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Paleoecology of Productacea (Brachiopoda) from the Permian Kapp Starostin Formation, Spitsbergen

ABSTRACT: Productacean brachiopod assemblages are described from 10 taphocoenoses from various facies of the Upper Permian Kapp Starostin Formation in Spitsbergen. Time and space relationships among the investigated phenomena are based upon a previously established chronostratigraphic correlation of the strata. 15 productacean species are distinguished, based upon analysis of their morphology and ecology. Their paleontological descriptions take into account the ranges of their ecophenotypic variation. Shells adapted to three modes of life are recognized among the considered Productacea: (1) forms stabilizing within loose bottom sediments, (2) forms floating at the surface of soft substrates, and (3) forms living just below the surface of quaggy substrates. Distribution of the productacean assemblages in the Kapp Starostin Formation is analyzed within the framework of a reconstruction of the history of the Permian sea in this area. The main ecological controls upon this distribution include stratification of the water, substrate suitability for settlement, and coastal influences on the marine environment. Because of their spatially limited distribution and unrecognized evolution within the considered time interval, the investigated brachiopods cannot be employed for biochronostratigraphy.

Key words: Arctic, Spitsbergen, Permian, facies, paleontology (Brachiopoda).

Introduction

The Upper Paleozoic strata deposited within the post-Variscan transgressive cycle and exposed in Spitsbergen contain abundant brachiopod assemblages (Gobbett 1963). The present study is devoted to the Productacea, which are particularly diverse and abundant in these strata. The focus is

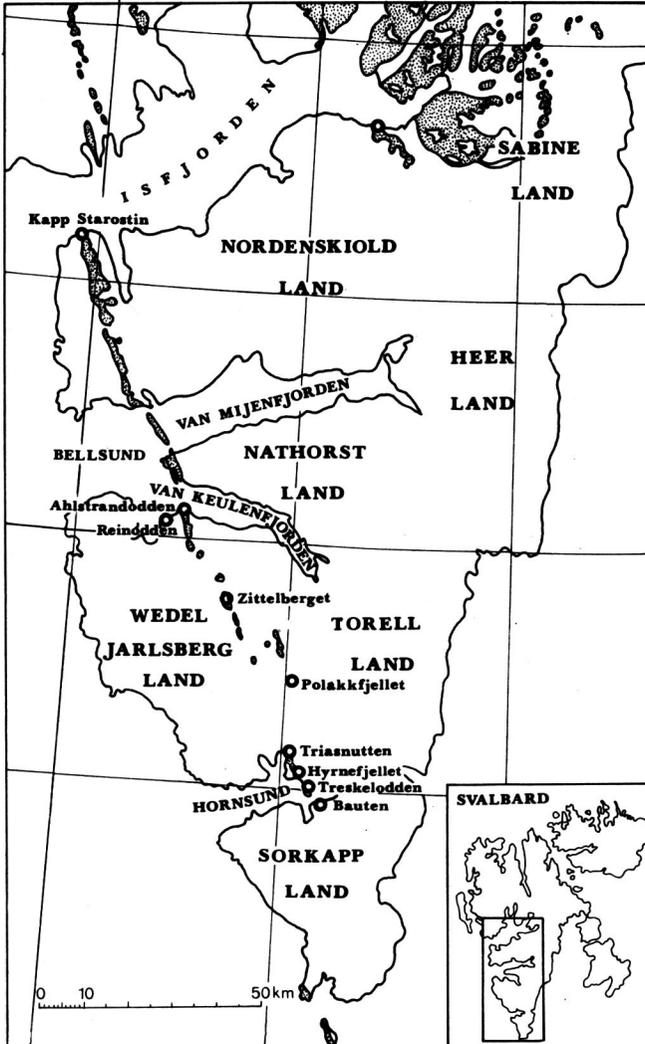


Fig. 1. Geographic extent of the Kapp Starostin Formation deposits (stippled)

primarily upon their paleoecology and intraspecific variation and the consequent taxonomic problems.

The study concerns materials collected from the Kapp Starostin Formation (Burov *et al.* 1965, Cutbill and Challinor 1965), which is well exposed in the central and western Spitsbergen (Fig. 1). The age of this formation was regarded as the Early to Late Permian transition (Stepanov 1957, 1973; Forbes *et al.* 1958; Ustritsky 1971). More recently, the base of the formation is attributed on the basis of its conodont fauna to the Roadian, or the uppermost Lower Permian (Szaniawski and Małkowski 1979),

while the demonstrably continuous sedimentary transition from the Kapp Starostin Formation to the overlying Triassic strata (Birkenmajer 1977) indicates that the formation encompasses the entire Upper Permian (Table 1).

Table 1

Stratigraphic position of the Kapp Starostin Formation within the Permian System

Russian Platform	Spitsbergen	Delaware Basin (USA)
TATARIAN KAZANIAN UFIMIAN	Kapp St. Fm. HOVTINDEN SVENSKEEGGA	OCHOAN GUADE- CAPITAN LUPIAN WORDIAN
KUNGURIAN ARTINSKIAN SAKMARIAN ASSELIAN		Roadian LEONARDIAN WOLFCAMPIAN

This study's focus upon paleoecology and paleobiology of the Productacea has been made possible by the author's two earlier studies: analysis of the facies distribution within the Kapp Starostin Formation (Małkowski and Hoffman 1979), and chronostratigraphic correlation of its various exposures and reconstruction of its depositional history (Małkowski 1982). The present study is distinctly bipartite in that the faunal distributions are analyzed separately from the facies development. These two analyses are linked together by the Productacea which are treated both as an object of paleobiological study and as a facies component. The empirical observations are then interpreted within the framework provided by a model of facies distribution in the Permian sea in the study area (Małkowski and Hoffman 1979). Ultimately, geodynamic processes are inferred as an explanation for these observations.

Brachiopod materials

The brachiopod collection taken from 10 exposures of the Kapp Starostin Formation (Fig. 1, Table 2) comprises over 2500 specimens, a couple of tens to a couple of hundreds per exposure (Fig. 2). The majority of the specimens are well preserved, often as single valves with clearly visible morphology and inner structure of the shell. Shell ornamentation is sometimes obliterated, and spines are preserved in only a few specimens, although they are abundant in the sediment. Shell microstructure is generally well preserved, except for partly silicified specimens where the original structure is partly replaced by chalcedonite spherulites.

The collected productacean brachiopods can all be attributed, on the

Table 2

Sample size (specimen number) of the brachiopods collected at various localities in the Kapp Starostin Formation

SPECIES	Lithological complexes									
	H-1	P-4b	V-1	A-1	F-5	P-3	Tr-2	F-8	F-1	P-1
<i>Horridonia timanica</i>	22	7	139	27	15				30	2
<i>Horridonia</i> aff. <i>horrida</i>			1				4			
<i>Svalbardoproductus arcticus</i>	3	76	45	10	22				21	
<i>Kochiproductus porrectus</i>	3		1	4	13		37	7		
<i>Waagenoconcha irginae</i>	18	15	32	12	12	11	22	7		23
<i>Yakovlevia impressa</i>			144	3						
<i>Yakovlevia duplex</i>	2	10		12	4					
<i>Yakovlevia mammata</i>					9					
<i>Megousia weyprechtii</i>	8	2	46	9	28		50		9	
<i>Megousia kulikii</i>			3	11			58			
<i>Linoproductus dorotheevi</i>										98
<i>Cancrinella spitsbergiana</i>			35	43			7	4		115
<i>Anemonaria pseudohorrida</i>	7	8	88	82	16		55		5	
<i>Liosotella robertiana</i>							25	9		
<i>Anidanthus aagardi</i>							2	1		
<i>Lingula frebaldi</i>										11
<i>Orbiculoidea winsensi</i>			5			2				
<i>Arctitreta kempei</i>	3	9	23	2	18				7	
<i>Pinegathyris royssiana</i>	1	13	10		11			3	12	
<i>Neophricadothyris asiatica</i>										32
<i>Pterospirifer cordieri</i>							2	3		7
<i>Spirifer striato-paradoxus</i>	6	12	39	5	12		7		17	
<i>Spirifer striato-plicatus</i>			26	4	10					
<i>Spiriferella keilhavii</i>	21	82	60		23					
<i>Spiriferella draschei</i>		13	5	9			70	5		27
<i>Rhynchopora variabilis</i>			25	30						350
	94	247	627	264	193	13	339	39	101	665
	Total									2582

basis of their morphology, to the species reported previously from Spitsbergen (Gobbett 1963; Biernat and Birkenmajer 1981). Their morphology and inner structure are satisfactorily known, and their taxonomy conforms to the standards accepted for the Productacea (Muir-Wood and Cooper 1960). Comparative studies have been made on the Permian brachiopods of the Arctic (Dunbar 1955, Gobbett 1963), and global distributions have also been compiled (Stehli 1973, Waterhouse 1973, 1976, Waterhouse and Bonham-Carter 1976). Nevertheless, the question arises concerning systematic relationships among morphologically similar phenotypes collected from neighboring localities. To give a species name to each morphologically distinct class of specimens rules out the possibility of clinal intraspecific variability as well as that of polytypic and evolving species (Mayr 1969).

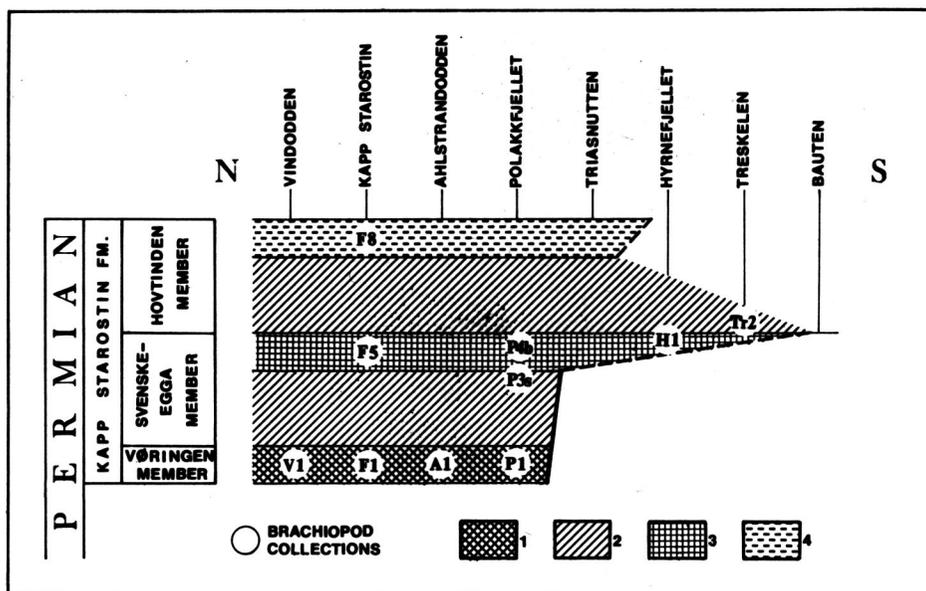


Fig. 2. Stratigraphic correlation and lithofacies of the investigated localities in the Kapp Starostin Formation. 1 — limestones, 2 — cherts, 3 — sandy limestones, 4 — marls and shales

Yet the ecological variation among brachiopods (Wright 1972), which has also been observed in the Productacea (Stepanov 1961, Gobbett 1961, Kaźmierczak 1967), calls for a consideration of these latter possibilities.

Up to date, several tens of productacean species have been described from the Permian of the Arctic (Ifanova 1972, Sarytscheva 1977, Ustritsky 1979), but their systematic and ecologic relationships remain thus far unknown. The present study is aimed to recognize the environmental controls upon the distribution of these Permian brachiopods and to establish their taxonomy allowing also for intraspecific variability.

¹ The investigated collection is housed in the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, and its symbol reads ZPAL Bp. 1—2500.

Methods

For the purposes of this study, 10 faunal localities have been selected within the Kapp Starostin Formation (Fig. 2). Their choice was based both on brachiopod abundance and preservation, and also on the absence of evidence for redeposition of fossils within particular taphocoenoses (Małkowski and Hoffman 1979). In each taphocoenosis, productacean phenae (*cf.* Camp and Gilly 1943, Mayr 1969) have been distinguished, and their systematic position is the subject of this study.

The author's previous investigations (Małkowski 1982) demonstrate that the strata constituent of the Kapp Starostin Formation were all deposited within a single epicontinental marine basin. Thus, all the faunal elements made part of a single ecosystem. The paleocological relationships among the productacean phena within an environmental continuum could therefore be also employed for their systematic analysis.

The criteria for species identification can thus be expanded to include not only morphological similarity but also ecological commonality of the living habits. The latter criterion approximates the neontological rule concerning the potential ability of interbreeding. Morphological variation among conspecific phena can reflect both genetic and environmentally controlled differences; the former cannot be directly studied in the fossil material but the latter can be estimated by analysis of covariation between morphology and environment. The author's explicit acceptance of a possibility of morphological differences between conspecific phena enforces the conclusion that species differences can be unequivocally identified solely for coexisting phena. In such a situation, a morphological gap separating particular phena is here assumed to indicate their differences at the species level. This assumption is supported by only minor significance of sexual dimorphism among the Productacea (Moore 1965, Ferguson 1969). For phena taken from separate localities of the formation, species or phyletic lineages are here recognized on the basis of similarity in both morphological and ecological characteristics. This method results in grouping together under one species heading forms that were previously attributed to different species or even genera.

Paleontological analysis of taphocoenoses from the Kapp Starostin Formation

Ten productacean phena have been distinguished in the taphocoenosis V-1 (from Vindodden), which happened to be the first to be studied. Each phenon has then been assigned a species name chosen after the diagnostic features of the species established previously in the paleontological literature. On the basis of the local phena, a set of index morphological traits have been determined for each of these species (Table 3). The index traits allow then for identification of presumably conspecific phena encountered in the other localities. The phena which could not be attributed to any of the species recognized in the previously analyzed localities have been regarded as representative of still another species, given the appropriate species name, and also assigned the set of index morphological traits. As a result, 15 productacean species have been distinguished in the brachiopod

Table 3

Index morphological features of the recognized productacean species

Species	Shell	Ornamenta- tion	Sinus	Umbo	Spines
<i>Horridonia timanica</i>	large, trapezoid, with auricles	absent or granular	distinct	narrow	thick and straight
<i>Svalbardoproductus arcticus</i>	large, sub-oval, with auricles	thick ribs (6—10 per cm)	distinct	massive	thick and straight
<i>Kochiproductus porrectus</i>	suboval, elongate, with a velum	short and straight, tuberculate ribs	shallow	massive	delicate
<i>Waagenoconcha irginae</i>	large, sub-oval, elongate	concentric	shallow	small	delicate, twisted
<i>Megousia weyprehti</i>	medium-sized, subrectangular, with large auricles	fine ribs	shallow	wide	few
<i>Megousia kulikii</i>	medium-sized, suboval	fine ribs	indistinct	wide	few
<i>Anemonaria pseudohorrida</i>	small, subrectangular	absent	distinct	narrow	long and straight
<i>Yakovlevia impressa</i>	large, trapezoid	fine ribs (16—30 per cm)	shallow	small	hinge margin only
<i>Yakovlevia duplex</i>	medium-sized, subrectangular, strongly coiled	fine ribs (c. 20 per cm)	distinct	small	few
<i>Yakovlevia mammata</i>	small, subrectangular, very wide	fine ribs (over 20 per cm)	shallow	small	few
<i>Liosotella robertiana</i>	small, trapezoid	bifurcating ribs	distinct	massive	thin and straight
<i>Linoproductus dorotheevi</i>	large, sub-oval, with a velum	fine ribs (12—20 per cm)	absent	small	few, straight
<i>Canocrinella spitsbergiana</i>	small, sub-oval, with a velum	short ribs and tuberculate intercalations	absent	massive	numerous, thin

materials from the Kapp Starostin Formation (Table 2). Nine species names which have been previously reported from this area are then considered as subjective synonyms.

The degree of morphological detail of the index traits distinctive of these productacean species roughly corresponds to the level generally accepted in the literature for genera. It nonetheless suffices for species identification within the Kapp Starostin Formation which represents an environmental continuum where closely related species would outcompete one another from similar habitats. The recognized productacean species include phena sharing the same qualitative features which are invariant relative to quantitative transformations of the shell form. Such invariant morphological traits had a functional significance (Ferguson 1978) and hence can be employed

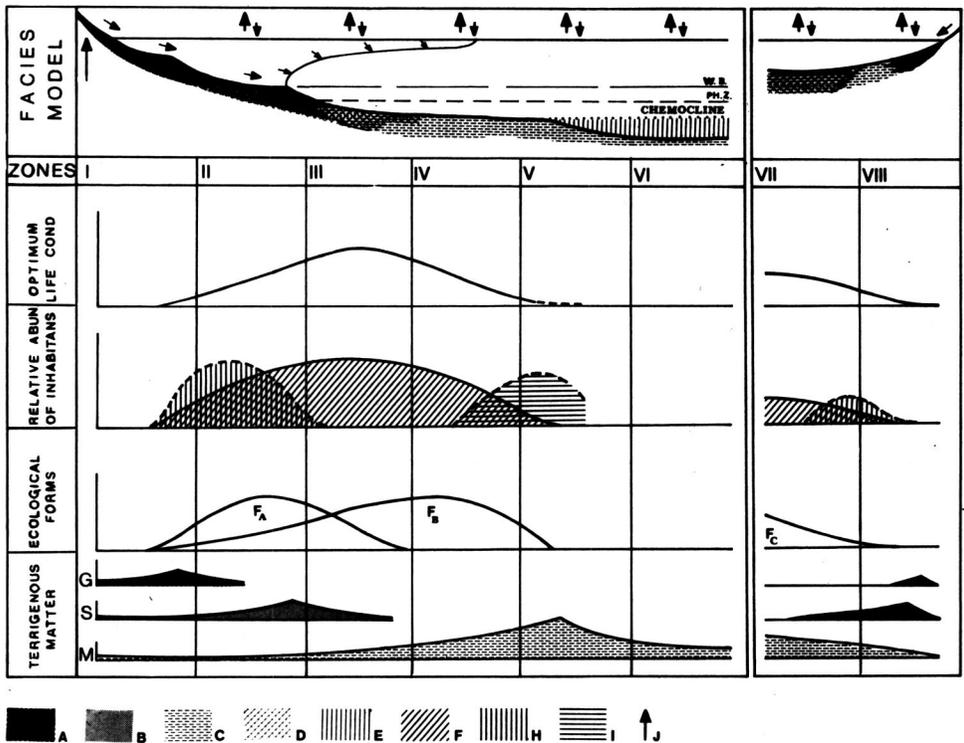


Fig. 3. Distribution of the main environmental factors and the corresponding biofacies in the Permian sea of Spitsbergen; facies zone identifications after Małkowski and Hoffman (1979). A — coarse terrigenous material, B — sand, C — silt and clay, D — carbonate deposition area, E — the zone below chemocline, F — brachiopod abundance curve, H — mollusc and crinoid abundance curve, I — sponge abundance curve, J — vectors of the main geodynamic agents in the Permian sea of Spitsbergen (diastrophic movements, precipitation and evaporation, nutrient supply, terrigenous material transport: G gravel, S sand, M silt), F_{ABC} — distribution of the productacean life forms (cf. Fig. 7)

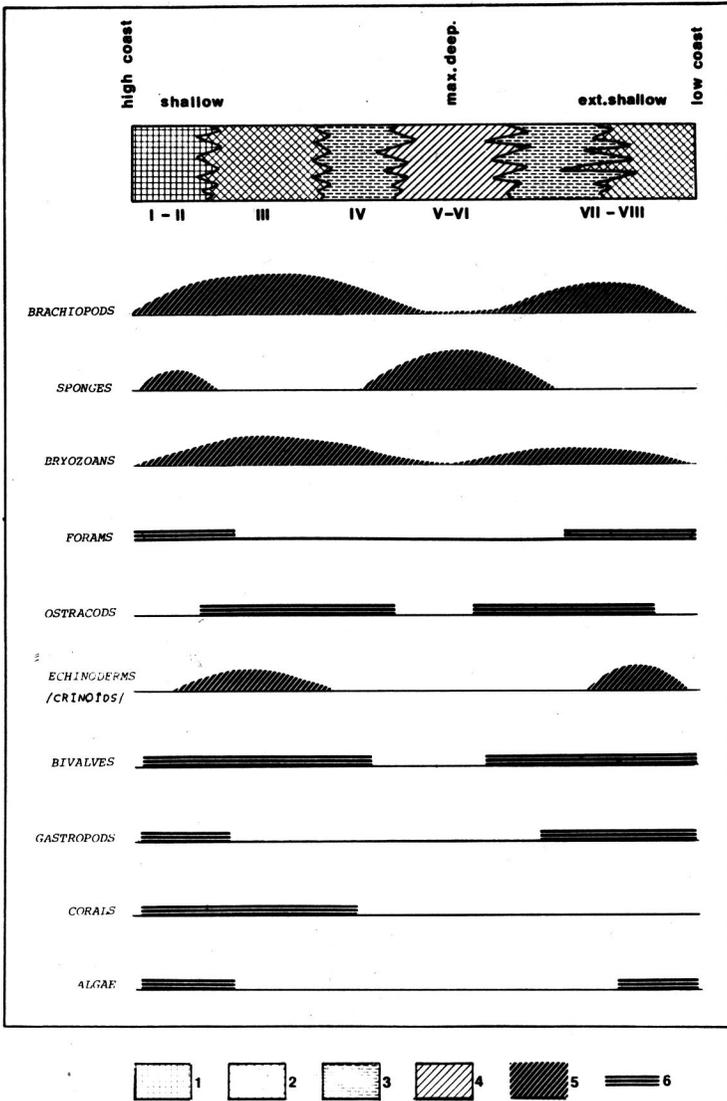


Fig. 4. Distribution of the main organic groups in various facies zones in the Kapp Starostin Formation; facies zone identifications as in Fig. 3. 1 — carbonate-clastic deposits, 2 — coquinas, 3 — marls and shales, 4 — cherts, 5 — abundance of the main groups, 6 — occurrence of the subordinate groups

for autecological characteristics of the mode of life in common to all conspecific organisms.

For each pair of the phena being compared for the sake of their species attribution, a synecological analysis of the associated biota and a reconstruction of the abiotic environment have been undertaken on the basis of a facies model of the Kapp Starostin Formation (Małkowski and

Hoffman 1979, Małkowski 1982; see Fig. 3 herein). The limits of distribution of the Productacea and their associated fauna depend chiefly upon gradients in such environmental factors as water eutrophication and oxygenation, bottom currents, and substrate mobility. The facies distribution, however — and hence also the faunal distribution — depends ultimately upon the paleogeographic position of any given area relative to the world's climatic zones, the ocean configuration, and the local topographic relief and tectonics. Because of the considerable effects the adjacent land had on the life conditions of the investigated fauna, the facies model (Figs. 4—5) is spanned between two endmember situations: high and active coast versus low coast (see Rollins *et al.* 1979).

By plotting the ranges of individual fossil species against the facies distribution, the environmental limits of coeval faunal assemblages have been recognized. These assemblages simply reflect the overlapping patterns of distribution of individual species within particular facies zones. The assemblages differ in the number and abundance of their constituent species, depending on the position of the habitat relative to the ecological optimum for the group. The marginal assemblages are less diverse but their species often are very abundant and show some unique adaptations. Neither direct interactions, nor phenomena of ecological succession have been observed among the investigated Productacea (see Johnson 1972). The only controls upon their distribution seem to consist in their variable tolerance of abiotic environmental parameters (see Liebig 1840, Shelford 1913). The observed

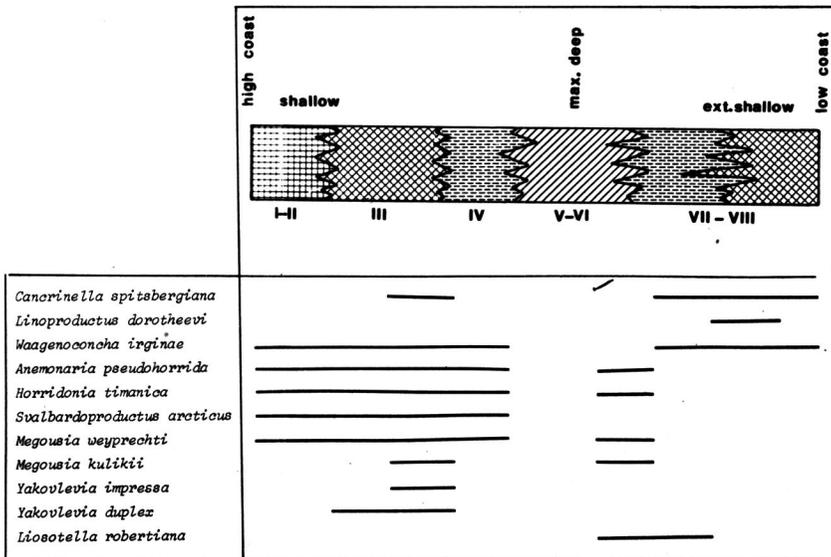


Fig. 5. Distribution of productacean species in various facies zones in the Kapp Starostin Formation; facies zone identifications as in Figs. 3—4

KAAP STAROSTIN FORMATION			LOCALITIES
Vorinen Mb.	Svenskeegga Mb.	Hovtinden Mb.	
			VINDODDEN
			KAPP STAROSTIN
			AHLSTRANDODDEN
			POLAKKJELLETT
			HYRNEJELLETT
			TRISKELEN

Fig. 6. The pattern of phenotypic variation of *Horridonia timanica* in the Kapp Starostin Formation; the variable features include: shell size and coiling, auricle size, ornamentation density, presence/absence of growth lines, spine distribution

recurrence of productacean assemblages in the Kapp Starostin Formation depends upon the recurrence of deposits representing particular facies areas and upon some larger-scale, global or macroregional, factors operating in the Permian sea.

The productacean species recognized in the Kapp Starostin Formation include each a number of phenotypes similar to each other in the majority of morphological features though sometimes differing in presence/absence and/or quantitative dimensions of one or more traits. Such phenotypes often are grouped together on the autecological and synecological criteria. Given that these criteria are valid, the following morphological features appear to be subject to much ecophenotypic variation: shell convexity, auricle size and shape, spine presence and distribution, growth line distinctness, density of ribs and tubercles. The most parsimonious explanation for the observed variation in these traits (Fig. 6) is the phenotypic reaction of individual brachiopods to a quantitative variation in environmental parameters among the investigated localities.

Three basic kinds of the shell form can be discerned among the Productacea; they correspond to three different modes of life (Fig. 7). On coarse-grained loose substrates rich in skeletal debris, the Productacea usually are able to stabilize the juvenile shell by anchoring and supporting it with long and thick spines which grow mainly on the margins of the ventral valve and on the auricle edges (Fig. 7a). Depending on the ontogenetic stage when the shell ultimately achieves stability in the sediment, the productaceans vary in the degree of shell coiling, commissure position relative to the sediment surface, and spine distribution (Każmierczak 1967). This life form is exemplified in the Kapp Starostin Formation by *Horridonia timanica*, *Svalbardoproductus arctius*, and *Anemonaria pseudohorrida* in the facies zones I—III (cf. Fig. 3).

On soft substrates where even the juvenile shell could not be stabilized, the Productacea typically develop a capability of floating partly within the sediment. During ontogeny, the center of gravity shifts forwards, thus allowing the commissure to maintain a constant position relative to sediment-water interface while the older parts of the shell coil around an axis parallel to the hinge margin (Fig. 7b). *Waagenoconcha irginae* and *Kochiproductus porrectus* well exemplify this adaptation; in *W. irginae* even the spines are twisted in concordance with the coiling direction of the shell, as it is also the case in some other productacean genera (Grant 1966, 1968).

Some other species inhabiting soft substrates lack the capability of floating and sink in the sediment in the course of ontogeny. They develop, however, an extended velum which permits them to survive even under the cover of a sediment layer up to a couple of centimeters thick (Fig. 7c). *Linoproductus dorotheevi* provides a good example of such a life form (Pl. 6, Fig. 11).

On loose substrates in shallow- but rather quiet-water environments, productacean assemblages are dominated by forms reclining at, or partly buried in, the sediment; they achieve stability of the shell solely by the

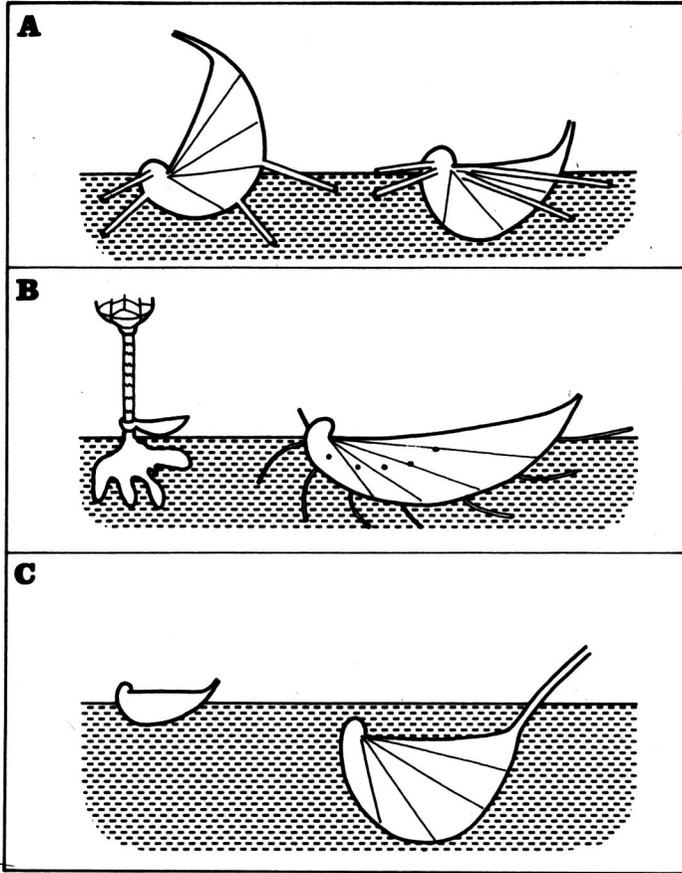


Fig. 7. Life forms among the Productacea. A — forms stabilized in the sediment with their long and straight spines, B — forms floating at the surface of soft substrates, C — velum-bearing forms sinking in the sediment

resistance of the ventral valve. They lack abundant spines and may therefore be able to shift the position by shifting the center of shell gravity in ontogeny; they can thus retain the position of commissure relative to the sediment surface. Such adaptations are characteristic of *Yakovlevia*, occurring in the facies zone III, often in association with other productacean as well as other brachiopods.

The productacean species adapted to float in quaggy substrates occur in the Kapp Starostin Formation in a wide range of facies zones — from nearshore sheltered embayments (zones I—II) and lagoons (zones VII—VIII) to wide area of the outer shelf (cf. Fig. 3). These forms include *Waagenoconcha irginae* and *Kochiproductus porrectus*, which show relatively little, and decreasing in ontogeny, convexity of the shell; their size may exceed 10 cm (Pl. 3, Fig. 9).

The forms sinking in the sediment — for example, *Linoproductus dorotheevi* — have a strongly convex ventral valve, usually lacking any spines. In the Kapp Starostin Formation, they are confined to lagoon facies zones (VII—VIII).

Bio- and lithofacies analysis of lithological complexes from the Kapp Starostin Formation

Fossils vary in abundance within the Kapp Starostin Formation; they are most abundant in carbonate and terrigenous rocks. The lithological complexes containing the richest and best preserved productacean taphocoenoses, without evidence for sorting or redeposition, have been the subject of detailed facies analysis. Cherts, in turn, although the dominant sediment type in the formation, are here largely neglected because they contain mainly sponge remains (Siedlecka 1970), while brachiopods are almost entirely absent. Marly cherts, however, are also taken into account as a transitional zone between the brachiopod-dominated facies and the zone of mass occurrence of sponges.

The lithological complexes and their biotic and abiotic characteristics are here described on the basis of field observations, some 200 thin sections, and microfossil collection obtained by dissolution of rock samples. The complexes are referred to by symbols, which are identical to those introduced in the author's earlier article (Małkowski 1982); the only exception is the complex V-1 from Vindodden section, which was first described only after that article had been submitted for publication.

Vindodden section: morphological edge and coastal cliff near Cape Vindodden in Isfjord.

V-1: The entire complex is equivalent to the Voringen Member in the type section of the formation; in terms of facies, it is typical of the so-called "Spirifer limestone" (Frebald 1937, Hoel and Orwin 1937). Successive portions of the section of the V-1 lithological complex designated as V-1a, b, c, and d. The faunal contents: Productacea — *Horridonia timanica*, *Horridonia aff. horrida*, *Svalbardoproductus arcticus*, *Yakovlevia impressa*, *Megousia weyprechtii*, *Megousia kulikii*, *Canocrinella spitsbergiana*, *Anemonaria pseudohorrida*, *Waagenoconcha irginae*, *Kochiproductus porrectus*; other brachiopods — *Aulosteges tholus*, *Arctitreta kempei*, *Derbya aff. grandis*, *Spiriferella polaris*, *Spiriferella keilhavii*, *Neophricadothyris asiatica*, *Pinegathyris royssiana*, *Spirifer striato-paradoxus*, *Spirifer striato-plicatus*, *Licharevia sp.*, *Rhynchopora variabilis*, *Dielasma itaitubense*, *Orbiculoidea winsensi*, *Pseudosyrinx sp.*; bryozoans, crinoids, and bivalves.

The V-1 lithological complex includes fossiliferous biocalcarenes and biomicrites interbedded with layers of nonfossiliferous marly sediments with

some gravel. Limestones at the base of the complex contain small-sized branching trepostome bryozoans which are replaced upwards by massive colonies often encrusting the brachiopod shells. Most limestone beds include broken bioclasts (up to 80% of the rock volume) embedded in sparitic matrix. The fossil assemblage is dominated by brachiopods occurring in the following sequence: *Cancrinella spitsbergiana*, *Rhynchopora variabilis*, and single specimens of *Horridonia timanica* in V-1a limestones; *Horridonia timanica* and *Arctitreta kempei* in V-1b biocalcarenes; *Waagenoconcha irginae*, *Megousia weyprechtii*, *Megousia kulikii*, and less abundant *Horridonia timanica* in V-1c biocalcarenes; *Yakovlevia impressa* and *Svalbardopproductus arcticus* in V-1d marly biomicrites at the top. *Spiriferella* occurs in small amounts in the beds with *Horridonia*, but it reaches mass abundance higher up in the section and its individual specimens range up to more than 5 cm in size. In the detrital limestones, the brachiopod density reaches several hundred large-sized specimens per square meter of the rock. These accumulations include whole shells as well as single valves and their fragments, and they sometimes exhibit imbrications. The brachiopod density is lower in biomicrites, where it ranges from several to several tens of predominantly large-sized specimens per square meter. The species content of the coquina does not differ from that of the assemblages preserved *in situ*. In thin sections, the rock is rich in brachiopod shell fragments (abundant spines), crinoid trochites, and bryozoan colony fragments; there are a few uniserial foraminifers. Some brachiopod shells display borings, these largely straight channels being usually less than 1 mm in diameter.

The productacean species recognized in this lithological complex come from a single facies zone which encompassed the nearshore area along with brachiopod beds forming sublittoral shoals. The coquinas originated by local winnowing during episodes of increased turbulence, but degree of shell transportation is insignificant as a factor biasing the initial community composition.

The collection of *Horridonia timanica* from this lithological complex comprises well over a hundred specimens, often preserved with spines at the auricle margins and with granular ornamentation of the shell surface (Pl. 1, Figs. 1—3, 6; Pl. 2, Fig. 9). The morphological variation within this phenon is relatively small and concerns chiefly the spine distribution, auricle shape, and the degree of ventral valve coiling. One specimen has numerous and regularly arranged spines on the ventral valve near the hinge margin (Pl. 1, Fig. 3), which make it to resemble *Horridonia horrida*. The other productacean phenon found in the V-1 lithological complex (Table 2) are separated by distinct morphological gap, so there can be no doubt about their genetic distinctness. The two cooccurring species of *Megousia* clearly differ in their shell outline, sinus development, and density and thickness of the ribs on the shell surface. The range of variation of the shell shape in particular

phena is illustrated by the measurements which have been taken on representative specimens. The V-1 lithological complex is attributed to the facies zones II—III (cf. Fig. 3).

Kapp Starostin section (known also as Festningen, as it makes part of the section described under this heading by Frebold in 1937): type section of the Kapp Starostin Formation (Cutbill and Challinor 1965), exposed several kilometers along the Linnaeus Valley south of Isfjord, more than 300 meters thick. The formation is subdivided into Voringen Member, Svenskeegga Member, and Hovtinden Member, which can be correlated from this section to the Central and Southern Spitsbergen (Cutbill and Challinor 1965). Fossils are most abundant and best preserved in limestones of the Voringen Member, at the top of the Svenskeegga Member, and in marls and marly shales at the top of the Hovtinden Member; these lithological complexes are designated as F-1, F-5, and F-8, respectively (Małkowski 1982). Characteristic, though uncommon, faunal elements of the carbonates are here solitary tetracorals, ranging up to the top of the formation.

F-1 (Voringen Member): the lowermost lithological complex of the Kapp Starostin Formation. It comprises detrital and micritic limestones rich in brachiopods, crinoids, and bryozoans; it is typical of the „*Spirifer* limestone” (Frebold 1937, Orwin 1940). The accumulations of brachiopod shells often form coquinas. The complex approximates 8 m in thickness. The faunal contents: Productacea — *Horridonia timanica*, *Svalbardoproductus arctitus*, *Anemonaria pseudohorrida*, *Megousia weyprechtii*; other brachiopods — *Pseudosyrinx wimani*, *Spirifer striato-paradoxus*, *Derbay* aff. *grandis*, *Arcitreta kempei*, *Spiriferella* sp., *Neophricadothyris asiatica*, *Pinegathyris royssiana*; bryozoans, crinoids, and occasional gastropods.

The fossils are very well preserved, often *in situ*, in the micritic limestones. Brachiopods, even such large-sized forms as *Horridonia timanica*, *Svalbardoproductus*, and *Spirifer striato-paradoxus*, occur in accumulations exceeding one hundred specimens per square meter; juvenile shells occur only rarely. In thin sections, very common are heavy brachiopod spines (*Horridonia*, *Svalbardoproductus*), crinoid trochites, and smooth and porous brachiopod shell fragments (*Dielasma*?). Brachiopod remains are a rock-building component, constituting up to 50% of the rock volume.

The four productacean phena found in the F-1 lithological complex do not differ in morphology from their equivalents found in the V-1 complex; the associated facies and faunal assemblage also are similar, thus supporting the assignment of these phena to the species recognized in the V-1 complex. It is worth noting, however, that productacean specimens from the F-1 complex generally have only indistinct growth lines, weakly developed auricles, and less numerous spines; all these features seem to be related to their unusually quiet life conditions. The F-1 lithological complex is attributed to the facies zone III (Małkowski 1982; Fig. 3 herein).

F-5, Svenskeegga Member: marly limestones with abundant large-sized brachiopods and bryozoans and also with considerable accumulations of crinoids; total thickness of the complex approximates 5 m. The faunal contents: Productacea — *Horridonia timanica*, *Svalbardoproductus arcticus*, *Kochiproductus porrectus*, *Anemonaria pseudohorrida*, *Yakovlevia duplex*, *Yakovlevia mammata*, *Waagenoconcha irginae*, *Megousia weyprechtii*; other brachiopods — *Arctitreta kempei*, *Spirifer striato-plicatus*, *Spiriferella keilhavii*, *Rhynchonella* sp., *Pinegathyris royssiana*, *Schelvienella* sp.; pectenid bivalves, cystoid crinoids, trepostome bryozoans, solitary tetracorals, and rare gastropods.

The marly limestones of this complex contain exceptionally large brachiopod, bivalve, and gastropod shells and bryozoan colonies. The contribution of terrigenous material is variable; crinoids occur in larger quantities in micrites with only a few per cent proportion of the fine-grained material. The majority of brachiopods are excellently preserved and *in situ*. The productaceans generally lack spines, which only sporadically occur in thin sections. Two phenotypes of the genus *Yakovlevia* occur in this lithological complex; their ranges of morphological variation are separated by a clear gap, so that their species distinctness appears to be unquestionable. They differ in the mean shell size and general shape as well as in rib thickness (Table 3; Pl. 5, Figs. 3–9; Pl. 6, Figs. 2, 4, 5, 7). One of these phenotypes has not been encountered in the complexes analyzed previously and is referred to the species *Yakovlevia mammata*. The productacean and their associated fauna are here larger-sized than in any other locality, which may indicate particularly favorable trophic conditions and a quiet-water habitat. This lithological complex is attributed to the facies zone III (Fig. 3).

F-8, Hovtinden Member: black marls and marly shales at the very top of the Kapp Starostin Formation, just below the Triassic strata (*cf.* Gaździcki and Trammer 1977, 1978; Birkenmajer 1977). This complex approximates 17 m in thickness. The faunal contents: Productacea — *Kochiproductus porrectus*, *Waagenoconcha irginae*, *Anidanthus aagardi*, *Liosotella robertiana*, *Canocrinella spitsbergiana*; other brachiopods — *Lissochonetes spitzbergianus*, *Camerophoria spitzbergiana*, *Pterospirifer cordieri*, *Spiriferella keilhavii*, *Rhynchonella* sp., *Pinegathyris royssiana*; a horizon with *Cladochonus*; fenestellid bryozoans, pectenid bivalves, and solitary corals.

Bryozoan colonies and *Cladochonus* (*cf.* Stasińska 1982) occur in this complex as thickets extending over several meters; brachiopods are scattered in the rock or occur in nests of several tens of specimens, usually a dozen to a few tens of specimens per square meter. In thin sections, some marly streaks show increased amounts of skeletal remains, sometimes containing also sponge spicules. Two of the productacean phenotypes encountered in this complex clearly differ in morphology from those found

in the previously discussed lithological complexes, and they are therefore attributed to other species. The other three phenotypes are grouped together with the phenotypes encountered in the other lithological complexes, in spite of some morphological differences. In contrast to the V-1, F-1, and F-5 complexes, which are interpreted as representative of shallow sublittoral habitats, the F-8 complex is assigned to the open marine facies zone V (Małkowski 1982; Fig. 3 herein). The difference in environmental conditions and also in preservation state (strong compaction) must have contributed to the morphological distinctness of the productacean phenotypes from the F-8 complex. The observed variation in such morphological traits as the degree of shell coiling, ornamentation density, shell thickness and sometimes also outline is therefore regarded as primarily ecophenotypic; it is particularly pronounced in *Kochiproductus porrectus* and *Waagenoconcha irginae* (Table 3; Pl. 4, Figs. 2–6; Pl. 5, Figs. 1, 4–5, 7a–b).

Ahlstrandodden section: southern coast of Van Keulenfjord.

A-1, Voringen Member: biocalcarenites and biocalcilites with abundant fauna, locally in the form of coquinas; in the upper part of this complex, limestones gradually give way to marly cherts. The complex approximates 4 m in thickness. The faunal contents: Productacea — *Svalbardoproductus arcticus*, *Horridonia timanica*, *Yakovlevia impressa*, *Yakovlevia duplex*, *Waagenoconcha irginae*, *Kochiproductus porrectus*, *Anemonaria pseudohorrida*, *Megousia weyprechtii*, *Megousia kulikii*, *Canocrinella spitsbergiana*; other brachiopods — *Spirifrella keilhavii*, *Spirifer striato-paradoxus*, *Spirifer striato-policatus*, ?*Orthotetes* sp., *Pinegathyris royssiana*, *Dielasma giganteum*, *Rhynchopora variabilis*; massive, branching, and fenestellid bryozoans, crinoids, bivalves, gastropods, and conodonts *Neostreptognathodus*.

The detrital limestones of this complex consist mainly of bioclasts (brachiopod shells and bryozoan colonies, crinoid trochites), whereas the sparitic, locally micritic, matrix accounts for some 25% of the rock volume. *Horridonia timanica* and *Yakovlevia impressa* have here smaller-sized shells than in the other localities (Table 4); in the former species, the auricles are very pronounced but lack spines on their margins. The other index morphological features and ecological similarities suggest that the productacean phenotypes should be attributed to the species encountered in the previously discussed lithological complexes of the facies zone III. Some brachiopod specimens have shells partly silicified. There is a succession of productacean assemblages, similar to the one observed in the V-1 complex: *Canocrinella spitsbergiana* and *Waagenoconcha irginae* dominate at the bottom, *Horridonia timanica* and *Svalbardoproductus arcticus* with minor amounts of *Yakovlevia impressa* occur higher up in the section, *Yakovlevia duplex* and *Megousia weyprechtii* dominate in the strata transitional to the overlaying cherts.

Polakkfjellet section: in the western part of Torrell's Land, between the glaciers Polakkbreen and Drevbreen, described by Birkenmajer (1977) and Nysaether (1977).

P-1, Voringen Member: light grey limestones passing upwards into darker limestones with siliceous lenses and giving finally way to the cherts of the Svenskeegga Member. Fossils are particularly abundant in the lowermost limestones; they occur more rarely and in the form of nests higher up in the section. Thin clastic interlayers appear in a couple of places. The richly fossiliferous limestones approximate 20 m in thickness. The faunal contents: Productacea — *Linoproductus dorotheevi*, *Horridonia timanica*, *Canocrinella spitsbergiana*, *Waagenoconcha irginae*, *Megousia kulikii*; other brachiopods — *Lingula* cf. *freboldi*, *Spiriferella draschei*, *Neophricadothyris asiatica*, *Dielasma plica*, *Rhynchopora variabilis*, *Pseudosyringothyris borealis*, *Lissochonetes spitzbergianus*, *Pinegathyris royssiana*; in- and epifaunal bivalves, gastropods, bryozoans, crinoids, sessile foraminifers, ostracodes, conodonts *Neostreptognathodus*, algal microlaminations.

The sandy calcarenites at the base of the complex contain strongly fragmented brachiopod shells, bryozoan branching colonies, and crinoids, the size of these bioclasts being largely uniform and approximating 2 mm. Higher up in the section, streaks of terrigenous material appear in larger amounts. The degree of skeletal fragmentation is proportional to the amounts of sand in the rock. Bioclasts have sometimes micritic coatings. Sessile foraminifers occur here abundantly. In the upper part of the section, the fossils are well preserved and the degree of sediment winnowing and redeposition is very minor. *Rhynchopora variabilis* occurs here in accumulations of several hundred specimens, with distances between the adjacent shells being no more than the shell diameter. A similar form of occurrence is characteristic also of the other brachiopods in these strata: *Linoproductus dorotheevi* occurs in nests of a dozen or so specimens, *Canocrinella spitsbergiana* and *Neophricadothyris asiatica* in groups of several tens of individuals. The brachiopod shells in such accumulations generally are well preserved, and the Productacea often are close to their life positions. Massive bryozoan colonies cooccur with *Rhynchopora*, *Neophricadothyris*, and algal microlaminations, whereas branching bryozoans cooccur with productaceans. There is a succession of brachiopod assemblages in this litological complex: *Rhynchopora variabilis*, *Neophricadothyris asiatica*, *Lingula* cf. *freboldi*, and *Dielasma plica* at the bottom, abundant *Waagenoconcha irginae*, *Canocrinella spitsbergiana*, and *Spiriferella draschei* higher up in the section, and *Linoproductus dorotheevi* in association with *Canocrinella spitsbergiana* at the top. The boundaries between these fossil assemblages are gradual, however. The amounts of bioclasts in the rock vary from 10 to 60%, with their composition being clearly dominated by brachiopod and crinoid fragments. Sessile foraminifers characteristically occur in thin sections from the lower

part of the complex, whereas free-living foraminifers and ostracodes appear in those from the upper part. The majority of skeletal remains have well preserved microstructure. Some thick brachiopod shells bear borings, 0.5—1.5 mm in diameter. Trace fossils *Zoophycos* occur in the upper part of this lithological complex.

Only one productacean phenon encountered in this lithological complex is assigned to a species (*Linoproductus dorotheevi*) which is not represented in the previously discussed complexes. The majority of the productaceans are here adapted to float at the sediment surface or to live partly sunk in the sediment. Other life forms (*Horridonia timanica*) occur only sporadically. The phenon *Horridonia timanica* of the P-1 complex is distinctive in its weakly coiled ventral valve (Fig. 6) and poorly developed auricles. The brachiopod adaptations and the sedimentological characteristics of this lithological complex suggest it is representative of sublittoral shoals (facies zones II—III) adjacent to some lagoons (facies zones VII—VIII).

P-3s, upper part of the Svenskeegga Member: black, marly, micritic (sometimes detrital) limestones with abundant fauna. This complex approximates 1.2 m in thickness. The faunal contents: Productacea — *Waagenoconcha irginae*, *Megousia kulikii*; other brachiopods — *Orbiculoidea winsensi*, *Pterospirifer cordieri*, *Rhynchopora* sp.; infaunal bivalves, abundant gastropods, bryozoans, foraminifers, some crinoid trochites.

The detrital layers contain very abundant gastropod shells, at various ontogenetic stages, associated with many foraminifers, both sessile and free-living. The black, bituminous micrites comprise accumulations of trepostome bryozoans accompanied by small-sized foraminifers, ostracodes, and single brachiopods, especially *Waagenoconcha irginae*; large-sized individuals of the latter species, however do not occur in association with bryozoans. As compared to the productacean from the other localities in the Kapp Starostin Formation, the phenon of the F-3 top complex have a less dense shell ornamentation and more convex ventral valve. Nevertheless, their other morphological features and the occurrence in a facies zone adjacent to those inhabited by comparable phenon in the other localities suggests they should be attributed to *Waagenoconcha irginae* and *Megousia kulikii*. The P-3s lithological complex is attributed to the facies zones IV—V (Małkowski 1982; Fig. 3 herein).

P-4b, top of the Svenskeegga Member: marly and sandy limestones above a massive bed of white-yellowish cherts. These sediments are cross-bedded at the bottom; the overlaying limestones are rich in brachiopods and bryozoans, interbedded with black marly shales in places. This lithological complex approximates 12 m in thickness. The faunal contents: Productacea — *Svalbardoproductus arcticus*, *Horridonia timanica*, *Anemonaria pseudohorrida*, *Waagenoconcha irginae*, *Yakovlevia duplex*; other brachiopods — *Arctitreta kempei*, *Pinegathyris royssiana*, *Derbyia* aff. *grandis*, *Spirifer striato-paradoxus*,

Pterospirifer cordieri, *Spiriferella keilhavii*; amplexoporoid, timanodictyoid, and fenestellid bryozoans, crinoids, bivalves, and foraminifers.

The preservation state of the fossils strongly depends on lithology in this complex. The limestones contain accumulations of small and often fragmented shells along with well-preserved large-sized specimens, sometimes in life position; the fossils contribute 15–60% of the rock volume. In the marly shales, in turn, the preservation state is generally very good, including delicate bryozoans; the fossils contribute, however, only 5–15% of the rock volume. Brachiopods and bryozoans dominate among the fauna, the latter occurring in large, often biostromal accumulations. A couple of bryozoan-brachiopod associations can be distinguished. Trepostomes cooccur almost exclusively with *Spiriferella keilhavii*, whereas *Fenestella* colonies are associated with a variety of small-sized brachiopods. Large-sized brachiopod shells often bear borings. Trace fossils *Zoophycos* appear in more sandy strata.

Among the productacean phena, *Svalbardoproductus arcticus* has unusually large and thick shells; *Waagenoconcha irginae* also attains large sizes (up to 10 cm). *Horridonia timanica* is here uncommon, and its specimens are smaller-sized, less convex; they lack spines, and the granular ornamentation is denser. The P-4b lithological complex is assigned to the facies zone III.

Hyrnefjellet section: southern slope of Hyrne massif, at the base of Treskelen Peninsula inside Hornsund.

H-1, lithological equivalent to the top of the Svenskeegga Member: conglomerates with abundant remains of large-sized and thick-shelled brachiopods are overlaid by limestones and marly cherts (Birkenmajer 1964). The fauna is derived chiefly from the limestones just above the conglomerates. The faunal contents: Productacea — *Waagenoconcha irginae*, *Horridonia timanica*, *Kochiproductus porrectus*, *Svalbardoproductus arcticus*, *Anemonaria pseudohorrida*, *Yakovlevia duplex*, *Megousia weyprechtii*, *Liosotella robertiana*; other brachiopods — *Arctitreta kempei*, *Pinegathyris royssiana*, *Spirifer striato-paradoxus*, *Pterospirifer cordieri*, *Spiriferella keilhavii*; bryozoans, ostracodes, and foraminifers.

The fossils in the conglomerates at the base of this complex show imbrication. In the overlaying calcirudites, however, no evidence for considerable transportation occurs. The lower parts of the complex contain an association of *Waagenoconcha irginae*, *Spiriferella keilhavii*, *Svalbardoproductus arcticus*, and *Horridonia timanica*, but diversity of the fossil assemblage increases higher up to the section. Encrusting amplexoporoid bryozoans and uniserial foraminifers are fairly abundant in the limestones; they are often associated with small-sized and thin-shelled *Liosotella robertiana*. Bioclasts contribute up to 70% of the rock volume. Brachiopod shells often bear borings.

All the productacean phenae of the H-1 lithological complex may be regarded as conspecific with those recognized in the earlier discussed complexes, although *Horridonia timanica* and *Svalbardoproductus arcticus* have more strongly coiled shells than usual. This lithological complex is assigned to the facies zones I—II.

Treskelen section: a morphological edge along Treskelen Peninsula inside Hornsund.

Tr-2, lower part of the Hovtinden Member: marly cherts with abundant fauna dominated by brachiopods and sponges. The thickness of the complex decreases southwards and it ultimately disappears at the base of Bauten Mt (Birkenmajer 1964, 1977); it approximates 6 m in Treskelen section. The faunal contents: Productacea — *Waagenoconcha irginae*, *Horridonia* aff. *horrida*, *Megousia weyprechtii*, *Megousia kulikii*, *Kochiproductus porrectus*, *Liosotella robertiana*, *Anidanthus aagardi*, *Yakovlevia duplex*, *Anemonaria pseudohorrida*, *Cancrinella spitsbergiana*; other brachiopods — *Spiriferella keilhavii*, *Neophri-cadothyris asiatica*, *Spirifer striato-paradoxus*, *Camerophoria spitzbergiana*, *Chonetes* sp., *Pterospirifer cordieri*; bivalves, gastropods, bryozoans, crinoids, conodonts *Neogondolella*, foraminifers, and ostracodes.

The fossils are in part preserved as internal moulds, but the brachiopods, which abundantly occur in sediments enriched in terrigenous material, are generally well-preserved. The majority of fossils, however, are at least partly distorted by compaction. The fossils contribute up to 50% of the rock volume. The sponges *Haplistion* are characteristic of the fossil assemblage (Siedlecka 1970). Fenestellid and delicate branching trepostome bryozoans occur in minor amounts. The rocks contain also abundant foraminifers (*Geinitzina*, *Nodosaria*, *Fronicularia*), ostracodes, and conodonts *Neogondolella*. Among the Productacea, *Megousia kulikii*, *Megousia weyprechtii*, *Anemonaria pseudohorrida*, *Kochiproductus porrectus*, and *Waagenoconcha irginae* are dominant. There are several to several scores of sponge individuals, up to 200 brachiopods (including a couple of large-sized *Spirifer* and *Kochiproductus*), some bryozoan colonies, and a couple of large (up to 40 cm in diameter) trace fossils *Zoophycos* per square meter of the rock; bivalves and gastropods occur only sporadically. Sponge spicules are in places an important rock-building element. The sponges are roughly uniformly distributed in the rock, whereas the brachiopods occur in clusters of several dozens. The productacean phenae occurring in the Tr-2 lithological complex are generally smaller-sized and considerably thinner-shelled than in other complexes; the forms with long and delicate spines dominate. *Horridonia* aff. *horrida* differs from *Horridonia timanica* in that it has a row of cardinal spines at the hinge margin, which is diagnostic of the species *Horridonia horrida* in the Permian of Central Europe (Malzan 1937). The Tr-2 lithological complex is assigned to the facies zone V.

Facies development of the Kapp Starostin Formation

Two diastrophic episodes occurred in Spitsbergen during deposition of the Kapp Starostin Formation: first, prior to sedimentation of the uppermost strata of the Svenskeegga Member, and second, prior to sedimentation of the uppermost strata of the Hovtinden Member. These two events can be employed for chronostratigraphic correlation of the diachronous lithostratigraphic divisions of the formation (Małkowski 1982). The facies development of the Kapp Starostin Formation can therefore be portrayed as three successive transgressive sequences (Fig. 8), separated from each other by local tectonic uplift episodes (Mackenzie and Pigott 1981).

The investigated Permian basin was a rather small epicontinental sea at least partly separated from the ocean (Harland 1973, Scotese *et al.* 1979). It was located in a warm climatic zone, probably around 30–40 N (Stehli 1970, Harland 1973, Birkenmajer 1977), and it was migrating northwards during deposition of the Kapp Starostin Formation. At the same time, its connections to the Cisuralian area were disrupted (Fig. 9). In such a spatially restricted sea, under warm climate and poor water exchange with the ocean, the conditions were met for development of a stratification of the water column and hence for appearance of poorly oxygenated or even anoxic waters below the pycnocline (Degens and Stofers 1976, Byers 1979, Demaison and Moore 1980). That it indeed developed is supported by the facies characteristics of the deeper parts of the investigated basin and by the facies sequence in the investigated geological sections (Małkowski and Hoffman 1979). The biofacies distribution in marine basins with stratified waters depends upon the anoxic zone which sets the limit to the occurrence of Metazoa. The oxygen concentration in water, however, may decrease gradually (Byers 1977), and the zonal distribution of benthic organisms depends then on their tolerance to oxygen deficiency (Rhoads and Moore 1971). Presence/absence of the pycnocline and its associated phenomena is controlled by the climate and, locally, also by the feasibility of other mechanisms of water stratification. In the investigated basin, the diastrophic episodes presumably disturbed the oceanographic conditions, including water stratification (Fig. 10), because they led to increased fresh water and terrigenous influx from land (*cf.* Walker 1978) and perhaps also to a change in the pattern of coastal currents.

The position of the investigated marine basin relative to the adjacent land masses and to the ocean underwent a considerable change (Dietz and Holden 1970, Irving 1977) during the Late Permian when the Kapp Starostin Formation was deposited (Szaniawski and Małkowski 1979). The

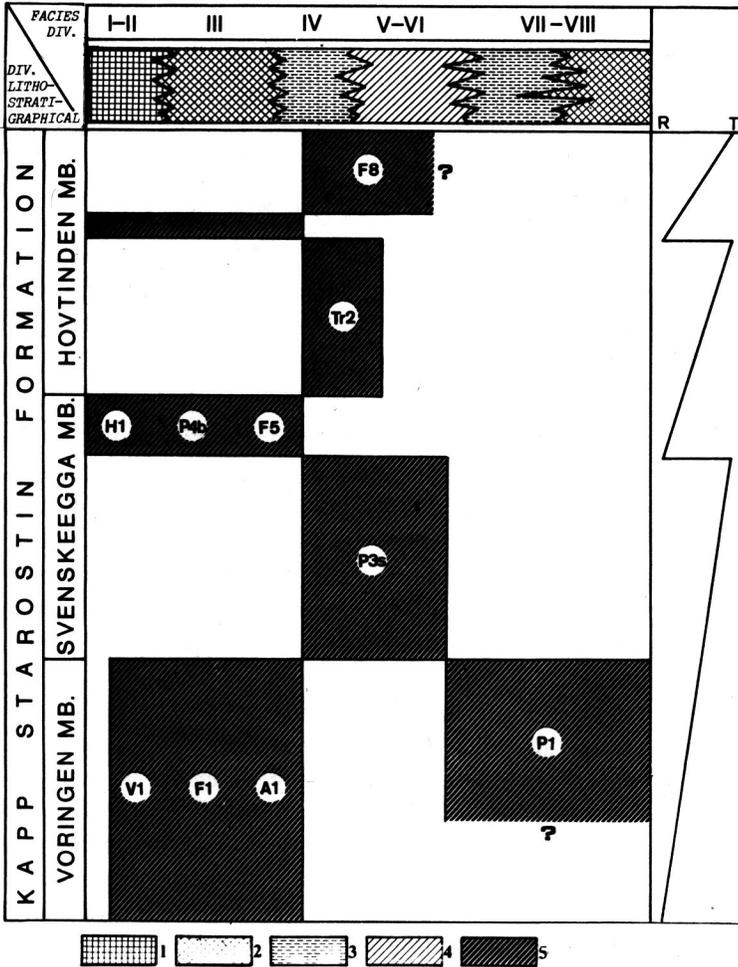


Fig. 8. Position of the investigated lithological complexes of the Kapp Starostin Formation to the facies zones and the transgressive-regressive cycles. 1 — nearshore facies, under strong terrigenous influences, 2 — shallow facies, weakly affected by terrigenous influences, 3 — soft-substrate facies of the open sea, 4 — open marine facies below the chemocline, 5 — lithological complexes R and T symbolize regression and transgression, respectively

drift of this area northwards probably was accompanied by a climatic cooling, a change in rock weathering (from chiefly chemical to primarily mechanical), and perhaps also an increase in precipitation. The conditions thus arose for a decrease in water salinity in the basin, which had initially had at least temporarily negative water balance (Fig. 10). This change must have had an impact on facies development in this Permian basin and on life conditions of the fauna.

The environmental changes in the Permian sea could eliminate species whose limits of tolerance were insufficient to allow them to occupy newly

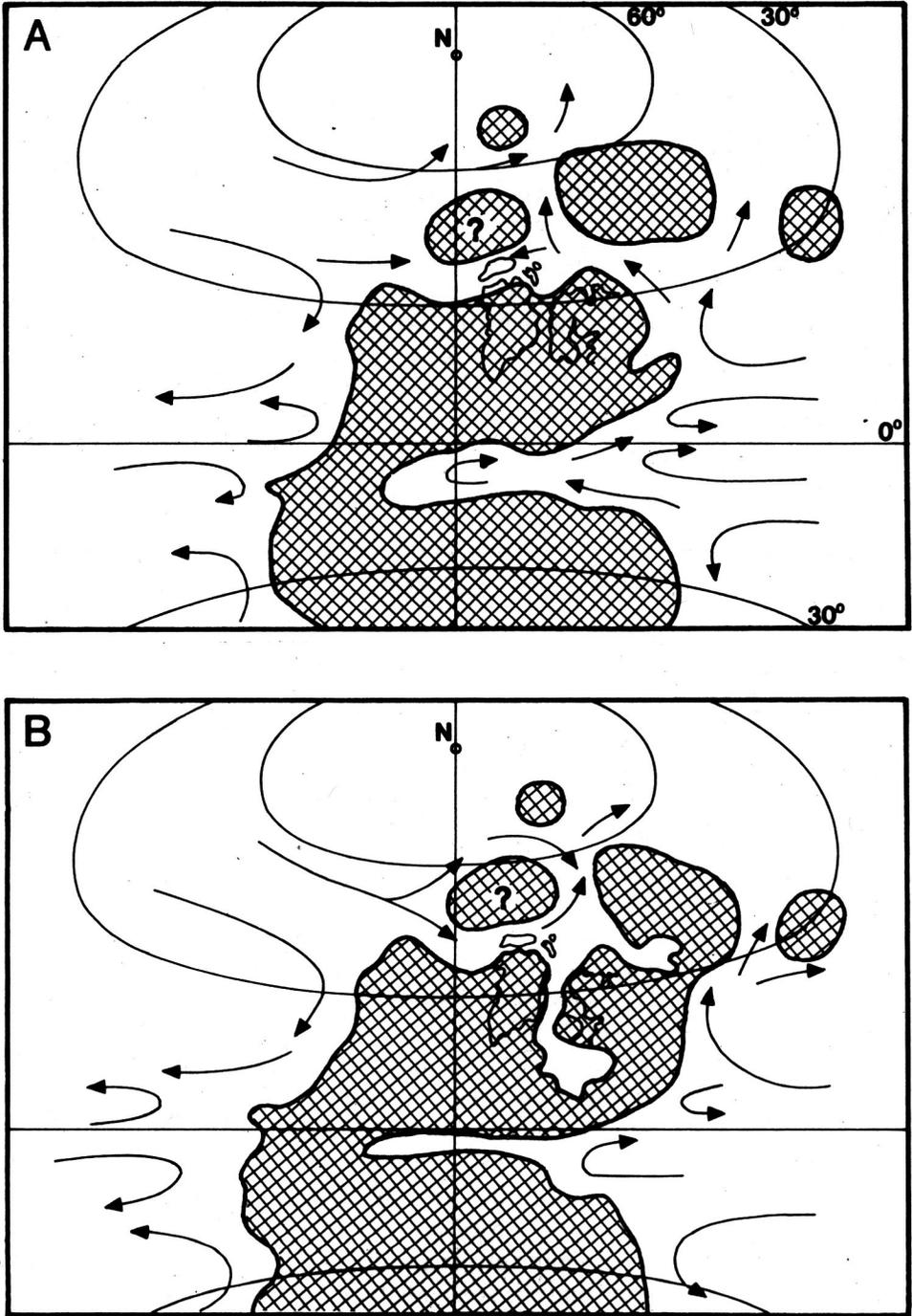


Fig. 9. Earliest (A) and latest (B) Permian paleogeography of the study area (cf. C. Ross and J. Ross (1985))

emerging habitats. They thus could constitute the ecological driving force of evolution, since they could deplete some bioprovinces from a part of their faunas (see Kauffman 1976). The area investigated in the present study, however, is too small to permit the author to recognize ultimate extinction of any species; the observed facies changes imply a shift of the habitats beyond the study area's borders rather their total destruction. It is only the terminal Paleozoic macroregional, or even global, changes (Valentine 1973, of ecosystems and thus had very far-reaching evolutionary consequences.

The local environmental changes, however, explain the pattern of replacement of the fossil assemblages in the investigated basin. The 10 localities from which the Productacea of the Kapp Starostin Formation have been collected represent various facies zones of the Permian sea (Figs. 2, 8). The most distinctive fossil assemblages have been distinguished in these facies zones; their index species are those most abundantly represented in the rock, rather than biologically dominant in the original ecological communities.

The strata of the Voringen Member contain fossil assemblages of nearshore, shallow-water areas and lagoons which were only under a weak terrigenous influence. Water salinity and temperature presumably were directly controlled by the climate. The assemblage *Linoproductus dorotheevi* — *Cancrinella spitsbergiana* includes forms with a velum, and hence adapted to life within the sediment, which permitted them to survive episodes of unfavourable environmental conditions. The assemblage *Horridonia timanica* — *Svalbardoproductus arcticus* — *Waagenoconcha irginae* inhabited nutrient-rich nearshore environments, where the main limiting ecological factors were water turbulence and substrate nature. The first two of the index species were equipped to live under such circumstances due to their long and strong spines which allowed for firm anchoring in the sediment. *Waagenoconcha irginae*, in turn, was able to settle soft substrates between skeletal banks dominated by *Horridonia timanica* and *Svalbardoproductus arcticus*.

The majority of the cherts of the Svenskeegga and Hovtinden Members contain abundant sponges, which probably were adapted to life around the chemocline; there was only a limited water circulation in that zone, but also little competition from other organisms. Brachiopods presumably had greater oxygen requirements, as they are very rare or entirely absent from this facies zone.

The widespread occurrence (lithological complexes H-1, P-4b, F-5) of the assemblage *Horridonia timanica* — *Svalbardoproductus arcticus* — *Waagenoconcha irginae* in isochronous sediments at the top of the Svenskeegga Member (Małkowski 1982) suggests that the zone inhabitable by brachiopods expanded; this phenomenon may have been caused by lowering, or even partial disappearance of the chemocline, during a diastrophic episode (Fig. 10). This situation did not persist for long, water stratification reappeared,

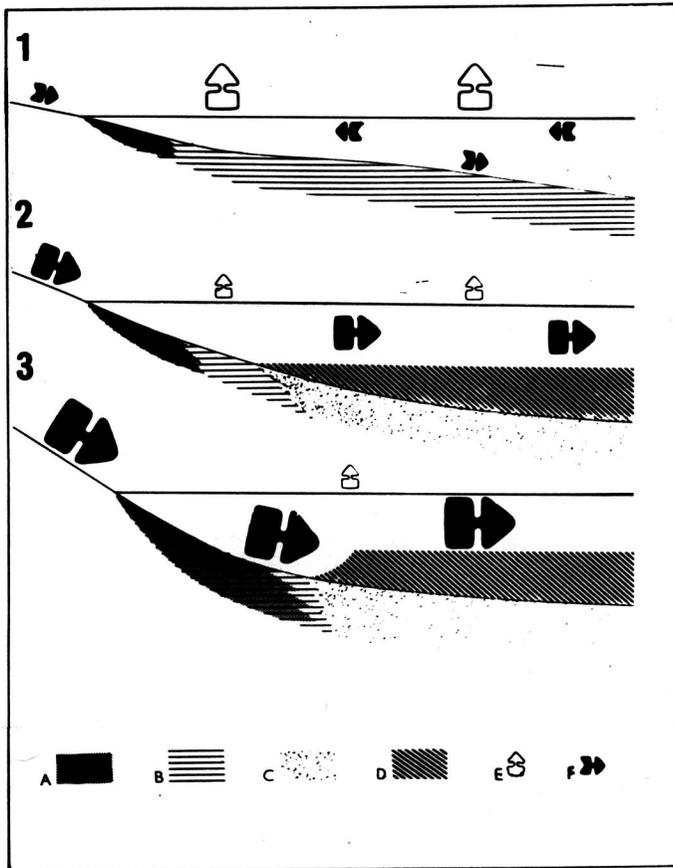


Fig. 10. A model of the Permian sea of Spitsbergen in the times of negative water balance and unstratified water column (1), positive water balance and stratified water column (2), increased terrigenous influence and the consequent local disappearance of water column stratification (3) A — terrigenous deposits, B — carbonates, C — cherts, D — the zone below chemocline, E — evaporation, F — freshwater influx

and brachiopod habitats shifted again shorewards, beyond the limits of the study area. The F-5 complex well illustrates these environmental changes, for its fossiliferous rocks border both at the top and at the base with deposits indicative of anaerobic conditions. As a result of such migrations of the brachiopod-crinoid-bryozoan biofacies (equivalent to „*Spirifer limestone*”), the *Horridonia timanica* — *Svalbardoproductus arcticus* — *Waagenoconcha irginae* assemblage appears twice in the Kapp Starostin Formation in Central Spitsbergen; while there are indications (Burov *et al.* 1965, Ustritsky 1979) that it appears also in the uppermost Permian strata in northeastern Svalbard. An occurrence of this characteristic fossil assemblage can thus be related to migration of the shallow sublittoral zone during the diastrophic episodes (Fig. 11) in the study area (see Whittaker 1975).

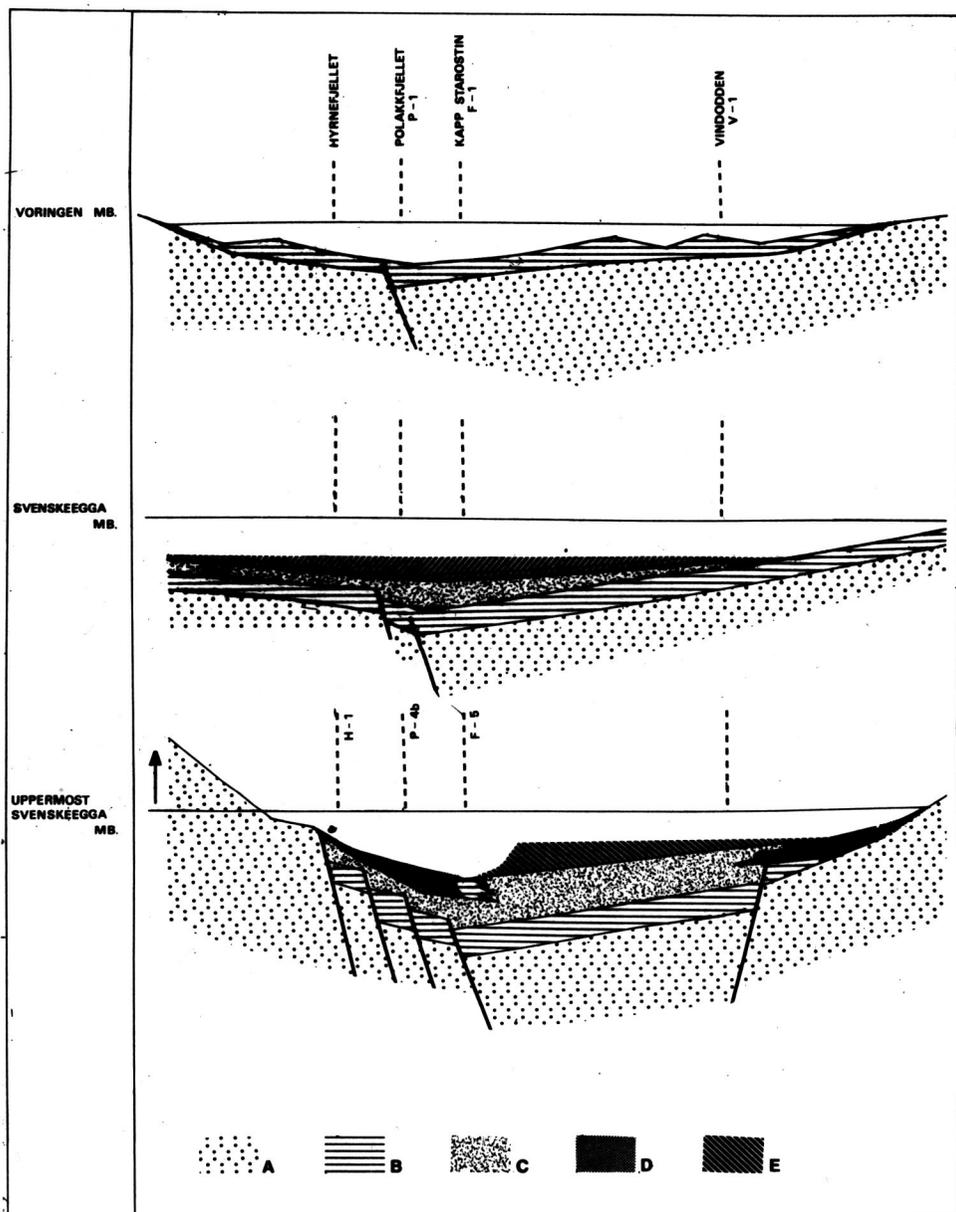


Fig. 11. Facies development stages of the Kapp Starostin Formation, at which the richest productacean taphocoenoses accumulated. A — basement rocks, B — carbonates, C — cherts, D — terrigenous deposits, E — the zone below chemocline

The sediments belonging in the investigated area to the Hovtinden Member were deposited at a distance from the shoreline, presumably under somewhat cooler climatic conditions. The climate allowed for at least episodic

mixing of the water and hence for colonization of this area by brachiopods. The assemblage living in this environment must have been dominated by forms capable of life on soft, perhaps even quaggy, substrates. This is why the assemblage is dominated by *Waagenoconcha irginae* and *Kochiproductus porrectus*.

The assemblage *Megousia weyprechtii* — *Megousia kulikii* — *Yakovlevia duplex* inhabited environments less favorable for brachiopods, in the vicinity of the chemocline, that is, under limited oxygen and nutrient concentrations. Its typical typhocoenoses occur at the transition between the Voringen and Svenskeegga Members in Ahlstrandodden section and in the Tr-2 lithological complex in the Hovtinden Member.

During deposition of the Hovtinden Member, the contribution of terrigenous sediments considerably increased, perhaps in association with a climatic cooling and disappearance of water stratification. These phenomena may have played crucial roles in the sharp faunal change at the Permian/Triassic boundary, at least in the investigated area.

Final remarks

The pattern of distribution of the productacean phenon in the Kapp Starostin Formation can be explained by environmental changes during deposition of this formation, without any reference to evolutionary processes which may have had little impact on adaptive morphology of the Productacea in the considered time interval. Taxonomic composition of the productacean assemblages occurring in particular lithological complexes was primarily controlled by the limiting factors (Liebig 1840, Shelford 1913) specific to the individual species. The pattern of appearance/disappearance of these assemblages was controlled by environmental change triggered by regional geodynamic processes. There is no reason to consider fossil assemblages, constructed on the basis of overlapping distributions of individual species, as units of biosphere organization (Hoffman 1979). Coexistence of species must be referred to the entire ecosystem rather than merely to their local ecological interrelationships.

Acceptance of the view that the particular productacean species are confined each to a certain facies zone leads also to the conclusion that their evolutionary transformations must be studied within such a zone; whereas each facies zone shifts in space in the history of sedimentary basin. Evolutionary analysis of morphological changes, therefore, should generally not be done along the sedimentary sequence in a section. According to the Walther Law, a vertical sequence of facies corresponds to the lateral facies variation in the basin; it is therefore appropriate

to decipher the environmental distribution of group of organisms but not to study its evolutionary history.

In the Kapp Starostin Formation, the nearshore deposits known as „*Spirifer* limestone” were often regarded as isochronous (Ustritsky 1967, Biernat and Birkenmajer 1981). Actually, however, they occur a few times during deposition of the formation, also in its uppermost part (Ustritsky 1962), due to repeated local marine regressions (Małkowski 1982). However, the assemblage *Horridonia timanica* — *Svalbardopproductus arcticus* — *Waagenconcha irginae*, which is characteristic of these strata, did not undergo any significant change over this time interval. Because of the facies distribution of Productacea in the investigated area, they are useless for local chronostratigraphic correlation. These brachiopods, however, are very good paleoecological indices and hence can well be employed for paleoenvironmental reconstruction.

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Systematic paleontology

Superfamily **Productacea** Waagen, 1883

Genus *Horridonia* Chao, 1927

Type species: *Productus horridus* J. Sowerby, 1923

Horridonia timanica (Stuckenberg, 1875)

(Pl. 1, Figs. 1—2, 4—6; Pl. 2, Figs. 3—4)

1963. *Horridonia timanica*; Gobbett: 94, pl. 10, 1—4, with synonymy.

1972. *Horridonia timanica*; Ifanova: 127, pl. 9, 1—3.

1972. *Horridonia granulifera*; Ifanova: 124, pl. 8, 1—7.

1980. *Burovia selenderensis*; Ustritsky: 26, pl. 1, 1—2; pl. 2, 1—3.

Material: 242 well-preserved specimens.

Biometry¹:

Specimen identification number	shell length	shell with	shell thickness	surface length of ventral valve
V-114	46.0	65.0*	29.0	92.0
V-146	54.4	75.5*	25.6	93.0
V-283	55.0	79.8*	26.9	96.0
V-343	50.8	73.0*	21.6	74.0
V-345	44.8	65.3*	18.0	65.0

V-347	56.8	75.9*	25.8	90.0
V-350	49.8	64.0*	20.6	76.0
V-356	38.2	55.2*	24.0	77.0
V-371	62.0	70.7*	29.7	95.0
V-414	52.7	83.4*	27.3	63.0
V-420	52.8	79.0*	20.8	88.8
V-426	25.3	39.2*	10.0	32.5
V-1168	14.8	18.2	5.8	22.0
A-177	29.2	27.9	12.2	48.0
A-312	26.0	28.0	15.3	57.0
A-319	33.6	35.8	25.3	72.0
A-331	28.6	27.3	13.6	62.0
P-303	50.6	53.6	20.8	82.0
P-835	40.0	43.0	17.3	62.0
S-263	68.6	81.0*	32.2	123.0
R-1	64.3	62.0	39.0	130.2
R-2	64.0	61.0	43.6	129.0
R-3	74.0	59.1	30.0	133.0
H-120	48.0	41.0	26.5	102.0
H-214	49.0	46.2	28.3	101.0

¹ Letter symbols in specimen identification numbers refer to particular localities in the Kapp Starostin Formation: V — Vindodden, L, G, S, K — Kapp Starostin, A — Ahlstrandodden, O, P — Polakkfjellet, H, R — Hyrnefjellet, Tr — Treskelen.

* width included the auricles

Index morphological features: Shell provided with auricles; shell surface almost smooth to finely granular. Ventral valve strongly convex, with a distinct sinus. Umbo narrow. Dorsal valve slightly concave, with a low median fold. Auricle margins bear long and straight spines in the dorsal valve; but no spines occur at the ventral valve.

Intraspecific variation: In the V-1 lithological complex, *H. timanica* has numerous spines symmetrically arranged at the auricle margins in the dorsal valve. Distinct growth lines correspond to each pair of the spines (Pl. 1, Fig. 5; Pl. 2, Fig. 3). Well-developed spines and auricles appear at shell sizes exceeding 30 mm in length. The degree of shell coiling — or the ratio of the ventral valve actual length, as measured at the shell surface, to its projection on the plane — ranges between 1.5 and 2.0. The taphocoenosis in this lithological complex contains abundant single dorsal valves (Pl. 1, Fig. 1), which are thicker than the ventral ones (they attain 8 mm in thickness, as contrasted to 2—3 mm in ventral valve thickness) and hence more easily preservable. *H. timanica* from the F-1 lithological complex resembles its conspecific phenon from V-1 in shell outline, but it has less pronounced growth lines and less numerous spines. In the A-1 complex, the specimens are generally smaller (no more than 40 mm in length), but they have unusually long auricles (Pl. 1, Fig. 2) and more strongly coiled shells (the degree of coiling exceeds 2.0). They show no growth lines no spines on the auricle margins. The specimens from P-1 are relatively small-sized (below 40 mm in length), without visible growth lines and spines, but the degree of their coiling does not exceed 1.8. In the F-5 lithological complex, *H. timanica* achieves the largest size (up to 80 mm in length), but its morphology resembles the intermediary ontogenetic stages (at less than 30 mm in length) recorded in the other complexes (Pl. 1, Fig. 4); it has poorly developed auricles with only cardinal spines at the margins, and weakly convex ventral valves. The density of granular shell sculpture is here lower than in V-1 and F-1 (Pl. 1, Figs. 4—5; Pl. 2, Fig. 3), and the dorsal valve thickness

reaches 10 mm. The specimens from F-4b are less than 45 mm in length, poorly developed auricles, relatively little shell coiling (below 1.8), and distinct growth lines at the shell surface (Pl. 1, Fig. 6). The shells of *H. timanica* from H-1, in turn, reach the length of 80 mm, are strongly coiled (above 2.0), but have no growth lines or spines.

Ecology: The species *H. timanica* inhabits a wide range of environments, from near-shore habitats (H-1) and shoals (V-1) to open marine areas with loose substrates, good water circulation, adequate food and oxygen levels (F-5). Its individuals lived anchored at the sediment surface, with commissure kept above the sediment-water interface. The ecophenotypic variation of *H. timanica* concerns the degree of shell coiling, maximum size, ornamentation density, spine presence, number and distribution, and auricle shape and size. The species is often dominant in taphocoenoses from nearshore habitats. Its specimens in particular taphocoenoses generally are uniform in size, which may — given the absence of taphonomic biases — suggest only a little of mortality during growth. — The negligibility of taphonomic biases is indeed indicated by the cooccurrence of *H. timanica* with such small- and thin-shelled forms as *Anemonaria pseudohorrida*. *H. timanica* most commonly occurs in association with *Svalbardoproductus arcticus* and *Arctitreta kempei*.

Remarks: The form *Burovia selenderensis*, described by Ustritsky (1980) from late Permian strata of Spitsbergen, is here included to the synonymy of *H. timanica*, because its morphology and the associated fauna suggest it falls within the range of variation accepted for the latter species. Differences in thickness between the dorsal and the ventral valves, which Ustritsky (1980) regards as diagnostic of the genus *Burovia*, are subject to ecophenotypic in the species *H. timanica*.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, A-1, F-1, P-1; Svenskeegga Member — F-5, F-4b, H-1.

Horridonia aff. *horrida* (Sowerby, 1923)
(Pl. 2, Figs. 1, 2a-b)

Material: 5 specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
V-361	40.7	44.4	24.0	82.0
T-47	38.0	40.4	17.0	62.0
T-703	50.8	44.5	24.2	95.0

Discussion: A number of *Horridonia* specimens found in the V-1 and Tr-2 lithological complexes have spines on the auricles of the ventral valve. According to the diagnosis of *H. horrida* given by Gobbett (1961), this is the diagnostic feature of this species. A specimen from V-1 has a row of spines on the auricles of the ventral valve (Pl. 2, Fig. 1) and symmetrical spine rows at both sides of the sinus. All the other morphological traits of this specimen agree with those of the cooccurring specimens of *Horridonia timanica*. The specimens from Tr-2 have cardinal spines at the hinge margin of the ventral valve and pairs of spines on the auricles of the dorsal valve (Pl. 2, Fig. 2a-b). The degree of their shell coiling is 1.5, and the auricle shape and size resemble the specimens from V-1.

Remarks: The similarity in shell form between *H. timania* and *H. aff. horrida*, their cooccurrence in V-1, and the wide variation in spine number and distribution in *H. timanica* may suggest that these forms are very closely related to each other or even conspecific. Yet the paleogeographic ranges of both these taxa are clearly separated (Malzahn 1937, Gobbett 1961), and hence they may indeed be distinct, even if only at the level

of geographic races. The specimens of *H. aff. horrida* from the Tr-2 lithological complex occur in strongly marly sediments; they lived on soft substrates where shell stabilization was more difficult to achieve than in the habitat of *H. timanica*. Their life environment resembled the Zechstein facies, which was typical of the habitat of *H. horrida* (Kaźmierczak 1967).

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1; Hovtinden Member — Tr-2.

Genus *Svalbardopproductus* Ustritsky, 1962

Type species: *Productus semireticulatus arcticus* Whitfield, 1908

Svalbardopproductus arcticus (Whitfield, 1908)

(Pl. 1, Figs. 1—3; Pl. 3, Figs. 1—5)

1962. *Svalbardopproductus striatoauritus*; Ustritsky: 74—89, pl. 2, 1a.
 1963. *Costinifera arctica*; Gobbett: 90, pl. 9, 2—6, with synonymy.
 1969. *Costiferina arctica*; Birkenmajer and Logan: 37.
 1972. *Thuleproductus arcticus*; Sarytscheva and Waterhouse: 71, pl. 7, 9; pl. 8, 4—5, with synonymy.
 1977. *Thuleproductus subarcticus*; Sarytscheva: 78, pl. 9, 1—3.
 1977. *Thuleproductus arcticus*; Sarytscheva: 74, pl. 7, 6—8.
 1977. *Thuleproductus crassauritus*; Sarytscheva: 76, pl. 8, 1—4.
 1981. *Thuleproductus cf. crassauritus*; Biernat and Birkenmajer: 13, pl. 2, 2; pl. 3, 1—3.
 Material: 177 well-preserved specimens, including some ventral valves with internal mould of morphology of the dorsal valve (Pl. 3, Fig. 4).

Biometry:

Specimen identification number	shell length	shell with	shell thickness	surface length of ventral valve
V-172	44.6	48.4	27.0	89.0
V-173	52.0	39.0	26.3	91.0
V-296	21.0	33.5	—	—
V-340	35.5	78.3	24.9	73.0
V-465	36.2	33.5	21.8	69.0
V-477	40.9	50.4	30.0	74.0
A-127	43.0	72.0	26.5	75.0
A-128	48.3	42.0	19.0	81.0
L-57	39.0	41.2	24.8	76.0
L-58	36.8	38.3	18.3	72.0
P-256	46.1	58.4	19.7	75.0
P-264	38.7	41.8	25.4	78.0
P-271	46.0	55.0	28.8	96.0
P-274	39.0	40.8	27.2	67.0
P-293	44.7	48.0	26.2	95.0
P-305	43.0	43.6	25.4	92.0
P-307	48.0	45.4	39.6	88.0
H-46	62.1	53.0	32.0	120.0
H-74	47.0	46.5	25.0	88.0
H-99	45.0	47.3	29.0	98.0
S-11	73.3	71.0	38.0	173.0
S-48	71.6	—	43.0	186.0
S-56	61.3	65.1	40.3	116.0
S-182	52.0	60.1	41.1	127.0
G-9	85.6	79.9	40.8	135.0

Index morphological features: Well-developed auricles. 6—8 strong, thick ribs per centimeter. Ventral valve convex, with a low median fold. Spines straight and long (though variable in length), particularly numerous on the margins and auricles of the ventral valve. Reticulated shell sculpture in the umbonal part of the shell. Ribs on the auricles parallel to the hinge margin.

Intraspecific variation: In the V-1, F-1, and A-1 lithological complexes, *Svalbardopproductus arcticus* does not exceed 56 mm in shell length; rib density ranges between 7 and 10 per centimeter (Pl. 1, Figs. 3; Pl. 3, Figs. 1—2), ventral valve thickness approximates 1.5—2.0 mm, but up to 5 mm in its umbonal part, dorsal valve thickness is 2 mm. The spines reach 50 mm in length, umbonal angle approximates 100, and the degree of shell coiling ranges between 1.7 and 1.9. Even articulated shells usually lack spines and auricles. Shell thickness at the auricle margins is less than 1 mm. Many ribs bifurcate in the anterior part of the dorsal valve; such bifurcations are less common in the ventral valve. The specimens from P-4b and H-1 have a narrower umbo, with the umbonal angle ranging from 80 to 90 (Pl. 3, Fig. 2). *S. arcticus* attains the greatest size in F-5, here it may reach 90 mm in length. Its specimens in the latter complex have large auricles and 6—8 thick ribs per centimeter (Pl. 3, Fig. 3), and the degree of their shell coiling approximates 2.0.

Ecology: The species *S. arcticus* inhabits shallow nearshore environments (H-1, V-1, F-1, A-1) as well as open marine areas subject to terrigenous influence (F-5, P-4b). The shell size and the long and straight spines indicate adaptation to life at the surface of loose sediments. Ecophenotypic variation of the species concerns primarily the maximum shell size and rib density. *S. arcticus* often occurs in clusters of a dozen or so adult specimens. It is commonly associated with *Horridonia timanica* and *Waagenoconcha irginae*.

Remarks: Minor differences in shell morphology, which are herein regarded as ecophenotypic variation, constituted the basis for establishing three congeneric species: *S. arcticus*, *S. subarcticus*, and *S. crassauritus* (Sarytscheva 1972, 1977). One of the diagnostic, for example, was the number of ribs per centimeter, which seems to depend in the Kapp Starostin Formation upon the maximum shell size in particular localities. The genus *Thuleproductus* was erected by Sarytscheva and Waterhouse (1972) for material from the Canadian Arctic, without taking notice of the older name *Svalbardopproductus* (Ustritsky 1962). The authors of *Thuleproductus* assigned to their new genus also the species *arcticus*, which had been repeatedly described from Spitsbergen (see Gobbett 1963). Ustritsky (1979) emphasized taxonomic priority of the name *Svalbardopproductus* and attributed to this genus all species described under the name *Thuleproductus*.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, F-1, A-1; Svenskeegga Member — H-1, F-5, P-4b.

Genus *Kochiproductus* Dunbar, 1955

Type species: *Productus porrectus* Kutorga, 1844

Kochiproductus porrectus (Kutorga, 1844)

(Pl. 4, Figs. 1, 3, 5—6; Pl. 5, Fig. 5)

1963. *Kochiproductus porrectus*; Gobbett: 80, pl. 7, 1—3.

Material: 65 specimens, in part preserved as internal moulds with shell fragments, sometimes distorted by compaction.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
V-474	70.0	61.0	30.8	116.0
V-578	63.0	70.0	24.5	85.0

A-330	22.8	31.6	10.4	42.0
P-841	115.0	105.0	48.2	164.0
H-169	36.0	41.3	14.1	57.0
T-6	40.8	45.4	16.9	61.0
T-406	51.0	46.0	18.4	82.0
T-429	43.1	44.8	20.3	78.0
T-447	47.0	40.6	19.0	71.0
T-857	53.6	51.0	27.0	85.0
T-711	52.0	51.2	—	—
K-351	60.6	51.3	—	—
K-365	56.4	54.0	—	—
K-373	31.0	46.7	—	—

Index morphological features: Shell oval in outline, with a long velum and covered with thick, undulated ribs bearing tubercles at the base of the spines. Ventral valve convex but flattening in ontogeny. Sinus wide and shallow. Umbo massive. Dorsal valve almost flat. Spines thin.

Intraspecific variation: In the V-1 and A-1 lithological complexes, *K. porrectus* reaches up to 80 mm in length. It has up to 8 ribs per centimeter; the ribs often bifurcate in the anterior part of the shell, while the spine bases are poorly developed. The specimens from H-1 and F-5 have similar shell size and outline, but the rib density is smaller (6–7 per centimeter). The majority of the specimens from Tr-2 and F-8 are preserved as internal moulds distorted by compaction; there are only shell fragments covered with distinctive ornamentation (Pl. 4, Figs. 3, 6; Pl. 5, Fig. 5). These specimens reach at most 60 mm in length. In F-8, delicate auricles with traces after spines occur on some specimens (Pl. 4, Figs. 1, 5).

Ecology: The species *K. porrectus* inhabited soft substrate areas in the nearshore zones (H-1) as well as on the outer shelf (Tr-2, F-5, F-8). The shell shape suggests its ability to float at the sediment surface, but the long velum indicates that some specimens were also capable of living partly buried in the substrate. In outer shelf areas, the species occurs rather abundantly — a dozen or so individuals per square meter in Tr-2.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, A-1; Svenskeggga Member — H-1, F-5; Hovtinden Member — Tr-2, F-8.

Genus *Waagenoconcha* Chao, 1927

Type species: *Productus humboldti* d'Orbigny, 1842

Waagenoconcha irginae (Stuckenbergh, 1898,
emend. Tschernyshev, 1902)

1963. *Waagenoconcha irginae*; Gobbett: 76, pl. 5, 7; pl. 6, 1–5, with synonymy.

1963. *Waagenoconcha wimani*; Gobbett: 75, pl. 5, 1–2.

1969. *Waagenoconcha irginae*; Birkenmajer and Logan: 36; pl. 1, 3a-d.

1972. *Waagenoconcha humboldti*; Ifanova: 103, pl. 3, 14–16.

1972. *Waagenoconcha wimani*; Ifanova: 105, pl. 3, 17–18.

Material: 152 specimens, in part distorted by compaction.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
V-6	46.0	53.0	—	—
V-253	60.2	48.4	28.8	103.0

V-338	43.2	48.0	16.5	62.0
V-1193	41.2	41.8	15.8	62.0
V-1194	18.4	16.0	7.9	24.0
V-1195	19.3	22.2	8.0	25.0
P-212	30.4	36.6	16.5	57.0
P-215	37.4	39.4	16.3	64.0
P-269	—	29.0	9.2	—
P-290	33.0	34.0	14.5	50.0
P-551	53.2	60.7	20.6	91.0
P-589	61.4	51.0	21.3	93.0
P-842	69.5	72.4	23.2	109.0
P-873	78.5	66.0	24.4	120.0
T-1	31.4	37.0	11.4	42.0
T-2	33.0	34.1	13.3	57.0
T-3	38.0	40.2	17.0	58.0
T-31	28.5	28.9	8.2	40.0
T-470	40.7	36.2	17.0	62.0
T-501	36.2	36.1	19.0	66.0
T-701	30.6	30.4	12.0	42.0

Index morphological features: Shell oval in outline, covered with concentric lamellae each with a row of fine spines. Ventral valve moderately convex, flattening in ontogeny. Dorsal valve flat. Spines curved, pointing towards the shell growth direction.

Intraspecific variation: The specimens from V-1 range from 10 to 60 mm in shell length. Their surface ornamentation is distinct, with spine bases arranged alternately in rows parallel to concentric lamellae; spine density attains 100 per square centimeter. In the H-1, A-1, and P-1 lithological complexes, *Waagenoconcha irginae* does not exceed 50 mm in shell length, but its sculpture density resembles that recorded in V-1. The specimens from P-4b and F-5 achieve larger size (more than 70 mm) and their shell outline is somewhat different than in those from the other localities (Pl. 4, Fig. 4). The specimens of *W. irginae* from P-3 have particularly thick shells, whereas those from Tr-2 and F-8 are no more than 45 mm long and with spine density less than 80 per square centimeter.

Ecology: The species *Waagenoconcha irginae* occurs in all the environments inhabited by brachiopods in the Permian sea of Spitsbergen. Its capability of floating at the sediment surface allowed it to successfully enter many habitats inaccessible to the other productaceans. The largest shell sizes occur among individuals which lived in the outer shelf zone.

Remarks: The variable maximum shell size and ornamentation density in different localities were previously taken as the basis to distinguish between *Waagenoconcha humboldti*, *W. irginae* and *W. wimani*. In the Kapp Starostin Formation, however, the pattern of variation in these characters is most easily explained as ecophenotypic reaction of conspecific organisms to environmental differences.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, A-1, F-1; Svenskeegga Member — H-1, P-4b; F-5; Hovtinden Member — Tr-2, F-8.

Genus *Yakovlevia* Fredricks, 1925

Type species: *Yakovlevia kaluziensis* Fredricks, 1925

Yakovlevia impressa (Toula, 1875)

(Pl. 5, Fig. 2; Pl. 6, Figs. 1, 3, 6)

1963. *Yakovlevia impressa*; Gobbett: 114, pl. 14, 1—4.

1972. *Yakovlevia impressa*; Ifanova; 122, pl. 7, 6—8.

Material: 147 well-preserved specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
V-298	52.2	82.4	25.0	77.0
V-360	46.9	63.0	18.0	65.0
V-374	46.9	67.6	21.2	70.0
V-442	54.8	66.3	23.2	81.8
V-445	63.0	70.7	25.4	82.0
V-448	58.2	71.0	26.0	90.2
V-457	50.8	73.8	28.0	75.0
V-459	52.5	70.7	16.0	66.0
A-75	41.3	48.8	16.3	62.0
A-80	34.0	50.0	—	—

Index morphological features: Shell trapezoid in outline, covered with fine ribs. Ventral valve convex, with a shallow sinus. Umbo small and wide. Dorsal valve strongly concave, with a low median fold. Short spines at the hinge margin.

Intraspecific variation: The majority of the collection comes from V-1, where *Y. impressa* shows a considerable variation in shell length to width ratio (0.6 to 0.9) and in auricle size (Pl. 6, Figs. 1, 3, 6), Rib density ranges from 16 to 30 per centimeter, and the maximum shell length approximates 65 mm. In the A-1 lithological complex, the specimens of *Y. impressa* are smaller-sized (no more than 45 mm in shell length) and less convex.

Ecology: In the Kapp Starostin Formation, the species *Yakovlevia impressa* is confined to loose but rather stable substrates in shallow-water areas. It may form large monospecific accumulations.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, A-1.

Yakovlevia duplex (Wiman, 1914)
(Pl. 5, Fig. 3; Pl. 6, Figs. 2, 4—5, 7)

1963. *Muirwoodia duplex*; Gobbett: 113, pl. 14, 5—6.

Material: 28 well-preserved specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
A-28	28.3	39.2	20.5	61.0
A-46	25.6	34.4	13.0	53.0
A-314	30.4	38.7	17.8	60.0
A-324	31.2	43.1	20.1	61.0
A-333	28.6	38.7	16.4	52.0
S-270	35.0	43.0	—	—
H-17	26.5	32.2	18.0	60.0
H-80	29.5	33.0	16.0	54.0
H-133	23.4	31.2	12.0	52.0
P-196	28.0	34.2	16.4	46.0
P-287	21.9	26.8	11.5	46.0
P-295	28.9	36.7	17.7	61.0
P-301	23.0	35.7	11.6	36.0
P-421	29.2	37.0	16.1	54.0

Index morphological features: Shell subrectangular, covered with fine ribs. Ventral valve strongly convex, with a distinct and deep sinus. Umbo small and wide. Dorsal valve strongly concave. Few spines at the sides of the ventral valve.

Intraspecific variation: In the A-1 lithological complex, the specimens of *Y. duplex* are no more than 30 mm long, have 17–20 ribs per centimeter (Pl. 4, Figs. 4, 6) and 0.5–0.8 shell length to width ratio, and the degree of their shell coiling ranges from 1.8 to 2.0. In H-1 and P-4b, the shell size and outline (Pl. 6, Figs. 4–5) are very much like in A-1, but the degree of shell coiling exceeds 2.0. The largest shell sizes (up to 40 mm in length) occur in F-5, where the rib density is the smallest (no more than 16 per centimeter).

Ecology: The species *Yakovlevia duplex* is restricted in its occurrence to loose but rather stable terrigenous substrates in shallow-water areas. It occurs in clusters of up to a dozen or so specimens per square meter.

Remarks: The generic identity of *Muirwoodia* and *Yakovlevia* is here accepted, as in Ifanova (1972).

Occurrence: In the Kapp Starostin Formation: Voringen Member — A-1; Svenskeegga Member — H-1, P-4b, F-5.

Yakovlevia mammata (Keyserling, 1846)

(Pl. 5, Fig. 6)

1963. *Muirwoodia mammata*; Gobbett: 112, pl. 13, 23–28.

1972. *Yakovlevia mammata*; Ifanova: 121, pl. 7, 4–5.

Material: 9 specimens derived from a single cluster.

Index morphological features: Shell subrectangular, very wide, covered with fine ribs. Ventral valve strongly convex, with a pronounced sinus. Dorsal valve convex. Some spine bases at the sides of the ventral valve.

Remarks: The shells of *Y. mammata* are relatively small-sized, with shell length to width ratio of less than 0.6. They cooccur in F-5 with *Y. duplex*, from which they differ in shell size and outline as well as in a distinct geniculation of the dorsal valve (Pl. 5, Fig. 6).

Occurrence: In the Kapp Starostin Formation: Svenskeegga Member — F-5.

Genus *Megousia* Muir-Wood and Cooper, 1960

Type species: *Megousia auriculata* Muir-Wood and Cooper, 1960

Megousia weyprechtii (Toula, 1874)

(Pl. 7, Figs. 7, 11)

1963. *Megousia weyprechtii*; Gobbett: 107, pl. 12, 27–29; pl. 13, 1–6.

1977. *Megousia weyprechtii*; Grigorjeva and Kotlar: 63, pl. 6, 1–3.

Material: 152 well-preserved specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
V-56	15.6	20.1	8.2	31.0
V-70	12.8	18.0	7.1	27.0
V-76	18.6	—	8.4	41.0
V-207	24.8	25.2	9.1	47.0
V-221	21.1	26.3	11.3	41.0
H-115	23.0	31.5	14.1	44.0

H-419	21.3	30.8	13.2	43.0
H-229	31.4	36.9	15.0	54.0
P-450	22.2	32.0	12.0	40.0
P-453	28.0	31.4	16.2	48.0
S-47	26.7	26.2	11.2	44.0
S-76	29.6	26.8	15.2	48.0
S-345	23.0	26.5	—	—
T-4	21.8	30.2	14.2	42.0
T-5	22.0	29.8	11.8	37.0
T-473	24.1	29.0	11.3	41.0
T-648	24.1	26.6	13.1	43.0
T-717	24.3	30.8	14.2	46.0
T-743	22.6	32.1	14.3	41.0

Index morphological features: Shell subrectangular, with well-developed auricles, covered with fine ribs which run parallel to the hinge margin on the auricles. Ventral valve strongly convex, with a shallow sinus. Umbo small and wide. Dorsal valve weakly concave, with a low median fold. Few spine bases near the hinge margin. Ribs often bifurcate in the anterior part of the shell.

Intraspecific variation: In the Kapp Starostin Formation, this species is rather uniform in size (up to 30 mm in shell length) and in rib density (15–20 per centimeter). It shows a variation in the degree of shell coiling (1.7–2.0), with a maximum reached in V-1 and H-1.

Ecology: The species *Megousia weyprechtii* occurs in a very wide range of environments, from nearshore to the outer shelf, under a variety of substrate, food availability, and turbulence conditions. Its individuals lived at the sediment surface, anchored with their spines, and perhaps also supported by the large auricles.

Remarks: The large auricles of *M. weyprechtii* (Pl. 7, Fig. 11) were interpreted as a brood chamber, and hence as an expression of sexual dimorphism (Ferguson 1969). The present material does not allow for a description of these delicate structures, because they are too poorly preserved.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, F-1, A-1; Svenskeegga Member — H-1, P-4b, F-5; Hovtinden Member — Tr-2.

Megousia kulikii (Fredricks, 1915)

(Pl. 7, Fig. 8)

1963. *Megousia kulikii*; Gobbett: 110, pl. 13, 7–15.

1972. *Megousia kulikii*; Ifanova: 114, pl. 5, 1–14.

1977. *Megousia kulikii*; Grigorieva and Kotlar: 61, pl. 5, 17.

Material: 72 specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
V-131	25.6	36.0	14.4	50.0
V-221	20.6	27.0	13.0	38.0
V-319	20.3	28.0	15.1	42.0
P-569	17.3	18.2	10.4	44.0
T-492	13.4	12.3	8.0	26.0
T-497	12.3	14.3	6.0	22.0
T-502	13.2	16.0	8.0	26.0

T-565	14.8	28.0	13.6	8.9
T-713	13.6	15.2	8.4	21.0
T-718	14.8	15.0	8.6	26.0

Index morphological features: Shell suboval, with pronounced auricles, covered with fine ribs. Ventral valve strongly convex, with a weakly developed sinus. Umbo small and wide. Dorsal valve weakly concave. Few thin spines at the sides of the ventral valve and on the hinge margin.

Intraspecific variation: In the V-1 and A-1 lithological complexes, *M. kulikii* attains 30 mm in shell length, 15 ribs per centimeter, and 1.9–2.0 in degree of shell coiling. The specimens from Tr-2 are smaller-sized (no more than 15 mm in shell length), but the other quantitative traits are similar to those observed in the other localities.

Ecology: The species *M. kulikii* inhabited quiet-water environments rather distant from the shoreline.

Occurrence: In the Kapp Starostin Formation: Voringen Member — A-1, V-1; Svenskeegga Member — P-3s; Hovtinden Member — Tr-2.

Genus *Anemonaria* Cooper and Grant, 1969

Type species: *Anemonaria inflata* Cooper and Grant, 1969

Anemonaria pseudohorrida (Wiman, 1914)

(Pl. 7, Figs. 2–4, 6)

1963. *Liosotella pseudohorrida*; Gobbett: 62, pl. 3, 27–34.

1977. *Anemonaria pseudohorrida*; Sarytscheva: 120, pl. 17, 4–5; pl. 18, 1–4, with synonymy.

Material: 181 well-preserved specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
V-317	22.1	24.2	14.6	46.0
V-464	14.6	23.3	7.5	23.0
V-1178	16.2	17.1	11.6	38.0
V-1202	20.0	23.8	10.2	38.0
A-4	17.3	19.0	9.8	35.0
A-25	20.0	24.1	10.2	44.0
A-98	19.0	24.8	8.0	32.0
A-137	19.0	32.0	13.5	41.0
A-302	11.0	14.0	7.9	26.0
A-340	19.2	20.9	14.3	42.0
A-353	17.2	22.6	11.3	43.0
A-356	16.4	20.2	8.4	35.0
G-5	22.0	25.0	9.9	37.0
G-20	20.8	24.4	12.0	41.0
G-21	24.6	26.0	14.1	43.0
S-212	15.0	18.1	6.2	24.0
T-513	19.6	19.0	11.0	32.0
T-706	14.2	20.0	9.7	27.0
T-714	18.1	19.2	10.1	26.0
T-743	16.1	20.0	9.2	26.0

Index morphological features: Shell trapezoid or subrectangular, smooth. Ventral valve strongly convex, with a distinct sinus. Umbo small and narrow. Dorsal valve concave, with a low median fold. Small auricles. Long and straight spines along the hinge margin and a few of them also on the visceral surface of the ventral valve.

Intraspecific variation: The shells of *A. pseudohorrida* from V-1, A-1, and F-1 attain 20 mm in length; they have distinct auricles, and the degree of their coiling varies from 1.8 to 2.4. In the lithological complex F-5, the shells reach 25 mm in length, approximate 2.0 in degree of coiling, and their auricles are smaller than in the other localities.

Ecology: The species *A. pseudohorrida* occurs in a wide range of shallow sublittoral environments, particularly in relatively quiet-water areas. Its individuals lived at the sediment surface, stabilized by their long cardinal spines. The species has a rather narrow range of ecophenotypic variation.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, A-1, F-1; Svenskeegga Member — F-5, P-4b, H-1; Hovtinden Member — Tr-2.

Genus *Liosotella* Cooper, 1953

Type species: *Liosotella rugosa* Cooper, 1953

Liosotella robertiana (De Koninck, 1850)

(Pl. 7, Figs. 1, 5, 9, 12)

1963. *Liosotella robertiana*; Gobbett: 66, pl. 4, 1—7.

Material: 34 specimens, in part distorted by compaction.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
K-347	13.0	17.6	—	—
K-381	13.6	18.4	—	—
K-399	14.4	19.6	—	—
T-634	9.7	9.8	5.0	15.0
T-651	12.2	11.6	9.6	21.0
T-679	11.2	11.1	6.0	18.0
T-692	12.6	14.2	8.3	22.0
T-723	11.2	13.9	6.9	21.0
T-729	11.6	12.8	5.6	19.0
T-741	10.0	12.8	5.0	15.0

Index morphological features: Shell small, trapezoid in outline, with rather small auricles. Valves covered with ribs which bifurcate, more rarely trifurcate, in the anterior parts. Ventral valve strongly convex, with a distinct but narrow sinus. Umbo massive. Dorsal valve concave, with a distinct median fold. A few long and straight spines.

Intraspecific variation: The specimens from Tr-2 have up to 15 mm in shell length and approximate 0.9 in shell length to width ratio (Pl. 7, Figs. 1, 5, 9). Rib density variable, dependent upon the rate of rib subdivision. The specimens from F-8, generally flattened by compaction (Pl. 3, Fig. 13), have the shell length to width ratio of no more than 0.8.

Ecology: The species *Liosotella robertiana* is confined in its occurrence to soft substrates in stable offshore environments. Its shells were stabilized in the sediment by long spines, especially if compared to the small weight of these thin shells.

Occurrence: In the Kapp Starostin Formation: Hovtinden Member — Tr-2, F-8.

Genus *Canocrinella* Fredricks, 1928, emend. Sarytscheva, 1937

Type species: *Productus cancrini* De Koninck, 1842

Canocrinella spitsbergiana Gobbett, 1963

(Pl. 8, Figs. 2, 4—8, 11)

1963. *Cancrinella spitsbergiana*; Gobbett: 104, pl. 12, 8—12.

1963. *Cancrinella singletoni*; Gobbett: 102, pl. 12, 1—7.

1977. *Cancrinella spitsbergiana*; Grigorieva *et al.*: 132, pl. 19, 13—15.

1977. *Cancrinella singletoni*; Grigorieva *et al.*: 133, pl. 19, 16—17.

1981. *Cancrinella spitsbergiana*; Biernat and Birkenmajer: 15, pl. 5, 1—8; pl. 6, 1—6.

Material: 204 generally well-preserved specimens.

Biometry:

Specimen identification	shell length	shell width	shell thickness	surface length of ventral valve
V-173	24.6	26.6	14.7	47.0
V-1173	13.6	12.4	6.1	22.0
V-1175	23.0	21.2	12.3	43.0
V-1182	20.8	19.2	10.4	37.0
V-1183	15.9	18.3	—	—
A-301	24.4	27.1	11.9	48.0
A-303	19.4	18.0	10.5	34.0
A-305	17.9	19.4	12.6	41.0
A-315	20.0	17.9	10.4	44.0
O-40	19.0	18.0	9.5	39.0
P-830	20.8	17.0	8.0	38.0
T-696	22.0	20.9	13.1	39.0
T-699	19.0	18.2	—	—
T-712	15.8	17.0	—	—
T-721	20.6	23.3	—	—
T-747	17.0	21.6	—	—
T-778	19.4	16.7	7.3	28.0
K-272	19.0	17.0	—	—
K-352	21.0	29.3	—	—

Index morphological features: Shell circular, covered with short ribs with alternating intercalatory ones and tubercles at the spine bases. Spines oblique to the shell surface, regularly arranged (quincunical). Ventral valve strongly convex, with a massive and wide umbo. Dorsal valve concave. Sinus and median fold absent.

Intraspecific variation: In the V-1, A-1, P-1 lithological complexes, the specimens have up to 25 mm in shell length, approximately 1.7—2.2 in shell coiling degree, and 20 spines per square centimeter (Pl. 8, Figs. 2, 4, 8). The specimens from Tr-2 and F-8 have similar dimensions but are generally less coiled (no more than 1.8), and there are also some differences in spine density and obliqueness (Pl. 8, Figs. 5, 7, 11).

Ecology: The species *Cancrinella spitsbergiana* inhabited the areas marginal relative to the ecological optimum of the Productacea. Its ability to live below the sediment surface, due to the presence of a velum, allowed it to survive periods of environmental stress caused by changes in water temperature and salinity in lagoon habitats or by oxygen deficiency in the vicinity of the pycnocline.

Remarks: The two species names *C. spitsbergiana* and *C. singletoni* were erected by Gobbett (1963) for two endmembers of a morphological continuum observed in the Kapp Starostin Formation. The present material provides evidence for continuity in variation in shell outline, ornamentation density, and spine obliqueness relative to the shell surface, which are the features Gobbett (1963) considered as distinctive between his two species.

This morphological continuity and the synecological similarity of the two morphotypes make the basis for the present author's decision to regard them as conspecific.

Occurrence: In the Kapp Starostin Formation: Voringen Member — V-1, A-1, P-1; Hovtinden Member — Tr-2, F-8.

Genus *Linoproductus* Chao, 1932Type species: *Productus cora* d'Orbigny, 1842*Linoproductus dorotheevi* (Fredricks, 1932)

(Pl. 8, Figs. 1, 3, 9—10)

1963. *Linoproductus dorotheevi*; Gobbett: 98, pl. 10, 8—9; pl. 11, 1—5.1981. *Linoproductus dorotheevi*; Biernat and Birkenmajer: 14, pl. 4, 1—5.

Material: 98 well-preserved specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
P-712	48.1	58.0	27.0	95.0
P-731	42.3	43.2	32.0	68.0
P-729	48.2	61.3	24.0	80.0
P-754	48.0	53.0	23.0	73.0
P-861	86.5	68.0	7.0	113.0
P-897	48.7	66.0	25.0	76.0
P-934	32.0	53.0	13.0	47.0

Index morphological features: Shell circular in outline, usually large-sized, with a pronounced velum, covered with fine, irregular in places ribs. Ventral valve strongly convex, with a wide umbo but without sinus. Dorsal valve almost flat. A few spines at the hinge margin of the dorsal valve and in the anterior part of the ventral valve.

Intraspecific variation: The species *L. dorotheevi* occurs in the Kapp Starostin Formation solely in P-1. It shows there some variation in ventral valve convexity (1.9—2.1 in degree of shell coiling) and rib density (15—20 per centimeter).

Ecology: This species inhabited nearshore and lagoon areas. It was capable of living buried in the sediment. It occurs in clusters of up to a dozen or so individuals, often in association with *Cancrinella spitsbergiana*.

Occurrence: In the Kapp Starostin Formation: Voringen Member — P-1.

Genus *Anidanthus* Whitehouse, 1928Type species: *Linoproductus springsurensis* Booker, 1932*Anidanthus aagardi* Toula, 1875)

(Pl. 7, Fig. 10)

1963. *Anidanthus aagardi*; Gobbett: 106, pl. 12, 22—26, with synonymy.

Material: 3 specimens.

Biometry:

Specimen identification number	shell length	shell width	shell thickness	surface length of ventral valve
T-734	10.2	11.2	—	—

Index morphological features: Shell small, subrectangular, with pronounced auricles, covered with ribs including intercalatory ones. Ventral valve strongly convex. Dorsal valve concave, covered with distinct concentric lamellae. Spines at the hinge margin.

Ecology: The material comes from deposits representative of a stable environment in the outer shelf zone.

Remarks: The lamellar sculpture of the dorsal valve of *A. aagardi* probably reflects a succession of velum formation periods during ontogeny (Muir-Wood and Cooper 1960).

Occurrence: In the Kapp Starostin Formation: Hovtinden Member — Tr-2, F-8.

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Streszczenie

Opisano kolekcje ramienionogów (Productacea) z dziesięciu, różnych facjalnie, tafocenozy późnego permu Spitzbergenu (fig. 1—2, tab. 1). Palinspastyczne relacje badanych tafocenozy i odpowiadających im biofacji odniesiono do wcześniej wykonanej litochronostratygraficznej korelacji utworów formacji Kapp Starostin (Małkowski 1982). Wyróżniono piętnaście gatunków Productacea na podstawie analizy ich cech morfologicznych, autekologicznych i synekologicznych (fig. 4—5, tab. 2—3). W paleontologicznych opisach zbadanych gatunków (pl. 1—8) uwzględniono zakresy ich ekofenotypowej zmienności (fig. 6—7). Wśród opisanych muszli Productacea wyróżniono trzy przystosowawcze formy: 1 — zakotwiczone na zwięzłym osadzie, 2 — unoszące się na powierzchni miękkiego osadu, 3 — przystosowane do życia bezpośrednio poniżej powierzchni grząskiego dna (por. fig. 7).

Schemat rozprzestrzenienia zespołów Productacea w utworach formacji Kapp Starostin odniesiono do rekonstrukcji etapów rozwoju morza permskiego (fig. 8—10, zob. także Małkowski 1982). Ekologiczne ograniczenia środowiska życia, wynikające ze stratyfikacji wód morza permskiego, zróżnicowanej przestrzennie podatności dna na zasiedlenie oraz ze zmiennego w czasie wpływu czynników strefy przybrzeżnej, uznano za podstawowe dla wyjaśnienia prawidłowości rozprzestrzenienia zbadanych fenonów Productacea w obrębie utworów formacji Kapp Starostin (fig. 11).

Wskazano brak możliwości zastosowania zbadanej grupy ramienionogów we wnioskowaniach biochronstratygraficznych, ze względu na facjalne ograniczenia stref ich występowania oraz brak danych o ich ewolucyjnym rozwoju w zbadanym zakresie.

Praca została wykonana w ramach problemu MR. I. 29. Polskiej Akademii Nauk.

Explanation of the plates

All specimens are from the Kapp Starostin Formation (Upper Permian), Spitsbergen, Svalbard.

Pl. 1.

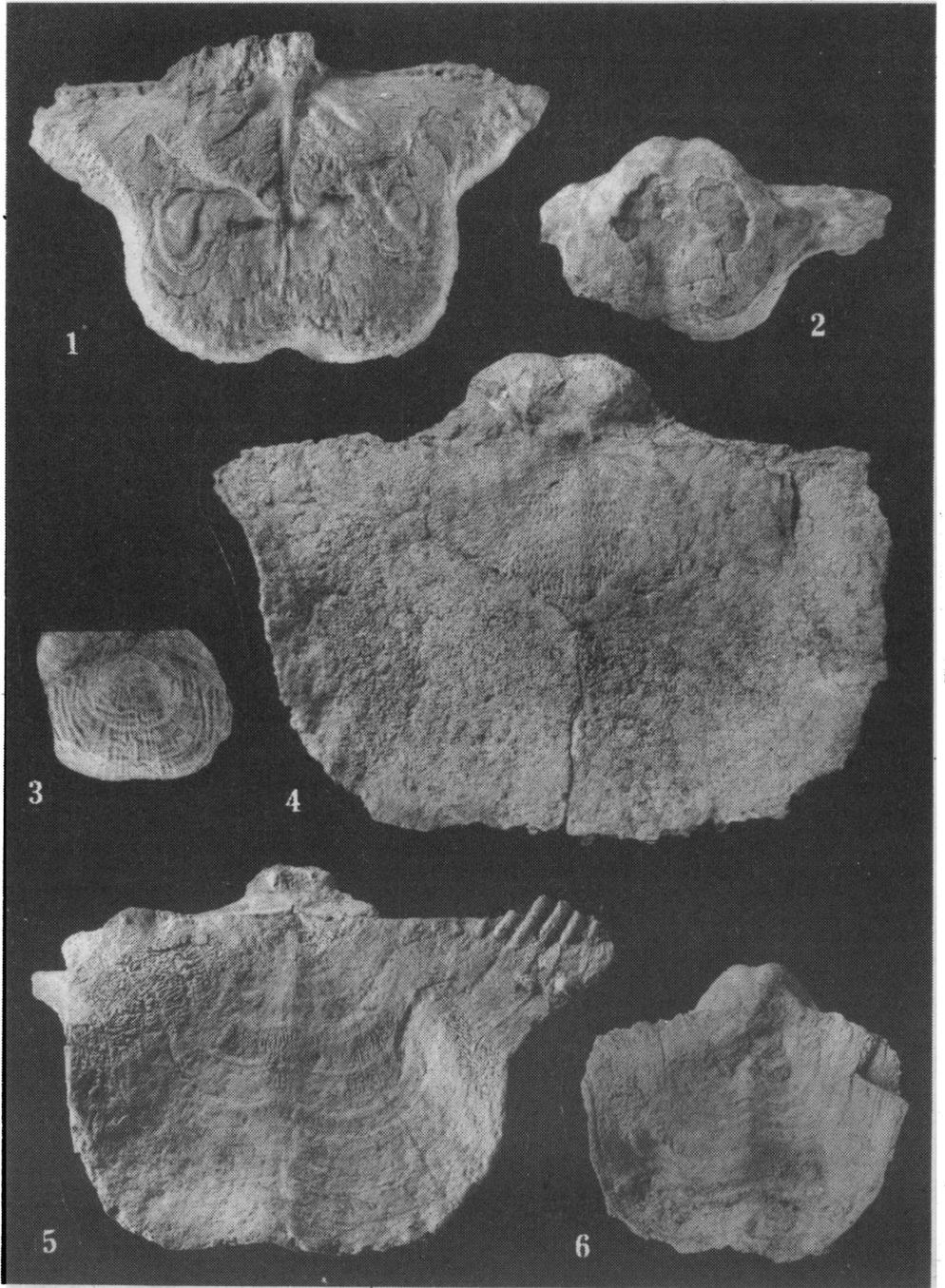
1. *Horridonia timanica* (Stuckenberg), internal mould of the dorsal valve, Vindodden (V-1), ZPAL. Bp. XXX/V-2, x 1.
2. *Horridonia timanica* (Stuckenberg), ventral valve, Ahlstrandodden (A-1), ZPAL. Bp. XXX/A-312, x 1.
3. *Svalbardoproductus arcticus* (Whitfield), umbonal view of the ventral valve, Vindodden (V-1), ZPAL. Bp. XXX/V-1170, x 1.
4. *Horridonia timanica* (Stuckenberg), dorsal valve, Kapp Starostin (F-5), ZPAL. Bp. XXX/S-263, x 1.
5. *Horridonia timanica* (Stuckenberg), dorsal valve, Vindodden (V-1), ZPAL. Bp. XXX/V-5, x 1.
6. *Horridonia timanica* (Stuckenberg), dorsal view, Polakkfjellet (P-4b), ZPAL. Bp. XXX/P-835, x 1.

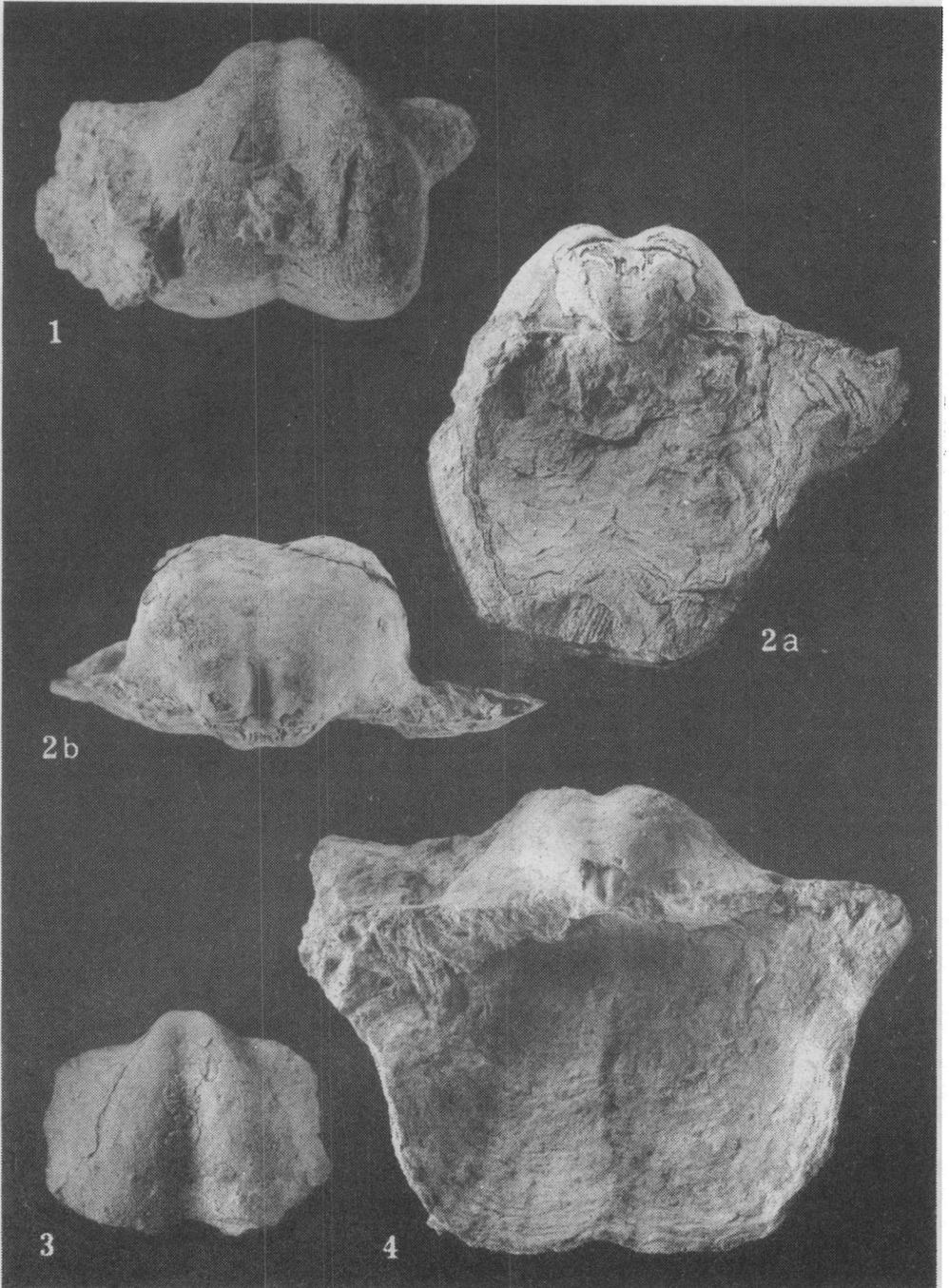
Pl. 2.

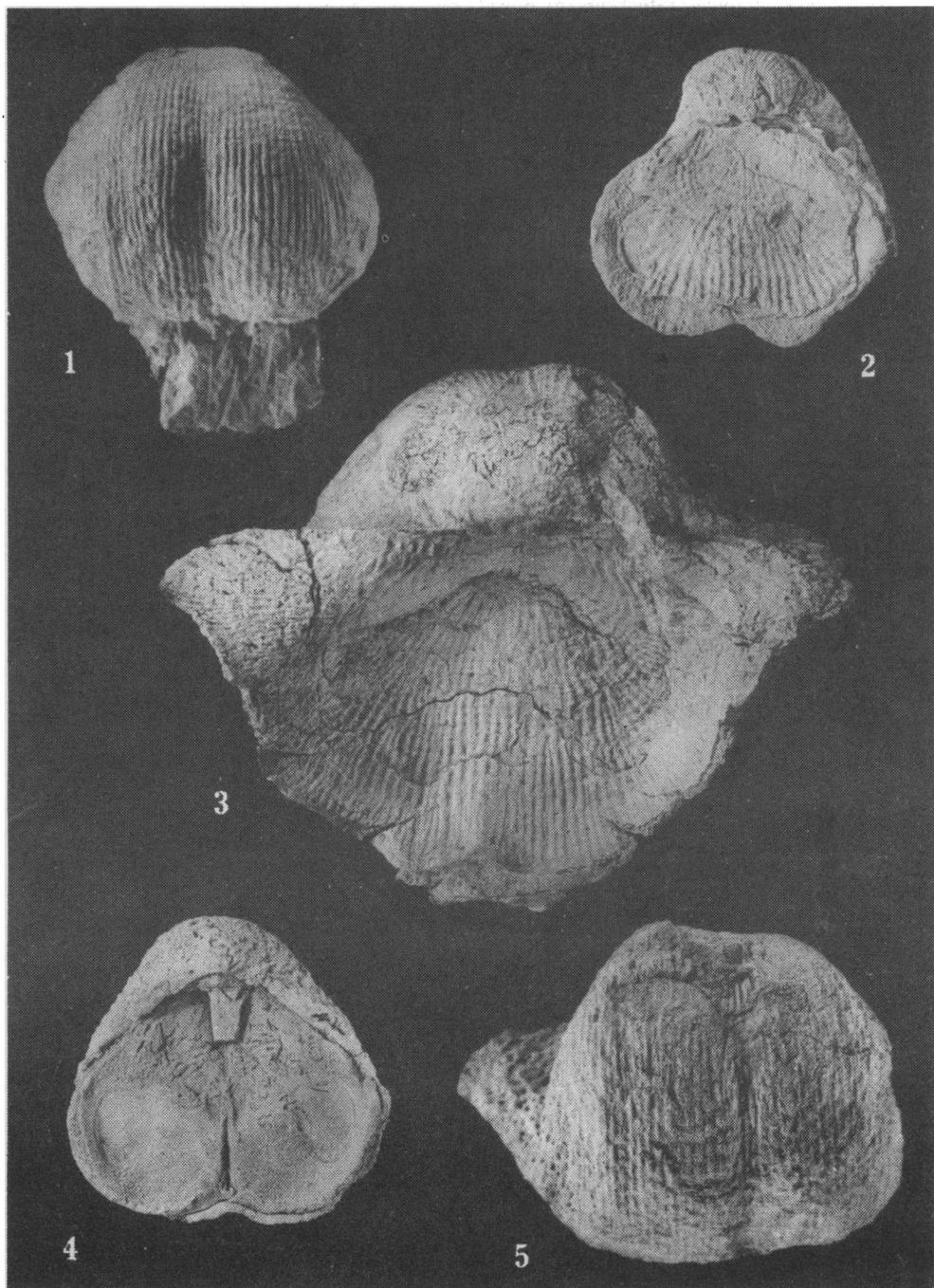
1. *Horridonia* aff. *horrida* (Sowerby), ventral valve, Vindodden (V-1), ZPAL. Bp. XXX/V-361, x 1.
2. *Horridonia* aff. *horrida* (Sowerby), a — dorsal view, b — umbonal view, Treskelen (Tr-2), ZPAL. Bp. XXX/T-703, x 1.
3. *Horridonia timanica* (Stuckenberg), ventral valve of juvenile specimen, Vindodden (V-1), ZPAL. Bp. XXX/V-1168, x 1.
4. *Horridonia timanica* (Stuckenberg), dorsal view, Vindodden (V-1), ZPAL. Bp. XXX/V-3, x 1.

Pl. 3.

1. *Svalbardoproductus arcticus* (Whitfield), ventral valve with spines, Kapp Starostin (F-1), ZPAL. Bp. XXX/L-57, x 1.
2. *Svalbardoproductus arcticus* (Whitfield), dorsal view, Polakkfjellet (P-4b), ZPAL. Bp. XXX/P-263, x 1.
3. *Svalbardoproductus arcticus* (Whitfield), dorsal view, Kapp Starostin (F-5), ZPAL. Bp. XXX/S-11, x 1.
4. *Svalbardoproductus arcticus* (Whitfield), internal mould of the dorsal valve, Polakkfjellet (P-4b), ZPAL. Bp. XXX/P-305, x 1.
5. *Svalbardoproductus arcticus* (Whitfield), ventral valve, Vindodden (V-1), ZPAL. Bp. XXX/V-172, x 1.







Pl. 4.

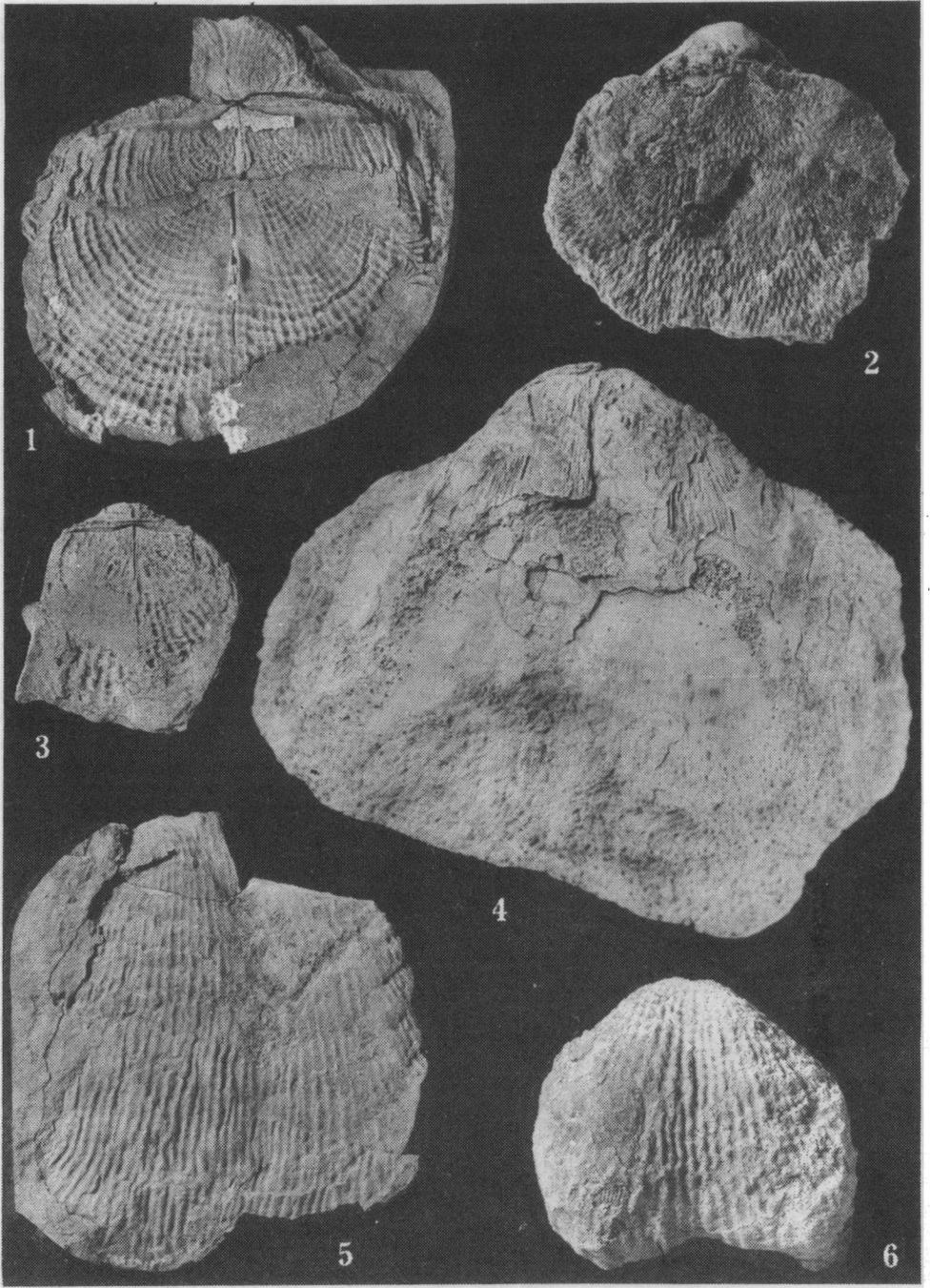
1. *Kochiproductus porrectus* (Kutorga), dorsal valve, Kapp Starostin (F-8), ZPAL. Bp. XXX/K-365, x 1.
2. *Waagenoconcha irginae* (Stuckenberg), dorsal view, Vindodden (V-1), ZPAL. Bp. XXX/V-1189, x 2.
3. *Kochiproductus porrectus* (Kutorga), internal mould of the dorsal valve, Treskelen (Tr-2), ZPAL. Bp. XXX/T-31, x 1.
4. *Waagenoconcha irginae* (Stuckenberg), internal mould with shell fragments, ventral view, Polakkfjellet (P-4b), ZPAL. Bp. XXX/P-858, x 1.
5. *Kochiproductus porrectus* (Kutorga), ventral view, Kapp Starostin (F-8), ZPAL. Bp. XXX/K-366, x 1.
6. *Kochiproductus porrectus* (Kutorga), ventral valve, Treskelen (Tr-2), ZPAL. Bp. XXX/T-6, x 1.

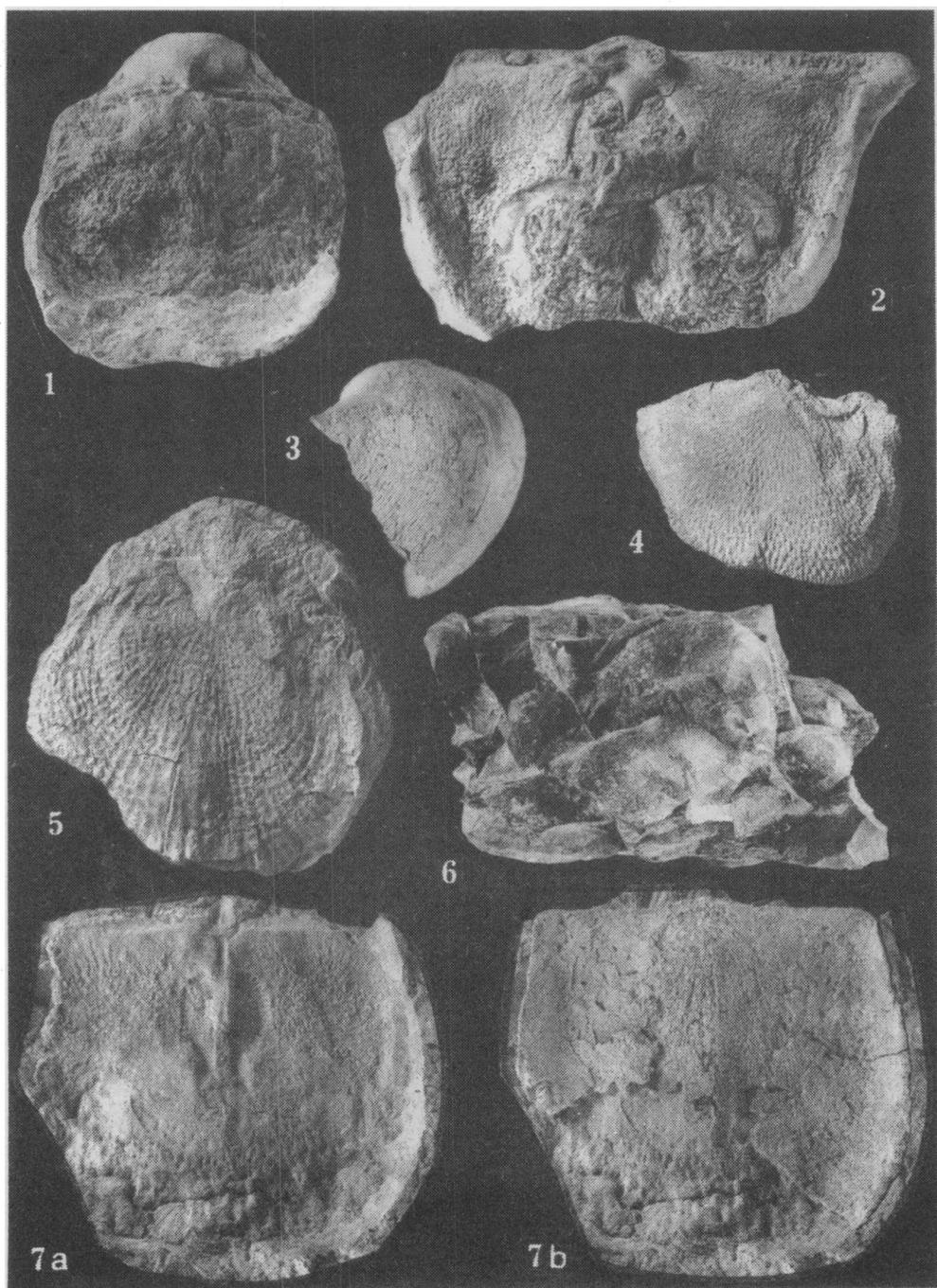
Pl. 5.

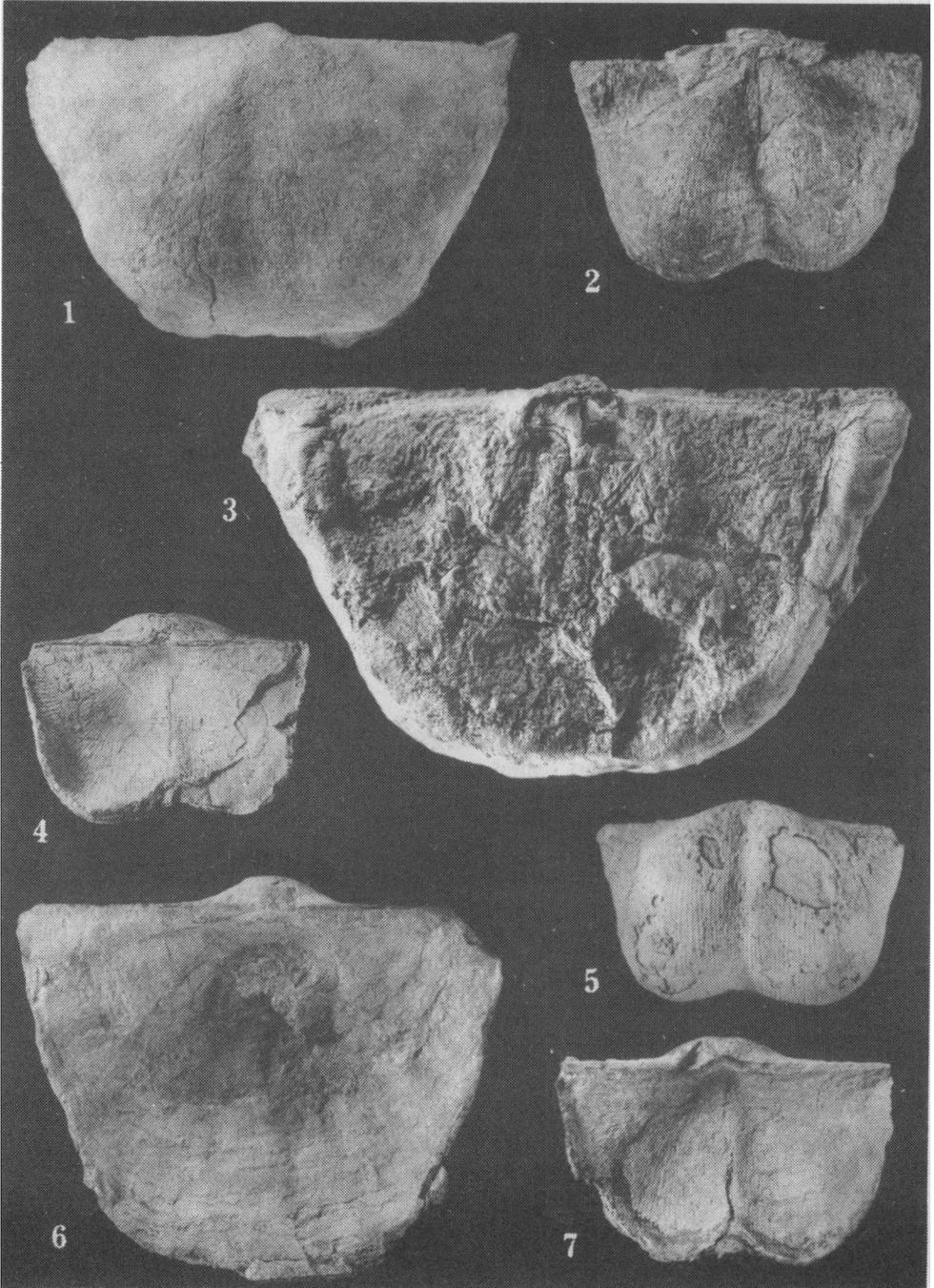
1. *Waagenoconcha irginae* (Stuckenberg), dorsal view, the velum preserved, Vindodden (V-1), ZPAL. Bp. XXX/V-1188, x 1.
2. *Yakovlevia impressa* (Toula), internal view of the dorsal valve, Vindodden (V-1), ZPAL. Bp. XXX/V-1187, x 1.
3. *Yakovlevia duplex* (Wiman), ventral valve, Polakkfjellet (P-4b), ZPAL. Bp. XXX/P-295, x 1.
4. *Waagenoconcha irginae* (Stuckenberg), mould of the dorsal valve sculpture, Treskelen (Tr-2), ZPAL. Bp. XXX/T-8, x 1.
5. *Kochiproductus porrectus* (Kutorga), dorsal view of the internal mould with shell fragments, Treskelen (Tr-2), ZPAL. Bp. XXX/T-711, x 1.
6. *Yakovlevia mammata* (Keyserling), shell accumulation, Kapp Starostin (F-5), ZPAL. Bp. XXX/S-350, x 1.
7. *Waagenoconcha irginae* (Stuckenberg), a — internal mould of the dorsal valve, b — dorsal valve, Vindodden (V-1), ZPAL. Bp. XXX/V-6, x 1.

Pl. 6.

1. *Yakovlevia impressa* (Toula), ventral valve, Vindodden (V-1), ZPAL. Bp. XXX/V-1185, x 1.
2. *Yakovlevia duplex* (Wiman), ventral valve, Kapp Starostin (F-5), ZPAL. Bp. XXX/S-270, x 1.
3. *Yakovlevia impressa* (Toula), internal mould of the dorsal valve, Vindodden (V-1), ZPAL. Bp. XXX/V-1186, x 1.
4. *Yakovlevia duplex* (Wiman), dorsal view, Polakkfjellet (P-4b), ZPAL. Bp. XXX/P-295, x 1.
5. *Yakovlevia duplex* (Wiman), ventral valve, Polakkfjellet (P-4b), ZPAL. Bp. XXX/P-296, x 1.
6. *Yakovlevia impressa* (Toula), dorsal view, Vindodden (V-1), ZPAL. Bp. XXX/V-1184, x 1.
7. *Yakovlevia duplex* (Wiman), dorsal view, Ahlstrandodden (A-1), ZPAL. Bp. XXX/A-324, x 1.







Pl. 7.

1. *Liosotella robertiana* (De Koninck), dorsal view, Treskelen (Tr-2), ZPAL. Bp. XXX/T-725, x 2.
2. *Anemonaria pseudohorrida* (Wiman), dorsal view, Kapp Starostin (F-5), ZPAL. Bp. XXX/G-21, x 2.
3. *Anemonaria pseudohorrida* (Wiman), ventral view Treskelen (Tr-2), ZPAL. Bp. XXX/T-714, x 2.
4. *Anemonaria pseudohorrida* (Wiman), internal mould of the ventral valve, Kapp Starostin (F-5), ZPAL. Bp. XXX/G-5, x 2.
5. *Liosotella robertiana* (De Koninck), ventral valve, Treskelen (Tr-2), ZPAL. Bp. XXX/T-710, x 1.5.
6. *Anemonaria pseudohorrida* (Wiman), dorsal view, Vindodden (V-1), ZPAL. Bp. XXX/V-1178, x 2.
7. *Megousia weyprechtii* (Toula), ventral view, Treskelen (Tr-2), ZPAL. Bp. XXX/T-735, x 1.5.
8. *Megousia kulikii* (Fredricks), ventral valve, Vindodden (V-1), ZPAL. Bp. XXX/V-1179, x 1.
9. *Liosotella robertiana* (De Koninck), ventral valve, Treskelen (Tr-2), ZPAL. p. XXX/T-719, x 2.
10. *Anidanthus aagardi* (Toula), internal view of the dorsal valve, Treskelen (Tr-2), ZPAL. Bp. XXX/T-734, x 2.
11. *Megousia weyprechtii* (Toula), internal view of the dorsal valve, Kapp Starostin (F-5), ZPAL. Bp. XXX/S-345, x 2.
12. *Liosotella robertiana* (De Koninck), ventral valve, Kapp Starostin (F-8), ZPAL. Bp. XXX/K-347, x 2.

Pl. 8.

1. *Linoproductus dorotheevi* (Fredricks), dorsal valve, Polakkfjellet (P-1), ZPAL. Bp. XXX/P-286, x 1.
2. *Cancrinella spitsbergiana* (Gobbett), ventral valve, Vindodden (V-1), ZPAL. Bp. XXX/V-1183, x 1.
3. *Linoproductus dorotheevi* (Fredricks), umbonal view of the internal mould, Polakkfjellet (P-1), ZPAL. Bp. XXX/P-306, x 1.
4. *Cancrinella spitsbergiana* (Gobbett), ventral valve, Vindodden (V-1), ZPAL. Bp. XXX/V-1173, x 2.
5. *Cancrinella spitsbergiana* (Gobbett), internal mould of the ventral valve, Treskelen (Tr-2), ZPAL. Bp. XXX/T-712, x 2.
6. *Cancrinella spitsbergiana* (Gobbett), dorsal valve, Kapp Starostin (F-8), ZPAL. Bp. XXX/K-352, x 2.
7. *Cancrinella spitsbergiana* (Gobbett), internal mould of the dorsal valve, Treskelen (Tr-2), ZPAL. Bp. XXX/T-788, x 2.
8. *Cancrinella spitsbergiana* (Gobbett), ventral view of the internal mould, Vindodden (V-1), ZPAL. Bp. XX/V-1182, x 2.
9. *Linoproductus dorotheevi* (Fredricks), ventral valve with velum, Polakkfjellet (P-1), ZPAL. Bp. XXX/P-270, x 1.
10. *Linoproductus dorotheevi* (Fredricks), dorsal view of the internal mould, Polakkfjellet (P-1), ZPAL. Bp. XXX/P-228, x 1.
11. *Cancrinella spitsbergiana* (Gobbett), dorsal view of the internal mould, Vindodden (V-1), ZPAL. Bp. XXX/V-1174, x 2.

