Pl. 10, Fig. 3). Close

terrace lines on doublure. Wider spaced terrace lines on cranial surface, running more or less transversely, except where bowed forwards on posterior part of glabella. Pits in lines just posterior to terrace lines, in the position illustrated by MILLER (1975). Internal mould finely punctate, except on median smooth line running sag. on forward part of glabella.

Free cheek about as long (exsag.) as wide (tr.) in plan view, genal angle only slightly rounded. Sculpture as on cranidium except terrace lines absent around base of eye.

Hypostoma smooth, maximum width at anterior wings only slightly exceeding sagittal length. Anterior lobe of middle body circular, gently convex, equally so sag. and trans. Anterior margin bowed backwards medially. Furrow defining anterior half of middle body shallow. Middle furrow narrow and deep (exsag.), shallowing posteromedially to cut off low, crescentic posterior lobe of middle body. Length of posterior lobe about one-third that of anterior lobe (sag.). Narrow downturned rim around posterior lobe of middle body. Evidence of maculae is lacking on the exterior cuticular surface, although there is a circle of small, faint pits on the anterior lobe of the middle body that may represent muscle insertion areas. Posterior hypostomal margin transverse.

Pygidium of length slightly more than half maximum width, less convex (sag.) than cranidium. Axis occupies 0.3 pygidial width at anterior margin, convexity (tr.) slight, initial taper rapid, but soon becoming parallel-sided. Although posteriorly not distinct from pleural fields extent of axis is marked by termination of some of the terrace lines, showing that it extends to half pygidial length (dorsal view); axial definition is clearer on internal moulds. Steeply downturned facet, not extending far across anterior pygidial margin. Terrace lines and pits as on cephalon, except only half as closely spaced on axis, not on facet. Doublure (Pl. 10, Fig. 12) steeply reflexed beneath dorsal surface, gently cusped around tip of axis, with sparse terrace lines (12 to 18 on larger specimens examined). There is a median groove in the doublure running sag. behind the axis almost to the posterior pygidial margin, interrupting the course of the terrace lines.

Discussion. — This species belongs within the *Illaeus sarsi* species group of JAANUSSON (1957, p. 110), which includes a number of species with a cusped inner margin of the pygidial doublure. WHITTINGTON (1965, p. 385) has suggested that a notch in the anterior margin of the hypostoma is associated with species having an axe-shaped rostral flange. The similarity of our hypostoma to that of *I. consimilis* BILLINGS (*ibid.* Pl. 52, Figs. 6–13) indicates a rostral development of this type in *I. oscitatus*. In view of the numerous described species of *Illaeus* it is a little surprising to find that the species from Spitsbergen is a new one. *I. sarsi* JAANUSSON 1954, itself is closely similar to our species in general proportions but differs significantly in having facial sutures that are scarcely divergent behind the palpebral lobes, and in lacking the coarse pits that cover the external surface of *I. oscitatus*. The convexity (particularly seen in lateral view) of the cranidia of *I. sarsi* and *I. oscitatus* is similar. Since the size series of cranidia of *I. oscitatus* shown on Pl. 10, Figs. 2, 6, 7

demonstrates that convexity (sag.) decreases with increase in size it is obviously important to compare cranidia at the same approximate size. Of the species from the Lower Head Boulder, western Newfoundland, described by WHITTINGTON (1963) *I. oscitatus* compares in some general features with *I. tumidifrons* BILLINGS, but this species has deep dorsal furrows, lacks an anterior cranial border, has a different surface sculpture, and a fork-like median extension of the pygidial doublure. WHITTINGTON (1965) described five named species from the Middle Table Head Formation, western Newfoundland. *I. fraternus* BILLINGS is probably the most similar of these to the Spitsbergen form, but it is less convex, has a different surface sculpture, the free cheek is much narrower, with a prominent flange, and the outline of the pygidial doublure is like that of *I. tumidifrons*. A species recorded as *Illaeus* sp. ind. 2 (WHITTINGTON 1965, Pl. 54, Figs. 4, 6, 7) evidently had exterior punctae on the cranidium, and has a narrow glabella of about the same (sag.) length as that of *I. tumidifrons*, but the eyes of this species are so far back as to reduce the postocular cheek to a spine. *I. auriculatus* Ross (1967, p. 16–17, Pl. 5, Figs. 1–32, 36, 40) from a Whiterock horizon in California has outward-bowed glabellar furrows, at least on larger cranidia, the anterior cranial border is not defined, the pygidium is transversely wider, and the free cheek has a broad lateral flange. Ross (1972) has also described seven *Illaeus* species from the Meiklejohn bioherm, Nevada, six under open nomenclature. One of these, *Illaeus* sp. c (Ross 1972, p. 33, Pl. 14, Figs. 7–12) may be conspecific with *I. oscitatus*, judging from the glabellar profile, the forward position of the palpebral lobes, divergent postocular sutures, and definition of the glabella. Fragments of exoskeleton adhering to Ross' Fig. 9 show a comparable surface sculpture. The lunettes are slightly more impressed on the Nevada material, and the anterior cranial border is not clearly visible, so that specific identity must remain in doubt.

Family AULACOPLEURIDAE ANGELIN 185-

Subfamily SCHARYIINAE OSMOLSKA 1957

Genus *Oenonella* n. gen.

Type species. — *Oenonella paulula* n. sp.

Diagnosis. — Scharyiine trilobites with long, gently tapering glabella; palpebral lobes relatively short, less than half length of glabella. 1P glabellar furrows short. Postocular fixed cheeks acutely pointed. Anterior branches of facial sutures not highly divergent. Pygidium large, resembling that of *Scharyia*.

Discussion. — THOMAS and OWENS (1978, p. 75) included four genera of scharyiine trilobites as a subfamily of the Aulacopleuridae. They suggested that *Panarchaeogonus* ÖPIK 1937, might include species at the root of later genera. *Panarchaeogonus* has not yet been recorded in rocks of pre-Llandeilo age. The new genus from Spitsbergen takes the history of the group back to the Arenig. The tapering glabella, long preglabellar field, and large, long pygidium,

indicates that *Oeononella* is allied to the scharyiines rather than the aulacopleurines. *Scharyia* itself includes species in which the glabellar furrows are subdued (OWENS 1974); in *Oeononella paulula* a short section of the 1P furrow remains, but this is entirely different from the deep, backward curving 1P furrow characteristic of aulacopleurines. All *Scharyia* species have well developed cedariiform facial sutures, with strongly divergent anterior branches, whereas the sutures of *Oeononella* are of a usual opisthoparian type. *Panarchaeogonus* (type species *P. parvus* ÖRİK 1937, Pl. 1, Fig. 3) is similarly opisthoparian, but differs from *Oeononella* in the structure of the glabella, in the large palpebral lobes close to the glabella, and in the comparatively short preglabellar field. On balance *Oeononella* shares more morphological features with *Scharyia* than with *Panarchaeogonus*. THOMAS and OWENS (1978) indicated that the latter may have included species ancestral to *Scharyia*. *Oeononella* now seems a more plausible alternative. In any case the discovery of *Oeononella* supports OWENS' (1974, p. 687) belief that "the ancestors of *Scharyia* presumably had ... a normal opisthoparian suture".

Oeononella is also present in Nevada, in the beds flanking the Meiklejohn bioherm. A good cranium is in the collections of the British Museum (Natural History) (No. It 9810).

Oeononella paulula n. gen., n. sp.
(Pl. 11, Figs. 1-8, 11; Fig. 7)

Stratigraphic range. — Only found in one bed on Profilbekken, not in measured section, but from the associated fauna certainly in the uppermost part of the Olenidsletta Member or very lowest Profilbekken Member (latest Arenig, Valhallan).

Material. — Holotype, cranium PMO NF 1324; cranidia: PMO NF 1327-8, 1343; pygidia: PMO NF 1325, 1337.

Diagnosis. — As this genus is so far monotypic, diagnosis follows that of genus above.

Description. — All specimens are small, cranidia 2 mm long or less, and it is probable that this small size is characteristic of the genus, because a second undescribed species from the 'flanking beds' at Meiklejohn Peak, Nevada, is of similar proportions. Largest pygidium slightly shorter than cranium, and it is considered that this species was probably subisopygous, like *Scharyia*. Maximum cranial width at posterior margin slightly exceeding sagittal length. Glabella convex (tr.) posteriorly, decreasingly so anteriorly, extending to three fifths cranial length (dorsal view), tapering gently and uniformly forwards, axial furrows enclosing an angle of 20 degrees or less. Front margin truncate to gently rounded on largest cranium (Pl. 11, Fig. 1). Only one pair of glabellar furrows at all well-defined, and these are short, inward-backward directed at about 0.4 glabellar length (including occipital ring); faint indication of second pair of furrows opposite forward parts of palpebral lobes.

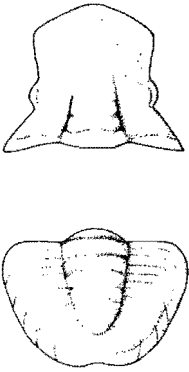


Fig. 7. Cranidium and pygidium of *Oenonella paulula* n. gen., n. sp. restored approx. $\times 12$.

Slightly inflated glabellar lobe in front of 1P furrow. Lateral parts of occipital furrow curve backwards parallel to 1P; mid-part curves forwards so that occipital ring widest medially (sag.), where about one-quarter total glabellar length. Axial furrows deepest posteriorly; preglabellar furrow shallow. Small palpebral lobes placed opposite mid-part of pre-occipital glabella, width (tr.) of intraocular cheek about half that of adjacent glabella. Palpebral furrow deep. Faint eye ridges run inwards and forwards from anterior limits of palpebral lobes to meet axial furrows shortly behind anterolateral corners of glabella. Preglabellar field broad, continuing downward and forward slope of front part of glabella, faintly caecate. Anterior border nearly flat, widening medially, slightly acuminate. Border furrow shallow. Posterior border elevated above postocular cheek, widening laterally. Anterior branches of facial suture diverge slightly in front of palpebral lobe, posterior divergence much greater, suture running almost straight to posterior margin, which is cut at an acute angle. Cuticle thin, and there is little difference between external surface and internal mould. Surface sculpture lacking except for caeca.

Larger pygidium about two-thirds as long as wide, axis standing well above pleural fields, occupying about one-third pygidial width at first axial ring. Axis tapers posteriorly, axial furrows enclosing an angle of about 25 degrees, to acutely rounded tip at about three-quarters pygidial length. Four (? five) axial rings, only the first two defined across mid-part of axis, ring furrows shallowing medially. Articulating half ring prominent, length (sag.) about equal to that of axial rings. On the pleural fields the first two segments are clearly delimited by interpleural furrows, almost like unreleased thoracic segments. Pleural furrows shallow on these segments, extending almost to pygidial margin. Ridges marking the intersegmental boundaries run across the pleural fields and on to the pygidial margin to delineate the third, fourth and fifth pleural segments, their tips strongly deflected posteriorly. Convex posterior border narrowing anteriorly, and not present adjacent to first two pleural segments.

Minute, immature pygidium almost twice as wide as long and with relatively shorter axis than above (Pl. 11, Fig. 11), generally more proetid-like. Five pleural segments are still visible at this size. Partially revealed doublure is narrow, concave-upwards, ventrally coincident with pygidial border.

Discussion. — The affinities of this species have been discussed above. It is worth remarking that it occurs in Spitsbergen with an assemblage of trilobites (*Triarthrus*, *Hypermeccaspis*, *Ampyx* and Nileidae) of transitional type between olenid and nileid community types. Aulacopleurids, including *Aulacopleura* itself, have a long subsequent history in the equivalents of the olenid community (FORTEY and OWENS 1975).

Family DIMEROPYGIDAE HUPÉ 1953
Subfamily DIMEROPYGINAE HUPÉ 1953
Genus *Ischyrotoma* RAYMOND 1925

Type species. — *Ischyrotoma twenhofeli* RAYMOND 1925

Ischyrotoma twenhofeli RAYMOND 1925
(Pl. 11, Figs. 9, 10, 12–21)

Stratigraphic range. — Profilbekken Member, V₄b, 65 m to 75 m from base (Whiterock *Orthidiella* zone).

Material. — Cephalo: PMO NF 138, SMA 84345; pygidia: PMO NF 3113, SMA 84346.

Discussion. — The type species of *Ischyrotoma* has been redescribed by WHITTINGTON (1963, P. 45–48, Pl. 7). I cannot distinguish the cephalo from the Profilbekken Member from similarly preserved material of the type species from the Lower Head Boulder, western Newfoundland. The eyes are not preserved on the material available to us. Glabellar tuberculation is particularly coarse and reflected in a more subdued fashion on the internal mould. A deep preglabellar furrow separates the convex well-defined border from the glabella, and there is no preglabellar field, these characters serving to distinguish *I. twenhofeli* from *I. anataphra* FORTEY 1979, from an earlier horizon in the St George Group of western Newfoundland. An incomplete cephalon (Pl. 11, Figs. 12, 15) has only one free cheek, and the doublure has been prepared to show the connective suture anteromedially. From its position near the midline the rostral plate can only have been excessively narrow, as shown by WHITTINGTON (1963, Pl. 7, Fig. 13) for *I. twenhofeli*.

WHITTINGTON (1963) did not have complete information on the pygidium. Two well-preserved examples are known from Spitsbergen. They are assigned here rather than to *Ischyrophyma* ? *borealis* n. sp. because they resemble pygidia of other *Ischyrotoma* species described by ROSS (1951), HINTZE (1953) and FORTEY (1979). A pair of tubercles was present on the terminal piece of one specimen, but they were unfortunately destroyed during preparation.

Pygidium with broadly triangular outline, convex, of sagittal length about two-thirds its maximum width at the anterior margin. Axis broad, of maximum transverse width slightly less than half that of pygidium, tapering posteriorly. Three convex (sag., trans.) axial rings which are bowed forwards slightly

medially, of decreasing length (sag.) posteriorly. Ring furrows deep, shallower medially. Crescentic articulating half ring of sagittal length equal to that of the axial ring immediately behind it, from which it is separated by a deep furrow. The first ring furrow contains a transverse, inflated ridge medially, probably representing a vestigial articulating half ring. Pleural fields with narrow (trans.) adaxial horizontal part, laterally and postaxially steeply downwards sloping. The structure of the anterior pair of pygidial pleurae is complex and probably closely reflects the thoracic structure. A posterior adaxial convex band, almost horizontal, terminates in a tubercle, and is continued laterally as a downward sloping triangular raised band, the point of this triangular band joining the posterior border of the pygidium. In front of the triangular band there is a broad (exsag., trans.) triangular facet which slopes downwards to the front of the pygidium (Pl. 11, Fig. 16). The adaxial part of the convex band is bounded anteriorly by a deep, transverse pleural furrow which shallows laterally. In front of this furrow is a narrow (exsag.) anterior convex band which bears a prominent node (possibly an articulating boss), this band being truncated laterally by the facet. The structure of the second pygidial pleurae is similar, although the anterior convex band and pleural furrow is feebly developed. Shallow furrows run along the mid line of the lateral, triangular parts of the posterior convex bands, dying out abaxially. On the posterior three pygidial pleurae these details are not visible, and the posterior bands only are developed, these being progressively more backward directed, the fifth pair almost parallel to the sagittal line; the bands are separated by broad furrows. An indistinctly defined sixth pair of pleural bands may be present behind the axis. A narrow (sag., exsag.) convex rim runs along the posterior margin of the pygidium, which joins the tips of the pleural bands.

I. twenhofeli has been fully discussed by WHITTINGTON and his account does not require repetition. Ross (1967, p. 21, Pl. 7, Figs. 1–7) has described a species, *Ischyrotoma* sp., from the *Orthidiella* zone of the western United States. The specimens are immature, but they seem to have more in common with *I. twenhofeli* than any other species. *Ischyrotoma* thus ranges from probably late zone G of Ross 1951 to the early Whiterock, i.e. throughout the Arenig and just into the Llanvirn.

Subfamily CELMINAE JAANUSSON 1956
(nom. transl. herein *ex* Celmidae JAANUSSON 1956)
Genus *Ischyrophyma* WHITTINGTON 1963

Type species. — *Ischyrophyma tuberculata* WHITTINGTON 1963.

Discussion. — I regard *Ischyrophyma* as related to *Celmus* ANGELIN 1854, and incorporate both genera in the Dimeropygidae. *Celmus* has a peculiar pygidium consisting of a single segment. FORTEY and OWENS (1975, p. 232) presented arguments to show that this form could have been derived from a dimeropygid ancestor. Unfortunately, the pygidium of the type species of *Ischyrophyma* is not known. Cranidial characters of *Celmus* and *Ischyrophyma* are similar: hook-

like 1P glabellar furrows and a short 2P, similar course of the facial sutures and similar position of palpebral lobes. The glabella of *Celmus* (JAANUSSON 1956, Pl. 1, Figs. 3, 6, 9) is anteriorly truncate, while that of *Ischyrophyma* has a broadly parabolic outline and may be inflated anteriorly. A species from Spitsbergen is included, cautiously, in *Ischyrophyma*. The 1P glabellar furrows are less incised than in the type species and the palpebral lobes are further from the glabella.

Ischyrophyma? borealis n. sp.
(Pl. 12, Figs. 1–7)

Stratigraphic range. — Profilbekken Member, 45 m to 65 m from base (Whiterock, *Orthidiella* zone).

Material. — Holotype, cranidium, SM A 84343; cranidia: SM A 84344, 84359, PMO NF 3258 free cheek: SM A 84347.

Diagnosis. — A species referred with caution to *Ischyrophyma* with weakly impressed lateral glabellar furrows. Surface sculpture of tubercles of two sizes.

Description. — Cranidium with maximum width at posterior border. Glabella of transverse width at occipital ring slightly less than half the maximum width of the cranidium, highly convex (sag., trans.), expanding slightly in width in front of the occipital ring, anteriorly tapering to broadly rounded front. Two pairs of weakly impressed lateral glabellar furrows, transverse line joining the abaxial ends of furrows 1P is about mid-length of glabella in dorsal view. Outer part of glabellar furrow 1P almost transverse, curving sharply backwards and shallowing, not reaching occipital furrow. Furrow 2P short, transverse. Occipital furrow deep, straight. Occipital ring narrower laterally, in lateral view slightly lower than posterior part of glabella. Axial and preglabellar furrows deep and wide. Fixed cheeks slope steeply downwards in front of palpebral lobes, posterior parts slope more gently outwards and downwards. Posterior limit of palpebral lobe opposite furrow 1P, anterior limit slightly in front of furrow 2P. Lobe is defined by a distinct, outward bowed furrow, broadest medially, and is directed upwards from cheek. From midpart of palpebral furrow a short, outward-directed branch furrow bisects palpebral lobe. Anterior border of the cranidium convex, defined by deep border furrow confluent with preglabellar furrow medially. Facial sutures cut the posterior border at about 70 degrees, running inwards at about 20 degrees to the sagittal line, in front of the palpebral lobes converge forward and curve adaxially after crossing the border furrow to meet on mid line.

Lateral border of free cheek strongly convex, separated from cheek by broad furrow. The lateral outline of the cheek is evenly rounded in this species so that the genal angle is not identifiable. I agree with JAANUSSON (1956, p. 43) that the facial suture should be regarded as opisthoparian. Doublure of free cheek narrow, curved upwards sharply beneath border and continued adaxially

beneath anterior border of cranidium. Subsemicircular eye elevated above free cheek on narrow, convex socle, and shows no lenses, in spite of excellent preservation. The lenses were probably extremely minute.

Sculpture of coarse tubercles, quite widely spaced, interspersed with finer granules. The tubercles are reflected on internal moulds, granules not visible internally. Furrows, palpebral lobes and adaxial part of posterior borders smooth, and there are broad, smooth bands surrounding the eyes on the free cheeks (Pl. 12, Fig. 1). The lateral border bears low ridges anteriorly in addition.

Pygidium not known, but if it were the minute, single segment structure of *Celmus* type, this is scarcely surprising.

Discussion. — The type species, *I. tuberculata*, from the Lower Head boulder, western Newfoundland, has a convex, forward-protruding glabella, deep 1P glabellar furrows, and a coarsely tuberculate sculpture (WHITTINGTON 1963, Pl. 8, Figs. 1–10). The first two features also distinguish *I. tumida* WHITTINGTON (1965, Pl. 19, Figs. 6–12, 15) from *I. ? borealis*.

Ischyrophyma marmorea DEAN (1970) from northeastern Newfoundland and *I. deserta* (BILLINGS) (DEAN 1970, Pl. 1, Figs. 2–4, 7–9, 11–13; Pl. 2, Figs. 1–3, 5, 7, 9, 10, 12, 13) also have deep 1P furrows which are isolated within the glabella, and these may be bicomposite. The pygidium attributed to *I. marmorea* by DEAN is very different from the single segment of *Celmus*. I have recently discovered a typical *Ischyrophyma* from a silicified fauna in north-western Newfoundland in which the pygidium is again a single segment similar to that figured by FORTEY and OWENS (1975, Fig. 1B) for *Celmus* sp. This leads me to suspect that *I. marmorea* is not a true *Ischyrophyma*, if its pygidium is correctly associated. Its isolated 1P furrow inclines me to the view that it is a glaphurid.

Family BATHYURIDAE WALCOTT 1886
Subfamily BATHYURINAE WALCOTT 1886
Genus *Acidiphorus* RAYMOND 1925

Type species. — *Acidiphorus spinifer* RAYMOND 1925.

Discussion. — WHITTINGTON (1965) has redescribed the type species of *Acidiphorus*, from the Lower Table Head Formation, western Newfoundland. *Acidiphorus* was considered to be the senior synonym of *Goniotelus* ULRICH, and this is accepted here. Two species assigned to *Acidiphorus* occur in the Profilbekken Member in Spitsbergen. One of these, *Acidiphorus ?ligo* n. sp., retains a short preglabellar field and a pointed anterior border, in these respects more closely resembling the type species of *Goniotelina*, *G. williamsi* (ROSS 1951, Pl. 14, Figs. 16–22, 25). The forward expansion of the glabella of *Acidiphorus ?ligo* suggests that assignment to *Acidiphorus* is more appropriate, although the species is evidently transitional with the somewhat older genus *Goniotelina*.

Acidiphorus brevispicatus n. sp.
(Pl. 12, Figs. 8–17)

Stratigraphic range. — Profilbekken Member, 65 m to 85 m from base (White-rock).

Material. — Holotype, cranium: PMO NF 1353. Cranidia: PMO NF 3129, 143, 3259, SM A 84360; pygidia: PMO NF 1349, 1396, 135; free cheeks: PMO NF 124, 135, 147b.

Diagnosis. — *Acidiphorus* species with short genal and pygidial spines. Anterior border of cranium medially tumid; coarse glabellar tuberculation replaced by ridges anteriorly. Posterior part of pygidial axis tumid; pygidial spine comes off border.

Description. — Most of the available material of this species is exfoliated, but in spite of the thick cuticle the internal surfaces seem to match the externals except that the surface sculpture is only weakly reflected. Cranidia highly convex, glabella sloping down especially in front of palpebral lobes, slightly overhanging anterior border in lateral view but with a truncate forward outline in dorsal view. Glabella not greatly vaulted transversely, with characteristic slight expansion in width opposite centre points of palpebral lobes. It narrows again at the front of the palpebral lobes, only to expand around the frontal glabellar lobe, where it is broadly rounded about the mid-line. Two pairs of glabellar furrows are imperfectly indicated by smooth areas on the glabella. 1P commences at wide point of glabella opposite palpebral lobe, curves inwards and backwards in a deep hook to a point about opposite posterior end of palpebral lobe; 2P shorter and fainter with similar form, commencing near anterior limit of palpebral lobe. Occipital ring only slightly wider medially; ring furrow deep. Axial furrows deepest at front and back ends of palpebral lobes, preglabellar furrow shallow. Palpebral lobes semi-circular, almost touching axial furrows at both ends, inclined towards glabella, length (exsag.) about one-third total glabella length in dorsal aspect, and rather far advanced for *Acidiphorus*. Palpebral rims well-defined, narrow, without tubercle. Narrow, downsloping preocular cheeks widen forwards into preglabellar field which is virtually absent medially. Narrow (trans.) anterior cranial border carries fine terrace ridges and is swollen medially (Pl. 12, Fig. 10). Narrow (exsag.) and acutely pointed postocular cheeks not as wide as occipital ring, largely composed of convex posterior border which apparently lacks tubercles. The rest of the dorsal surface carries surface sculpture: discrete, large tubercles over most of glabella and occipital ring, a few of the same on palpebral lobes, irregular ridges on forward part of glabella. An internal mould of a free cheek (Pl. 12, Fig. 12) shows a short, curved genal spine with a medial keel, narrow border steeply downturned towards front, with the border furrow fading out near genal spine. Reflection of surface sculpture on internal surface suggests that posterior part of field carried scattered tubercles like those on glabella.

Triangular pygidium prolonged into posterior spine of about same length or less as pygidial axis. Spine is a prolongation of the border, tapers rapidly at first into circular cross section, inclined upwards. Axis occupies half or somewhat less pygidial width at anterior margin, tapers very slightly anteriorly through two axial rings of similar width (sag.) Posterior part of axis tumid and barrel shaped, carrying obscure indications of up to six segments. Pleural fields steeply declined abaxially, with anterior facet swept far back, indicating a narrow thoracic axis at rear. Two pairs of pleural furrows are strongly backward-directed and fade out on border, one weak pair interpleural furrows. Dorsal sculpture not known from internal moulds, but included lines of tubercles on first two axial rings and posterior part of axis, traces of which are seen on the internal mould.

Discussion. — This is a distinctive species of *Acidiphorus*, which is easily distinguished by its short pygidial spine and rounded, prominent tubercles on the glabella. The convex nub on the anterior cranial border is also unique to *A. brevispicatus*. *Acidiphorus spinifer* (WHITTINGTON 1965, Pl. 44, Figs. 3–16) has a stout and long pygidial spine, narrow cranial anterior border, and the glabella carries a dense mosaic of flat-topped tubercles. Of the several species of *Acidiphorus* (formerly *Goniotelus*) described by WHITTINGTON 1963, from the Lower Head boulder, western Newfoundland, *A. brevispicatus* is closest to *A. rostratus*, which displays glabellar furrows of like form, palpebral lobes similar in size and position, narrow anterior cephalic borders and apparently short genal spines. However, *A. rostratus* is densely and finely tuberculate right to the front of the glabella, and the cranial border is prolonged into a spikelike projection medially (WHITTINGTON 1963, Pl. 15, Fig. 4).

SHAW (1974) has described *Goniotelina* cf. *G. williamsi* (ROSS) from the Joins Formation, Oklahoma. Most of the material described under this name bears no resemblance to the species under discussion, however one pygidium figured by SHAW (Pl. 5, Fig. 26) is very like that of *A. brevispicatus*, and differs in its lack of pleural furrows and posterior axial furrows from other pygidia attributed to *Goniotelina* cf. *G. williamsi*. It is probably more correctly referred to a species like that from Spitsbergen, and differs from the pygidium of *A. brevispicatus* only in the lack of a second pair of pleural furrows. The fact that the Oklahoma specimen occurs with *Carolinites angustagena* ROSS (= *C. sibiricus* CHUGAEVA), which is present in Spitsbergen along with *A. brevispicatus*, indicates a similar age for the similar pygidia.

Acidiphorus ? *ligo* n. sp.
(Pl. 13, Figs. 1–9)

Stratigraphic range. — Profilbekken Member, 40 m to 75 m from base (Whiterock, *Orthidiella* zone).

Material. — Holotype, cranidium, PMO NF 126; cranidia: PMO NF 30, 33, 340, SM A 84361–5; thorax (partial) and pygidium: PMO NF 127; free cheeks: PMO NF 31, 116, 1341, 3191; pygidia: PMO NF 126a, 888, 1756, SM A 84366–9.

Diagnosis. — *Acidiphorus* with short (sag.) preglabellar field, flat, sharply acuminate cranial border. Sculpture on glabella of scattered tubercles especially sparse posteriorly. Genal spines long, flat. Pygidium with up to four axial rings, narrow posterior border.

Description. — Glabella expanding in width (trans.) gently forwards to antero-lateral corners, broadly rounded in front, not overhanging anterior border. Glabellar furrows not incised, except for faint indications of furrows opposite anterior end of palpebral lobe and again opposite mid-point of palpebral lobe. Occipital ring slightly wider medially, defined by deep, transverse or forward-arched occipital furrow. Axial furrows slightly deeper and wider anteriorly around anterolateral corners of glabella. Palpebral lobe large, length (exsag.) half that of pre-occipital glabella, forward end closer to glabella than back end, outline a deep, transverse U-shape. Narrow well-defined rims carry a row of small tubercles. Palpebral lobes far back, transverse line connecting posterior limits only slightly in advance of occipital furrow. Preocular cheeks very narrow (trans.), sloping downwards into preglabellar field, which is a narrow and gently forward-sloping band in front of frontal glabellar lobe. Horizontal anterior cranial border very narrow laterally, medially expanding into a flat obtuse triangle. Facial suture of usual course for genus. Surface sculpture on glabella of rather sparse tubercles, which may be almost absent posteriorly, although median occipital tubercle present. Fine anastomosing raised lines also on frontal lobe of glabella and preocular fixed cheek, continuing on to librigenal borders.

Free cheek equipped with a long and gently curved genal spine which in lateral view forms a nearly flat plane with the sharp edge facing outwards. Posterior and lateral borders fade out when approaching spine, which runs without a break into the genal field. Lateral border narrow in dorsal view, steeply inclined downwards along cephalic margin, and bowed down below level of genal spine. Eye elevated on low, smooth eye socle, dorso-ventrally high, so it must have occupied a relatively elevated position above most of cephalon except midpart of glabella. Minute crowded lenses, at least twenty per dorso-ventral row. Genal field carries line of tubercles beneath eye like a row of beads, over rest anastomosing ridges. Ridges on lateral border in ranks oblique to margin, on spine in a series of forward-pointing chevrons.

Thorax incomplete, showing seven posterior segments, pleurae wider than axis, outer half downturned from small articulating process. Pleural tips minutely spinose. Pleural furrows not extending quite to tip. Anterior and posterior pleural bands may carry tubercles, as does axis.

Triangular pygidium about two-thirds as long as wide (excluding spine); angle enclosed by backward convergence of borders variable. Convex axis has three or four rings defined progressively fainter backwards; all carry tubercles in lines with raised lines additionally on terminal piece. Axis is set off from terminal spine by shallow furrow. Spine is presumed to be an extension of border, circular to oval cross section, length up to twice that of axis. Sculpture on spine of fine forward-pointing lines in chevron pattern. Anterior pleural

segment well-defined and interpleural furrow encroaches on border, pleural furrow deep. Posterior two segments progressively shorter, anterior pleural band of third segment only developed. Few tubercles on ribs of pleural field, anastomosing raised lines may be present on narrow, convex border.

Discussion. — As noted above this species falls between typical *Goniotelina* and *Acidiphorus* species. It differs from the type species of *Acidiphorus*, *A. spinifer* RAYMOND (WHITTINGTON 1965, Pl. 44, Figs. 3–16) especially in having a short preglabellar field, palpebral lobes further back, and the pygidial spine being clearly differentiated from the axis. The type species of *Goniotelina*, *G. williamsi* (Ross 1951, Pl. 14, Figs. 16–22, 25), resembles the new species in these same features, but has a parallel sided glabella with a deeply rounded anterior profile. Other *Goniotelina* species in HINTZE (1953) have similar glabellar form to *G. williamsi*. *G. brighti* resembles the Spitsbergen species most closely, but has finely granulate sculpture, strongly recurved genal spines, and only one segment clearly defined on the pygidial pleurae. The one described species with an intermediate set of characters like *A. ?ligo* is *Goniotelina hesperia* Ross 1967 (Pl. 6, Figs. 10–15) from the *Orthidiella* zone in Nevada. This species was described from small, and rather coarsely silicified specimens. They resemble *A. ?ligo* closely in the forward-expanding glabella, long, flat genal spines and acuminate cranidial border. The palpebral lobes are perhaps larger, but this may be accounted for by size difference, since during ontogeny the eyes of bathyurids become reduced in size (e.g. WHITTINGTON 1963, Pl. 11, Fig. 9). Ross (1967) states, however, that the surface of the glabella of *G. hesperia* is “not pustulose” and that the pygidial spine is “rooted in axis” rather than separated from the axis by a furrow as in *A. ?ligo*. These features would preclude identity of the Nevada and Spitsbergen species. It is possible that the small size and poor silicification of available material of *G. hesperia* is responsible for the supposed differences, and the discovery of larger and better preserved material of *G. hesperia* may establish the identity of the widely separated forms. The best recourse for the moment seems to be to establish *A. ?ligo* for our well-preserved material.

Bathyurine gen. et sp. indet
(Pl. 13, Figs. 10, 11)

Stratigraphic range. — Lower part of Olenidsletta Member early Arenig (V₁a).

Material. — Cranidium, PMO NF 2767; cephalon, PMO NF 3113.

Discussion. — This species is incompletely known, and without a pygidium cannot be certainly assigned to a genus. It is of interest as the only bathyurid found in the Olenidsletta Member, at the base presumably “carried over” from the facies of the underlying Kirtonryggen Formation. It is remarkable for its complete lack of surface sculpture except for parallel striae on the anterior border. This smoothness, and the deep border furrow recall *Strigigenalis* (see FORTEY, 1979, for a re-evaluation of this genus), but the broadly rounded, long glabella is significantly different from described species of that genus.

Subfamily BATHYURELLINAE HUPÉ 1953

Genus *Punka* FORTEY 1979

Type species. — *Bathyurellus nitidus* BILLINGS 1865

Discussion. — FORTEY (1979) redescribed the type species of *Bathyurellus*, *B. abruptus* BILLINGS, from the St George Group, western Newfoundland. This species proved to be very different from most of those assigned to *Bathyurellus* in the past, and for the reception of these the genus *Punka* was proposed. *Punka* species have wide cephalic borders and transverse pygidia often with a fan-like arrangement of furrows, but without the strongly concave border typical of *Uromystrum*.

Punka caecata n. sp.
(Pl. 14, Figs. 1–12)

1972 *Bathyurellus* sp. 4 Ross; p. 35, Figs. 13–16 (? non Fig. 20).

Stratigraphic range. — Profilbekken Member 50 m to 108 m from base. This species is one of the few identifiable from the uppermost part of the Valhallfonna Formation.

Material. — Holotype, incomplete cranidium: PMO NF 243; incomplete cranidia: PMO NF 131, 242, 1243 1255, 1887, 1974; pygidia: PMO NF 117, 136, 1227, 1393, 1948, 1950, 3112; free cheeks: PMO NF 1231, 3109, 29.

Diagnosis. — *Punka* with highly caecate preglabellar field and free cheeks (inside border). Preglabellar field long (sag.).

Description. — Cranidium convex (sag.) but this varies with size, and the most convex are the smallest. Glabella with maximum transverse convexity posteriorly, extends to about two-thirds cranial length in dorsal view, twice as long as wide, parallel sided or slightly tapering forwards to rounded but acuminate front. Smooth areas on side of glabella (Pl. 14, Fig. 7) homologous with glabellar furrows: 1P somewhat elongate and inclined backwards, 2P circular, opposite anterior end of palpebral lobes. Axial furrows uniformly deep around glabella. Occipital furrow shallower, especially laterally, where there may be another muscle insertion area. Palpebral lobes about one-third length of glabella, and with strongly curved outline, especially posteriorly. Postocular cheeks incompletely preserved, evidently narrow (exsag.) and long like other *Punka* species. Preocular cheeks slope down to merge with preglabellar field, gently convex. Preglabellar field long (sag.) but length less than that of border. Eye ridges present. Anterior border wide (sag.), gently downsloping and sharply demarcated from preglabellar field, flat to slightly concave. Sculpture on glabella of fine terrace ridges concentric with axial furrows, which break up into a fine honeycomb arrangement of ridges over the mid part. Prominent pitted caeca over preocular cheeks and preglabellar field. These stop abruptly at border which carries sparse, interrupted terrace ridges parallel to cranial

margin, 8–11 across border. Fine and crowded ridges on palpebral lobes. Anterior branches of facial sutures diverge at up to 60 degrees to sagittal line in dorsal view. Small cranidia (Pl. 14, Fig. 9) are more convex (sag.), with longer palpebral lobes, more vaulted glabella (trans.), and the caeca may be faint or absent.

Free cheek continues cranidial border towards short, triangular genal spine, where it rapidly narrows near genal angle. Eye a low and convex strip, lenses minute. Caeca (including principal genal vein) on convex genal field, extending on to proximal part of spine, where overlain by terrace ridges, but on inflated posterior part of spine they disappear. Terrace ridges continue from cranidial border on to lateral border, abruptly curving upwards over posterior lobe on genal spine.

Pygidium is probably correctly associated because it compares in abundance with cephalic parts, and shows a closely similar sculpture around its periphery to that on cephalic borders. Width about twice length, axis extends to somewhat more than half pygidial length. Axis tapers gently, broadly rounded posteriorly, with four axial rings of decreasing width (sag.) backwards, and almost semicircular terminal piece almost twice length of preceding ring. Pygidial ribbing deepest on slope to border fading out before margin. Anterior pygidial segment relatively clearly defined, distally elevated above pygidial border. Three posterior pairs of interpleural furrows slope progressively steeply backwards and widen on to inner part of border, faint or absent on dorsal surface of adaxial part of pleural fields. Pleural furrows distinct on first segment only. Internal mould (Pl. 14, Fig. 10) shows deeper furrows on flat, adaxial part of pleural fields including up to three pairs pleural furrows. Edge of the slope to border is marked by drop-like, inflated areas lying between first interpleural and second pleural furrows and between second interpleural and third pleural furrows. These inflated areas show only faintly on dorsal surface. Sparse terrace ridges on border subparallel to margin, discontinuous like those on cephalic border. More crowded ridges on adaxial part of pleural fields and mid-part of axis.

Discussion. — Apart from the relatively long (sag.) preglabellar field this species is typical of *Punka* as defined by FORTEY (1979). The type species, *P. nitida* (BILLINGS) (WHITTINGTON 1953, Pl. 67, Figs. 9, 13–15; 1963, Pl. 10, Figs. 8, 9, 11, 12, 14–17; Pl. 11, Figs. 1–12, 14, 15), has larger eyes, a down-sloping cephalic border, less distinctly furrowed pygidium, and some specimens at least have shorter genal spines. No other species that can be assigned to *Punka* has the highly caecate preglabellar area and free cheeks, which serves as the defining character of the new species. However, Ross (1972, p. 35, Pl. 15, Figs. 13–16) has described a cranidium (as *Bathyporellus* sp. 4) from the bioherm at Meiklejohn Peak, Nevada, which appears to be caecate like the Spitsbergen form, and has a preglabellar field that is “long for the genus”. The border of Ross’ specimen is broken off. The only difference is the tendency for the glabella to expand slightly in width near the forward end of the palpebral lobes in the Nevada specimen. The important shared characters between

the Spitsbergen form and the Nevada specimen are regarded as compelling evidence for their conspecificity. Ross (*ibid.* Pl. 15, Fig. 20) also figured a pygidium which he assigned to *Bathyuirellus* sp. 4, which differs in almost every detail from the one assigned to *Punka caecata* herein, and having well-developed pleural and interpleural furrows on the adaxial pleural fields, is unlike *Punka* pygidia in general. If the attribution is correct the Nevada species cannot be the same as the one from Spitsbergen, but it seems more probably incorrect. A pygidium like that of Ross is also present in the Spitsbergen fauna, and is recorded below under open nomenclature. The most plausible explanation is that a second, and probably new type of bathyuirelline occurs in both Spitsbergen and Nevada, the remains of which are fragmentary in both localities.

That this species is truly caecate (rather than merely having pitted sculpture) is shown by two features: the principal genal vein is present on the free cheek running from the middle of the eye towards the front part of the inflated posterolateral border; and on the inner part of this border terrace ridges clearly run over the top of the caeca, which are therefore connected with a ventral structure. Caecate bathyurids are otherwise unknown, and in this case the dorsal expression of caeca is evidently a derived rather than primitive character.

Bathyuirelline gen. et sp. indet.
(Pl. 15, Figs. 6, 7)

Stratigraphic range. — Profilbekken Member 68 m to 75 m from base (Whiterock, *Orthidiella* zone).

Material. — Fragmentary pygidia: PMO NF 123; cranidial fragment: PMO NF 1392.

Discussion. — A distinct bathyuirelline is found as fragmentary and allochthonous debris in the illaenid-cheirurid lenses in the upper part of the Profilbekken Member. The material is inadequate for determination. As remarked in the previous paragraphs, a pygidium of similar type was figured by Ross (1972, Pl. 15, Fig. 20) from the Meiklejohn bioherm, Nevada. The pygidium differs from those assigned to *Punka* species in having four pairs of deeply incised but almost straight pleural furrows on the adaxial part of the pleural fields. Interpleural furrows are weaker and hardly extend on to the border. The pygidial axis is longer (sag.) than in *Punka* due to an extended terminal piece. Excessively fragmentary cranidia (Pl. 15, Fig. 6) have been found in the same beds and may belong here, having fine lines on the dorsal surface like those on the pygidia. Little can be said about the cranidia except that the glabella was evidently somewhat acuminate medially and closely approached the cranidial border. The pygidium is distinctive enough to suggest that the species may not fit into existing bathyurid genera, but the problems of its affinities cannot be resolved here.

Family HARPEDIDAE HAWLE and CORDA 1847

Family name. — The name Harpidae HAWLE and CORDA 1847, is preoccupied by a molluscan family based on the genus *Harpa*. The name Harpetidae has been proposed as a replacement for the trilobite family name (*Bull. Zool. Nom.* 29, p. 2 and p. 108; 30, p. 3), a spelling suggested to avoid confusion with Harpididae WHITTINGTON 1950b. The name Harpedidae has been in use for a long time (see WHITTINGTON 1950b, p. 4), and the earliest use I can find of the name in this form is in SALTER 1864. I prefer to adopt this spelling as a translation from Harpides HAWLE and CORDA.

Genus *Scotoharpes* LAMONT 1948

Type species. — *Scotoharpes domina* LAMONT 1948.

Discussion. — NORFORD (1973) has redescribed the type species of *Scotoharpes*, and suggested that *Scotoharpes* should have priority over *Selenoharpes* WHITTINGTON. Characteristic features of *Scotoharpes* include a girder that "joins the inner rim some distance in front of the tip" (*ibid.* p. 14), genal caeca that extend on to the brim, and, adjacent to girder and rims, "single rows of pits coarser than those elsewhere on the brim". A species from Spitsbergen could be referred to *Scotoharpes* in the light of this diagnosis. Development of caeca on the brim varies considerably, even within a species (WHITTINGTON 1965, Pl. 9, Fig. 6). NORFORD gives *Scotoharpes excavatus* (LINNARSSON) as the oldest species of the genus. One as old or older is *Harpes cassinensis* WHITFIELD 1897, from the Fort Cassin Formation, Vermont.

Scotoharpes aduncus n. sp.
(Pl. 15, Figs. 1–5)

Stratigraphic range. — Profilbekken Member, 60 m to 75 m from base (Whiterock, *Orthidiella* zone).

Material. — Holotype, large cephalon incomplete on right side, PMO NF 1356; other cephalae: PMO NF 115, 148, 1230, 1254, 1262.

Diagnosis. — *Scotoharpes* with well-defined, large alae. Genal prolongations at least as long as cephalon (sag.) and distally curved inwards. Brim less than twice as wide (sag.) as length of prelabellar area to girder.

Description. — Full descriptions of *Scotoharpes* spp. have been given by WHITTINGTON (1963, 1965) and NORFORD (1973) and only salient points are given here. Cephalon of transverse width at occipital ring slightly less than twice sagittal length. Length of glabella in dorsal view exceeds length (sag.) of brim. Glabella tapers to rounded front, with one pair of glabellar furrows defining slightly inflated glabellar lobes. Occipital furrow deepest laterally; occipital tubercle present. Alae prominent and well-defined. Eye ridges directed outwards and slightly forwards to small eye tubercles. Genae slope downwards most steeply laterally, less so in front of glabella, downward slope

continues into inner half to two-thirds of fringe. Caeca prominent on cheeks, genal roll and fringe; a stronger vein enters the axial furrow between eye ridge and ala. Genal prolongations exceed sagittal length of cephalon on larger specimens, converging backwards, steeply inclined except at concave outer edge. Girder curves upwards to join inner rim near proximal end of genal prolongation. Small specimen (Pl. 15, Fig. 4) still shows prominent alae, but genal prolongations may have been shorter and not inward-curved.

Discussion. — The type species, as described by NORFORD (1973, Pl. 1, Figs. 1–3) differs from *S. aduncus* in the shorter genal prolongations, with the outer flattened part proportionately much wider. Silurian species of the genus have generally broader and flatter brims, with shorter genal prolongations, although *S. loma* (LANE 1972, Pl. 62, Figs. 1–9; NORFORD 1973, Pl. 3, Figs. 1–11) has a similar glabella and alae. Ordovician species from western Newfoundland include *S. vitilis* (WHITTINGTON) (1963, Pl. 2, Figs. 4–8, Pl. 3, Figs. 2–4, 6–11), *S. fragilis* (RAYMOND) (WHITTINGTON 1963, Pl. 1, Figs. 18–20) and *S. singularis* (WHITTINGTON) (1965, Pls. 8, 9). *S. singularis* is most similar to *S. aduncus* but with the brim twice the width (sag.) of the area between the front of the glabella and the girder, shorter genal prolongations, and the alae are not defined as prominent smooth areas. *S. cassinensis* (WHITFIELD 1897, Pl. 5, Figs. 3, 4) is alate, but its shorter genal prolongations are also less vertically elevated, and the brim is hardly caecate. Scandinavian and Estonian harpids are in need of revision, but as WHITTINGTON (1950b, p. 24) noted, *Harpes excavatus* LINNARSSON (1875, Pl. 5, Figs. 1–3; WHITTINGTON 1950a, Pl. 1, Figs. 1–3) is an early *Scotoharpes* (= *Selenoharpes*); this species also has a broader, forward-expanding brim and more poorly defined alae than *S. aduncus*. Similar differences apply to *Scotoharpes spasskii* (EICHWALD) (see SCHMIDT 1894, Pl. 5, Figs. 3–9; NEBEN and KREUGER 1971, Pl. 23, Fig. 16). ROSS (1972, Pl. 16, Fig. 8) has figured a fragmentary cephalon which is like smaller ones from Spitsbergen, except that the alae are described as “inconspicuous” (p. 36).

There is little known about intraspecific variation in these harpids and specific distinctions based on the shape or convexity of the brim should perhaps be viewed with caution. The prominent alae of the species from the Valhallfonna Formation, and the narrow brim produced into exceptionally long, and steeply sloping genal prolongations, set it apart from any other early species.

Family CHEIRURIDAE HAWLE and CORDA 1847
Subfamily CHEIRURINAE HAWLE and CORDA 1847
Genus *Sycophantia* n. gen.

Type species. — *Sycophantia seminosa* n. sp.

Diagnosis. — Resembling *Geraurinella*, but with quadrate glabella and broad, ledge-like anterior cranial border, small eyes in an anterior position, eye ridges bisecting forward part of fixed cheek. Pygidium with three pairs of spines and small median knob. Hypostoma with broad, rounded posterior border.

Discussion. — This genus is obviously allied to *Ceraurinella*, a medial Ordovician genus of wide distribution. *Ceraurinella* constitutes a rather compact group of species, united by similar cephalic characters, including eyes in a much more posterior position than is the case in *Sycophantia*. LANE (1971, p. 75) has suggested that the evolution of *Ceraurinella* was accompanied by progressive suppression of the posterior pygidial spines. In *Sycophantia* these spines are well-developed, and there is in addition a small, posteromedian knob. It seems probable that *Sycophantia* represents an early stage in the evolution of the *Ceraurinella* group, in which the eyes were still in a forward position, resulting in very wide (exsag.) postocular cheeks, the cranial border was well-defined, and with a well-segmented pygidium. The quadrate glabella and ledge-like anterior border are other notable features of the new genus. *Ceraurinella polydorus* (BILLINGS 1865) from a slightly younger horizon in the Middle Table Head Formation, western Newfoundland (WHITTINGTON 1965), is similar to the Spitsbergen species in these cephalic characters, but in all other respects is a typical *Ceraurinella*.

To include *Sycophantia* within an extended concept of *Ceraurinella* would have the advantage of making the phylogenetic suggestions above implicit in the classification. On the other hand the morphology of *S. seminosa* differs in several important features from the closely knit *Ceraurinella* group, and it seems preferable to regard the differences as indicating separate generic rank. Discovery of other species of *Sycophantia* might be anticipated in shallow water limestones of Arenigian age.

Sycophantia seminosa n. gen., n. sp.
(Pl. 16, Figs. 1–11)

Stratigraphic range. — Upper part of Profilbekken Member 45 m to 70 m from base, V₄b, Whiterock (*Orthidiella* zone).

Material. — Holotype, cranidium, PM● NF 125; cranidia: PM● NF 120, 113, SMA 84384; pygidia: PM● NF 128, 140; hypostomata: PM● NF 145, 3192–3.

Diagnosis. — As this is the only described species of *Sycophantia* the diagnosis follows that of the genus given above.

Description. — The species is known from well-preserved material, but the exoskeleton tends to flake off during preparation, and so much of the material is internal. Cephalic convexity is not great for a cheirurid, but glabella deeply vaulted about mid-line. Width of cranidium at posterior border slightly more than twice sagittal length. Glabella occupies only about one-quarter cranial width (excluding spines), rectangular, length two-thirds width. The anterior margin of the glabella is transverse, slightly indented medially on some specimens, anterolateral corners rounded. Three pairs of glabellar furrows extend less than one-third across the glabella in dorsal view, length (exsag.) of glabellar lobes along axial furrows subequal. IP is deepest and slopes back

most strongly, faint backward extension extending to occipital furrow and cutting off basal lobes. 2P and 3P narrow, sloping gently inwards and backwards. Occipital ring occupying about one-sixth glabellar length, minute median tubercle; occipital furrow deeper and wider laterally, median narrowing produced by forward expansion of occipital ring.

Anterior cranial border outlined by deep preglabellar furrow, narrowest in front of glabella, laterally widening rapidly to form a flat ledge in front of the preocular cheeks. Palpebral lobes short, about one-sixth of glabella, situated opposite 3P glabellar lobes, distance from glabella (tr.) equal to about one-third glabellar width. Deep, straight palpebral furrows, outline crescentic, upward-tilted palpebral lobes, which pass into conspicuous eye ridges which run inwards and forwards to bisect the preocular fixed cheeks, terminating at the outer end of 3P. Strongly defined, smooth lateral and posterior borders expand in width towards the genal angle, the latter downward-deflexed beyond point of articulation with anterior thoracic segment at about two-thirds transverse width. Slight median forward bend in posterior border furrow. Powerful genal spines blade-like, flattened in dorso-ventral plane, extending (exsag.) to length somewhat less than that of glabella (sag.) Anterior sections of the facial sutures diverge slightly backwards, behind the eyes curving outwards and slightly forwards, making a right angle with anterior branches, and meeting the lateral cranial borders at an obtuse angle.

Sculpture on cheeks of a strong network of raised ridges which are reflected on internal moulds. On the ridges, and in the pits between some of them, are small round tubercles, which are not seen on the internal moulds. Sculpture on glabella of finer granules. On internal moulds (Pl. 16, Fig. 4) pits on the forward part of the glabella may represent the insertion points of cephalic (?oesophagal) muscles.

Hypostoma (Pl. 16, Fig. 6) occurs in a bed with numerous cranidia of this species (and without other cheirurids) and is associated with confidence. Middle body about three-quarters as wide as long, tapering posteriorly to a point, widest near anterior margin, which is bowed gently forwards. Convexity is greatest anteriorly, where the middle body overhangs the lateral borders. Middle furrows short and shallow, sloping inwards and backwards, outer ends at about two-thirds length of middle body. Borders wide and flat around much of the middle body, narrowing rapidly anteriorly, posterior margin rounded-acuminate. Border furrows shallower where joined by the furrows on the middle body. Surface sculpture on hypostoma like that on dorsal surface, discrete small tubercles, which, however, are absent on the middle body posterior to the furrows thereon. Tubercles are also coarser anteriorly and medially on middle body.

Pygidium with three pairs of spines and a small median knob. Outermost pair of spines much the longest, twice the (sag.) length of the pygidium, diverging outwards at first, distally curving gently adaxially. Two inner pairs of spines short, and about equal in length. Pygidial axis shows three pairs of axial rings, of progressively less width (tr.) posteriorly, with a small terminal piece passing into the median protuberance. Furrow between first and second

pygidial spines deeper adaxially; anterior spine is bisected proximally by a short furrow. Pygidial doublure with V-shaped outline (Pl. 16, Fig. 5), forming a raised bar with a posteromedian embayment.

Discussion. — *S. seminosa* is the only species which can be definitely referred to the genus. A pygidium from the early Middle Ordovician of Nevada figured by Ross (1967, Pl. 7, Fig. 32) may be referable to the new genus.

An additional distinction from *Ceraurinella* is also worth noting: hypostomata of species of that genus (e.g. WHITTINGTON and EVITT 1954, Pl. 11, Figs. 8, 14; SHAW 1968, Pl. 15, Fig. 27; CHATTERTON and LUDVIGSEN 1976, Pl. 8, Figs. 28, 31, 38, Pl. 9, Figs. 20, 22) have short (sag.) and truncate posterior borders. If the hypostoma illustrated here (Pl. 16, Figs. 3, 6) is correctly assigned to *Sycophantia*, its broad and rounded posterior border is probably of generic significance. The middle furrows are also shallower than is the case in *Ceraurinella* and the posterior lobe is smooth rather than granulate.

Subfamily PILEKIINAE SDZUY 1955

Genus *Parapilekia* KOBAYASHI 1934

Type species. — *Calymene* ? *speciosa* DALMAN 1827.

Discussion. — SDZUY (1955) and LANE (1971) regarded *Parapilekia* as a junior subjective synonym of *Pilekia* BARTON, but other authors (DESTOMBES 1970; HAMMANN 1971) have accepted its validity. Examination of the type and other species of *Pilekia* shows that this genus should be discriminated from *Parapilekia* on the basis of its tumid and expanded glabellar lobes, and anterior glabellar taper. This gives the cranidium an almost sphaerexochinid appearance. As thus limited *Pilekia* is confined to the North American craton and the Canadian Series, *Parapilekia* includes species with subquadrate glabella, generalised cheiruracean glabellar furrows similar to those of its pliomerid contemporaries, and four pairs of pygidial spines, like *Pilekia*. *Anacheirus* and *Metapilekia* both have three pairs of pygidial spines. Early species of *Parapilekia* show a bicomposite or branching 3P glabellar furrow, for example, *P. anxia* (SDZUY 1955). The anterior branch in this case represents a remnant of the 4P glabellar furrow, and presumably the primitive condition for the Cheiruracea. In *Parapilekia* ? *discreta* (see SDZUY 1955, Pl. 8, Fig. 16a) this fourth furrow is still separate from the third. A similar case is described elsewhere in this paper referring to early cybelines (p. 97).

Parapilekia includes the following species: *P. speciosa* (DALMAN), *P. bohémica* (RUŽICKA 1926), *P. olesnaensis* (RUŽICKA 1934), *P. anxia* (SDZUY 1955), *P. sougyi* DESTOMBES 1970, *P. afghanensis* (WOLFART 1970), *P. acetae* HAMMANN 1971, *P. jacquelinae* n. sp. and, more doubtfully, *P. discreta* (BARRANDE 1868). Two cranidia closely similar to *P. jacquelinae* have been figured by ROSS (1958, Pl. 84, Figs. 9, 10) from a pillow lava of early Ordovician age in Nevada.

P. jacquelinae occurs in the Profilbekken Member in beds which are probably of youngest Arenig age. It is the youngest known pilekiine. The geological

range of *Parapilekia* is thus a long one, spanning the Tremadoc and Arenig, with the type species lying at the centre, both morphologically and stratigraphically. *P. jacquelinae* differs from the older species mainly in having the eyes further from the glabella, and in a slightly more posterior position than *P. speciosa*, and in having fewer pygidial axial rings, but there is nothing to suggest that these should be regarded as of more than specific importance. The little known genus *Macrogrammus* WHITTARD (WHITTARD 1966, Pl. 49, Figs. 9, 10; LANE 1971, Pl. 7, Fig. 21) differs significantly from the Spitsbergen *Parapilekia* only in the even more posterior position of the palpebral lobes. LANE (1971) regarded *Macrogrammus* as a cheirurine, and the question of its affinities cannot really be resolved without the discovery of its pygidium.

Parapilekia jacquelinae n. sp.
(Pl. 17, Figs. 1-6)

Stratigraphic range. — Lower part of Profilbekken Member, V₄a, 20 m to 23 m, Valhallan, probably latest Arenig.

Material. — Holotype, cranidium, PMO NF 200; Cranidia: PMO NF 252, 292, 309, 1090; Pygidium: PMO NF 286.

Diagnosis. — *Parapilekia* with palpebral lobes far removed from glabella, opposite glabellar furrow 2P. Surface sculpture on glabella of coarse, scattered tubercles. Pygidial axis with four axial rings and minute terminal piece; slender pygidial spines posteriorly directed.

Description. — This distinctive species is the youngest pilekiine known. Excluding genal spines cranidium more than twice as wide as long (sag.), glabella of rather low transverse convexity, much of the cranidial convexity deriving from sharp downward turn of postocular cheeks. Glabella subsquare in front of occipital ring, length including occipital ring about 1.2 times maximum width at basal glabellar lobes. This width is rapidly attained in front of the occipital ring, only a slight taper anteriorly. Three pairs of deep glabellar furrows extend more than one-third across glabella; inner ends of 1P shallow abruptly, curve backwards parallel to sag. line, cutting off slightly inflated basal glabellar lobe. One specimen (Pl. 17, Fig. 4) shows a pathological effacement of this glabellar furrow abaxially. Truncate forward margin of glabella with slight median indentation and smooth area running sagittally backwards therefrom. Distinct platform-like anterior cranidial border widest exsag. and slightly downward curved laterally. Prominent eye ridge defined by deep furrow along anterior edge running outwards not quite at right angle to sag. line, total length about two-thirds that of adjacent glabella. Uprturned palpebral lobes opposite 2P glabellar furrow and anterior part of 2P glabellar lobe. Length (exsag.) of cheeks behind palpebral lobes half (sag.) length of glabella. Posterior border narrow, adaxially equal to width of posterior border furrow (exsag.), slightly wider laterally where curved very slightly forwards. Genal spine long and flattened, directed outwards. Surface sculpture on

glabella of scattered tubercles of variable size. Similar tubercles are present on the raised ridges between the reticulum on the fixed cheeks. Finer granules on anterior border and eye ridges.

Pygidium with pleural fields almost flat, axis of decreasing convexity posteriorly. Latter occupies about one-quarter total pygidial width anteriorly, tapers slightly to blunt posterior extremity. Four axial rings and minute, tubercle-like terminal piece. Ring furrows between first and second, and second and third axial rings conspicuously wider medially, representing the homologues of the thoracic articulating half rings. Slender, pointed pygidial spines all curved backwards distally, transverse adaxial part on first two pleural bands. Interpleural furrow shallowing abruptly abaxially between second and third spines.

Discussion. — Species here regarded as belonging to *Parapilekia* have been discussed above. *P. jacquelinae* differs from the type species *P. speciosa* (MØRBERG and SEGERBERG 1906, Pl. 7, Figs. 15–17) in the eyes being further from the glabella and slightly further back, in the relatively great (trans.) width of the anterior cranial border, and in the short pygidial axis with no more than four axial rings. Similar differences apply to other Tremadocian *Parapilekia*, although *P. afghanensis* (WOLFART 1970, Pl. 15, Figs. 5, 6) has a similar abbreviated pygidial axis.

Closely similar cranidia, possibly conspecific, have been figured as ‘unidentified proparian species’ by Ross (1958, Pl. 84, Figs. 9, 10). These occur in a pillow lava of extra-cratonic origin in Nevada of “Late Tremadoc or pre-Llandeilo age”. If this specific identity is correct it would seem that the fauna is of latest Arenig (Valhallan) age. *Parapilekia* is accompanied there by a pliomerid that resembles *Europeites hyperboreus* from a similar part of the Valhallfonna Formation to *P. jacquelinae*. On the other hand another species in the same fauna is a *Benthamaspis* close to *B. conica* FORTEY 1979, which is from an early Arenig horizon in Newfoundland.

Parapilekia jacquelinae is the only cheirurid definitely associated with the nileid facies in Spitsbergen, and, like *Europeites hyperboreus* n. sp., is related to forms from the Ceratopyge Limestone of Scandinavia rather than the shelf faunas of the North American plate.

Subfamily SPHAEREXOCHINAE ÖPIK 1937

Genus *Kawina* BARTON 1913

Type species. — *Cheirurus vulcanus* BILLINGS 1865.

Kawina wilsoni Ross 1972

(Pl. 18, Figs. 1, 3, 4, 7)

Stratigraphic range. — Profilbekken Member (V₄b, *Orthidiella* zone, early Whiterock) 50 m to 75 m from base of Member.

Material. — Cranidia: PMO NF 146, 1267; pygidia: PMO NF 137, 1249, 1394.

Discussion. — This species was described by Ross (1972, p. 38–39, Pl. 17, Figs. 1–16) from the bioherm at Meiklejohn Peak, Nevada. The material from Spitsbergen agrees closely with Ross' description. In particular Ross describes the surface sculpture as "very finely granular with widely scattered large pustules". The material illustrated here shows an exactly similar sort of surface sculpture on pygidium and cranidium. Because other *Kawina* species, including those from the Valhallfonna Formation, vary widely in the coarseness and density of exoskeletal tuberculation, the similarity of the sculptural pattern of the present material and that from Nevada is regarded as a good indication of specific identity. Our most complete cranidium (Pl. 18, Figs. 1, 3) is slightly crushed anteriorly, but the right lateral profile is probably not greatly distorted, and shows that the Spitsbergen specimen is somewhat less convex across the basal glabellar lobes, so that the upward bulge of the glabella in front of the occipital ring is less pronounced. Ross describes the pygidial axial furrows as enclosing an angle of approximately 60°. On our material this angle is obviously obtuse, but the Nevada specimen illustrated by Ross (*ibid.* Pl. 17, Fig. 4) is similar or even more obtuse, and it is therefore concluded that the axial taper in the species was subject to intraspecific variation. The other two species of *Kawina* from the Profilbekken Member are both characterised by denser and coarser dorsal tuberculation. An unnamed pygidium figured by WHITTINGTON (1965, Pl. 62, Figs. 5, 7) from the Lower Table Head Formation, Western Newfoundland, is also granulate, but instead of having scattered tubercles, as in *K. wilsoni*, the granulation is interrupted by smooth, oval areas. Differences from other described species have been summarized by Ross (1972).

Kawina? sp. aff. *K. sexapugia* Ross 1951
(Pl. 18, Figs. 10, 11)

Stratigraphic range. — Olenidsletta Member, 75 m from base (Middle Arenig).

Material. — One cranidium PMO NF 245.

Discussion. — A single small cranidium from the Olenidsletta Member is not enough for precise determination. Among early cheirurids it can only be compared with *Kawina sexapugia* Ross 1951, from a zone J horizon in Utah and Nevada. Like that species the eyes are far further forward than in any later species attributed to *Kawina*, and it has broad (trans.) postocular fixed cheeks equipped with stout, laterally directed genal spines. Several minor differences from *K. sexapugia* are noted: the 1P glabellar furrows of the Spitsbergen specimen are evenly backward-curved where the same furrow on *K. sexapugia* is nearly straight, and the latter has a finely granulate sculpture on the fixed cheeks where our species has the rather coarse genal reticulum found on many cheirurids. *Kawina? webbi* HINZE 1953, from a similar horizon to *K. sexapugia* is less like the Spitsbergen species, having an elongate and tumid glabella with poorly defined glabellar furrows.

WHITTINGTON (1965, p. 411) and LANE (1971, p. 79) have suggested that *K. sexapugia* is different enough from later sphaerexochindids to be generically distinct from *Kawina* and the allied genera *Cydonocephalus* and *Xystocrania*. The cranidium from Spitsbergen may belong within the same genus, but the material is inadequate to clarify the relationships of these early Sphaerexochinae.

Kawina sp. A
(Pl. 18, Figs. 6, 8, 9, 12)

Stratigraphic range. — Profilbekken Member, 60 to 68 m from base (White-rock, high *Orthidiella* zone).

Material. — Cranidium, PMO NF 1250 (incomplete); pygidium: PM● NF 1258.

Discussion. — Although this seems to be a new species, the few specimens available and their fragmentary nature makes the use of open nomenclature advisable. Cranidium and pygidium are associated because they both carry a crowded tuberculate unlike that of *K. wilsoni* above. On the cranidium the maximum glabellar convexity occurs in front of the 1P glabellar lobes; this was used by WHITTINGTON (1963, p. 97) as a discriminating character of *Cydonocephalus*, to which the present species might therefore be referred. However, the degree of inflation of the glabella across the basal glabellar lobes seem to vary widely in *Kawina*/*Cydonocephalus*, and as a generic character glabellar convexity is not entirely satisfactory. The pygidium of our species is like those attributed to *Kawina* species, and because the pygidium of *Cydonocephalus* is not known, it seems preferable to refer the new form to *Kawina* for the present. The cranidium compares most closely with those of *Cydonocephalus griphus* WHITTINGTON 1963 and *C. torulus* WHITTINGTON 1963, from the Lower Head boulder, Western Newfoundland, both of which have a tuberculate surface sculpture, but differs from both in the relatively low transverse convexity across the 1P glabellar lobes. The 1P glabellar furrow of the Spitsbergen species has a sharp backward turn at its inner end and is not conspicuously sigmoidal, both the Newfoundland species having sigmoidal 1P furrows that curve backwards in a uniform arc towards the occipital furrow. The pygidium differs from that of *Kawina wilsoni* in the sculpture, and in the more widely splayed pygidial spines, but resembles that of *K. wilsoni* more than any other described species. *K. arnoldi* WHITTINGTON 1963 (Pl. 27, Figs. 2, 8) has a long terminal piece, and none of the unassigned pygidia figured by WHITTINGTON (1963, Pl. 31, Figs. 1–17, 19, 20) from the Lower Head boulder are closely similar to the present form. *Kawina divergens* REED 1945 (see LANE 1971, p. 57) from the Arenigian Tourmakeady Limestone of western Eire, is the only species with more widely splayed pygidial spines than *Kawina* sp. A, and has a large terminal piece and is not tuberculate. Both *Kawina* sp. A and *K. divergens* retain a proximal remnant of the pleural furrows on the anterior pygidial pleural spines.

Kawina sp. B
(Pl. 17, Figs. 7, 8)

Stratigraphic range. — From first Illaenid-cheirurid lens in the Profilbekken Member, 42 m from base (Whiterock, *Orthidiella* zone).

Material. — One pygidium, PMO NF 317.

Discussion. — This species is known from a single example of a pygidium. As was the case for *Kawina* sp. A it differs from all described species but cannot be formally named without further material. The surface sculpture is distinctive, consisting of a fine ground of granules with very large, flat-topped smooth tubercles much larger and more closely spaced than in *K. wilsoni*. This sculpture distinguishes *K. sp. B* from all other *Kawina* or *Cydonocephalus* species, indeed, it is probably coarser than on any other early sphaerexochinid.

Genus *Cydonocephalus* WHITTINGTON 1963

Type species. — *Cydonocephalus griphus* WHITTINGTON 1963.

Cydonocephalus sp. A
(Pl. 18, Figs. 13, 14)

Stratigraphic range. — Olenidsletta Member, V_{4a}, about 90 m from base of Member (middle Arenig).

Material. — Cranidium, PMO NF 244.

Discussion. — This cranidium records the rare occurrence of a cheirurid within the Nileid community of the Olenidsletta Member. It is an internal mould, which carries no indication of dorsal sculpture, which is unlikely to have been more than finely granulate. Since the maximum convexity of the glabella lies in front of the basal glabellar lobes it conforms to *Cydonocephalus* rather than *Kawina* (but see *Kawina* sp. A above). Of the six species of *Cydonocephalus* described by WHITTINGTON (1963) from the Lower Head boulder, western Newfoundland, *C. sp. A* compares most closely with *C. prolificus* (BILLINGS 1865), which has a subdued sculpture and a lesser degree of glabellar inflation compared with other species of the genus. *C. sp. A* differs from *C. prolificus* and all the other species from Newfoundland in the forward position of the palpebral lobes opposite the 2P glabellar furrows. The evolution of several early groups of cheirurids seems to have been accompanied by a backward migration of the eyes (see *Sycophantia*, p. 78) and *Cydonocephalus* sp. A is probably another example of an early representative of the group with eyes in an advanced position.

Genus *Kolymella* CHUGAEVA 1973

Type species. — *Kawina plana* CHUGAEVA 1964.

Kolymella ? sp. indet.
(Pl. 18, Figs. 2, 5)

Stratigraphic range. — Profilbekken Member, 42 m from base.

Material. — Fragmentary cranidium PMO NF 246.

Discussion. — This fragmentary specimen is attributed with question to *Kolymella*, because of the exceptionally low convexity of the glabella (sag., trans.) particularly across the basal lobes, in which it resembles the type species, *K. plana* (CHUGAEVA 1964, Pl. 4, Figs. 2, 3; 1973, Pl. 10, Figs. 1–7). The strongly curved 1P glabellar furrow is more like that of *Kawina* or *Cydonocephalus*, however, and the attribution to the Siberian genus must therefore be tentative.

Family PLIOMERIDAE RAYMOND 1913
Subfamily PLIOMERINAE RAYMOND 1913
Genus *Europeites* BALASHOVA 1966

Type species. — *Cyrtometopus primigenus lamanskii* SCHMIDT 1907.

Remarks. — *Europeites* was originally proposed as a subgenus of *Pliomeroides* HARRINGTON and LEANZA 1957. Discovery of the new species from Spitsbergen suggests that it may now properly be regarded as of generic rank. This is more fully discussed after the description of *Europeites hyperboreus* n. sp. below.

Europeites hyperboreus n. sp.
(Pl. 19, Figs. 1–8; Pl. 20, Figs. 1–8)

1973 *Europeites* sp. FORTEY and BRUTON, p. 2235 (in error).

Stratigraphic range. — Almost throughout the Profilbekken Member, V₄a–b 3 m to 70 m extending from upper Valhallan to Whiterock.

Material. — Holotype, cranidium, PMO 1102; among abundant further material are cranidia: PMO NF 163–4, 329, 1104, 1107, 1269, 2456, 3194, SMA 84370–3; pygidia: PMO NF 1106, 1109, 1110, 1369b, 2406, SMA 84374–7; free cheeks: PMO NF 1108, 3195, 185; hypostomata: PMO NF 1103, 1105.

Diagnosis. — *Europeites* species with glabella rounded anteriorly; 3P glabellar furrow sigmoidal or distally terminating in a pit. Pygidium with rounded spines, terminal piece with a pair of pits on internal mould. Surface sculpture of minute granules.

Description. — One imperfect articulated exoskeleton (PMO NF 1248) shows that this species has the elongate form characteristic of the Pliomeridae and reached a length of about 12 cm. Cranidium of low convexity, with only the postocular cheeks steeply downward deflexed, glabella barely elevated above

cheeks. Glabella occupies between 0.25 and 0.30 maximum cranial width at occipital ring, expanding in width gently forward to maximum at 3P glabella lobes, broadly rounded anteriorly. Glabellar furrows deep, especially the posterior two pairs, extending more than one-third across glabella. 1P curves backwards, particularly at its inner end, where it is deepened, but does not reach occipital furrow. 2P almost transverse except for backward curve at inner end, sited at midlength of preoccipital glabella. 3P sloping inwards and backwards, directed towards anterolateral corner of glabella, and exhibiting variation in form. It is generally gently sigmoidal, but on larger crania the outer end, which invariably does not reach the preglabellar furrow, is deepened into a pit (Pl. 19, Fig. 3). On the largest crania this pit may become altogether detached from the rest of the furrow, giving the appearance of a fourth glabellar furrow. The exoskeleton of this species is remarkably thick, and generally flakes off, for good dorsal surfaces we have had to rely on silicified specimens. However, the form of the glabellar furrows on internal surface apparently matches that on the exterior. Occipital furrow deepest laterally, arched forwards medially. Occipital ring one-fifth or less total glabellar length, with small median tubercle visible on internal moulds, representing a site of thinning of the dorsal exoskeleton.

Axial furrows deep and narrow, further deepened near anterolateral corners of glabella to apodemes; preglabellar furrow deepened medially, where it indents the frontal glabellar lobe. Convex anterior border with vertical anterior "wall", bowed gently forwards medially, widest opposite forward continuation of axial furrows. Preocular cheeks slope downwards and forwards, more or less bisected by prominent eye ridges. Palpebral lobes far back opposite outer ends of 1P glabellar furrows, semicircular and upward-tilted. Postocular cheeks slope downwards laterally, and the adjacent posterior border flattens and expands in width here, passing without a break into short section of lateral border of similar width. Minute genal spine on smaller cranium (Pl. 20, Fig. 4). Anterior branches of facial sutures diverge slightly backwards behind the eyes swinging forwards again.

Surface sculpture on glabella and anterior border of minute granules. Similar granules cover the fixed cheeks, which are additionally pitted. The pits do not extend on to the eye ridges, nor on to the perimeter of the cheeks adjacent to the axial and border furrows. The pits, but not the granules, are reflected on the internal mould, especially anteriorly. Internal mould of glabella shows scattered, fine pits representing needle-like invaginations of the exoskeleton.

Free cheeks carry a similar sculpture to that on the fixed cheeks. Border widens anteriorly, and slopes more steeply outwards.

Hypostoma of maximum transverse width at anterior margin slightly exceeding sag. length. Egg-shaped middle body widest and most convex anteriorly. Short, lateral, middle furrows hardly defined, at about three-quarters sag. length of middle body. The internal surface of the middle body carries numerous scattered thickened areas which show as depressions on the internal mould. These may be the sites of muscle attachments connected with the

support and dilation of the oesophagus. Anterior wings wide (tr.), triangular, steeply downsloping, invaginated into extremely deep apodemes which project anteriorly near lateral margins. Narrow anterior border which is bowed forwards. Lateral borders narrowest and steeply inward-sloping anteriorly, flattening out posteriorly. Margin carries three pairs of angulations (Pl. 20, Fig. 6), and the posterior tip is also acute. Border furrow shallow posteriorly, deepened anteriorly into apodemes adjacent to mid-part (sag.) of middle body. Sculpture on borders of granules like dorsal exoskeleton; posterior part of middle body smooth.

Thoracic segments long and narrow, at least 12 on complete specimen. Axis narrower than pleurae in dorsal view, which are turned down strongly distally at about half their length. Posterior pleural band convex, more than twice as wide as anterior band (exsag.), pleural furrows deep. Posterior aspect (of PMO NF 162) shows narrow articulating groove extending on to proximal portion of downturned part of pleura.

Pygidium about one and a half times as wide as long, peripherally steeply downsloping. Axis occupies about one-third total pygidial width anteriorly, tapering and progressively less convex posteriorly, axial furrows enclosing an angle of 20–30 degrees. Ring furrows deep, especially laterally, defining five axial rings curving gently forwards medially. Articulating half ring prominent, about half (sag.) length of anterior axial ring. Long terminal piece one-third axial length acutely pointed posteriorly, showing a deep pair of pits on the internal mould. On some specimens the pits are united within a horseshoe-shaped depression, and the sides of the terminal piece may be slightly concave. The only dorsal surface available (Pl. 20, Fig. 5) shows a single transverse depression in the terminal piece. Pleural ribs terminate in rounded spines; smaller specimens somewhat more pointed. Adaxial part of anterior rib horizontal, transverse, distally curving downwards and backwards; this rib widest medially, separated by a deep furrow from narrow anterior border. Adaxial horizontal part decreases progressively backwards, so that the posterior pair of ribs are subparallel to the sag. line. In posterior view this pair of ribs does not extend as far ventrally as other pairs. Narrow strip of doublure (Pl. 19, Fig. 4) connects ribs inside free ends, and carries a prominent, median ventrally-projecting ridge. It is presumed that during enrollment this ridge engaged with the anterior cranial border leaving the free edges of the pygidial spines projecting above the cranial margin. Dorsal surface of pygidial axis is granulate like the glabella, abaxial parts of ribs smooth. Internal moulds show obscure depressions along middle of ribs.

Discussion. — The type species of *Europeites*, *E. primigenus lamanskii* (SCHMIDT 1907, Pl. 1, Fig. 3) is not fully known. The available cranidia of the subspecies have been re-illustrated by BALASHOVA (1966, Pl. 1, Figs. 3–6), but the pygidium never seems to have been discovered. Nor has ANGELIN's species *Pliomera primigena* been redescribed in recent years. ANGELIN's (1854, Pl. 41, Fig. 15) illustration is of a pygidium which shows acutely pointed pygidial spines, and a triangular axial terminal piece with a distinct 'dimple'. MÖBERG

and SEGERBERG (1906, Pl. 7, Figs. 13, 14) give a good drawing of a pygidium of similar type, here associated with a cranidium. Both pygidium and cranidium suggest that the Spitsbergen species should be referred to the same genus: the palpebral lobes are in a similar somewhat posterior position, with the eye ridges bisecting the preocular fixed cheeks, glabellar furrows are similar, and the pygidium of our species has a terminal piece on the axis with a comparable, often horseshoe-shaped depression. Examination of material referred to "*Cyrtom'opus*" *primigenus* from the Ceratopyge limestone of the Oslo region has confirmed the assignment. Cranidia there include specimens in which the 3P glabellar furrow does not quite extend to the axial furrow, as in the Spitsbergen form. Posterior pleural bands are developed on the pygidia of the Oslo specimens, a primitive character which can be matched on early cybelines, and which are almost obsolete on the later species from the Valhallfonna Formation. NEBEN and KREUGER (1971, Pl. 1, Fig. 22) illustrate a cranidium of *primigenus* type from erratic material, on which the 3P glabellar furrow is isolated within the glabella, but the pygidium (*ibid.* Fig. 24) associated with the cranidium by them lacks the typical terminal piece of the species, and probably belongs to another pliomerid. On the subspecies *E. primigenus lamanskii* both 3P and 2P are isolated from the axial furrow, and the palpebral lobes are larger and further back than in ANGELIN's subspecies. It is unfortunate that BALASHOVA nominated this subspecies as type of the genus, because of the incomplete information on the pygidium. The new species from Spitsbergen is certainly congeneric with *E. primigenus primigenus*, and should therefore be referred to *Europeites*.

Pliomeroides is another incompletely understood genus, known only from its Argentine type species, *P. deferrariisi* (HARRINGTON) (see HARRINGTON and LEANZA, 1957, Figs. 120, 121, 2a-c). The cranidium (in HARRINGTON and LEANZA's reconstruction) has a tapering glabella and long genal sinues, and the pygidium (HARRINGTON in MOORE 1959, p. 443) does not have the characteristic axial structure of *Europeites*. These features are considered sufficient to justify separate generic status for *Europeites*.

Europeites hyperboreus is of particular interest because, with *Parapilekia jacquelinae*, it shows affinities with species of the Upper Tremadocian Ceratopyge Limestone of Scandinavia. Like *P. jacquelinae* it is abundant in the Nileid community type of the Profilbekken Member, and serves to confirm the similarities of this facies fauna with that of the Asaphid Province.

Genus *Pliomerops* RAYMOND 1905

Type species. — *Amphion canadensis* BILLINGS 1859.

Pliomerops praematura n. sp.
(Pl. 21, Figs. 7-15)

Stratigraphic range. — Profilbekken Member 46 m to 65 m from base, V₄b, Whiterock (*Orthidiella* zone).

Material. — Holotype, cranidium, PMO NF 1120; cranidia: PMO NF 1121–2; pygidium: PMO NF 1198; hypostoma probably referable here: PMO NF 1129.

Diagnosis. — *Pliomerops* with convex anterior border distinctly set off from glabella; 3P glabellar furrow deep, straight. Eyes opposite glabellar lobe 2P. Hypostoma with anterior boss on middle body.

Description. — This species does not approach the large size of *Europeites hyperboreus*, largest cranidia sagittal length about 1 cm. Cranidium about twice as wide as long, lateral genal areas steeply inclined downwards. Glabella flat-topped, about eight-tenths as wide as long, front margin rounded to truncate about mid-line. Glabellar furrows very deep, both on dorsal surface and internal mould, all three pairs sloping inwards and backwards at about 80 degrees to sag. line (3P subtending a more acute angle on larger cranidia). Of glabellar lobes 1P is the smallest (exsag.) Furrow 3P directed towards anterolateral corner of glabella, closely approaching preglabellar furrow but not joining it. Axial furrows of great depth; preglabellar furrow deepening greatly laterally into apodemes opposite outer ends of 3P glabellar furrows. Anterior cranial border not completely preserved on available material, convex and bowed strongly forwards medially. Preocular fixed cheeks widening backwards, crossed by strong eye ridges near forward margin. Palpebral furrow deep, palpebral lobe with forward limit opposite 2P glabellar furrow, and hind limit not reaching back as far as 1P. Deep posterior border furrow curves forwards rapidly into lateral border furrow abaxially; posterior border widens laterally. Coarse reticulum on cheeks; fragments of cuticle adhering to glabella show rather scattered, pointed granules.

Hypostoma is attributed to this species because it resembles that of *P. canadensis* (BILLINGS) figured by SHAW (1968, Pl. 2, Figs. 1, 2), has coarse granules on the middle body like those on the glabella, and differs from that of the other possibility, *Ectenonotus* (Ross 1967, Pl. 8, Fig. 14). Oval middle body three-fifths as wide as long, most convex (tr.) medially, but projecting backwards anteriorly to overhang the anterior border (somewhat as the rhynchos of encrinurids). Middle furrows not defined or represented by obscure depressions far posteriorly. Anterior wings narrow (tr.) and steeply down-sloping, passing into anterior border which is very narrow medially. Lateral border furrows deepest medially, furrow shallow around end of middle body. Lateral borders follow outline of middle body, converging gently backwards, widening posteriorly; prominent posteromedian point. Granules on border finer and more crowded than those on middle body (posterior part of middle body smooth). Internal surface of middle body irregularly pitted.

Pygidium known from a single example, not as well-preserved as cranidia, highly convex, about two-thirds as wide as long, distal parts of ribs forming a steep posterior wall. Ribs remain in contact until almost at tips. Posterior pair enclose terminal piece, which is not clearly preserved but evidently nearly an equilateral triangle.

Discussion. — The types species of *Pliomerops*, *P. canadensis* (BILLINGS), has been given a full redescription by SHAW (1968, p. 87–89, Pl. 1, Figs. 3–14, Pl. 2, Figs. 1, 2) and BILLINGS' original material has been illustrated by WHITTINGTON (1961). This is a Chazy species, in which the anterior cephalic border continues the forward slope of the front of the glabella, and the 3P glabellar furrow is far forwards. In *P. praematura* the cephalic border is distinct and the 3P glabellar furrow is directed towards the anterolateral corner of the glabella. In these respects it is probably closer to *P. senilis* (BARRANDE) (SHAW 1968, Pl. 1, Figs. 1, 2) from the Llanvirn of Czechoslovakia, in which the 3P furrow is only slightly more advanced, but which has the palpebral lobe far further forward than in *P. praematura*, and with a forward expanding glabella. *Pliomerops escoti* (BERGERON) (redescribed by DEAN 1966) resembles *P. senilis* in the position of the eye, and has much more delicate pygidial spines than the new species. In both *P. canadensis* and *P. senilis* the pygidium is steeply declined posteriorly, and the pleural ribs run nearly parallel to the posterior margin. The same is true of the pygidium from the Profilbekken Member. This provides a distinction from some other early species that have been attributed to *Pliomerops* in which the pygidial spines are markedly splayed (and which are closer to *Pseudomera*), for example, *Pliomerops shangortensis* REED 1945 (REED 1909, Pl. 6, Fig. 5) and "*Pliomera*" *dactylifera* POULSEN 1927. *Pliomerops siensis* CHUGAEVA 1964, is a true *Pliomerops* very similar to the type species, and differing from *P. praematura* in the same features.

The difference in the position of the 3P glabellar furrow in the new species compared with other *Pliomerops* spp. does not constitute a generic distinction, particularly considering the similarity of the pygidium and hypostoma to those of the type species.

Subfamily CYBELOPSINAE FORTEY 1979

Genus *Ectenonotus* RAYMOND 1920

Type species. — *Amphion westoni* BILLINGS 1865.

Ectenonotus connemaricus (REED, 1909)

(Pl. 21, Figs. 1–6)

1909 *Cybele connemarica* sp. nov. REED, p. 146–7, Pl. 6, Figs. 6, 7.

1945 *Ectenonotus connemaricus*, REED, p. 56–57.

Stratigraphic range. — Profilbekken Member, V₄b, 36 m to 70 m, *Orthidiella* zone (Whiterock).

Material. — Cranidia: PMO NF 134, 143, 1245, 3197; Pygidia: PMO NF 3130, 3196, 326.

Description. — Cranidium twice as wide as long in dorsal view. Glabella occupying one-third cranidial width, slightly longer than wide, gently rounded about mid-line anteriorly. Three pairs of glabellar furrows extending to less

than one-third glabellar width. Glabellar lobes 1P slightly shorter than 2P measured along axial furrow (exsag.) 1P and 2P furrows equal in length, deep, and sloping slightly backwards-inwards. 3P reduced to a pit far forwards on glabella, not reaching preglabellar furrow, deep on the external surface, but shallow on the internal mould. Occipital furrow deep and transverse laterally, shallowing and arched forwards medially. Complex surface sculpture on glabella of granules of two sizes generally distributed, with scattered low tubercles in addition each of which is perforated at the tip (Pl. 21, Fig. 5), this presumably representing the site of a seta. Anterior border nasute, narrow and highly convex, separated from the glabella by a deep preglabellar furrow. Fixed cheeks slope down towards the glabella adaxially, posterolateral parts sloping steeply downwards and outwards. Palpebral lobes extend backwards as far as anterior part of glabellar lobes 1P, forward limits opposite forward part of 2P. Palpebral furrow continues forward to define a short eye ridge, which is effaced adaxially. Cheeks deeply pitted, the pits reflected on the internal mould, the intervening ridges being covered with granules like those on the glabella, but coarser adjacent to the axial furrows. Posterior border widening and curving forwards laterally, without surface sculpture.

Pygidium of length about equal to width in dorsal view. Axis tapering backwards, axial furrows enclosing an angle of about 30 degrees, transverse convexity decreasing posteriorly. There are eleven or twelve axial rings defined by deep ring furrows, the last six gradually narrower (sag.) backwards. The best specimen shows nine pairs of pygidial pleurae, the last three pairs very short, which posteriorly run almost exsagittally and join with the posterior parts of the appropriate axial ring. The furrows separating the first six pleural ribs are deep, and run to the pygidial margin. The last three furrows are progressively shorter, so that there is a posterior, unfurrowed area behind the pygidial axis. This area is also slightly inflated, and, on the internal mould, densely pitted. Pleural ribs terminate in blunt spines; broad triangular articulating facet. Posterior pygidial margin upward arched about mid-line. Fragments of cuticle show that the axis is covered with granules; the pleural ribs are apparently smooth except for granulose tips. The internal mould shows a line of prominent pits on each axial ring (tubercles on the ventral surface of the exoskeleton), pleural ribs more finely and densely pitted.

Discussion. — Six species of *Ectenonotus* have been described, all probably from Whiterock occurrences: *E. westoni* (BILLINGS 1865), *E. connemarius* (REED 1909), *E. octocostatus* (REED 1910), *E. marginatus* HOLLIDAY 1942, *E. raymondi* HOLLIDAY 1942, and *E. whittingtoni* ROSS 1967.

The type species, *E. westoni*, has been redescribed by WHITTINGTON (1961, p. 915–6, Pl. 99, Figs. 1–4, 6–9). The species from Spitsbergen is obviously congeneric, but the type species has fifteen or sixteen axial rings on the pygidial axis, and the cephalic anterior border is medially flattened and acuminate where it is gently rounded on our specimens. FORTEY (1979) has suggested that *Ectenonotus* was derived from a more usual pliomerid ancestor by progressive expression of additional pygidial segments, a suggestion supported by some

intermediate forms in the upper Canadian. The number of pygidial segments is accordingly regarded as of particular importance in specific determinations. *E. connemarus* (REED 1909, p. 146–7, Pl. 6, Figs. 6, 7; Pl. 21, Fig. 6 herein) from the Shangort beds, Co. Galway, western Eire, has twelve or thirteen rings on axis, and nine or ten pleural ribs, and the specimens from Spitsbergen fall within this range of variation. *E. octocostatus* (REED 1910) is reputed to have only eight pleural ribs. REED (1910, Pl. 22, Figs. 5, 6) also illustrated cranidia, originally attributed to *Pliomera pseudoarticulata* (PORTLOCK), but subsequently (REED 1945, p. 57) assigned to *E. octocostatus*, which are not unlike cranidia from Spitsbergen, but are not well-preserved or complete. The identity of pygidia of *E. connemarus* with those of the Spitsbergen species justifies the use of REED's specific name for the new material.

E. whittingtoni ROSS (WHITTINGTON 1961, Pl. 99, Figs. 5, 10–15; ROSS 1967, Pl. 7, Figs. 33, 34, Pl. 8, Figs. 1–22) from the *Orthidiella* zone of Nevada is an exact contemporary of our Spitsbergen form. The mature pygidium of this species has "twelve segments and a minute terminal piece" and "eight pairs of pleura with suggestions of a ninth at posterior end". Except for the lesser backward curve of the pygidial pleurae it is difficult to distinguish the larger pygidium of ROSS (1967, Pl. 3, Figs. 1–3) from the Spitsbergen specimens. The anterior border on the larger cranidia of *E. whittingtoni* (ibid., Pl. 7, Figs. 33, 34) is wider (sag.) than on our material, and the 3P glabellar furrow is not pit-like, but other cranidia from Nevada (ibid., Pl. 8, Figs. 5, 9) are not so different in this regard. Perhaps of more significance is the fact that the surface sculpture of *E. whittingtoni* consists of rather coarse granules, unlike the distinctive, fine scale sculpture reported for our material.

E. raymondi HOLLIDAY 1942 is reported to have as many as 22 axial rings on the pygidium, a number exceeding any other species. *E. marginatus* HOLLIDAY 1942 is known from rather poorly preserved material, and may prove to be conspecific with either *E. connemarus* or *E. whittingtoni*, but the question of its identity cannot be resolved without the collection of more and better material.

Genus *Strotactinus* BRADLEY 1925

Type species. — *Amphion salteri* BILLINGS 1861

Strotactinus sp. A
(Pl. 20, Figs. 9–11)

Stratigraphic range. — Olenidsletta Member, 102 m from base, latest Canadian (late Arenig, V₂b).

Material. — Cranidium, PMO NF 85; pygidium, PMO NF 98; hypostoma, PMO NF 105.

Discussion. — The type species of *Strotactinus*, from the early upper Canadian of eastern Canada, has been redescribed by LUDVIGSEN (1979); *S. insularis* (BILLINGS) from the St George Group, western Newfoundland, has been revised

by FORTEY (1979). There is no doubt that a species from Spitsbergen should be referred to the same genus, although it is only represented by fragmentary material and cannot be formally named. Typical features of *Strotactinus* shown by the Spitsbergen species are the recurved anterior cranial border overlapping on to the frontal glabellar lobe, and the long terminal piece on the pygidial axis which carries one (and a faint second) transverse furrow. *Strotactinus* sp. A is the youngest species of the genus known. Several features show that it is a new species. The 3P glabellar furrows are short and isolated within the glabella. A unique feature is a pair of protruberances of the forward margin of the glabella opposite the outer ends of the 3P furrows. These may have served as buttresses between the glabella and the recurved border. The incomplete pygidial material shows that the terminal piece of the axis on *Strotactinus* sp. A was relatively long and narrow (trans.) and not greatly inflated, as it is in *S. insularis* (FORTEY 1979, Pl. 15, Fig. 6). The free ends of the pygidial spines are long and slender, and not curved as in other species of *Strotactinus*. A hypostoma occurs in the same bed as the partial cranidium and pygidium, and resembles that attributed to *S. insularis* by FORTEY (1979).

Family ENCRINURIDAE ANGELIN 1854

Subfamily CYBELINAE HOLLIDAY 1942

Genus *Cybelurus* LEVITSKIY 1962

Type species. — *Cybelurus planus* LEVITSKIY 1962 (= *Cybele planifrons* SEMENOVA 1960, p. 426, plate 0–XX, Figs. 8, 9 non VEBER 1948, p. 64, plate X, Fig. 20).

Discussion. — The type species of this genus was described by SEMENOVA (1960) under the name *Cybele planifrons* VEBER 1948. LEVITSKIY (1962) proposed the genus *Cybelurus*, gave the new name *Cybelurus planus* to SEMENOVA's material, which he regarded as distinct from *Cybele planifrons* VEBER, and nominated *Cybelurus planus* as the type species of the new genus. WHITTINGTON (1965) redescribed *Encrinurus mirus* BILLINGS 1865, and referred this species to a new genus, *Miracybele* (with *M. mirus* as type species). Comparisons of the type species of *Miracybele* and *Cybelurus* are hindered by the poor illustration of the Russian material, but it is clear that *Cybelurus planus* possesses many of the characters regarded by WHITTINGTON (1965, p. 423) as distinguishing *Miracybele* from other cybelines, notably a deep pit in the preglabellar furrow, and a furrow running back from this pit on to the frontal lobe of the glabella, and branched 3P glabellar furrows. BURSKY (1970), DEAN (1973), and TRIPP (1976) have regarded *Miracybele* as a junior synonym of *Cybelurus*, and this procedure is followed here. It is noted that there is much variation in *Cybelurus* as thus constituted, especially in the anterior cephalic border, and in the relative development of the pleural bands on the pygidium (ROSS 1970).

Cybelurus species are widespread, occurring in the U.S.S.R. in the Altai Mountain region (SEMENOVA 1960; LEVITSKIY 1962) and Pai-Khoya, North-west Arctic region (BURSKY 1970), in Norway (NIKOLAISEN 1961, p. 295), Sweden (Dr. T. TJERNVIK written communication 1971), Newfoundland

(WHITTINGTON 1965), Western U.S.A. (ROSS 1967), Scotland (ROSS and INGHAM 1970; TRIPP 1976), and the Yukon (DEAN 1973). Two new species are described below from the upper part of the Valhallfonna Formation.

Cybelurus halo n. sp.

(Pl. 22, Figs. 1–15; Pl. 25, Fig. 12)

Stratigraphic range. — Profilbekken Member, V₄b (Whiterock: *Orthidiella* zone) 30–100 m from base.

Material. — Holotype, part and counterpart of complete exoskeleton (except free cheeks) PMO NF 1278. Abundant further material includes cranidia: SMA 84321–3, 84327–8, 84329, 84378–80, PMO NF 1274, 3199, 1397; pygidia: SMA 84330, 84332, PMO NF 3200, SMA 84381–3; free cheeks: SMA 84324, 84326; hypostome: SMA 84331.

Diagnosis. — *Cybelurus* species with anterior border on cranium greatly expanded on mid-line, forming a semicircular brim around front of glabella. Pygidium of width slightly greater than length of axis. Axial rings 11 or 12, except for anterior two faintly defined over mid-part of axis. Four pairs of convex pleural bands separated by very low interpleural bands. Surface sculpture of fine, densely spaced granules.

Description. — Cephalon about twice as wide as long. Glabella gently convex (sag., tr.) hardly elevated above level of cheeks, expanding evenly and gently forwards, maximum width at anterolateral corners between 0.75 and 0.8 times sagittal length. Front margin very gently rounded. Three pairs of glabellar furrows extend one-third across glabella, 1P and 2P deepened and slightly wider at their inner ends. Distance between the outer ends of lateral glabellar furrows 1P and 2P subequal to distance between 1P and occipital furrow, but less than that between 2P and 3P. 1P directed gently backwards, 2P crosses glabella transversely, while 3P bifurcates at its midpoint, posterior branch slightly backwardly directed, anterior branch running forwards and dying out on frontal lobe of the glabella. Glabellar lobes progressively larger (exsag., tr.) anteriorly, slightly inflated, 3P most noticeably so. Axial furrows narrow, deep, running in gentle curve outwards-forwards to anterior margin of cranium, deepened greatly to form an apodeme immediately in front of eye ridge. Preglabellar furrow shallow laterally, medially deepened into an elongate (tr.) pit. From this pit a fairly deep furrow runs backwards on the sagittal line to bisect frontal lobe of the glabella. Occipital furrow curving forwards and shallowing medially. Occipital ring broadest (sag.) medially, bearing a small median tubercle. Fixed cheek triangular, posterolaterally very narrow (exsag.), sloping downwards in all directions from palpebral lobe, which forms the highest point on the cranium. Palpebral lobe far back on the cheek, opposite glabellar lobe 2P, outline subcircular, sloping upwards at a steep angle to adjacent areas of the fixed cheek. From anterior limit of the palpebral lobe a prominent eye ridge runs inward and forwards across cheek to meet axial

furrow opposite outer end of lateral glabellar furrow 3P. On late cranidia genal spine stout, on specimens from lower in the Profilbekken Member it may be more slender. Posterior border furrow fairly wide and deep. Posterior border convex, sloping slightly backwards laterally, not sharply delimited from occipital ring. Anterior border broad, greatly expanded medially so that its sagittal length is 0.27 to almost 0.40 sagittal length of glabella (excluding occipital ring) laterally continuing the downward slope of the anterolateral parts of the frontal lobe of the glabella, medially almost horizontal, downturned at its anterior edge.

Free cheeks triangular, with convex lateral border, beneath which doublure closely reflexed. Anteriorly doublure broadens and flattens out, passing horizontally beneath expanded anterior border to form a 'doubled back' structure. If the lateral boundary of the doublure of the free cheek shown on Pl. 22, Fig. 13 represents the connective suture the rostral plate so outlined would be forward tapering; preservation is not good enough to be certain of this detail. Facial suture proparian, with shallow V-shaped outline, posterior branch cutting lateral border in front of genal spine, anterior branch crossing axial furrow where it meets the lateral border furrow and curving adaxially to pass along the anterior margin of the anterior border, the medial, transverse part presumably being the rostral suture. Surface sculpture consisting of a coarse raised network on cheeks, which is reflected on internal moulds, and fine granulation over dorsal surface of the cephalon (except in furrows). Around anterior margin of expanded anterior border there are irregularly distributed tubercles, which are visible also on internal moulds. Tips of tubercles perforated. From their confinement only to the anterior part of the cephalon, and their connection with the ventral surface of the exoskeleton, it seems possible that these tubercles bore sensory setae.

Thorax of 12 segments, the sixth segment bearing long pleural spine.

Hypostoma (Pl. 22, Fig. 3) with oval (long axis sag.) middle body, which bears prominent, bulging maculae, set off from the middle body anteriorly by deep straight middle furrows, which converge backwards at an angle of about 60 degrees to sag. line. Posterior part of middle body crescentic, gently inflated. Lateral border furrows deepened anteriorly to form an apodeme. Anterior margin almost straight, of transverse width more than twice that of the middle body. Anterior wings large, curving steeply upwards. Posterior border incompletely preserved, fairly wide and gently concave. External surface granulate anteriorly and around posterior border. A pair of subcircular smooth areas adjacent to the anterior margin on either side of the middle body probably represent sites of muscle attachment. This hypostoma is comparable with that described by WHITTINGTON (1965, Pl. 66, Figs. 5-8) for *Cybelurus mirus*, differing from it in having larger bulging maculae, deep middle furrows, and a shorter posterior border.

Pygidium gently convex (tr.), of maximum width anteriorly, this slightly greater than length of axis. Axis tapering gently and of decreasing convexity (tr.) posteriorly, with 11 or 12 axial rings, of which only the first two are defined over mid part of axis on dorsal surface (Pl. 22, Fig. 15). Ring furrows

deep laterally, forming paired apodemes, progressively narrower (exsag., tr.) posteriorly. Terminal piece of axis bears two pairs of shallow pits only discernable on dorsal surface. Axis continued posteriorly by a narrow tapering post-axial ridge. Pleural fields of maximum width at about mid-length, this being slightly less than the maximum width of the axis, almost horizontal or sloping slightly inwards and downwards adaxially, laterally curving steeply downwards. Four segments in the pleural regions defined by fairly deep interpleural furrows. Pleurae divided by deep pleural furrows which separate narrow anterior pleural bands from broader, highly convex posterior pleural bands, which are continued beyond the margin of the pygidium as long, slightly upward-directed spines. Anterior bands present on the first three segments only, and more prominent on internal mould than on dorsal surface. The posterior bands are anteriorly continuous with the first four axial rings (Pl. 22, Fig. 15). The most anterior of these is adaxially directed transversely, soon curving posteriorly and directed slightly inwards. In posteriorly succeeding bands this proximal transverse part decreases in width, so that fourth pair is directed immediately backwards adjacent to the axial furrows, converging backwards and touching postaxially.

Smallest cranidium (Pl. 22, Fig. 8) is of much greater convexity than larger specimens. Glabella highly convex (tr.) with three pairs of short (tr.), deep glabellar furrows. A fourth furrow is possibly present anteriorly, though very faint. The furrow bisecting the frontal lobe is still present, although shallow. Eyes further forward than on large cranidia. Genal spine short, stout. It may be noted that there is some resemblance between this cranidium and that figured by POULSEN (1965, Pl. 8, Fig. 10) from the early Ordovician of Bornholm.

Discussion. — Only one named species of *Cybelurus*, *C. sokoliensis* BURSKEY (1970) from the earliest Ordovician of Pai-Khoya, has an expanded anterior border like that of *C. halo* n. sp. It differs from *C. halo* n. sp. in having a weakly developed anterior branch of furrow 3P, and in having a broader pygidium with fewer axial rings well defined over mid part of axis. The cranidium and pygidia figured by Ross (1967, Pl. 8, Figs. 23–25) as *Miracybele* ? sp. 1 are closely similar to those of *Cybelurus halo*, and the species are probably conspecific.

The pygidia of the Nevada *Cybelurus* appear to be longer, and the pygidial axis broad posteriorly. Further *Cybelurus* from the Western United States have been figured by Ross (1970, Pl. 18, Fig. 6; 1972, Pl. 17, Fig. 26), who (1972, p. 40) regarded all the Nevada specimens as belonging to a single species. There is a tendency on this material for the anterior and posterior branches of the 3P glabellar furrows to be developed as separate pits. A similar tendency is shown on a cranidium from the Valhallfonna Formation figured on Pl. 22, Fig. 2 (also PMO NF 3199). Apart from the expanded anterior border the cranidium is similar to that of *C. mirus* BILLINGS (WHITTINGTON 1965, Pl. 64) and to that of the type species *C. planus* (SEMENOVA 1960, Pl. 0–XX, Figs. 8, 9). Generic separation of *C. halo* n. sp. on the basis of the very wide anterior border

does not seem justified, although it is unusual among encrinurids. The relationships of *C. halo* n. sp. to *C. brutoni* n. sp. are discussed in the following paragraphs.

Cybelurus brutoni n. sp.
(Pl. 23, Figs. 1-6)

Stratigraphic range. — Profilbekken Member, lower part, V₄a (Valhallan), preceding *C. halo* in the sections 2 m to 26 m from base.

Material. — Holotype: partly exfoliated cranidium SMA 84333; cranidia: SMA 84334, PMO NF 151, 157, 174, 176, 2441, 2462a, 239; free cheek: PMO NF 353; pygidia: PMO NF 178, 172, SMA 84335; hypostomes: PMO NF 267, 219.

Diagnosis. — A *Cybelurus* species, with broad anterior cranial border, of subequal width (sag. exsag.) in front of mid-part of glabella. Transverse pit in preglabellar furrow very long, and deep. Genal spine lacking. Pygidium closely similar to that of *C. halo* n. sp. but transversely broader.

Discussion. — This species occurs immediately below *C. halo* n. sp., to which it is similar, differing principally in having a broad, but not medially expanded anterior border, and a long, transverse pit in the preglabellar furrow. A graph showing the relative length of the anterior border on the sagittal line plotted against stratigraphic occurrence is given for *C. halo* n. sp. and *C. brutoni* n. sp. in Fig. 8. Available material shows an increase in the relative length of the anterior border on the sagittal line upwards in the sections. Early cranidia of *C. halo* are more like those of *C. brutoni* also in having a relatively longer (tr.) pit in the preglabellar furrow than later cranidia (Pl. 22, Fig. 9). With such

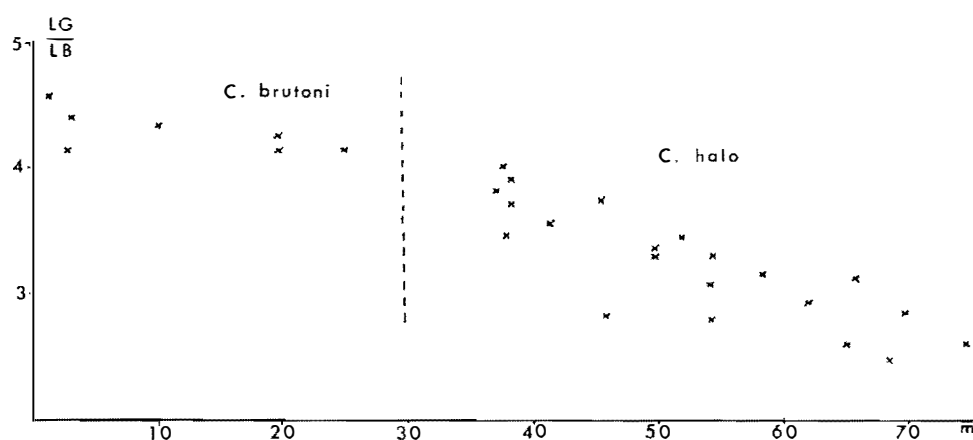


Fig. 8. Plot of ratio of length of glabella (LG, measured from the middle of occipital furrow to front margin) to width of anterior border (LB = border + anterior pit), sag., against stratigraphic occurrence of *Cybelurus* in the Profilbekken Member (m from base). Increase in width from the Valhallan form *C. brutoni* to early Whiterock form *C. halo*.

intergrading characters, it seems possible that *C. brutoni* gave rise to *C. halo* by a median expansion of the anterior border. Pygidia are similar to those of *C. halo*, but relatively wider (tr.), and it is difficult to discern more than ten axial rings.

Cybelurus cf. *mirus* (BILLINGS 1865)
(Pl. 23, Figs. 7–9)

Stratigraphic range. — Profilbekken Member, V₄b, 70 m from base, Whiterock, early Llanvirn.

Material. — A single cranidium PMO NF 1265.

Discussion. — This single specimen occurs with stratigraphically high specimens of *C. halo*, but is clearly distinct. In particular, the anterolateral parts of the anterior border are narrow (exsag.), and it can be inferred that the median part was not expanded in the same way as *C. halo*. The forward expansion of the glabella is more rapid, and the inflation of the 3P glabellar lobe is especially marked, so that this lobe is proportionately longer (exsag.). The posterior branch of the 3P glabellar furrow is more noticeably backward-directed. In front of the 3P lobe the axial furrows do not diverge forwards so rapidly. The postocular part of the fixed cheeks are wider (exsag.). Of the species of *Cybelurus* discussed previously the cranidium most resembles that of *C. mirus* (see WHITTINGTON 1965), but there is insufficient material to make more than a tentative determination.

Genus *Lyrapyge* n. gen.

Type species. — *Lyrapyge ebriosus* n. sp.

Diagnosis. — Glabella with three pairs of lateral glabellar furrows, the anterior of which have short, shallow, forward-directed branches commencing near their outer ends. Anterior border indistinctly defined, incorporated in glabella. Mid part of border furrow slightly deepened, from which a furrow runs upwards and slightly backwards to bisect the front part of the glabella. Pygidium very wide, axis gently tapering, with 8 or 9 axial rings. Pleural fields gently convex, crossed by four pairs of stout raised ribs, which distally converge backwards and are continued beyond the pygidial margin as upward-turned spines. Anterior to the first three pairs of ribs, and well separated from them, are three pairs of much narrower, lower ribs, not extending beyond pygidial margin.

Included species: *Lyrapyge ebriosus* n. sp., *Dindymene* (?) *areonosa* LISOGOR 1965.

Discussion. — The very wide pygidium with its distinctive, widely spaced pleural ribs, axis with relatively few axial rings, and the peculiar anterior border of the cranidium distinguish this genus from other cybelines. The furrow

bisecting the frontal lobe of the glabella, and the general form of the lateral glabellar furrows, fixed cheeks and hypostoma suggest that it is most nearly related to *Cybelurus*. The occurrence in the middle Arenig makes it among the earliest known encrinurids, perhaps only predated by *Cybelurus sokoliensis* Bursky (1970). *Dindymene* (?) *areonosa* Lisogor (1965, Pl. 2, Fig. 7) from the early Ordovician of Kazakhstan, of which only the pygidium is known, is similar to the pygidium of *Lyraphyge ebriosus* n. sp., differing in having more closely spaced pleural ribs and apparently a greater number of axial rings. It should probably be referred to the same genus. From a similar horizon to *Dindymene* (?) *areonosa* Vebek (1948, Pl. X, Fig. 20) described the species *Cybele planifrons*, known only from an incomplete cranidium, which has similar glabellar furrows to those of *Lyraphyge* n. gen., and may represent the cranidium of *Dindymene* (?) *areonosa*.

Lyraphyge ebriosus n. gen., n. sp.

(Pl. 23, Figs. 10–14; Pl. 24, Figs. 1–9)

Stratigraphic range. — Mid part of Olenidsletta Member 80–100 m from base, V_{1a} (middle Arenig).

Material. — Holotype: cranidium, largely exfoliated PMO NF 2131. Other material includes cranidia: PMO NF 2139, 2143, 1666, 2042, 2309, 497, 2132, SMA 84336–7; pygidia: PMO NF 2151, 2112, 2136, 2133, 2154, 2110, 3261, 2120, 2668, SMA 84338–9; free cheeks: PMO NF 2099, 2129, SMA 84341; hypostomata: PMO NF 2149, 3114.

Diagnosis. — See that of genus.

Description. — Cranidium moderately convex (sag., tr.), more than three times as wide as long. Glabella convex (tr.), with highest part on sagittal line, in lateral view (Pl. 24, Fig. 5) posterior two-thirds of profile horizontal, anteriorly steeply downcurved so that front part of frontal lobe of glabella is vertical. Glabella expands in width gently forwards reaching maximum width at rounded anterolateral corners. Three pairs of lateral glabellar furrows, which extend less than one-third across glabella, distance between outer ends of furrows 3P and 2P being greater than that between 2P and 1P and that between 1P and occipital furrow. Furrow 1P gently backward directed, 2P transverse, while outer end of furrow 3P deepened adjacent to axial furrow, from which a very shallow, short branch runs forward on to the frontal lobe of the glabella. Deep, inner part of furrow 3P shows a tendency to become isolated from adaxial pit. Glabellar lobe 3P slightly inflated. Occipital ring convex (tr.), widest medially, with tubercle. Axial furrows fairly deep, greatly deepened immediately anterior to furrows 3P to form a pair of apodemes. Preglabellar furrow very faint, in anterior view with broadly V-shaped outline (Pl. 23, Fig. 13), slightly deeper across mid-part of glabella, where broad-based furrow runs upwards and slightly backwards to bisect anterior, steeply sloping part of frontal glabellar lobe, this furrow narrowing and deepening inwards. Anterior

border continuing anterior slope of glabella, and narrowing and curving downwards medially. Fixed cheeks crossed by prominent, convex eye ridge, commencing opposite outer end of lateral glabellar furrow 3P and running slightly backwards to upward-turned palpebral lobe about halfway across the cheeks opposite glabellar furrow 2P. Posterior border narrow and convex adaxially, broadening and curving posteriorly laterally. Border furrow narrow and deep adaxially, wider and shallower laterally. Genal spine variable, quite stout on the cranium on Pl. 23, Fig. 10, but slender on some larger crania. Posterolateral part of the fixed cheek narrow (exsag.). Surface sculpture on the cranium consisting of a raised network on the cheeks, and apparently rather coarse granulation over the whole dorsal surface, preserved as isolated patches in available material.

Free cheek triangular, with narrow convex lateral border continued anteriorly as a broad vertical flange (Pl. 23, Fig. 12) which fitted vertically beneath lateral part of anterior border in front of glabella. Doublure narrow, turned up vertically beneath border. Facial suture cuts lateral border at an acute angle, curving adaxially to run transversely to palpebral lobe, in front of which it runs inwards at about 20 degrees to sagittal line, crossing axial furrow where it meets the border furrow, and curving adaxially to run in front of anterior border. Ventral sutures not known.

Hypostoma (Pl. 24, Figs. 6, 8) generally similar to that of *Cybelurus*, with broad, triangular anterior wings, convex, oval middle body, narrow steep lateral borders, and a wide (sag.) posterior border with gently rounded outline and posteromedian point. Macular small, like those of *Cybelurus mirus* (WHITTINGTON 1965, Pl. 66, Fig. 8). Anterior part of lateral border furrow deepened conspicuously to form an apodeme.

Pygidium broadly triangular, with maximum transverse width shortly behind anterior margin, this being between 1.6 and 1.8 times length of axis. Axis tapering, of decreasing convexity posteriorly, with 8 or 9 axial rings, first two curving slightly forwards medially. Ring furrows deep laterally, forming paired apodemes, fainter across mid-part of axis. Terminal piece of axis small, with two pairs of pits. Axial furrows deep anteriorly, shallowing rapidly adjacent to tip of axis. Pleural fields gently convex, most steeply downward-sloping posteriorly. Four pairs of convex ribs originate adaxially adjacent to first four axial rings, and are continued posteriorly as long, tubular, upward directed spines (Pl. 24, Fig. 7), which are broadened at their bases. Proximal part of anterior rib is transversely directed, laterally curving backwards and slightly inwards to broadened base of posterior spine. Proximal end of second rib runs gently backwards at about 80 degrees to sagittal line before curving posteriorly, that of third rib at about 60 degrees and the fourth only at about 20 degrees, so that curvature of ribs decreases progressively posteriorly. Irregular postaxial corrugation may represent the remnant of a fifth pair of ribs. Anterior to first three pairs of ribs and about midway between successive pairs there are much narrower, lower ribs which are not continued as spines. Surface sculpture of the pygidium comparable to that of cephalon consisting of a raised network bearing coarse granules.

Discussion. — The only other species which may be attributed to this genus, *Dindymene* (?) *areonosa* LISOGOR, has been discussed above (p. 100). It is of particular interest to note the resemblance of this trilobite to the pliomerid *Europeites* BALASHOVA 1966. The pygidium of *Europeites primigenus* (ANGELIN) from the Ceratopyge limestone of Scandinavia has a similar arrangement of paired convex pleural bands. The cranium of a new species of *Europeites* from the Profilbekken Member has the eyes in a posterior position, and a prominent eye ridge crossing the preocular cheek (Pl. 19, Fig. 1). In these features it is very like *Lyrapyge* n. gen. and distinct from other Pliomeridae. It is considered possible that the Cybelinae were derived from the Pliomeridae, and that *Lyrapyge ebriosus* retains some of the primitive characters.

Family ODONTOPLEURIDAE BURMEISTER 1843

Genus *Ceratocephala* WARDER 1838

Type species. — *Ceratocephala goniata* WARDER 1838

Ceratocephala sp. indet.

(Pl. 25, Figs. 8–10)

Stratigraphic range. — Olenidsletta Member, horizon about 92 m from base (middle Arenig).

Material. — small pyritised specimens. Cranidia: PMO NF 3168–9; pygidium: PMO NF 3170.

Discussion. — This species is known only from a number of small, pyritised specimens, and this is not enough to permit its formal naming. It is of interest as the earliest *Ceratocephala*, which now has a range from early Ordovician to Devonian. Silicified Ordovician *Ceratocephala* species have been described by WHITTINGTON and EVITT (1954), WHITTINGTON (1956) and CHATTERTON and LUDVIGSEN (1976). The incomplete pygidium from Spitsbergen shows the three barbed spines typical of the genus, although the median and left spines are broken off. The right hand spine is shorter and more incurved than in other species of the genus. On the largest cranidial fragment the glabellar lobes are quite well-defined at their inner ends; a pair of occipital spines but no median spine is present. In these respects the Spitsbergen form is perhaps closest to *C. laciniata* WHITTINGTON and EVITT 1954, although the glabellar taper is less than on later Ordovician *Ceratocephala* species and the 2P lobes are relatively large. Tuberculation is rather subdued on the material from the Olenidsletta Member.

Genus *Diacanthaspis* WHITTINGTON 1941

Type species. — *Diacanthaspis cooperi* WHITTINGTON 1941.

Diacanthaspis sp. indet.
(Pl. 25, Figs. 1, 2)

Stratigraphic range. — Profilbekken Member, 40 m from base.

Material. — Silicified pygidium, PMO NF 3105.

Discussion. — A single specimen of a pygidium is referred to *Diacanthaspis*. The specimen is silicified, with two greatly elongate posterior spines between which there are two pairs of spines (the inner pair almost broken off), a third pair almost hidden behind the elongate spines, and two pairs exterior to them.

It is assigned to *Diacanthaspis* because it resembles the pygidium of *D. ulrichi* WHITTINGTON 1956 (but not other *Diacanthaspis* spp.), except for the additional pair of spines half concealed beneath the elongate pair. *Primaspis primordialis* (BARRANDE) (BRUTON 1968, p. 11–13, Pl. 1, Figs. 8, 9, 11, 12) has a pygidium which is not unlike that of the Spitsbergen form, but with three pairs of spines exterior to the long pair. The Spitsbergen occurrence is an early one, but note that HINTZE (1953, Pl. 19, Fig. 16) has figured a probable *Diacanthaspis* cranidium (as “*Dicantaspis*”) from a still earlier horizon in Utah.

V. Revisions and corrections to Parts I & II

Additional notes on described species

Ampyxoides inermis FORTEY 1975. — In the original description of this species I indicated that the lack of a frontal spine was one of the defining characters. I noted there (p. 75) that most of the material was phosphatised, but that the lack of the spine was not considered to be only a product of the phosphatic internal mould in which the material was preserved. This supposition was wrong. Now (Pl. 17, Fig. 9) further breakage of material has shown that there are small cranidia with slender frontal spines, slightly declined, and so the original description must be accordingly modified. This is unfortunate, because it makes the specific name inappropriate. The spine was probably reduced on the larger cranidia.

Carolinites species. — I have stressed that *Carolinites* species are particularly widespread, and of corresponding stratigraphic importance. Since the publication of the second part of this monograph several more descriptions of *Carolinites* species have been published, and it may be of use to place them in the context of the Spitsbergen succession of species, which is the most complete anywhere. LEGG (1976) has described the type species, *C. bulbosus*, from material from northwestern Australia, but unfortunately without re-illustration of material from the type area in Tasmania. As LEGG noted, this material is indistinguishable from *Carolinites genacinaca* Ross *sensu lato*. The slightly flattened cranidium (LEGG 1976, Pl. 1, Fig. 6) is identical to that of a stratigraphic-

ally early specimen of *C. genacinaca genacinaca* from Spitsbergen (FORTEY 1975, Pl. 38, Fig. 1). A free cheek from Australia (LEGG 1976, Pl. 1, Fig. 29) shows a prominent subocular ridge, which therefore places it close to *C. genacinaca nevadensis* HINTZE. It seems probable that both subspecies are present in Australia, and it is to be anticipated that when the material from Tasmania is redescribed that *C. genacinaca* will enter into synonymy with *C. bulbosus*. The species *C. pardensis* LEGG, which lies stratigraphically above *C. bulbosus* in Australia, seems to be indistinguishable from *C. ekphymosus* FORTEY 1975, from a similar stratigraphic position in Spitsbergen. The information on this species from Australia is incomplete, however. LU (1975) has described several species from central and southwest China. *C. ichangensis* again falls within the limits of variation of *C. genacinaca* as shown in Spitsbergen, and probably the nominate subspecies. Furthermore, the re-illustration of *C. minor* (SUN) a small cranidium, shows that this species, too, could well prove to be identical to *C. genacinaca genacinaca*, in which case this name will have priority even over *C. bulbosus* KOEYASHI.

Note that LU (1975, p. 290) uses small differences in the relative width of the fixed cheeks to discriminate the several species of *Carolinites* in China. I have shown (1975, p. 105, Fig. 14) that this is not a reliable way of distinguishing the various species of *Carolinites*, as it is subject to much intraspecific variation. *C. subcircularis* LU, 1975, is known from small specimens, and at this size the specific characters are not fully expressed. An associated pygidium is incomplete, but does seem to taper backwards rather rapidly, a particular feature of *Carolinites killaryensis killaryensis*. It is my opinion that the evidence supports the widespread distribution of *Carolinites* species, and I regard it as unfortunate that the species names have proliferated in the way that they have.

Cloacaspis ekphymosa FORTEY 1974. — Previous illustrations of this species were of slightly flattened material, and I have taken this opportunity to illustrate a specimen preserved in relief (Pl. 9, Fig. 8).

Errata from Parts I and II

A number of errors, mostly concerning specimen numbers, have been detected during curation of material described in the first two parts of this monograph. Correct specimen numbers are listed as follows family by family.

Olenidae (FORTEY 1974)

- p. 33. *Balnibarbi scimitar*, holotype, PMO NF 2785. Fused cheeks Pl. 7, Fig. 4, PMO NF 2779.
- p. 47. Smallest cranidium (line 6) should be Pl. 13, Fig. 7.
- p. 55. *Psilocara comma* (Pl. 17, Figs. 1–10 etc.), line 5, numbers transposed, that of holotype being NF 2544.
- p. 62. PMO NF 3000 is a pygidium.

Asaphidae, etc. (FORTEY 1975)

- p. 6. "*Svalbardaspis*" error *pro Svalbardites* FORTEY 1975.
- p. 41. Pygidium of *N. glazialis costatus* should be PMO NF 1664, Pl. 10, Fig. 18.
- p. 49. Delete, pygidium PMO NF 374.
- p. 58. Add PMO NF 1345 to list of pygidia.
- p. 73. PMO NF 1330 should be added to cranidia of *A. toxotis*.
- p. 76. Line 14, for *occipatalis* read *occipitalis*.
- p. 92. "*Alsataspididae*" error for *Alsataspididae*.
- p. 95. Line 17: "*Oopsites gladiator* n. sp." *nom. nud.* synonym of *O. hibernicus* (REED).
- p. 100. Holotype, cranidium, *Oopsites squamosus* PMO NF 2879. Pygidium correctly PMO NF 1576.
- p. 105. Figured *Rhombampyx rhombos* also on block PMO NF 1192.
- p. 115. Delete PMO NF 785 from list of cranidia.
- p. 116. ●GIENKO in ZANINA published 1972.
- p. 128. Add Fig. 7 to Fig. 2.
- p. 182. Fig. 16, should read 332b.
- p. 189. Figs. 5–16, *Endymionia clavaria*.
- p. 198. Figs. 1–3. For Profilbekken read Profilstranda.
- p. 204. *Carolinites sibiricus* is described on p. 111.

Glossary of new names; Origin of names

acuticaudata (Latin) — "sharp tail".

aduncus (Latin) — bent inwards.

bellatula (Latin) — diminutive of beautiful.

borealis (Latin) — northern.

brevilingua (Latin) — short tongue.

brevis (Latin) — short.

brevispicatus (Latin) — "short spine".

brutoni — after D. L. Bruton.

caecata — with caeca.

ebriosus (Latin) — a guzzler, referring to the swollen glabella of *L. ebriosus*.

falcatus (Latin) — provided with scythes, the broad cheeks of the type species.

halo — referring to the broad anterior border of *Cybelurus halo*.

hinlovensis — after Hinlopenstretet, along which the Valhallfonna Formation outcrops.

hyperboreus (Latin) — very far north.

inexpectata (Latin) — unexpected.

jacquelinae — after my wife, who produced a daughter on the day this species was conceived.

ligo (Latin) — a grubbing mattock, referring to the spade-like anterior border of *Acidiphorus? ligo* n. sp.

lundehukensis — after Lundehuken, a promontory near the type locality.

Lyrapyge (Greek) — “Lyre tail” [Fem.]; in *L. ebriosus* the specific name is a noun in apposition.

minaretta — hybrid word referring to the minaret-shaped glabella of *Shumardia minaretta* n. sp.

Oenonella — diminutive from the Phrygian nymph Oenone.

oscitatus (Latin) — liable to provoke a yawn.

paulula — small, tiny.

phalloides (Latin) — phallus-shaped, of the glabella of *Shumardia phalloides*.

praematura (Latin) — premature, coming early.

proxima (Latin) — near, in close proximity, referring to its closeness to *A. danica danica*.

seminosa (Latin) — full of potential to produce offspring.

serus (Latin) — late.

Sycophantia (Latin) — deceit, knavery, referring to the problem of deciding whether this form was distinct from *Ceraurinella*.

tuber (Latin) — a root.

Turgicephalus (Latin) — swollen or turgid head.

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Plates 1—25

Specimens blackened with photographic opaque and then whitened with ammonium chloride sublimate before photography. Dorsal and other orientations are in line with the previous part of this monograph. Illumination is by ring light, except where special lighting has been used to record a particular feature. Where no orientation is mentioned in the descriptions dorsal orientation is assumed. PMO = Paleontologisk Museum, Oslo, Norway. SMA = Sedgwick Museum, Cambridge, England.

PLATE 1

- Figs. 1–14, 16. *Micragnostus serus* n. sp. (p. 21)
- Figs. 1, 6. Cephalon with cuticle, $\times 12$. PMO NF 2671. Olenidsletta Member on Olenidsletta at mouth of stream B, about 106 m from base of Member.
- Figs. 2–5. Holotype, well-preserved pygidium with cuticle, PMO NF 404; Figs. 2, 5, $\times 20$, oblique view showing sculpture, and dorsal view, Figs. 3, 4, posterior and lateral views, $\times 8$. Olenidsletta Member on Profilstranda, V_{2a}, 92 m from base.
- Figs. 7, 10. Pygidium, $\times 8$, lateral and dorsal views. Horizon and locality as holotype, Figs. 2–5. PMO NF 402.
- Fig. 8. Stratigraphically low cephalon, $\times 8$. PMO NF 3142. Profilstranda 30 m from base of Olenidsletta Member, V_{1b}.
- Fig. 9. Stratigraphically high cephalon with narrow borders, $\times 9$, about 100 m from base of Olenidsletta Member on Profilstranda, PMO NF 3135.
- Fig. 11. Stratigraphically low pygidium, $\times 8$. PMO NF 3140. Olenidsletta Member, V_{1c}, 60 m from base on Profilstranda.
- Fig. 12. Pygidium, $\times 9$, PMO NF 1747. Stratigraphically low (slightly flattened) 25–30 m from base of Olenidsletta Member on Profilstranda.
- Fig. 13. Cephalon, $\times 8$. PMO NF 2927. Same bed as cephalon, Fig. 1.
- Fig. 14. Cephalon, largely decorticated, $\times 9$. PMO NF 3134. 70 m from base of Olenidsletta Member on Profilstranda.
- Fig. 16. Incomplete pygidium, with slightly longer terminal piece, $\times 12$. PMO NF 1456. 95 m from base of Olenidsletta Member.
- Fig. 15. *Micragnostus calvus* (LAKE) (p. 23)
- Fig. 15. Lectotype, original of LAKE 1906, Pl. 2, Fig. 18, $\times 7$. Tremadoc of Nant rhos ddu, Arenig, North Wales. Sedgwick Museum Coll.
- Figs. 17, 18. *Micragnostus* sp. A. (p. 24)
- Fig. 17. Partial pygidium, PMO NF 601, $\times 12$. 75 m from base of Olenidsletta Member on Profilstranda.
- Fig. 18. Incomplete pygidium, $\times 8$. 70 m from base of Olenidsletta Member on Profilstranda, V_{1c}. PMO NF 3133.

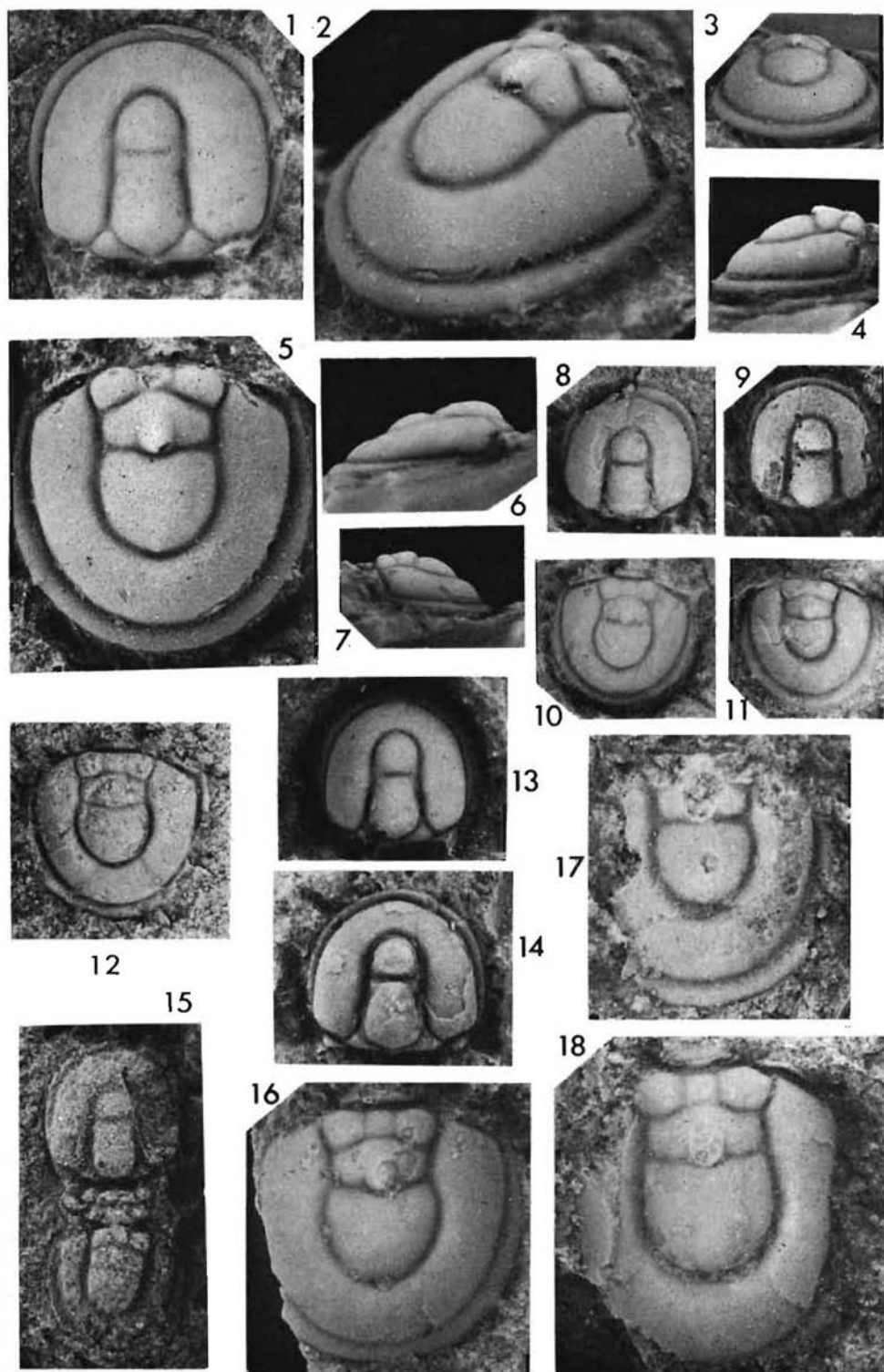


PLATE 2

- Figs. 1–9, 11, 12. *Arthrorhachis danica proxima* n. subsp. (p. 29)
- Fig. 1. Internal mould of cephalon, PMO NF 401b, from same rock fragment as holotype pygidium, Fig. 7, $\times 8$.
- Fig. 2. Largely exfoliated cephalon showing muscle impression, $\times 9$. PMO NF 3138. Olenidsletta Member, V₂b on Profilstranda, about 90 m from base.
- Fig. 3. Latex cast from slightly flattened, entire exoskeleton preserving external surface of cuticle, $\times 9$. Stream E on Olenidsletta, horizon about 80–90 m from base of Olenidsletta Member, V₂a. PMO NF 2044.
- Figs. 4, 8. Internal mould of pygidium, $\times 9$. Shore section on Olenidsletta 80–85 m from base. Fig. 8, detail of posterior part of axis photographed in strongly oblique light to show intranotular axis, $\times 15$. PMO NF 3141.
- Figs. 5, 6. Cephalon, internal mould, slightly caecate, $\times 9$. PMO NF 501. Olenidsletta Member on Profilstranda, V₂b, horizon as Fig. 12.
- Fig. 7. Holotype, internal mould of pygidium, $\times 8$. PMO NF 401a. Shore section on Profilstranda, 92 m from base.
- Figs. 9, 12. Pygidium, lateral and dorsal views, $\times 10$. Olenidsletta Member on Profilstranda, V₂b, 90 m from base. Note tripartition of terminal piece approaching the subspecies *brevis*. PMO NF 527.
- Fig. 11. Pygidium showing particularly broad axial furrows, $\times 10$. About 90 m from base of Olenidsletta Member. PMO NF 3111.
- Figs. 10, 13–15. *Arthrorhachis danica brevis* n. subsp. (p. 32)
- Fig. 10. Cephalon, internal mould, displaying all the muscle scars, $\times 10$. PMO NF 3137, about 106 m from base of Olenidsletta Member, V₂b/V₃a transition.
- Figs. 13, 14. Pygidium, internal mould, $\times 8$, dorsal and lateral view, PMO NF 70. Profilstranda, V₂b, 102 m from base of Olenidsletta Member.
- Fig. 15. Holotype, pygidium, $\times 12$. PMO NF 2664. Olenidsletta Member on Olenidsletta at mouth of stream B, 106 m from base.

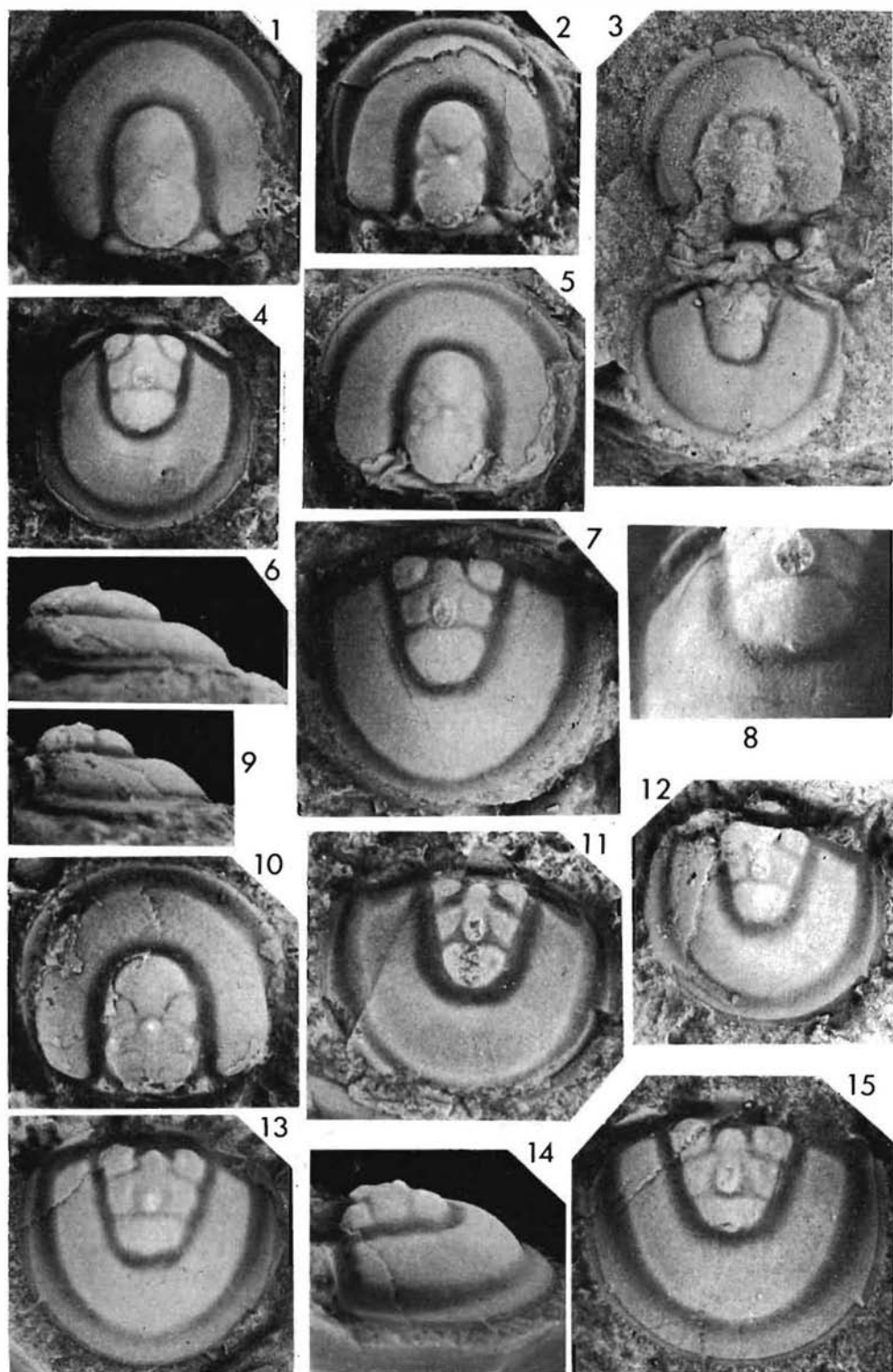


PLATE 3

- Figs. 1–10. *Shumardia minaretta* n. sp. (p. 35)
- Figs. 1–3. Holotype, cranium, dorsal, $\times 16$, anterior and oblique lateral views, $\times 12$. PMO NF 3126, 93 m from base of Olenidsletta Member on Profilstranda, V₂a.
- Figs. 4, 7. Latex cast from external mould of pygidium, oblique lateral and dorsal views, $\times 12$. PMO NF 3125. Horizon and locality close to that of holotype, Fig. 1.
- Figs. 5, 6. Well-preserved cranium, anterior and dorsal views, $\times 12$. PMO NF 3123. Horizon and locality as holotype, Fig. 1.
- Figs. 8, 10. Stratigraphically early cranium, anterior and dorsal views, $\times 12$. PMO NF 1874. Extension of glabella anteriorly not so long on this specimen, 80–85 m from base of Olenidsletta Member.
- Fig. 9. Incomplete pygidium with sparse tubercles, $\times 20$. PMO NF 1244, 92 m from base.
- Fig. 11. *Shumardia* cf. *minaretta*. Pygidium, $\times 8$, with longer axis and denser tuberculation than *S. minaretta* forma typica, and stratigraphically higher. PMO NF 1469. 100 m from base of Olenidsletta Member on Profilstranda.
- Figs. 12–18. *Shumardia acuticaudata* n. sp. (p. 34)
- Figs. 12, 16. Cranium, dorsal, oblique views, $\times 15$. Lower part of Profilbekken Member, V₄a, on Profilstranda 23–25 m from base of Member, PMO NF 300a.
- Figs. 13–15. Perfectly preserved cranium, dorsal view, $\times 20$, lateral and anterior views, $\times 15$. PMO NF 241, same bed as holotype, Fig. 17.
- Figs. 17, 18. Holotype, pygidium, dorsal and slightly oblique lateral views, $\times 12$. PMO NF 311. Lower Profilbekken Member on Profilstranda, 23–25 m from base.
- Figs. 19–24. *Shumardia phalloides* n. sp. (p. 36)
- Figs. 19–21. Holotype cranium, dorsal, anterior and lateral views, $\times 12$. Upper part of Profilbekken Member, V₄b, 50 m from base on Profilbekken. PMO NF 3128.
- Figs. 22, 23. Small cranium, PMO NF 3127, dorsal and anterior views, $\times 12$. Note buttresses interrupting course of axial furrows. Same bed as holotype, Fig. 19.
- Fig. 24. Small cranium, $\times 12$, PMO NF 1363. Locality as last, 40 m from base.
- Figs. 25–28. *Buttsia inexpectata* n. sp. (p. 37)
- Figs. 25–27. Holotype cranium, partly exfoliated, anterior and lateral views, $\times 5$, dorsal view, $\times 8$. NF 2879. Olenidsletta Member, V₁c, melt stream E on Olenidsletta, horizon about 75 m from base of member.
- Fig. 28. Internal mould of cranium, $\times 6$, PMO NF 1700. Same bed as holotype, Fig. 26.

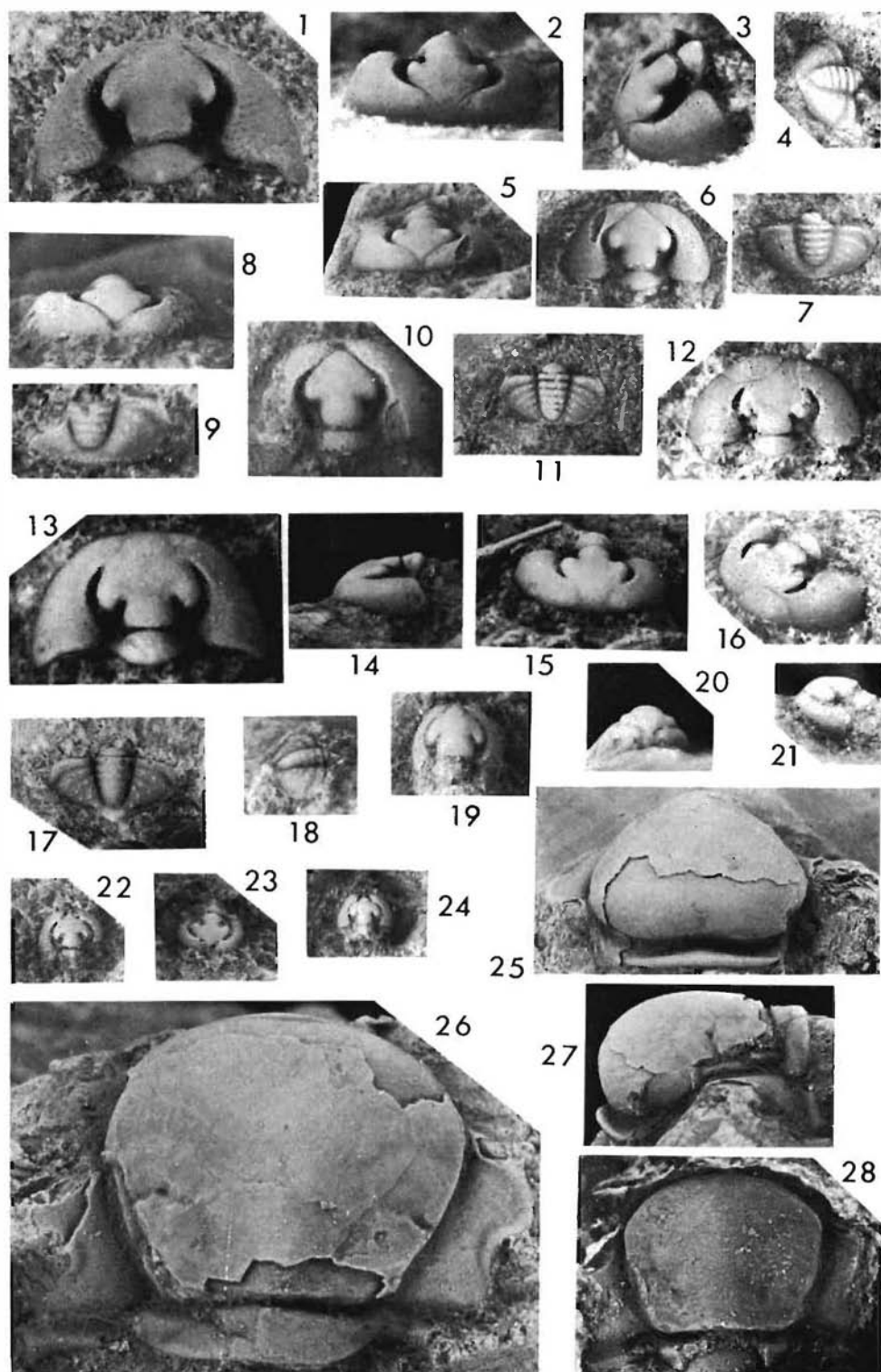


PLATE 4

- Figs. 1-5, 7, 8. *Lacorsalina ? bellatula* n. sp. (p. 39)
- Figs. 1, 4. Latex cast of holotype, external mould of cranium, PMO NF 96, dorsal and lateral views, $\times 10$. Profilstranda, V₂b, 102 m from base of Olenidsletta Member.
- Fig. 2. Fragmentary free cheek, PMO NF 75, $\times 10$. Same bed as holotype, Fig. 1.
- Fig. 3. Pygidium, $\times 10$. PMO NF 1596. Bed as holotype, Fig. 1.
- Fig. 5. Part of a thoracic segment, $\times 10$, PMO NF 91. Same bed as holotype, Fig. 1.
- Fig. 7. Small cranium, $\times 10$, PMO NF 97. Same bed as holotype, Fig. 1.
- Fig. 8. Pygidium showing broad doublure, $\times 6$. PMO NF 499. 92 m from base of Olenidsletta Member.
- Figs. 9-11 *Eorobergia* sp. A. (p. 41)
- Figs. 9-11. Cranium, internal mould, dorsal, lateral and anterior views, $\times 3$. PMO NF 3139. Olenidsletta Member, 75 m from base on Profilstranda.
- Fig. 6. Remopleuridid gen. and sp. indet. (p. 43)
- Fig. 6. Cranium, incomplete internal mould, $\times 7$. NF 3138, Olenidsletta Member 135 m from base, V₃b on Profilstranda.

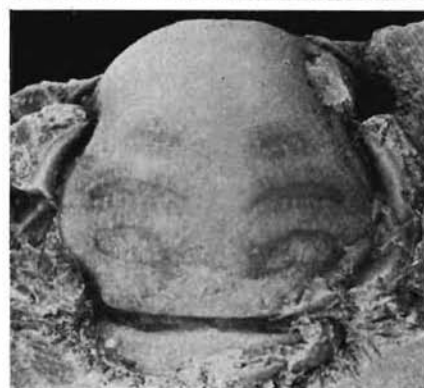
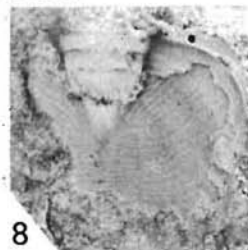
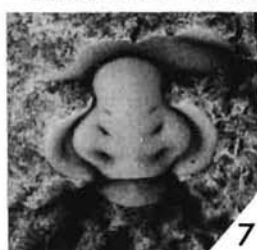
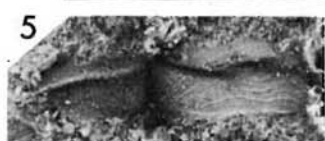
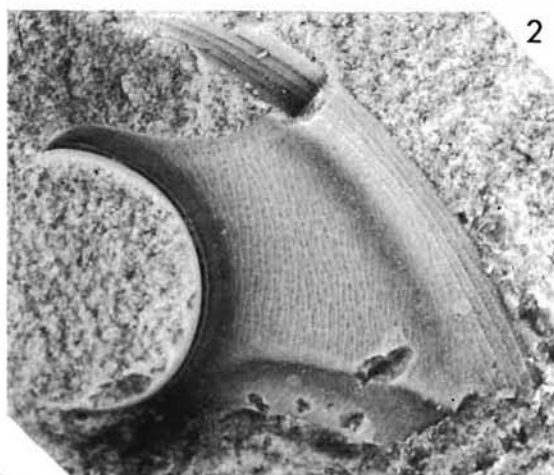


PLATE 5

- Figs. 1-8, 10, 11. *Robergiella brevilingua* n. sp. (p. 44)
- Figs. 1, 4, 11. Cranidium, dorsal and anterior views, $\times 12$, and lateral view, $\times 8$. Holotype, PMO NF 3143. Upper Profilbekken Member on Profilbekken, V₄b, 50 m from base.
- Fig. 2. Exfoliated large cranidium, $\times 10$, showing relatively deep glabellar furrows. Profilbekken Member on Profilbekken, 41 m from base of Member. PMO NF 3131.
- Figs. 3, 6. Cranidium, dorsal and antero-dorsal view to show border, $\times 12$. Profilbekken Member on Profilbekken, 50 m from base. PMO NF 1401.
- Figs. 5, 10. Cranidium preserving sculptural details, $\times 12$, anterior and dorsal views. PMO NF 3132. Horizon as Fig. 1.
- Figs. 7, 8. Free cheek, lateral, $\times 10$, and dorsal, $\times 12$, views. Profilbekken Member on Profilbekken. PMO NF 3110.
- Figs. 9, 12-14, 16. *Robergiella lundehukensis* n. sp. (p. 46)
- Fig. 9. Incomplete cranidium, $\times 12$, NF 2475. Horizon and locality as holotype, Fig. 12, in lower part of Profilbekken Member.
- Figs. 12, 16. Cranidium, holotype, dorsal and anterior views, $\times 12$. PMO NF 2405. Profilbekken Member, lower part on Stream A on Olenidsletta, 23 m from base.
- Fig. 13. Small free cheek, $\times 12$, PMO NF 2466. Horizon and locality as holotype.
- Fig. 14. Small cranidium, $\times 12$. PMO NF 2429. Horizon and locality as holotype, Fig. 12.
- Figs. 15, 17, 18. *Remopleurides* sp. A. (p. 43)
- Figs. 15, 17, 18. Cranidium, dorsal, oblique lateral and anterior views, $\times 12$. Profilbekken Member, V₄b, 60 m from base of Member on Profilbekken. PMO NF 1295.

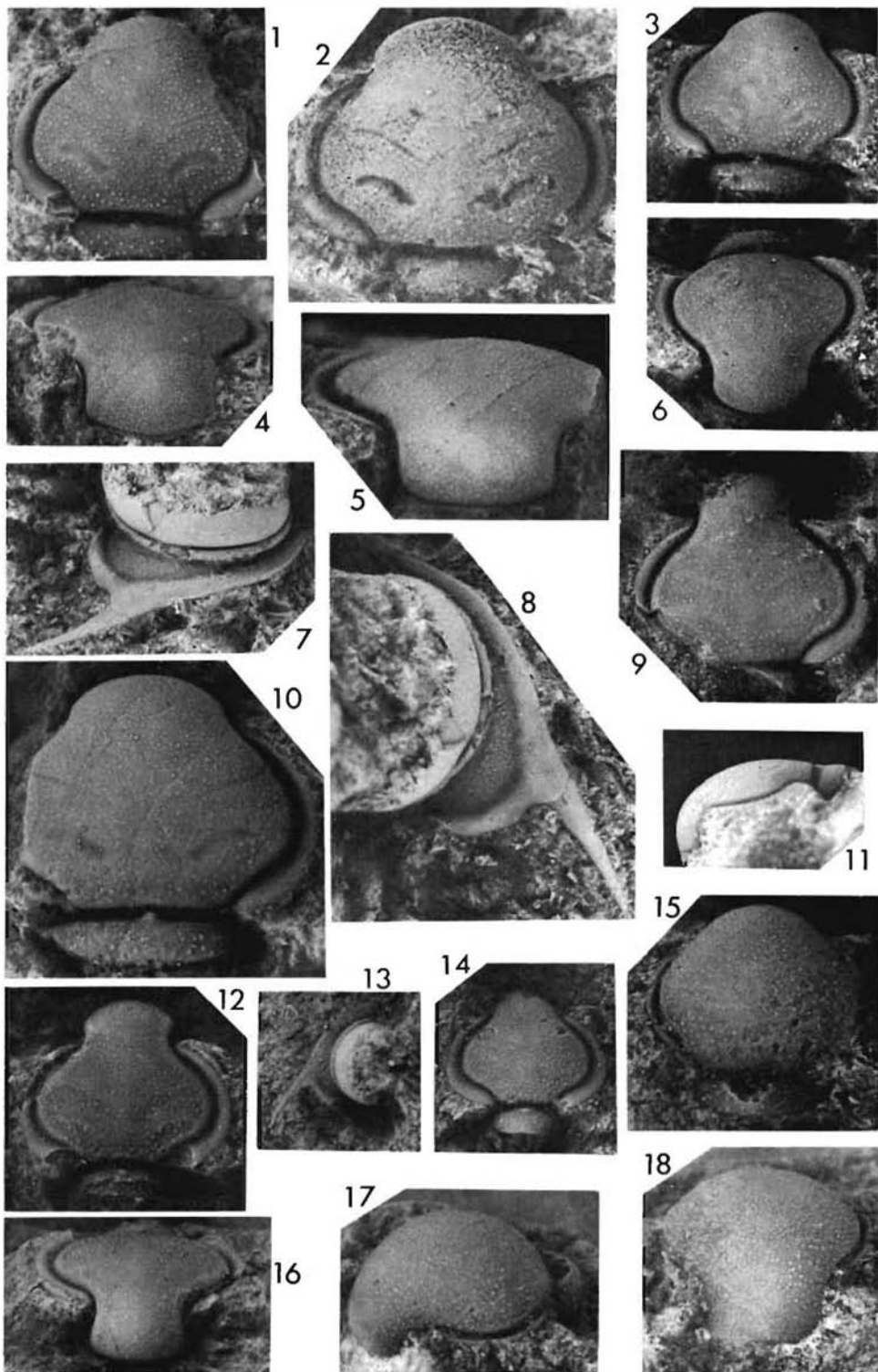


PLATE 6

- Figs. 1-8, 11. *Raymondaspis vespertina* ROSS (p. 50)
- Figs. 1, 2, 5. Cranidium, dorsal, lateral and anterior views, $\times 8$. Upper part of Profilbekken Member, V₄b, 40 m from base of Member, on Profilbekken. PMO NF 3117.
- Figs. 3, 7. Pygidium, dorsal and posterior views, $\times 8\frac{1}{2}$. PMO NF 3118. Same bed as cranidium, Fig. 1.
- Fig. 4. Pygidium, $\times 8$. PMO NF 3121. Profilbekken Member on Profilbekken, 38 m from base.
- Fig. 6. Free cheek, plan view, $\times 8$. PMO NF 3120. Same bed as cranidium, Fig. 1.
- Fig. 8. Small cranidium, $\times 5$, same bed as cranidium, Fig. 1. PMO NF 3119.
- Figs. 9, 13. *Opipeuter angularis* (YOUNG) (p. 48)
- Fig. 9. Cranidium, $\times 8$. Olenidsletta Member, V₁a, about 8 m from base on Olenidsletta. NF 2983.
- Fig. 13. Small, incomplete cranidium, $\times 8$. Same bed as Fig. 9. PMO NF 2986.
- Figs. 12, 14, 15. *Opipeuter inconnivus* FORTÉY (p. 47)
- Fig. 12. Free cheek viewed laterally, $\times 8$. Olenidsletta Member, V₁c, 68 m from base on Profilstranda. NF 648.
- Figs. 14, 15. Hypostoma, ventral view, $\times 12$, and enlargement, $\times 25$, showing maculae. PMO NF 769. Same bed as free cheek Fig. 12.
- Fig. 10. *Opipeuter* cf. *inconnivus* FORTÉY (p. 48)
- Fig. 10. Free cheek viewed laterally, $\times 8$. Compare Fig. 12. Same bed as free cheek, Fig. 12. PMO NF 690.

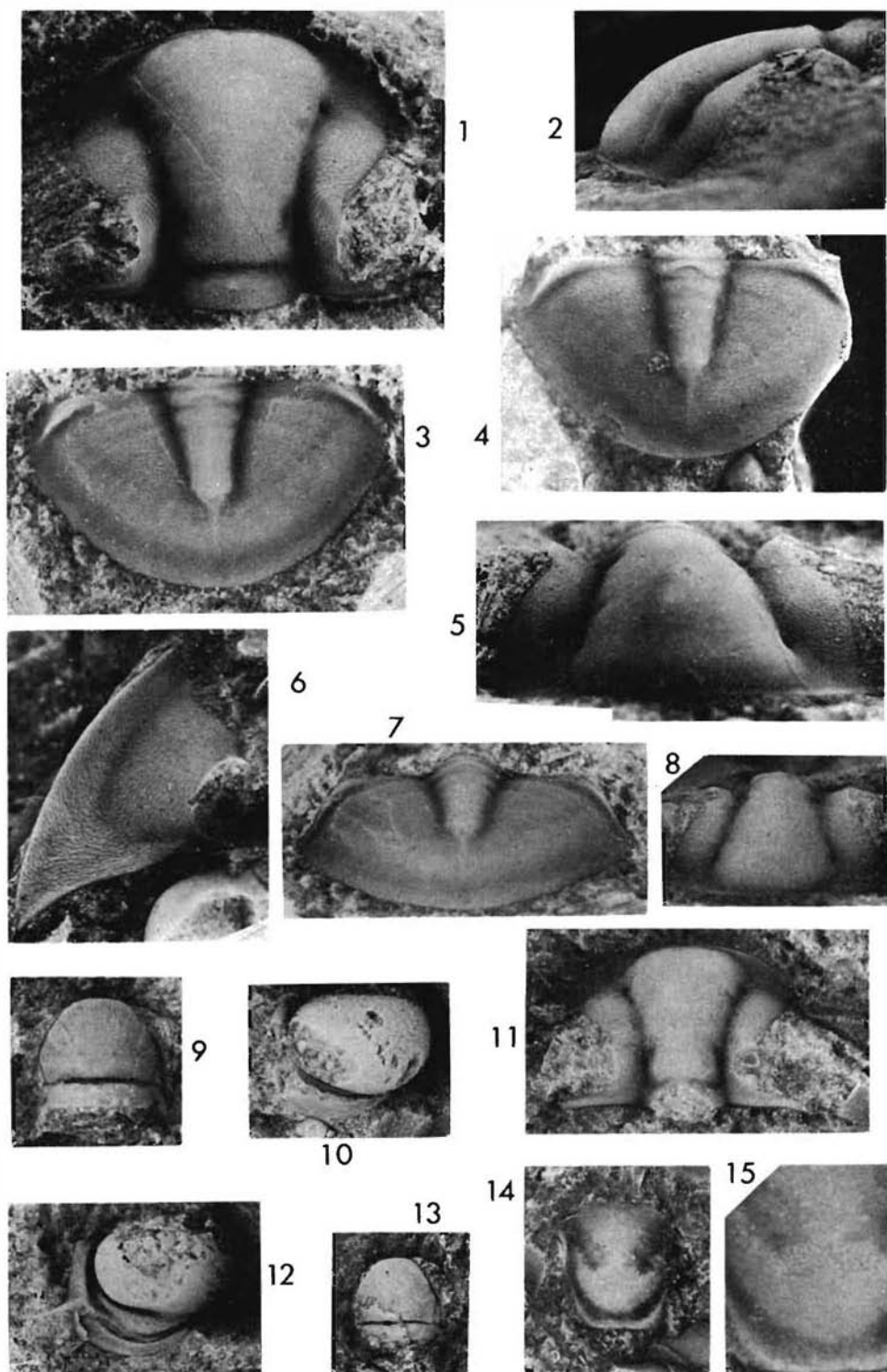
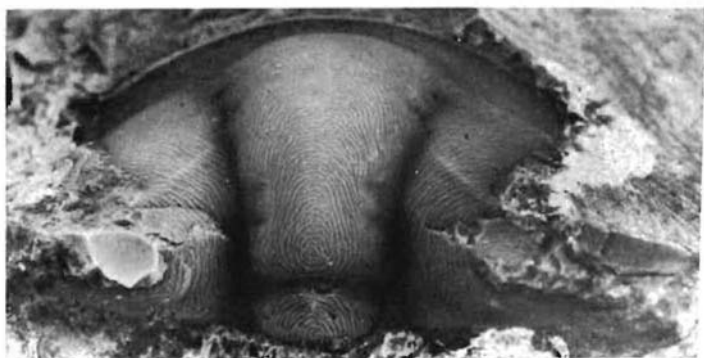


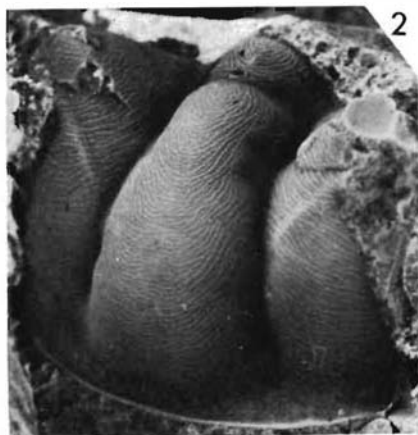
PLATE 7

- Figs. 1-4, 6. *Turgicephalus falcatus* n. gen., n. sp. (p. 52)
- Figs. 1-3. Holotype cranium, $\times 8$, dorsal, oblique lateral and anterior views. Compare with cranium of *Raymondaspis*, Plate 6. PMO NF 235. Lower Profilbekken Member on Profilstranda, V₄a, 20 m from base.
- Figs. 4, 6. Hypostoma, Fig. 6, ventral view, $\times 8$. Fig. 4, detail of sculpture and macula, $\times 20$. PMO NF 1840. Profilbekken Member on stream A on Olenidsletta, 23 m from base of Member.
- Figs. 5, 7. *Turgicephalus hinloppensis* n. gen., n. sp. (p. 55)
- Figs. 5, 7. Holotype, cranium, dorsal and anterior views for comparison with *T. falcatus*, $\times 10$. PMO NF 3122. Upper part of Profilbekken Member on Profilbekken, V₄b, 49 m from base.

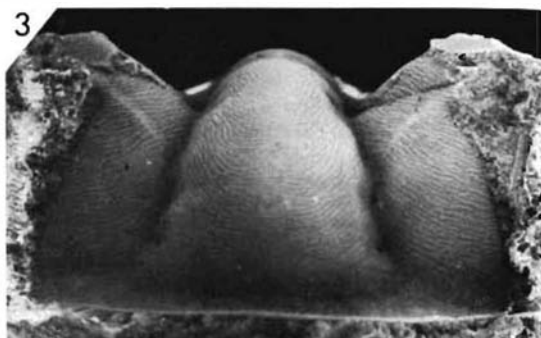
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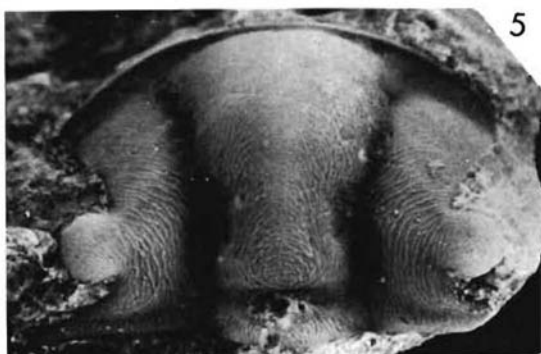
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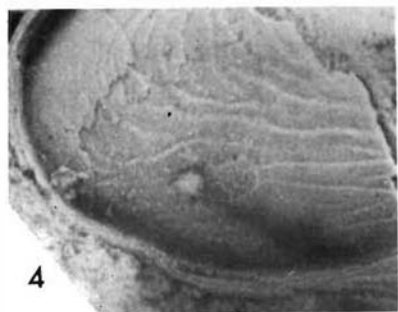
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PLATE 8

- Figs. 1, 2, 4-6, 8, 10. *Turgicephalus falcatus* n. gen., n. sp. (p. 52)
- Figs. 1, 2. Pygidium, dorsal, $\times 10$, posterior, $\times 5$, views. PMO NF 214. Lower part of Profilbekken Member, V₄a, on Profilstranda, about 20 m from base.
- Figs. 4, 5. Free cheek, dorsal and anterior views, $\times 8$. PMO NF 1879. Profilbekken Member on stream A on Olenidsletta, 23 m from base.
- Fig. 6. Pygidium showing doublure, $\times 5$. PMO NF 230. Profilbekken Member on Profilstranda, about 20 m from base of Member.
- Fig. 8. Small cranidium, $\times 6$. PMO NF 264. Horizon and locality as previous.
- Fig. 10. Free cheek showing doublure, $\times 6$. A second small cheek shown on same piece. PMO NF 284. Horizon and locality as Fig. 6.
- Figs. 3, 7, 9. *Turgicephalus hinloppensis* n. gen., n. sp. (p. 55)
- Figs. 3, 9. Pygidium, posterior and dorsal views, $\times 5$. PMO NF 1246. Upper part of Profilbekken Member, V₄b, on Profilbekken 70 m from base.
- Fig. 7. Internal mould of incomplete pygidium, $\times 8$. Note caeca, muscle scars on axis. PMO NF 1272, locality as previous 68 m from base.

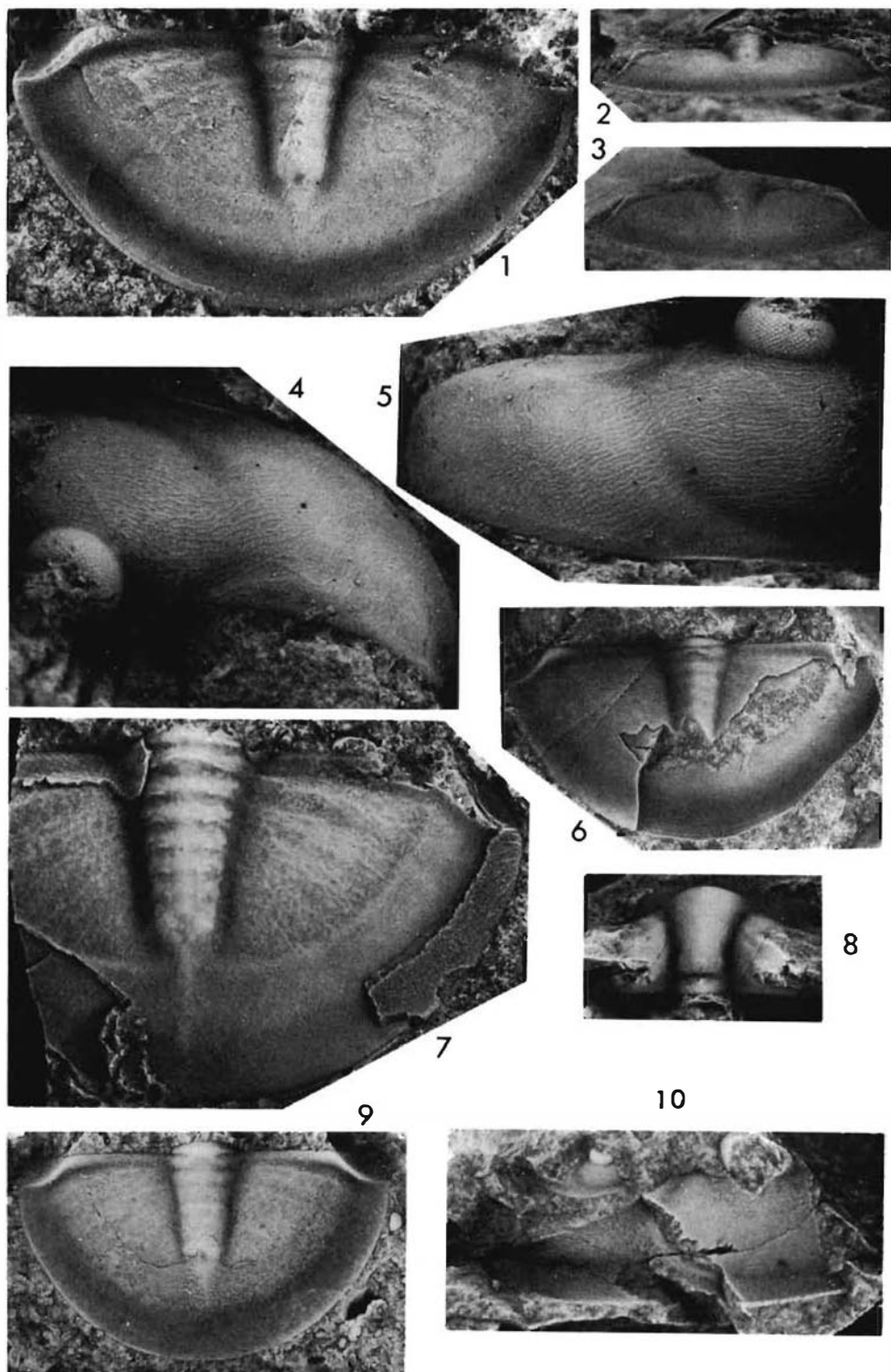


PLATE 9

- Figs. 1-3, 5. *Theamataspis tuber* n. sp. (p. 58)
 Figs. 1-3, 5. Holotype, cranidium with small patch of exoskeleton removed, dorsal, oblique lateral and anterior views, $\times 10$. Fig. 3. Oblique anterior view to show areas of muscle insertion, $\times 12$. PMO NF 510. Olenidsletta Member, V₂a, 89 m from base of Profilstranda.
- Fig. 4. ?*Protostygina* sp. ind. (p. 56)
 Fig. 4. Cranidium, $\times 13$. PMO NF 519a. Olenidsletta Member, V₂a, on Profilstranda, 85 m from base.
- Figs. 6-7. *Turgicephalus* cf. *hinloppensis* (p. 56)
 Fig. 6. Pygidium, dorsal view, $\times 3$. PMO NF 3316. Profilbekken Member, 35 m from base on Profilbekken.
 Fig. 7. Fragmentary and highly caecate large pygidium, $\times 2$. PMO NF 3315. Horizon and locality as previous.
- Fig. 8. *Cloacaspis ekphymosa* FORTEY. (p. 104)
 Fig. 8. Latex cast from cranidium, $\times 4$, better preserved than those illustrated in FORTEY (1974a). PMO NF 3108. V₃a on the shore at Olenidsletta.

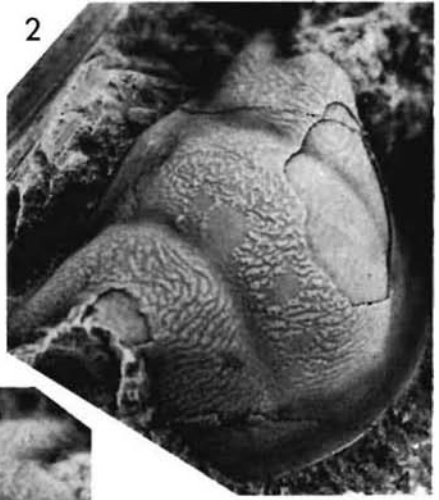


PLATE 10

- Figs. 1-13. *Illænus oscitatus* n. sp. (p. 60)
- Figs. 1-3. Holotype, cranidium preserving exoskeleton, palpebral, lateral and anterior views, $\times 6$. PMO NF 282. Profilbekken Member, V₄b, 60 m from base on Profilbekken.
- Figs. 4, 7. Exfoliated large cranidium, $\times 2$, palpebral and lateral views. Profilbekken, 38 m from base, of Profilbekken Member. PMO NF 226.
- Figs. 5, 6. Small cranidium dorsal and lateral views, $\times 8$. PMO NF 1347. 68 m from base of Profilbekken Member.
- Figs. 8, 10. Pygidium, incomplete on left side, posterior and dorsal views, $\times 6$. PMO NF 283. Profilbekken Member, 45 m from base on Profilbekken.
- Fig. 11. Hypostoma, ventral view, $\times 6$. PMO NF 227, locality and horizon as cranidium, Fig. 4.
- Fig. 9. Rostral plate, $\times 4$. 70 m from base of Profilbekken Member. PMO NF 147a.
- Fig. 12. Exfoliated pygidium showing doublure. Note pits on internal mould of exoskeleton. PMO NF 228. 65 m from base of Profilbekken Member, on Profilbekken.
- Fig. 13. Free cheek, plan view, $\times 6$. PMO NF 317. Locality and horizon as Fig. 12.

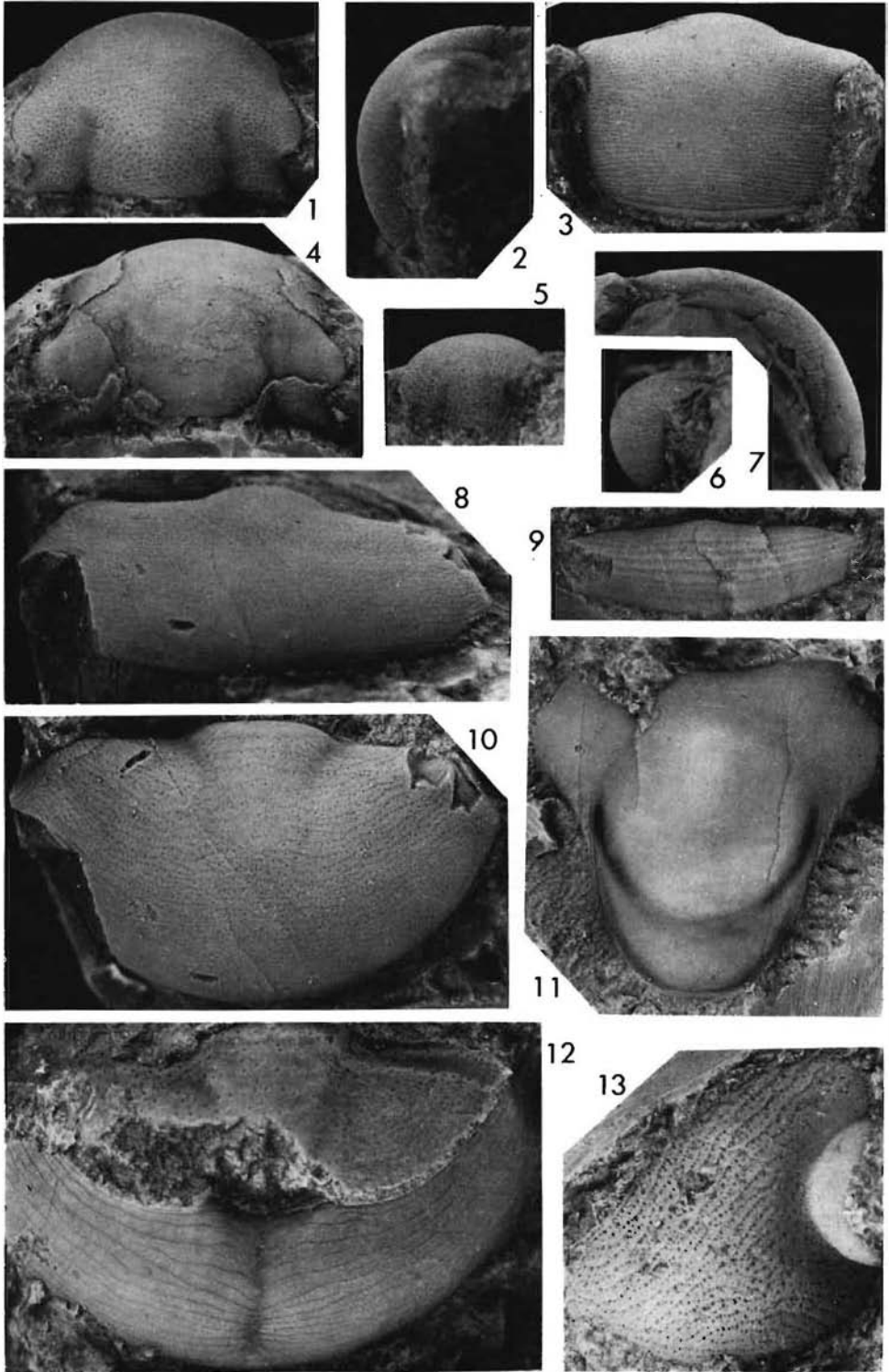


PLATE 11

- Figs. 1-8, 11. *Oenonella paulula* n. gen., n. sp. (p. 63)
- Fig. 1. Incomplete cranidium, $\times 15$. PMO NF 1327. Bed at transition from Olenidsletta to Profilbekken Member, in base of latter, isolated outcrop of Profilbekken.
- Figs. 2, 6. Cranidium, $\times 12$, dorsal, oblique anterior views. Locality and horizon as Fig. 1. Holotype, PMO NF 1324.
- Figs. 3, 7. Pygidium, dorsal, lateral views, $\times 15$. Locality and horizon as Fig. 1. PMO NF 1325.
- Figs. 4, 8. Cranidium, dorsal and lateral views, $\times 15$. PMO NF 1328. Horizon and locality as Fig. 1.
- Fig. 5. Partial cranidium showing some inflation of 1P glabellar lobe, $\times 15$. NF 1343. Locality as previous.
- Fig. 11. Small pygidium, $\times 15$. PMO NF 1337. Locality, horizon as previous.
- Figs. 9, 10, 12-21. *Ischyrotoma twenhofeli* RAYMOND (p. 65)
- Figs. 9, 10, 13. Cephalon, exfoliated except on genal borders, $\times 6$, lateral, dorsal and anterior views. PMO NF 138. Profilbekken Member on Profilbekken, V₄b, 68 m from base.
- Figs. 12, 14, 16, 17. Pygidium, lateral, dorsal and posterior views, $\times 6$. Fig. 16, detail of articulation. SM A 84346. Profilbekken Member on Profilbekken 46 m from base.
- Figs. 15, 18, 19. Incomplete cephalon, anterior, dorsal and lateral views, $\times 8$. Anterior view shows doublure and outline of rostral suture. SM A 84345, 65 m from base of Profilbekken Member.
- Figs. 20, 21. Pygidium, dorsal, posterior views, $\times 6$. PMO NF 3113. Profilbekken Member, 46 m from base.

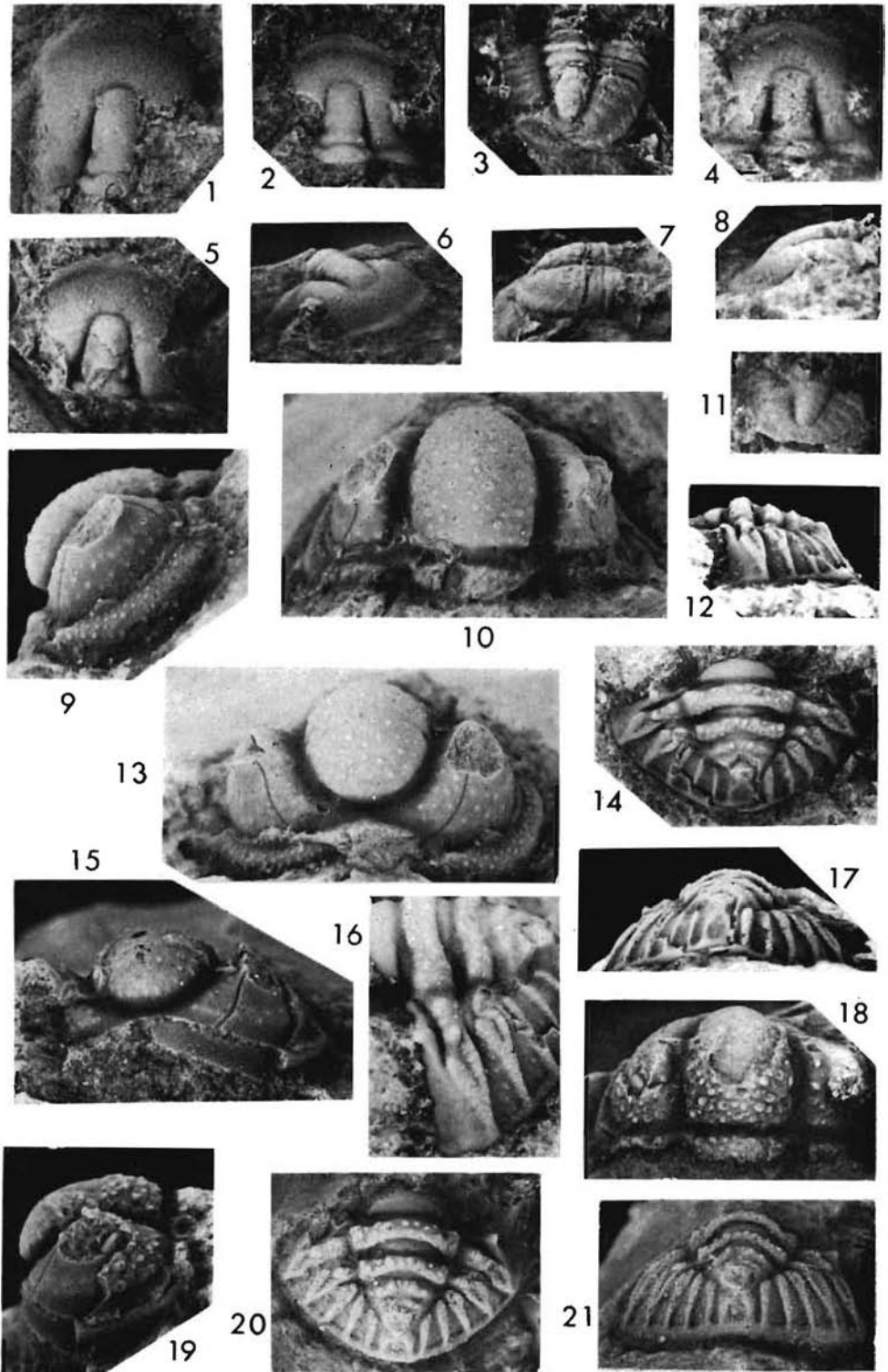


PLATE 12

- Figs. 1–7. *Ischyrophyma? borealis* n. sp. (p. 67)
- Figs. 1, 6. Free cheek, $\times 5$. SMA 84347. Profilbekken Member, V₄b, on Profilbekken 57 m from base of Member.
- Figs. 2, 3, 5. Holotype, cranidium, exfoliated over glabella, dorsal, anterior and lateral views, $\times 5$. SMA 84343. Profilbekken Member on Profilbekken 55 m from base of Member.
- Figs. 4, 7. Cranidium, dorsal, lateral views, $\times 6$. SMA 84344. Same bed as holotype, Fig. 2.
- Figs. 8–17. *Acidiphorus brevispicatus* n. sp. (p. 69)
- Figs. 8, 12. Free cheek, internal mould dorsal and lateral views, $\times 6$. PMO NF 147b. Profilbekken Member, V₄b, 65 m from base on Profilbekken.
- Figs. 9–11. Cranidium, dorsal, anterior and lateral views, $\times 4$. Anterior view shows median swelling on border. PMO NF 3129. 70 m from base of Profilbekken Member.
- Figs. 13, 14. Holotype, well preserved cranidium, oblique lateral and dorsal views, $\times 6$. Note hooked smooth areas. PMO NF 1353. 68 m from base of Profilbekken Member.
- Fig. 15. Internal mould of cranidium, $\times 6$. PMO NF 143. Same bed as free cheek, Fig. 8.
- Figs. 16, 17. Internal mould of pygidium incomplete on right side, lateral and dorsal views, $\times 6$. PMO NF 1349. Horizon as holotype, Fig. 13.

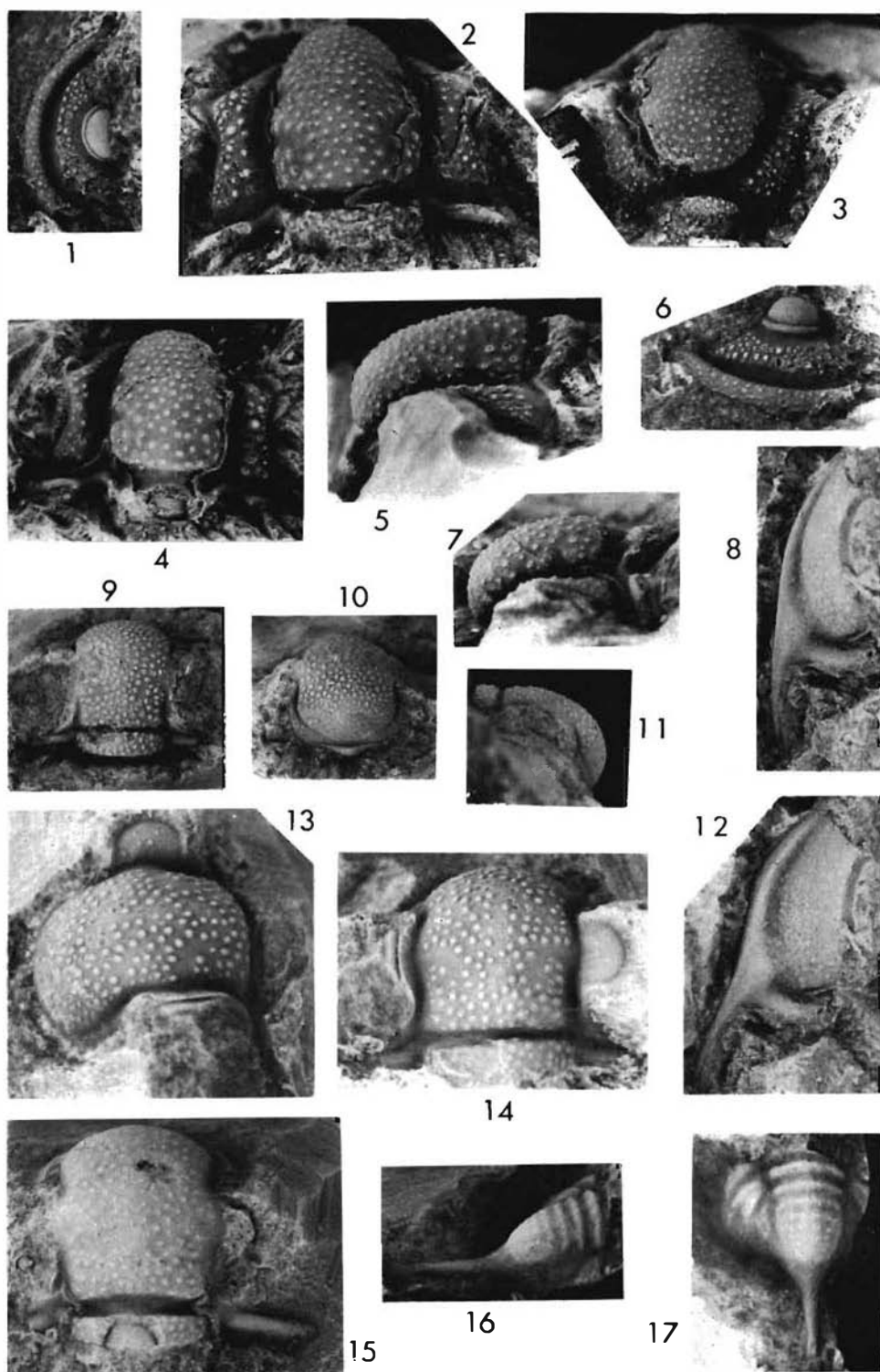


PLATE 13

- Figs. 1-9. *Acidiphorus* ? *ligo* n. sp. (p. 70)
- Figs. 1, 4. Holotype, cranidium, dorsal and anterior views, $\times 6$ and $\times 4$ respectively. PMO NF 126. Profilbekken, 68 m from base of Profilbekken Member, V₄b.
- Figs. 2, 9. Free cheek, dorsal and lateral views, $\times 8$. PMO NF 116. Same bed as Figs. 5, 7.
- Fig. 3. Small cranidium with more parallel sided glabella and longer preglabellar field, $\times 12$. PMO NF 33. Profilbekken, 63 m from base of Profilbekken Member.
- Figs. 5, 7. Pygidium showing caudal spine, dorsal and lateral views, $\times 4$. PMO NF 888.
- Fig. 6. Incomplete thorax and pygidium, $\times 4$. PMO NF 127. Locality as holotype, Fig. 1, 50 m from base.
- Fig. 8. Cranidium, showing both palpebral lobes, $\times 5$. PMO NF 30. Profilbekken, 65 m from base of Profilbekken Member.
- Figs. 10, 11. Bathyrine gen. and sp. indet. (p. 72)
- Fig. 10. Cranidium, $\times 3$, PMO NF 2767. Melt stream C on Olenidsletta, no more than 5 m from base of Olenidsletta Member, V₁a.
- Fig. 11. Slightly crushed cephalon, $\times 2\frac{1}{2}$. PMO NF 3113. Isolated outcrop of low Olenidsletta Member on Olenidsletta.

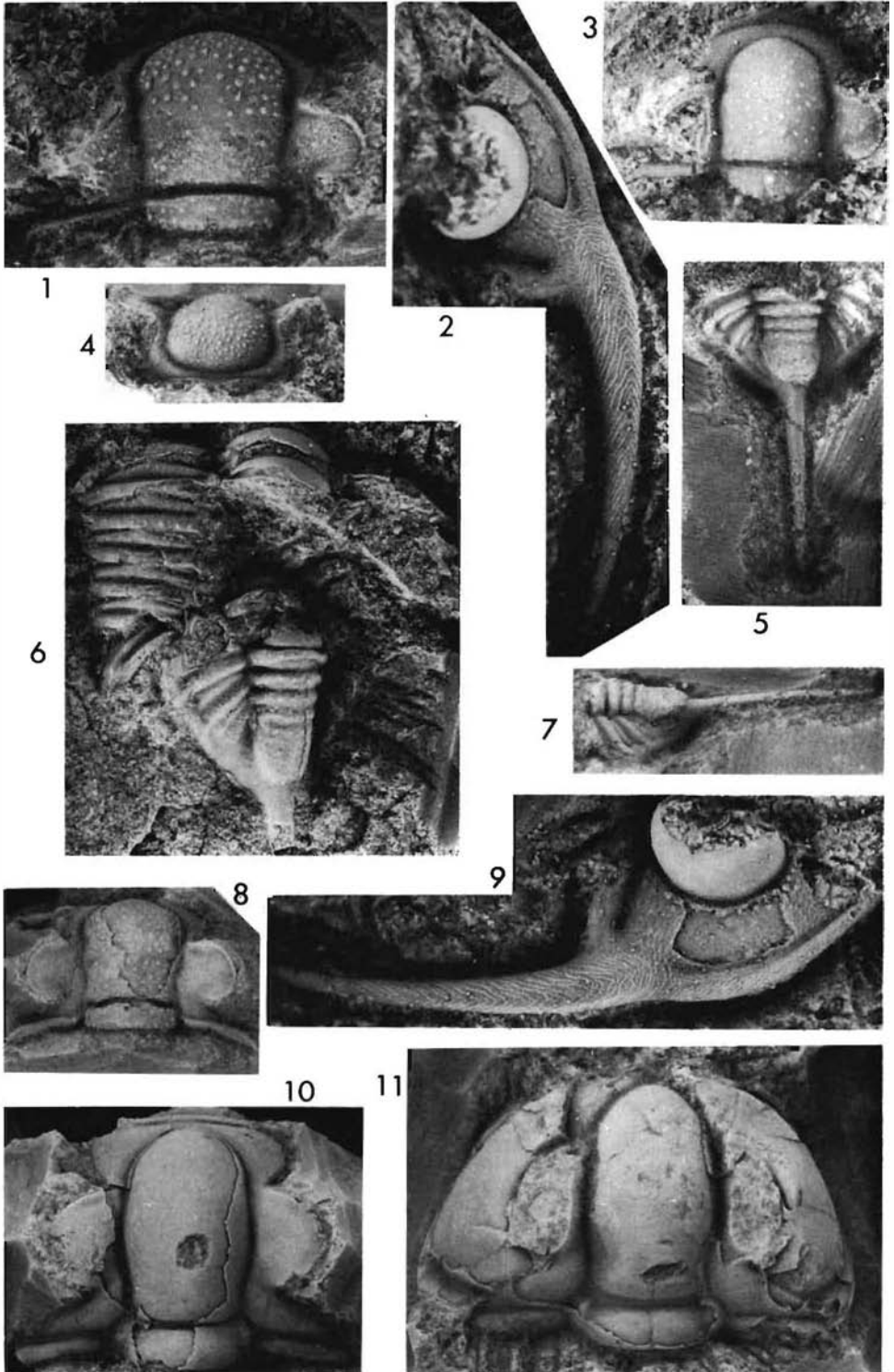


PLATE 14

- Figs. 1–12. *Punka caecata* n. sp. (p. 73)
- Figs. 1, 3, 4. Holotype, incomplete cranidium, dorsal, lateral views, $\times 4$. Fig. 4, detail of preglabellar field showing caeca, $\times 6$. PMO NF 243. Profilbekken Member, V₄b, 68 m from base on Profilbekken.
- Figs. 2, 5. Free cheek, plan view, $\times 6$, lateral view, $\times 4$. Note how terrace ridges pass over caeca, PMO NF 1231. Locality as holotype, Fig. 1, 70 m from base.
- Figs. 6–8. Cranidium, dorsal and lateral views, $\times 3$. Fig. 7, detail of glabella showing sculpture, $\times 7$. Locality and horizon as previous specimen. PMO NF 1243.
- Fig. 9. Small cranidium, $\times 8$, without conspicuous caeca. PMO NF 242. 68 m from base of Profilbekken Member on Profilbekken.
- Fig. 10. Pygidium, incomplete internal mould showing inflated areas on pleurae, $\times 6$. PMO NF 3112, Profilbekken, 50 m from base of Member.
- Figs. 11, 12. Pygidium preserving exoskeleton, dorsal, posterior views, $\times 6$. PMO NF 1393. Profilbekken Member on Profilbekken, 70 m from base.

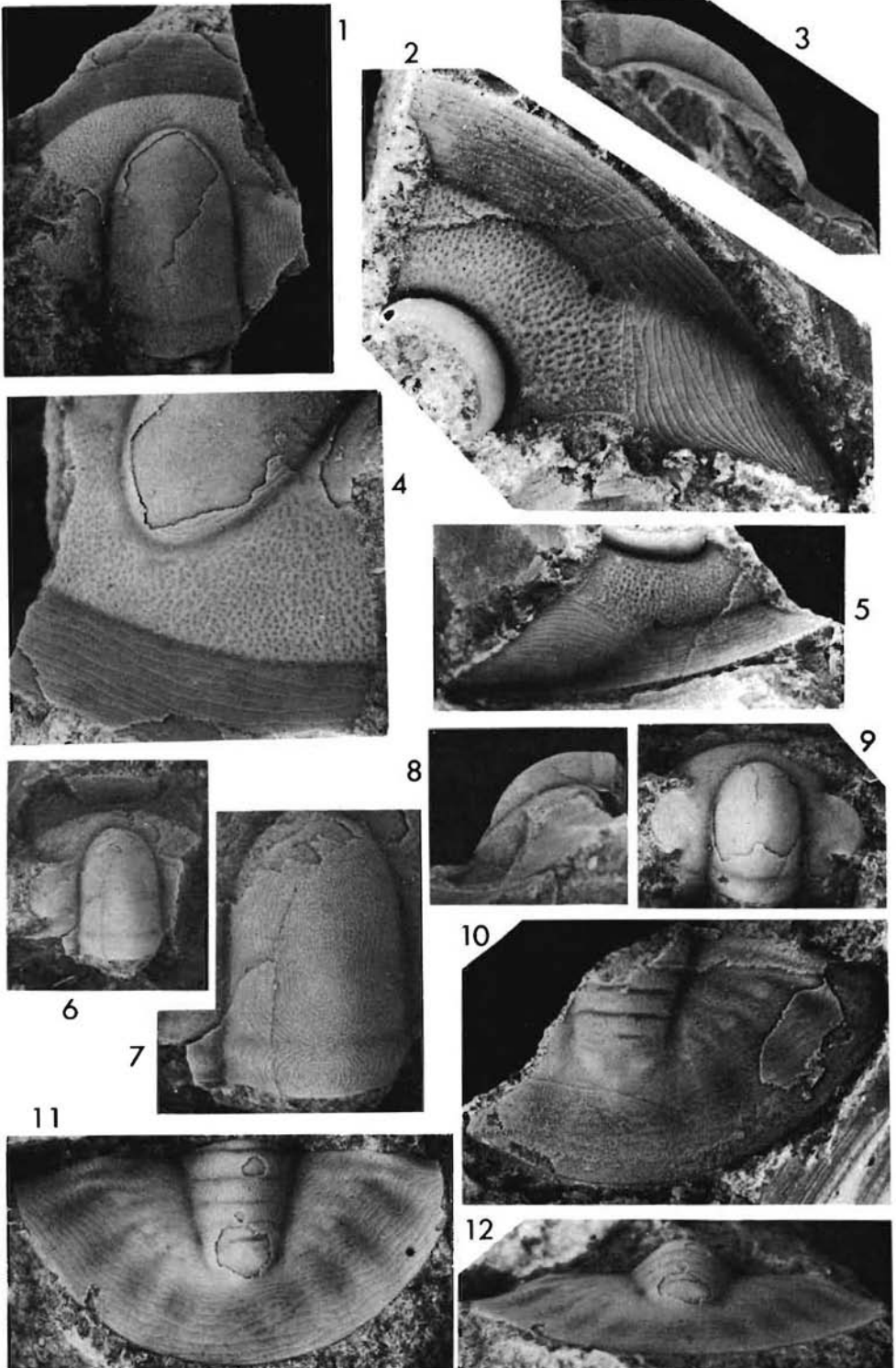


PLATE 15

Figs. 1-5. *Scotoharpes aduncus* n. sp. (p. 76)

Figs. 1, 5. Holotype, incomplete cephalon with long genal prolongation on left side almost to tip. Dorsal view, $\times 3$, lateral, $\times 2$. PMO NF 1356. Profilbekken Member, V₄b, on Profilbekken 64 m from base of Member.

Figs. 2, 3. Smaller cephalon than holotype, incomplete. Fig. 2, showing details of caeca, girder, upper lamella, Fig. 3, $\times 4$, latex cast from counterpart of Fig. 2, showing width of brim. PMO NF 115.

Fig. 4. Small cephalon, broken on right side, $\times 4$. PMO NF 148. Locality as holotype, 60 m from base of Profilbekken Member.

Figs. 6, 7. Bathyurelline gen. et sp. indet. (p. 75)

Fig. 6. Fragmentary cranidium, PMO NF 1392, $\times 6$. Profilbekken Member, V₄b, on Profilbekken, 68 m from base.

Fig. 7. Incomplete pygidium, $\times 6$, PMO NF 123. Locality and horizon as fragmentary cranidium, Fig. 6.

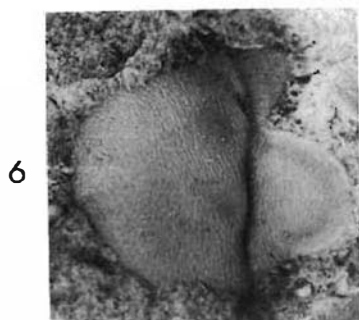
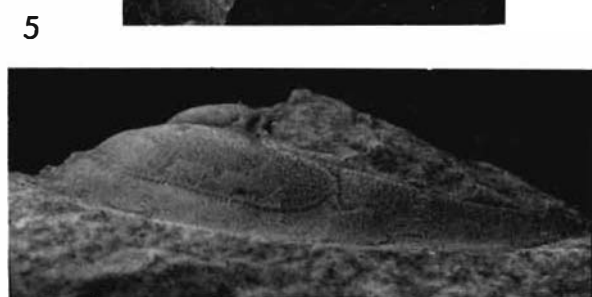
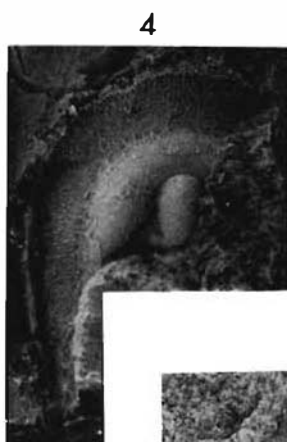
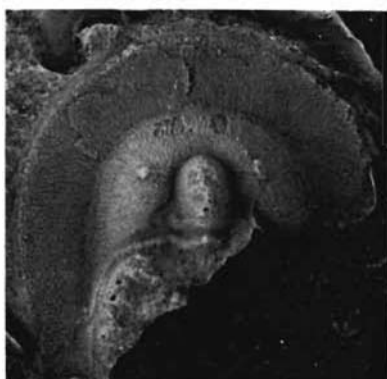


PLATE 15

- Figs. 1-11. *Sycophantia seminosa* n. gen., n. sp. (p. 78)
- Figs. 1, 7. Holotype, cranidium, dorsal and oblique lateral views, $\times 6$. PMO NF 125. Profilbekken Member, V₄b, 68 m from base of Member of Profilbekken.
- Figs. 2, 4. Incomplete cranidium, lateral and dorsal views, $\times 2$. PMO NF 120. Horizon and locality as holotype, Figs. 1, 7.
- Figs. 3, 6. Hypostoma, oblique lateral and ventral views, $\times 6$ and $\times 8$ respectively. PMO NF 145. Horizon and locality as holotype, Fig. 1.
- Fig. 5. Ventral view of pygidium, $\times 1\frac{1}{2}$. PMO NF 128. Horizon and locality as holotype, Fig. 1.
- Figs. 8, 10. Pygidium in anterior and dorsal views, $\times 4$. PMO NF 140. Isolated limestone block from the interval 35-70 m, Profilbekken Member.
- Figs. 9, 11. Fragmentary large cranidium, $\times 2$, dorsal, anterior views. PMO NF 113. Horizon and locality as holotype, Fig. 1.

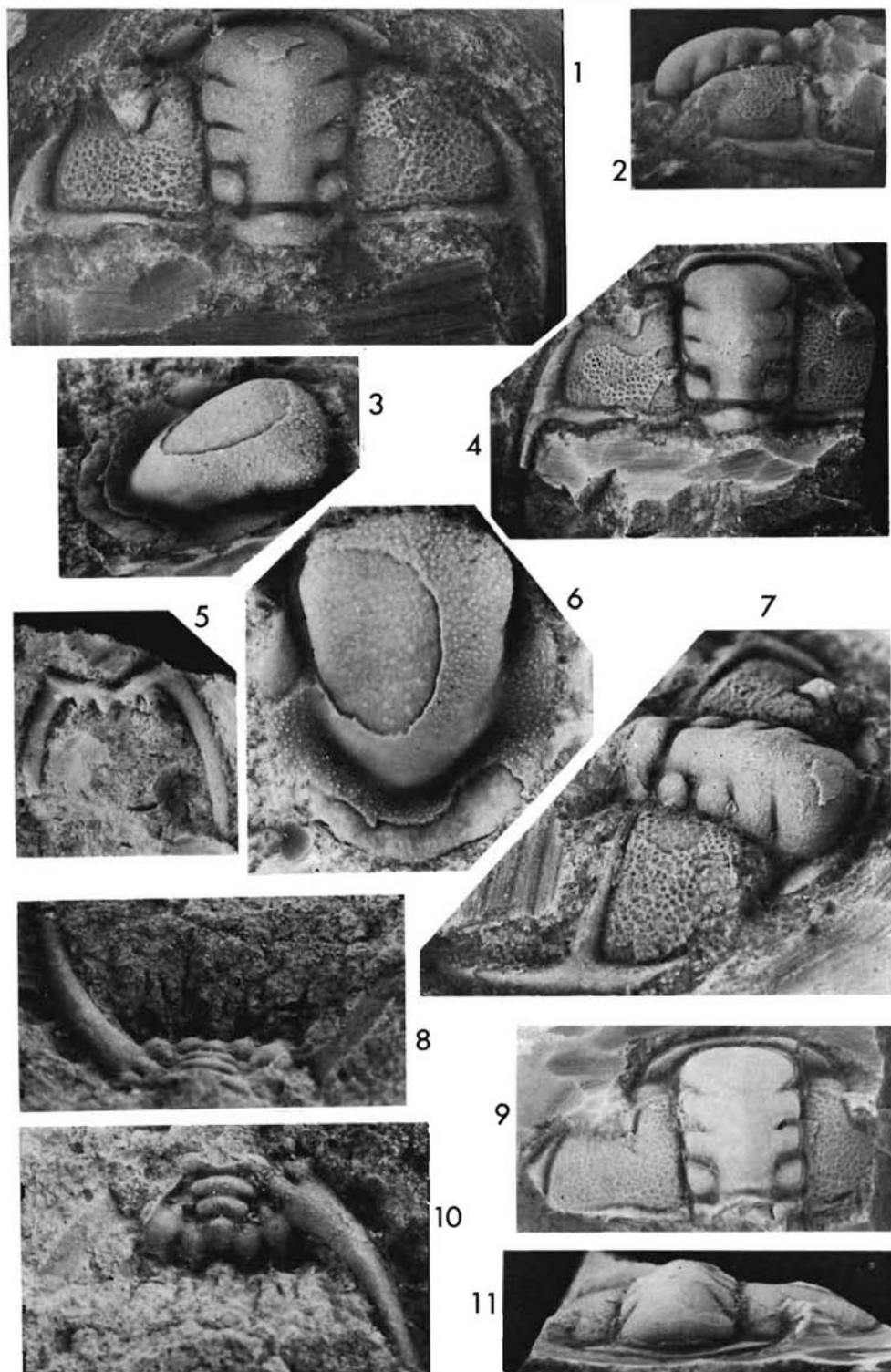


PLATE 17

- Figs. 1–6. *Parapilekia jacquelinae* n. sp. (p. 81)
- Figs. 1, 6. Holotype, cranidium, PMO NF 200, dorsal and lateral views, $\times 6$. Lower part of Profilbekken Member, V₄a, on Profilstranda, 20 m from base of Member.
- Figs. 2, 4. Cranidium, anterior, $\times 4$, and dorsal, $\times 6$, views. 1P furrow on right hand side pathologically developed. PMO NF 309. Same bed as holotype, Fig. 1.
- Figs. 3, 5. Pygidium, latex cast from external mould, $\times 8$, dorsal and lateral views. PMO NF 286. Same bed as holotype, Fig. 1.
- Figs. 7, 8. *Kawina* sp. B. (p. 85)
- Figs. 7, 8. Pygidium, dorsal and posterior, views, $\times 8$. PMO NF 317. Profilbekken Member, V₄b, 38–40 m from base on Profilbekken.
- Fig. 9. *Ampyxoides inermis* FORTEY (p. 103)
- Fig. 9. Small cranidium with frontal spine, $\times 8$; compare FORTEY 1975, Pl. 30, Fig. 12. Spine may be lost on larger cranidia. PMO NF 359. Low Profilbekken Member, V₄a on melt stream A on Olenidsletta, 12 m from base.

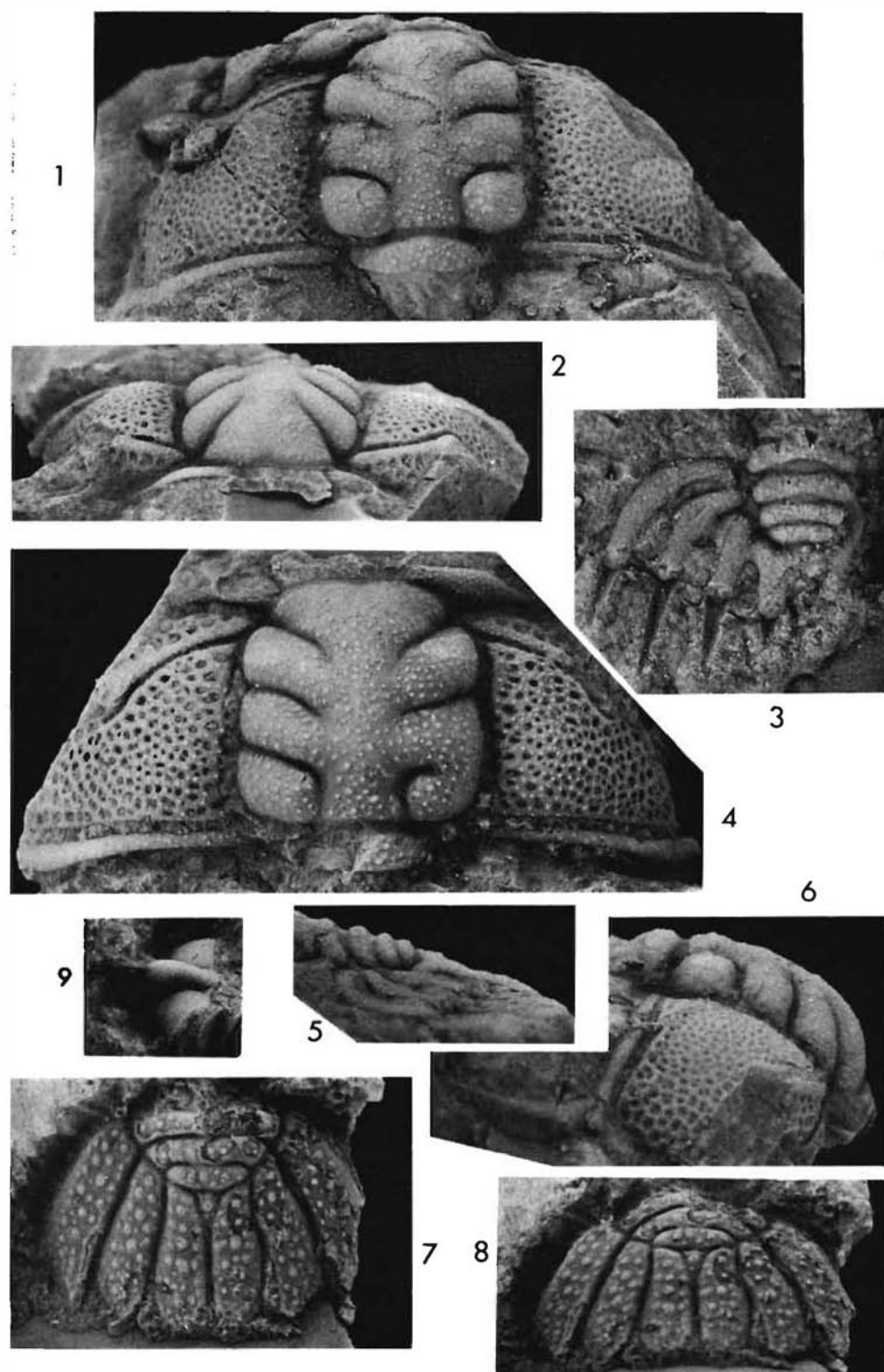


PLATE 18

- Figs. 1, 3, 4, 7. *Kawina wilsoni* Ross 1972 (p. 82)
- Figs. 1, 3. Cranidium, dorsal, $\times 6$ and lateral, $\times 4$ views. Specimen slightly crushed on left hand side. PMO NF 146. Profilbekken Member, V₄b, on Profilbekken 64 m from base of Member.
- Fig. 4. Pygidium, $\times 6$, from same bed as cranidium. PMO NF 137.
- Fig. 7. Fragmentary cranidium, $\times 6$. PMO NF 1267. 69-70 m from base of Member.
- Figs. 2, 5. *Kolymella* ? sp. indet. (p. 86)
- Figs. 2, 5. Incomplete cranidium, dorsal and lateral views, $\times 6$. Note fine granulation. PMO NF 246. Profilbekken Member, V₄b, 65 m from base on Profilbekken.
- Figs. 6, 8, 9, 12. *Kawina* sp. A. (p. 84)
- Figs. 6, 8. Cranidium, broken on right side, dorsal and lateral views, $\times 6$. PMO NF 1250. Profilbekken Member, V₄b, Profilbekken, 60 m from base.
- Figs. 9, 12. Pygidium, dorsal and posterior views, $\times 6$. PMO NF 1258. Profilbekken Member on Profilbekken, 68 m from base.
- Figs. 10, 11. *Kawina*? sp. aff. *sexapugia* Ross (p. 83)
- Figs. 10, 11. Cranidium, dorsal and anterior views, $\times 10$. Olenidsletta Member on Olenidsletta, V₁c, 75 m from base. PMO NF 245. The only example of a cheirurid associated with olenids in Spitsbergen.
- Figs. 13, 14. *Cydonocephalus* sp. A. (p. 85)
- Figs. 13, 14. Cranidium, dorsal and lateral views, $\times 4$. PMO NF 244. Olenidsletta Member, V₂a, about 85 m from base of Member on Profilstranda.

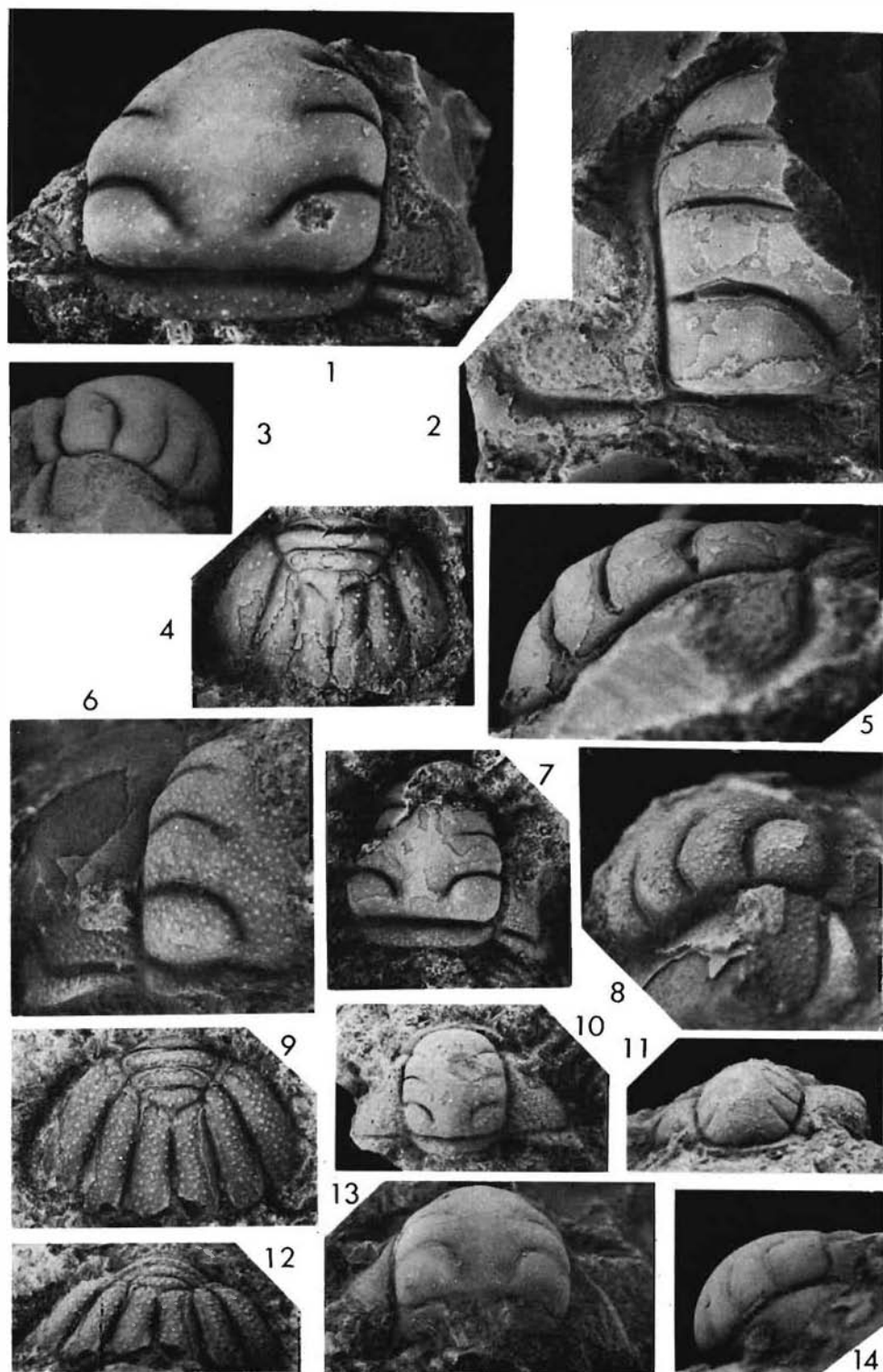


PLATE 19

- Figs. 1-8. *Europeites hyperboreus* n. sp. (p. 86)
- Figs. 1, 3, 8. Silicified, incomplete cranidium, preserving details of dorsal surface. Dorsal, anterior views, $\times 3$. Detail of left anterior shown on Fig. 8, $\times 6$, to shown granulation. PMO NF 1107. Profilbekken Member, low V₄b, 32-33 m from base of Member.
- Fig. 2. Free cheek (lacking eye) with cuticle, $\times 3$. PMO NF 1108. Horizon near Fig. 1.
- Fig. 4. Partial pygidium, dorsal surface removed to show ventral surface of spines and uniting strip of doublure, $\times 3$. PMO NF 1109. Profilbekken Member, 40 m from base on Profilbekken.
- Figs. 5-7. Internal mould of pygidium, dorsal, lateral and posterior views, $\times 2.7$. PMO NF 1110; same bed as cranidium, Fig. 1.

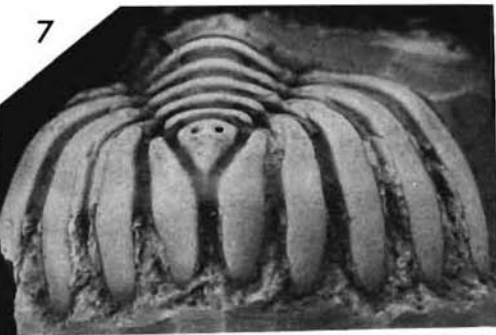
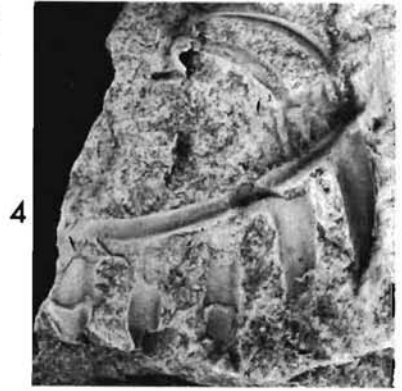
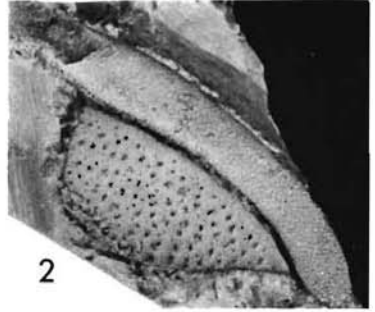


PLATE 20

Figs. 1-8. *Europeites hyperboreus* n. sp. (p. 86)

Figs. 1, 3. Holotype, cranidium, largely exfoliated and lacking left postocular limb. Dorsal and lateral views, $\times 2\frac{1}{2}$. Note sigmoidal 3P glabellar furrow. PMO NF 1102. Profilbekken Member, Profilbekken, 40 m from base.

Fig. 2. Hypostoma retaining exoskeletal posteriorly, ventral view, $\times 2\frac{1}{2}$. PMO NF 1103. 32-33 m from base of Profilbekken Member on Profilbekken.

Figs. 4, 7. Cranidium, left fixed cheek slightly displaced, dorsal and lateral views, $\times 2\frac{1}{2}$. Note straighter course of 3P furrow at this size. PMO NF 1104. 36 m from base of Profilbekken Member, Profilbekken.

Fig. 5. Latex cast from external mould of incomplete pygidium, $\times 2\frac{1}{2}$. PMO NF 1106. Locality as cranidium, Fig. 1.

Figs. 6, 8. Large exfoliated hypostoma, ventral and posterior views, $\times 2\frac{1}{2}$. Angulations on border shown on right. PMO NF 1105. Same bed as hypostoma, Fig. 2.

Figs. 9-11. *Strotactinus* sp. A. (p. 93)

Figs. 9, 10. Cranidium, postocular limbs not preserved, dorsal and lateral views, $\times 3$. PMO NF 85. Olenidsletta Member, V₂b, 102 m from base of Member on Profilstrenda.

Fig. 11. Fragmentary pygidium, $\times 5$. Note long terminal piece. PMO NF 98. Same bed as cranidium, Fig. 9.

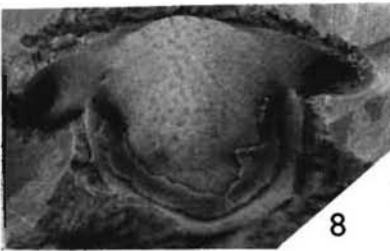
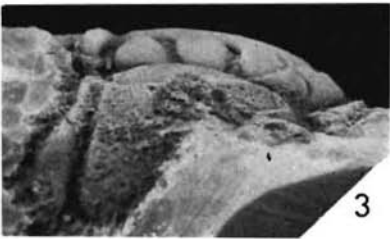


PLATE 21

Figs. 1–6. *Ectenonotus connemarus* (REED)..... (p. 91)

Figs. 1, 2, 5. Cranidium, dorsal, anterior views, $\times 2$, detail of glabella showing sculpture, $\times 8$. PMO NF 1245, Profilbekken Member on Profilbekken, V₄b, 70 m from base.

Figs. 3, 4. Pygidium, lateral and dorsal views, $\times 6$. Profilbekken Member, V₄ b, 36 m from base on Profilbekken. PMO NF 3130.

Fig. 6. Pygidium, *Cybele connemarus* of REED, 1909, $\times 6$. The outward turned pleural tips of this specimen compared with Figs. 3, 4, is a feature of the smaller size. Larger example of Irish material (SMA 10421) is not different in this regard. The specimen illustrated (SMA 10382b) shows the pygidial axis particularly well. Shangort beds, Co. Galway, western Eire.

Figs. 7–15. *Pliomerops praematura* n. sp. (p. 89)

Figs. 7, 9. Holotype, cranidium, incomplete on left side, lateral and dorsal views, $\times 6$. PMO NF 1120. Profilbekken Member, V₄b, on Profilbekken, 65 m from base.

Fig. 8. Fragmentary large cranidium, $\times 2$. PMO NF 1121. Horizon as holotype, Fig. 9.

Fig. 10. Fragmentary glabella and part of border, $\times 3$. PMO NF 1122. 50 m from base of Profilbekken Member, on Profilbekken.

Figs. 11, 15. Hypostoma, ventral and lateral views, $\times 5\frac{1}{2}$. PMO NF 1129. Same bed as holotype, Fig. 9.

Figs. 12–14. Pygidium, dorsal, posterior and lateral views, $\times 2\frac{1}{2}$. PMO NF 1198. 46 m from base of Profilbekken Member on Profilbekken.

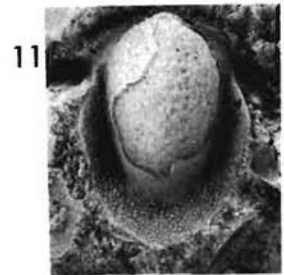
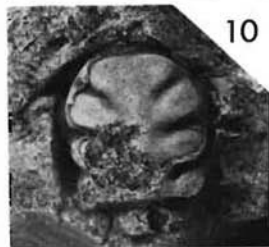
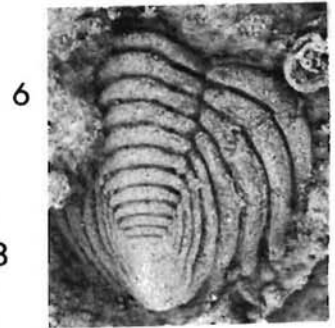
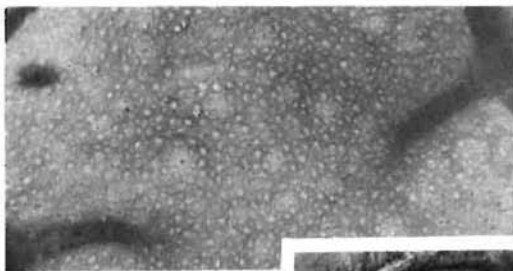
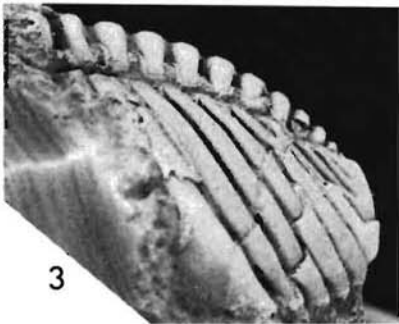


PLATE 22

- Figs. 1–15. *Cybelurus halo* n. sp. (p. 95)
- Figs. 1, 14. Holotype, internal mould of almost complete dorsal exoskeleton.
Fig. 1, latex cast from counterpart, $\times 4$. Fig. 14, pygidium, $\times 6$.
PMO NF 1278. 68 m from base of Profilbekken Member, V₄b,
on Profilbekken.
- Fig. 2. Incomplete exfoliated cranidium, showing isolation of posterior
part of 3P glabellar furrow, $\times 4$. SMA 84323. Locality as holotype,
57 m from base of Profilbekken Member.
- Fig. 3. Hypostoma, ventral view, $\times 8$. SMA 84331. 38 m from base of
Profilbekken Member.
- Figs. 4, 10, 12. Well-preserved cranidium, internal mould, dorsal, anterior and
lateral oblique views, $\times 3$. SMA 84321. 72 m from base of Profil-
bekken Member on Profilbekken.
- Fig. 5. Small exfoliated cranidium, $\times 4$. SMA 84328. 63 m from base of
Profilbekken Member.
- Figs. 6, 11. Internal mould of pygidium, dorsal and lateral views, $\times 4$. SMA
84330. 58 m from base of Profilbekken Member on Profilbekken.
- Fig. 7. Free cheek, $\times 4$. SMA 84324. 50 m from base.
- Fig. 8. Immature cranidium, $\times 25$. SMA 84327. Locality and horizon as
Fig. 9.
- Fig. 9. Stratigraphically early cranidium, $\times 3$. SMA 84322. 30 m from
base of Profilbekken Member.
- Fig. 13. Anteroventral view of free cheek, sutural outline on right, $\times 6$.
SMA 84326. 61 m from base of Profilbekken Member.
- Fig. 15. Latex cast taken from external mould of pygidium, showing sculp-
ture and spines, oblique view, $\times 10$. SMA 84332. Horizon and
locality as Fig. 9.

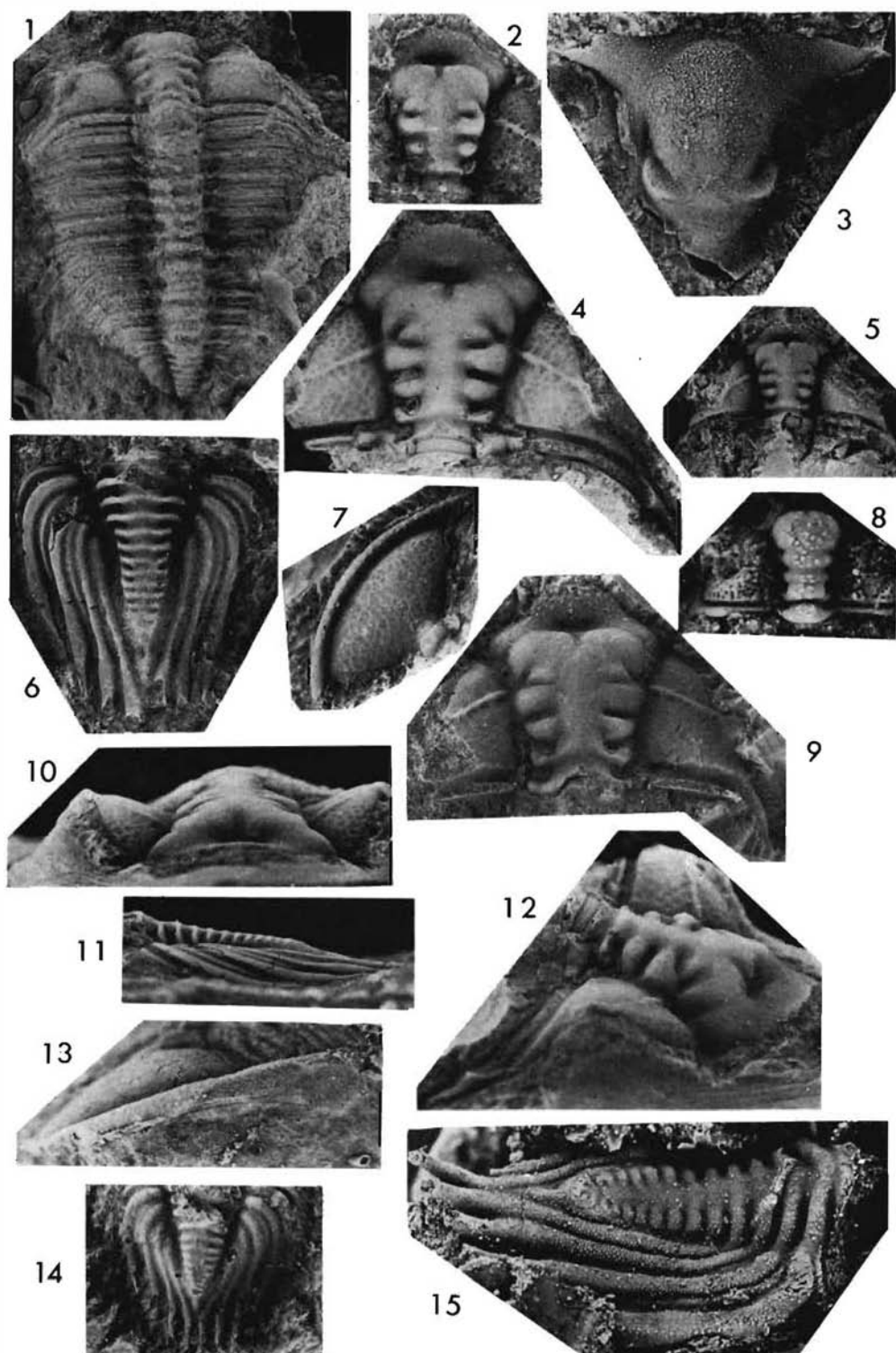


PLATE 23

- Figs. 1–6. *Cybelurus brutoni* n. sp. (p. 98)
- Fig. 1. Internal mould of incomplete cranidium, $\times 4\frac{1}{2}$, showing tubercles on internal surface of anterior border. SMA 84334. Lower part of Profilbekken Member, V_{4a}, on Profilstrenda, 20 m from base.
- Fig. 2. Pygidium, $\times 4$, same bed as cranidium, Fig. 1. SMA 84335.
- Figs. 3, 4. Holotype, cranidium, oblique lateral and dorsal views, $\times 6$. SMA 84333. Profilbekken Member, V_{4a}, on Profilstrenda, about 25 m from base.
- Fig. 5. Hypostoma, ventral view, $\times 6$. PMO NF 267. Locality as last, 20 m from base of Member.
- Fig. 6. Latex cast of internal mould of cranidium preserving palpebral lobes, $\times 4$. PMO NF 174. From an horizon very low in the Profilbekken Member, south of melt stream A on Olenidsletta.
- Figs. 7–9. *Cybelurus* cf. *mirus* (BILLINGS) (p. 99)
- Figs. 7–9. Cranidium, $\times 2$, dorsal, lateral, oblique views. PMO NF 1264. Profilbekken Member, V_{4b}, 68–70 m from base on Profilbekken.
- Figs. 10–14. *Lyrapsyge ebriosus* n. gen., n. sp. (p. 100)
- Fig. 10. Cranidium, slightly crushed but preserving genal spines, $\times 3$. PMO NF 497. Olenidsletta Member, V_{2a}, about 85 m from base of Member on Olenidsletta.
- Figs. 11, 14. Pygidium retaining some cuticle, $\times 3$, lateral, dorsal views. SMA 84338. Horizon and locality as previous.
- Fig. 12. Free cheek, anterior view, $\times 4$. SMA 84341. Horizon and locality as pygidium, Fig. 14.
- Fig. 13. Fragmentary cranidium in anterior view to show structure of anterior border, $\times 3$. SMA 84336. Horizon and locality as pygidium, Fig. 14.

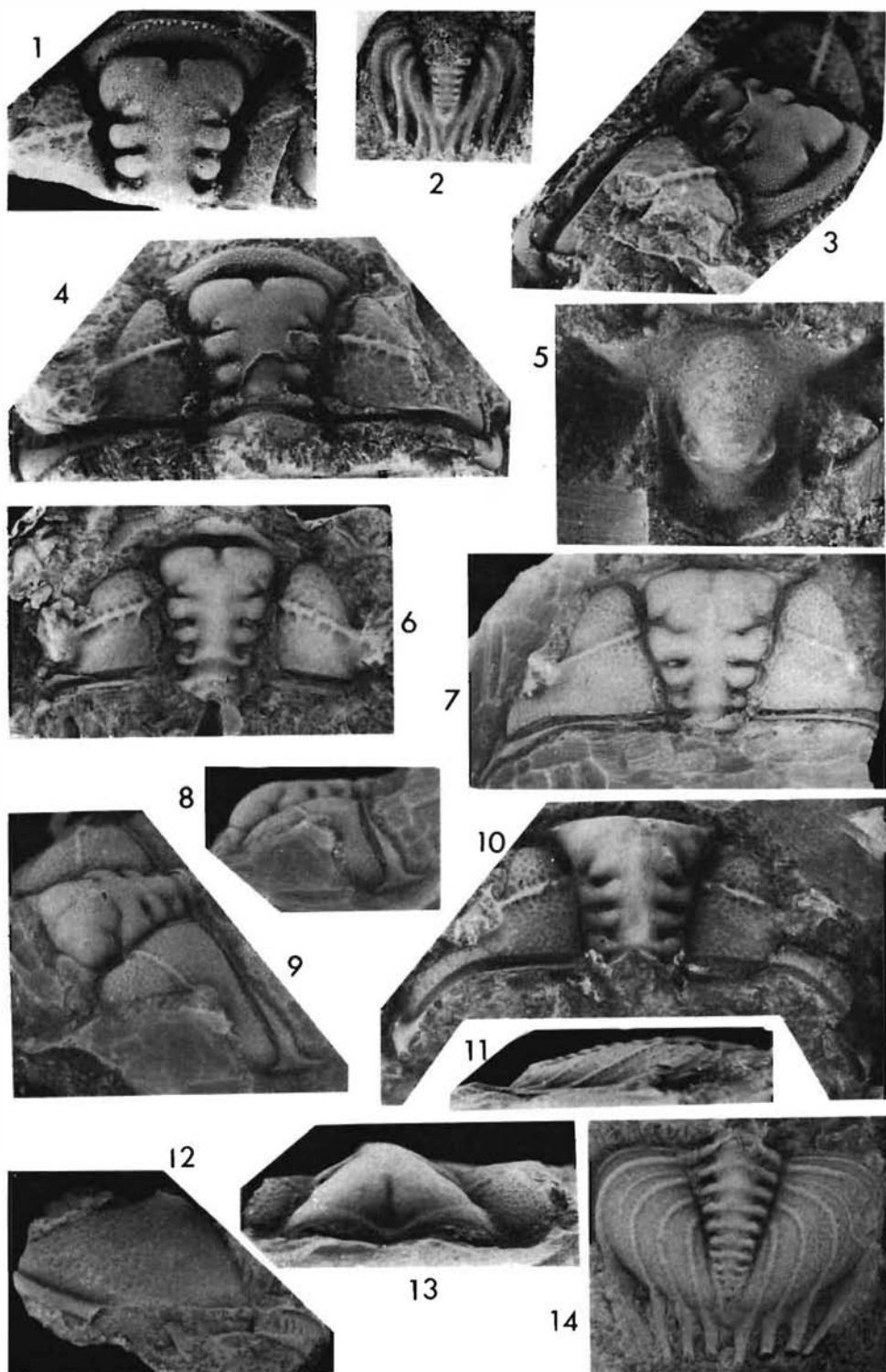


PLATE 24

- Figs. 1-9. *Lysiphe ebriosus* n. gen., n. sp. (p. 100)
- Figs. 1, 4, 5, 9. Holotype, exfoliated cranidium, dorsal, anterolateral, lateral and anterior views, $\times 3$. PMO NF 2131. Olenidsletta Member, V₃a, melt stream B on Olenidsletta, horizon 80-85 m from base of Member.
- Figs. 2, 6. Hypostoma, oblique lateral and ventral views, $\times 6$. PMO NF 2149. Same bed as holotype, Fig. 1.
- Figs. 3, 7. Pygidium, preserving spines particularly well, in oblique lateral, and anterior views showing upward curvature of spines. $\times 3$. PMO NF 2136. Same bed as holotype, Fig. 1.
- Fig. 8. Hypostoma, $\times 6$. PMO NF 3114. Olenidsletta Member on Profilstranda, 85 m from base.



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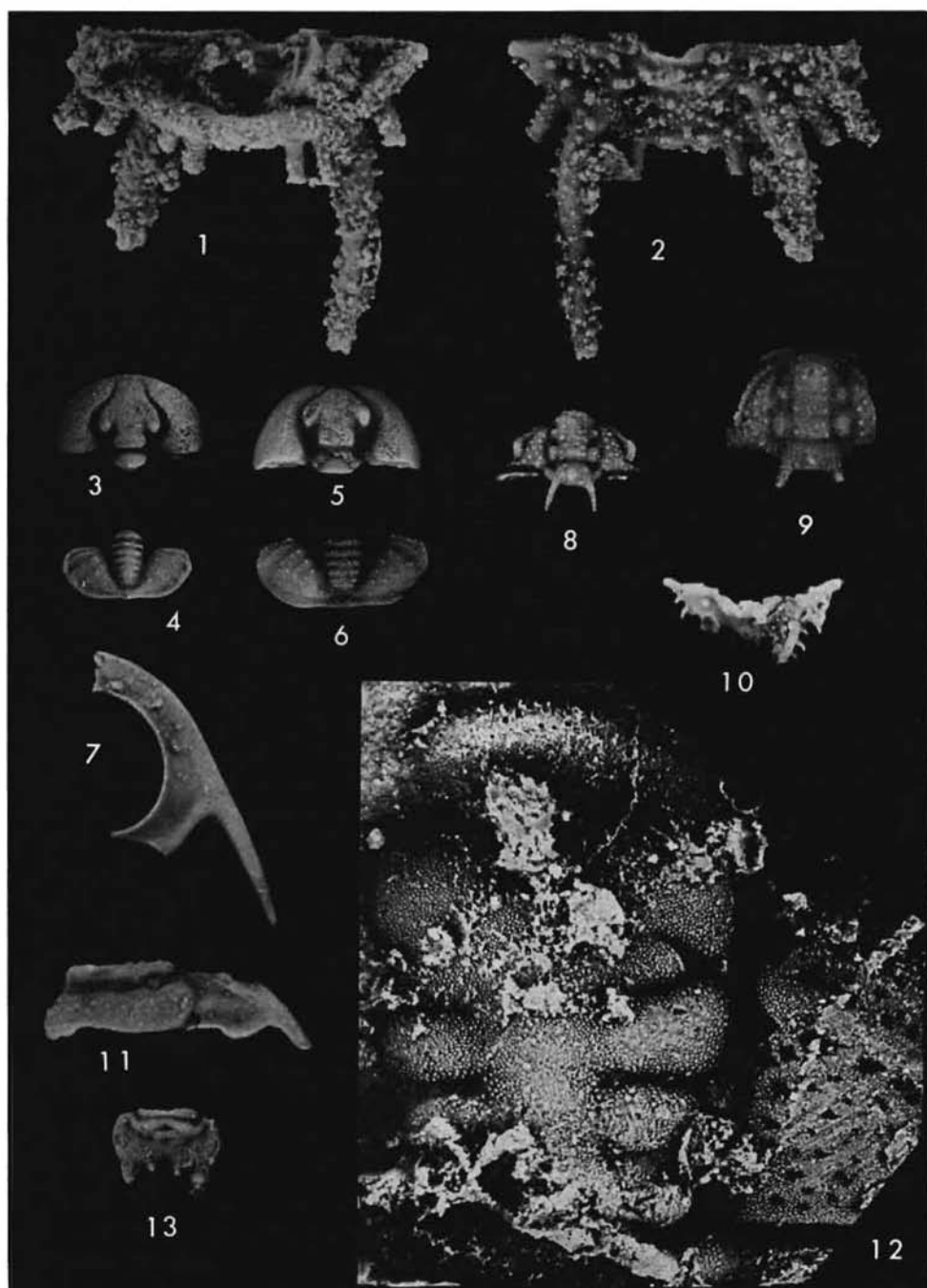
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PLATE 25

- Figs. 1, 2. *Diacanthaspis* sp. indet. (p. 103)
 Figs. 1, 2. Somewhat coarsely silicified pygidium, ventral and dorsal views,
 $\times 12$. PMO NF 3105. Profilbekken Member, V₄b, 40 m from base
 on Profilbekken.
- Figs. 3, 4. *Shumardia acuticaudata* n. sp. (p. 34)
 Fig. 3. Phosphatised and partially pyritised internal mould of cranium,
 $\times 12$. Basal Profilbekken Member, V₄a, on stream A on Olenid-
 sletta. PMO NF 3106.
 Fig. 4. Internal mould of pygidium, $\times 12$. Same bed as previous. PMO
 NF 3107.
- Figs. 5, 6. *Shumardia minaretta* n. sp. (p. 35)
 Fig. 5. Pyritised internal mould of cranium, $\times 12$. PMO NF 3144.
 Olenidsletta Member, V₂a, 90 m from base, on Profilstranda.
 Fig. 6. Pyritised internal mould of pygidium, $\times 12$. PMO NF 3146.
 Same bed as previous.
- Figs. 8–10. *Ceratocephala* sp. indet. (p. 102)
 Fig. 8. Pyritised internal mould of cranium, $\times 16$. PMO NF 3168.
 About 92 m from base of Olenidsletta Member on Profilstranda,
 V₂a.
 Fig. 9. Small pyritised cranium, $\times 16$. PMO NF 3169. Same bed as
 previous.
 Fig. 10. Imperfect pyritised pygidium, $\times 16$. PMO NF 3170. Same bed
 as Figs. 8, 9.
- Fig. 12. *Cybelurus halo* n. sp. (p. 95)
 Fig. 12. Latex cast taken from silicified external mould to show sculpture,
 $\times 10$ approx. SMA 84329. 30–32 m from base of Profilbekken
 Member.
- Figs. 7, 11, 13. *Robergiella brevilingua* n. sp. (p. 44)
 Fig. 7. Silicified small free cheek, $\times 20$. PMO NF 3171. Residue from
 limestone 35 m from base of Profilbekken Member, on Profilbekken.
 Fig. 11. Fragmentary thoracic segment, $\times 20$. PMO NF 3171a. Horizon
 and locality as last.
 Fig. 13. Silicified pygidium, $\times 15$. PMO NF 3172. From same bed as cheek
 and thoracic segment.



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