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LATE CARBONIFEROUS TO EARLY PERMIAN TABULATA FROM SPITSBERGEN

(TABULATA Z PÓŹNEGO KARBONU I WCZESNEGO PERMU SPITSBERGENU)

BY

ALEKSANDER NOWIŃSKI

(WITH 23 TEXT-FIGURES, 4 TABLES AND 23 PLATES)

WARSZAWA — KRAKÓW 1991
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ALEKSANDER NOWIŃSKI

LATE CARBONIFEROUS TO EARLY PERMIAN TABULATA FROM SPITSBERGEN

NOWIŃSKI, A.: Late Carboniferous to early Permian Tabulata from Spitsbergen. Palaeont. Polonica, 51, 3—74, 1991.

Twenty four species of Tabulata (including 13 new species and two species determined only at generic level) are described and illustrated. The new species are: *Roemeripora media* sp. n., *R. hornsundensis* sp. n., *Syringopora stuckenbergi* sp. n., *S. kruseryggensis* sp. n., *Neosyringopora spitsbergensis* sp. n., *Hayasakaia multispinosa* sp. n., *H. birkenmajeri* sp. n., *H. variabilis* sp. n., *Tetraporinus spitsbergensis* sp. n., *T. spinosus* sp. n., *T. kozlowskii* sp. n., *Neoroemeria spitsbergensis* sp. n., *N. permica* sp. n. The all specimens have been collected from the Lower Permian Treskelodden Formation ("Upper Treskelodden Beds") in Hornsund area, and from the Upper Carboniferous through Lower Permian "Wordiekammen Limestone" Formation in the Isfjorden area, in the southern and central parts of Spitsbergen. The paper also includes: (1) a historical review of investigations of the Tabulata from western Spitsbergen, (2) a discussion of biostratigraphical and palaeogeographical aspects of the studied fauna and (3) results of the studies of both skeletal growth periodicity and vegetative reproduction in Tabulata from the "Upper Treskelodden Beds". The Tabulata of Central Spitsbergen are strongly endemic, although some similarity to Upper Carboniferous and Lower Permian faunas of the N. Urals, Novaya Zemlya, Taymyr and Timan has been noted.

Key words: Coelenterata, Tabulata, taxonomy, growth periodicity, blastogeny late Carboniferous to early Permian, Spitsbergen.

Aleksander Nowiński, Polska Akademia Nauk, Instytut Paleobiologii, 02-089 Warszawa, Al. Żwirki i Wigury 93, Poland. Received: October, 1987.

TABULATA Z PÓŹNEGO KARBONU I WCZESNEGO PERMU SPITSBERGENU

Streszczenie. — W pracy przedstawiono wyniki badań nad Tabulata z dolnopermskich (asel, sakmar i być może część artinsku) osadów formacji „Treskelodden" („Upper Treskelodden Beds") z obszaru fiordu Hornsund oraz z górnego karbonu (?orenburg) i dolnego permu (asel i być może sakmar) formacji „Wordiekammen Limestone" („Lower", „Middle" and „Upper Wordiekammen Limestone" = ?górna część Cadellefiellet Member + Tyrrellefjellet Member) obszaru Isfjorden (Skanska Bukta, Linneus Valley), położonych w południowej i centralnej części Zachodniego Spitsbergenu. Opracowana kolekcja Tabulata została zebrana przez autora w czasie Polskiej Wyprawy Paleontologicznej na Spitsbergen w roku 1974.

W części systematycznej pracy opisano i zilustrowano 24 gatunki Tabulata (w tym 13 gatunków nowych i dwa gatunki w nomenklaturze otwartej) z rodzajów: *Roemeripora*, *Syringopora*, *Neosyringopora*, *Multithecopora*, *Hayasakaia*, *Tetraporinus* i *Neoroemeria*. Gatunki nowe: *Roemeripora media*, *R. hornsundensis*, *Syringopora stuckenbergi*, *S. kruseryggensis*, *Neosyringopora spitsbergensis*, *Hayasakaia multispinosa*, *H. birkenmajeri*, *H. variabilis*, *Tetraporinus spitsbergensis*, *T. spinosus*, *T. kozlowskii*, *Neoromeria permica*, *N. spitsbergensis*. Przeprowadzono również dyskusję oraz rewizję niektórych rodzajów Tabulata Spitsbergenu, o niepewnej pozycji systematycznej.

W części ogólnej pracy omówiono następujące zagadnienia:

1. Historię badań nad tabulatami Spitsbergenu. Przedstawiono pełną listę dotychczas opisanych lub tylko wymienianych w literaturze rodzajów i gatunków Tabulata z permokarbonu tego obszaru.

2. Pozycję stratygraficzną i charakterystykę osadów „Treskelodden Beds" i „Wordiekammen Limestone". Z dotychczasowych badań wynika, że osady „Treskelodden Beds" należą w całości do dolnego permu (asel + Sakmar i być może dolna część artinsku), o czym świadczy między innymi obecność w tych utworach charakterystycznej dla tego przedziału czasowego fauny koralowej i brachiopodowej. Opisane w niniejszej pracy Tabulata, pochodzące z utworów „Upper Treskelodden Beds", potwierdzają dolnopermski wiek tych osadów. Osady „Treskelodden Beds" stanowią kompleks sedymentacyjny o miąższości średnio ok. 100 m, złożony głównie z materiałów klastycznych (zlepieńce, grubo- i drobnoziarniste piaskowce kwarcowe, piaskowce wapniste, łupki), zawierający w środkowej i górnej części („Upper Treskelodden Beds") warstwy wapieni piaszczystych i wapieni, w których występuje licznie fauna koralowa. W obrębie „Upper Treskelodden Beds" wyróżniono pięć tzw. „poziomów koralowych" (Coral Horizons), w których występuje redeponowana fauna Tabulata i Tetracoralla. Typ sedymentacji tych osadów, szybka ich depozycja oraz redeponowana fauna koralowa wskazują na to, że obszar Hornsundu w okresie depozycji stanowił strefę marginalną morza, niezbyt odległą od lądu, której dno leżało poniżej strefy kipieli. Osady „Wordiekammen Limestone" (dolna część — Cadellefjellet member, środkowa i górna część — Tyrrellefjellet member) złożone z wapieni, dolomitów, piaskowców i łupków, zaliczane są do górnego karbonu i dolnego permu (Gzhelian-Sakmarian). Opisane dotychczas i w obecnej pracy gatunki Tabulata z tych osadów (poza gatunkami endemicznymi i o dużych zasięgach pionowych) potwierdzają ten wiek. O wczesnopermskim wieku stropowej części „Wordiekammen Limestone" mogłaby świadczyć obecność *Roemeripora wimani* Heritsch i *Hayasakaia elegantula* (Yabe et Hayasaka).

3. Rozmieszczenie stratygraficzne i charakterystyka Tabulata z „Upper Treskelodden Beds"

Zespół Tabulata z „Upper Treskelodden Beds" jest bogaty i zróżnicowany rodzajowo i gatunkowo, jednakże u większości okazów wewnętrzna budowa szkieletu uległa zniszczeniu pod wpływem procesów późnodiagenetycznych i rekrystalizacji. Wszystkie kolonie są redeponowane, przy czym stopień ich redepozycji maleje w kierunku stropu kompleksu. W poziomach koralowych I, II i III Tabulata występują rzadko i reprezentowane są głównie przez dwa rodzaje: *Roemeripora* i *Multithecopora*. W poziomach koralowych IV i V Tabulata występują bardzo licznie. W tych poziomach niektóre kolonie z rodzajów *Roemeripora* i *Multithecopora* osiągają bardzo duże rozmiary, do 2,5 m średnicy. Tabulatom w „Upper Treskelodden Beds" towarzyszy liczna fauna Tetracoralla, Crinoidea, Bryozoa, Gastropoda, Bivalvia, Trilobita, Hydrozoa, Foraminifera i detrytus roślinny.

4. Szkic paleogeograficzny.

Z korelacji paleogeograficznych wynika, że zarówno Tabulata rejonu Hornsundu, jak i obszaru Isfjorden, są w znacznym stopniu endemiczne i wykazują niewielkie powiązania z równowiekowymi zespołami tabulatowymi płn.-zachodniej Azji (płn. Ural, Nowa Ziemia, Tajmyr, Timan) i płd. Chin. Endemiczność zaznaczona jest wyraźniej w zespole Tabulata z „Upper Treskelodden Beds" (ok. 75% gatunków endemicznych) niż w zespole „Wordiekammen Limestone" (ok. 43% gatunków endemicznych). Ponadto zespół Tabulata z „Upper Treskelodden Beds", mimo ogólnego podobieństwa rodzajowego do zespołu „Wordiekammen Limestone", różni się od niego prawie zupełnie składem gatunkowym. Podobne, duże różnice rodzajowe i gatunkowe występują również pomiędzy zespołami Tetracoralla obu obszarów (Fedorowski 1965). Może to świadczyć o znacznej izolacji obu tych basenów sedymentacyjnych w górnym karbonie i dolnym permie (odległych o ok. 150 km) lub o bardzo różnych warunkach bytowania faun koralowych na tych obszarach.

Poza gatunkami endemicznymi, pozostałe części zespołów Tabulata z „Upper Treskelodden Beds" i „Wordiekammen Limestone" wykazują mniejsze lub większe powiązania z zespołami płn.-zachodniej Azji i Chin, co świadczyłoby o morskiej łączności pomiędzy tymi obszarami i Spitsbergenem w permo-karbonie. Łączność morska pomiędzy Spitsbergenem a Północnym Uralem i obszarami przyległymi w tym okresie wydaje się udowodniona (Scotese *et al.* 1979; Frakes 1979; Smith *et al.* 1982; Fedorowski 1981, 1986). Dyskusyjny pozostaje natomiast problem łączności morskiej w tym okresie pomiędzy Spitsbergenem i płd. Chinami. O względnej izolacji obu obszarów świadczą badania m. in. Bridena *et al.* (1974), Ramsbottoma (1979), Scotese'a *et al.* (1979) i Fedorowskiego (1981, 1986). Natomiast badania m. in. Frakesa (1979), Smitha *et al.* (1982) i Zonenshaina *et al.* (1985) wykazują, że jeszcze w dolnym permie istniało połączenie pomiędzy Europejską Arktyką i obszarem Paleo-Tetydy poprzez silnie już zwężony paleoocean Uralu.

5. Periodyczność wzrostową szkieletu.

Przedstawiono zarys dotychczasowych badań nad rytmicznością sezonalną w przyroście szkieletu u Tabulata w ogóle (w polskiej literaturze tabulatowej zjawiska te nie były dotąd sygnalizowane) oraz jakościowe i ilościowe charakterystyki pasm przyrostowych szkieletu w koloniach niektórych spitsbergeńskich gatunków Tabulata. Stwierdzono, że dolno-permski zespół Tabulata z „Upper Treskelodden Beds" w różnych poziomach koralowych złożony był z kolonii zróżnicowanych taksonomicznie i wiekowo. Wiek większości badanych kolonii z różnych poziomów koralowych, wyliczony z ilości pasm przyrostowych, wynosił od 3 do 40 lat, a niektórych, bardzo dużych kolonii płytowych (*Roemeripora*, *Multithecopora*) sięgał 100—150 lat. W koloniach różnych gatunków Tabulata z „Upper Treskelodden Beds" grubość poszczególnych pasm wzrostowych (średnie roczne tempo przyrostu tkanki szkieletowej) jest bardzo zmienna. Największa zmienność grubości tych pasm występuje przy porównaniu różnych rodzajów i różnych gatunków tego samego rodzaju, mniejsza — dla różnych kolonii tego samego gatunku, a najmniejsza — w astogenezie pojedynczej kolonii, na różnych jej poziomach. Natomiast w obrębie samych pasm wzrostowych (niezależnie od ich grubości i przynależności do określonego taksonu czy kolonii) stosunek grubości warstwy jasnej szkieletu do ciemnej jest stosunkowo stały.

6. Blastogenezę.

W rezultacie badań nad rozmnażaniem wegetatywnym stwierdzono w opracowanym zespole Tabulata dwa rodzaje pączkowania wewnątrzkielichowego (pączkowanie intrawisceralne i ekstrawisceralne) oraz pączkowanie zewnątrzkielichowe (stolonalne). Pączkowanie intrawisceralne występowało w koloniach z rodzaju *Roemeripora*. Pączek powstawał w dowolnym kącie ściennym komory wisceralnej kielicha macierzystego w wyniku połączenia się dwu wyrostków ściennych tego kielicha, tworzących rodzaj wypuklenia, narastającego w kierunku do środka tej komory. U pozostałych rodzajów, należących do rzędu Syringoporida, występowało pączkowanie ekstrawisceralne. Pączek powstawał w skierowanym na zewnątrz komory wisceralnej (odśrodkowo) wypukleniu ścianki kielicha macierzystego i oddzielając się własną ścianką i epiteką odsuwał się od niego, przekształcając się w młody polip. Pączkowanie zewnątrzkielichowe, występujące obok pączkowania wewnątrzkielichowego, zaobserwowano u gatunków: *Fuchungopora arctica*, *Tetraporinus spinosus* sp. n., *Neoroemeria spitsbergensis* sp. n. i *N. permica* sp. n. Młode osobniki odpączkowywały od rurek łączących lub od poziomo leżących rurek stolonalnych i rosnąc odginały się ku górze.

7. Zbadano i opisano niektóre charakterystyczne dla tabulatów Spitsbergenu cechy organizacji i rozwoju kolonii (występujące niezależnie od zjawisk periodyczności wzrostowej), takie jak: zmienny stopień integracji kolonii i jego wpływ na morfologię i wzrost pojedynczych koralitów, morfologiczno-funkcjonalną zmienność elementów łączących korality (pory, rurki, mostki, blaszki) w różnych typach kolonii i dwuwarstwową budowę ścianek koralitów. U Tabulata innych regionów Europy i Azji cechy te występują bardzo rzadko i nie są tak wyraźne.

General Part

Systematic Part

INTRODUCTION

The paper includes the results of studies on tabulate corals from the Lower Permian (Asselian + Sakmarian and ?lower part of Artinskian Treskelodden Formation („Upper Treskelodden Beds") of the Hornsund fjord region and the Upper Carboniferous through Lower Permian „Wordiekammen Limestone" Formation of Isfjorden region, in the southern part of Spitsbergen. The rich collection of Tabulata comprising 200 more or less complete colonies and a few tens of colonies of Chaetetida, Hydrozoa, Bryozoa and others, was gathered by the author during the four-months Polish Palaeontological Expedition to Spitsbergen in 1974, led by Professors G. BIERNAT and K. BIRKENMAJER. The bulk of the collection of Tabulata comes from four areas in Hornsund: Treskelen, Hyrnefjellet, Urnetoppen, Kruseryggen, and from two areas in Isfjorden: Skanska Bukta and Linnedalen.

Comparative studies have been done on the collections of Carboniferous Tabulata held in the Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, and on the known species of Tabulata occurring in the Carboniferous and Permian of Spitsbergen, Ural Mts., Donetsk Basin, China, Viet-Nam, Afghanistan, North America and Australia. More than 650 thin sections were done for morphological studies and identification of species, and more than 500 thin sections and polished sections for the study of structure and skeleton growth phenomena in colonies. Investigations of blastogeny and development of young corallites were carried out in serial thin sections, prepared from carefully chosen and oriented fragments of colonies. The distance between successive transverse sections (perpendicular to a corallite axis) was from 0.1 to 1.0 mm depending on diameter, blastogenetic stage and frequency of morphological changes at the particular developmental stage. 40 series of acetate imprints (ca 1200 peels) on celluloid films were done for these studies.

The tabulate corals of the Spitsbergen are relatively little known. All hitherto-described Permo-Carboniferous species, belonging to the genera *Roemeripora*, *Michelinia*, *Syringopora*, *Hayasakaia* and *Multithecopora*, come mainly from the Isfjorden and Bellsund regions (fig. 1). HOLTEDAHL (1912, 1913) briefly described several species of *Michelinia* and *Syringopora* from the Upper Carboniferous and Lower Permian. In the Permo-Carboniferous strata (Passage Beds, „Wordiekammen Limestone" and Brachiopod Cherts) of the Isfjorden area, HERITSCH (1939*a*) found the following species and subspecies: *Roemeripora wimani wimani* HERITSCH, *R. wimani minor* HERITSCH, *Michelinia tenuiseptata* (PHILLIPS), *Syringopora degeeri* HERITSCH, *S. eichwaldi* STUCKENBERG, *S. multattenuata* MC CHESNEY, *S. parallela* (FISCHER von WALDHEIM), *S. ramulosa* GOLDFUSS, *S. tchernychevi* STUCKENBERG, *Multithecopora yohi* CHI, and *Hayasakaia elegantula* YABE et HAYASAKA. PADGET (1954) presented a list of the Permo-Carboniferous coral fauna of the Isfjorden area (Bünsow Land and Tempelfjorden), that includes the following species of Tabulata: *Roemeripora wimani* Heritsch, *Syringopora ramulosa* GOLDFUSS and *S.* cf. *reticulata* GOLDFUSS. Twelve species and subspecies of Tabulata are included in the list of fauna from the Permo-Carboniferous strata (Passage Beds, „Lower", „Middle" and „Upper Wordiekammen Limestone", Lower Brachiopod Cherts) of the Isfjorden and Belsund regions, published by FORBES *et al.* (1958). These are: *Roemeripora wimani wimani* HERITSCH, *R. wimani* var. *fasciculata* WANG, *R. wimani* var. nov. WANG, *R. wimani* var. A, *Syringopora ramulosa* GOLDFUSS, *S. multattenuata* TCHERNYCHEV, *S. parallela* (FISCHER von WALDHEIM), *S. tchernychevi* STUCKENBERG, *S.* sp. A, *S.* sp. B, *Hayasakaia elegantula* (YABE et HAYASAKA) and *Cladochonus baccillaris* MC COY.

In contrast to those from the Isfjorden region, the Tabulata from the Hornsund region are almost unknown. FEDOROWSKI (1967) briefly described and illustrated five species of Tabulata from the Lower Permian of the "Upper Treskelodden Beds" of this area. These are: *Roemeripora wimani wimani* HERITSCH, *R. wimani minor* HERITSCH, *Michelinia abnormis* (HUANG), *Syringopora* cf. *ramulosa* GOLDFUSS and *Hayasakaia profunda* FEDOROWSKI. Recently, the present author (NOWIŃSKI 1982) described the following species of Tabulata from the "Upper Treskelodden Beds" of the Treskelen Peninsula: *Roemeripora aspinosa* NOWIŃSKI, *Armalites laminatus* NOWIŃSKI, *A.* sp., *Hayasakaia compacta* NOWIŃSKI, and *Fuchungopora arctica* NOWIŃSKI.

Moreover, SCRUTTON *et al.* (1976) reported the occurrence of coral fauna in Silurian strata (Holmeslettfjella Formation) in Oscar II Land (in the northern part of the Isfjorden region). This is the first discovery of Silurian corals in Spitsbergen. Besides several genera of Rugosa these authors report *Palaeofavosites* sp. and *Catenipora* sp.

The present work was done in the Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, abbreviated as ZPAL, where the collection is housed.

Abbreviations used:

A	— praecorallite
AC	— axial canal
ARC	— epitheca of a praecorallite
B	— bud chamber
BAG	— band of annual growth
CL	— clear layer
CO	— constriction between bud chamber and visceral chamber of a parent calice
CP	— connecting platform
CT	— connecting tube
D	— diaphragm

DL — dark layer
E — epitheca
EC — ephebic corallite
ES — ephebic stage
HNPA — hystero-neanic stage
HNPS — hystero-nepionic stage
I — invagination or evagination in the wall of a parent calice
P — connecting pore
PC — parent calice (corallite)
PEL — periepithecal layer
PS — preblastic stage
PVL — pervisceral layer
PT — disturbance in the structure of the wall of a parent calice (corallite)
SS — septal spine
T — tabula
V — visceral chamber of a calice (corallite)
VEC — visceral chamber of an ephebic corallite
VPC — visceral chamber of a parent calice
VT — vesicular tissue
WA — wall of a praecorallite
WC — wall of an adult corallite (calice)
WEC — wall of an ephebic corallite
WNC — wall of neighbour calice (corallite)
WO — wall outgrowths
WPC — wall of a parent calice
WT — wall of a tube

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GENERAL PART

OUTLINE OF STRATIGRAPHY AND LITHOLOGY OF "TRESKELODDEN BEDS" AND "WORDIEKAMMEN LIMESTONE"

Permo-Carboniferous deposits with corals cropping out in the central part of Spitsbergen occur in two belts forming a letter V, pointing toward the NW. The longer belt extends from the Hornsund area NNW through Kopernicusfjellet, Western Van Keulenfjorden, Lynnedalen, Kapp Starostin to Oscar II Land. The shorter one extends from Sassendalen NW through Tempelfjorden, Busnow Land, Dickson Land, Dicksonfjorden, Nordfjorden to Oscar II Land.

Hornsund area. — In the Hornsund area, Upper Carboniferous through Lower Permian deposits known as the Treskelodden Beds (Heintz 1953, Orvin 1958, Birkenmajer 1959*b*, 1960*a*, *b*, 1964*a*, 1981) or Treskelodden Formation (Cutbill and Challinor 1965), and containing coral fauna, occur north of Hornsund and extend from SSE toward NNW from Treskelodden Peninsula to Kopernicusfjellet (fig. 1). The best and well investigated outcrops

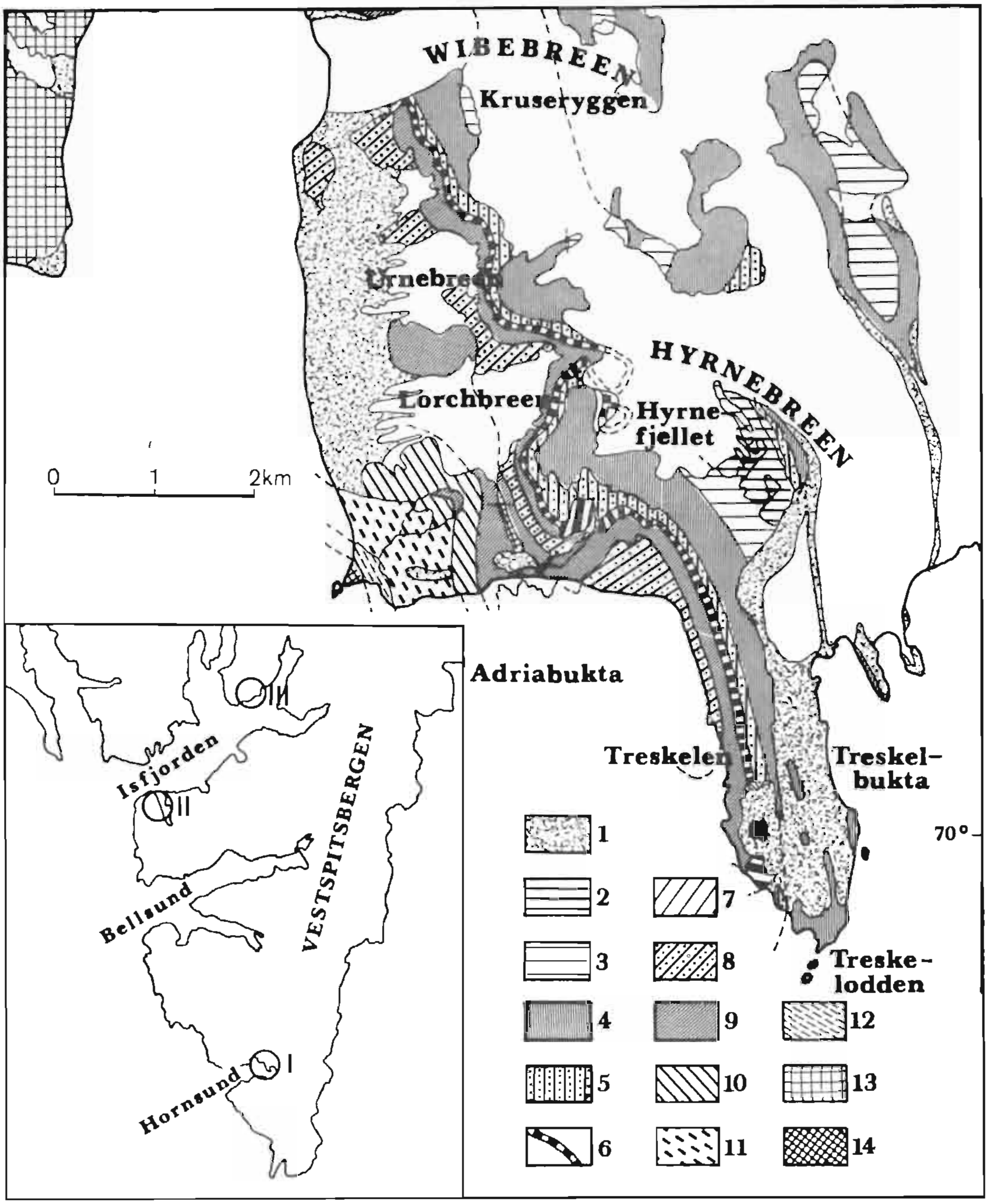


Fig. 1

A Collecting sites of tabulate corals in the southwestern Spitsbergen (I. Hornsund area, II. Linneus Valley, III. Skanska Bukta) and *B* Geological map of the North Hornsund area (after Birkenmajer 1964). 1. moraines, partly outwash; 2. Festningen Sandstone (Hauterivian to Barremian) and Ullaberget Series (Lower Neocomian); 3. Tirolarpasset Series (Volgian-Lower Neocomian), Ingebrigtsenbukta Series (Callovian-Kimmeridgian), Phosphorite Conglomerate (Callovian with Upper Toarcian) (redeposited fauna); 4. Middle to Upper Triassic (Rhaetic including); 5. Lower Triassic; 6. Brachiopod Cherty Limestone (Upper Permian); 7. Treskelodden Beds (Lower Permian); 8. Hyrnefjellet Beds (Lower Permian); 9. Adriabukta Series (Visean to Namurian A?); 10. Upper Marietoppen Series (Devonian: Grey Hock Series); 11. Middle Marietoppen Series (Devonian: Stjördalen Division?); 12. Lower Marietoppen Series (Devonian: Keltiefjellet Division?), Heckla Hock Succesion; 13. Sörkapp Land Formation (Ordovician); 14. Sofjebogen Formation (Precambrian to Eocambrian).

occur between Hyrnefjellet and Treskelen (Birkenmajer 1959*b*, 1964*a*, 1969*b*, 1981, Birkenmajer and Fedorowski 1980, Birkenmajer and Czarniecki 1960, Fedorowski 1982, Nowiński 1982). The main part of the investigated tabulate collection comes from this area.

The age of the "Upper" and "Lower Treskelodden Beds" is still disputable. Birkenmajer (1959*b*, 1960*a*, *b*, 1964*a*) based on lithostratigraphy, Fedorowski (1964, 1965, 1967) based on rugose corals, and Liszka (1964) who investigated foraminifers, include these deposits in the Lower Permian (Sakmarian and Lower Artinskian). Considering the lithology of Permo-Carboniferous strata of central Vestspitsbergen, Cutbill and Challinor (1965) included the "Treskelodden Beds" in the Artinskian. Waterhouse (1976), however, regards them as Lower Permian in age. Recently, Birkenmajer (1981) considers the age of this formation as Upper Carboniferous (Gzhelian) to Lower Permian (Sakmarian). At the top, the formation is separated from higher stratigraphical units of the Permian by a stratigraphical gap. More recent investigation (Birkenmajer 1979, Birkenmajer and Fedorowski 1980, Fedorowski 1981, 1982, 1986) show that the "Treskelodden Beds" are older than Artinskian. A rugose coral assemblage from the "Upper Treskelodden Beds" is closely comparable with the lowermost Permian (Asselian) coral fauna of the Ural Mts. (Fedorowski 1981, 1986). Also some common or closely related tabulate species occur in both areas (see p. 15 and 17).

On the other hand, Orvin (1940) and Czarniecki (1964, 1966, 1969) who investigated brachiopods from the "Treskelodden Beds", consider these deposits to be entirely of Upper Carboniferous age (Gzhelian). From the above discussion, it seems that the "Treskelodden Beds" belong to the Lower Permian. Also brachiopods described by Czarniecki (1969) are considered by Waterhouse (1976) as Lower Permian in age (Asselian). The investigated, highly endemic assemblage of tabulates may only crudely indicate stratigraphical position i.e. the Upper Carboniferous to Lower Permian.

The "Treskelodden Beds" consist mostly of clastics (conglomerates, coarse and fine grained quartzitic sandstones, carbonate sandstones, shales) and are rich in plant detritus. The thickness of these deposits, between Hyrnefjellet and Treskelodden, reaches 100 meters in average. The middle and upper parts ("Upper Treskelodden Beds") of this complex have intercalations of sandy limestones and limestones. In the "Upper Treskelodden Beds", five sedimentary cycles were distinguished (Birkenmajer 1964*a*, Siedlecka 1968, Nysaether 1977, Nowiński 1982). Each of them consists of both continental and marine strata. The name "Coral Limestone Horizon" was introduced (Birkenmajer 1964*a*) and subsequently used (Czarniecki 1964, 1969, Fedorowski 1964, 1965, 1967, Liszka 1964, Nowiński 1982) for marine carbonate deposits with corals, in the "Upper Treskelodden Beds". The first ("Lower Treskelodden Beds") and the second (lower part of the "Upper Treskelodden Beds") "sedimentary cycles" are practically devoid of marine deposits. "Cycles" 3 and 4 (middle part of the "Upper Treskelodden Beds") started with carbonate deposition and finished with clastics (conglomerates and sandstones), and the 5th "cycle" (uppermost part of the "Upper Treskelodden Beds") consists nearly entirely of carbonate deposits. As the two lowermost layers with corals (in the 2nd "cycle") of the "Upper Treskelodden Beds" contain no limestones and tabulate colonies and rugose corals are embedded in clastics, Siedlecka (1968) described them as "Coral Horizons". This term was used by Fedorowski (1982) and is also accepted in the present paper. According to recent investigations by Fedorowski (1982) the "Treskelodden Beds" show no features of cyclicity of the type "continental-marine-continental", and so-called "Coral Horizons" are better described as sets of layers, not horizons. Resulting from the present authors investigations, the existence of such cyclicity cannot be excluded, however, in the "Upper Treskelodden Beds". It may be only poorly expressed, as very gradual changes in the ratio of clastic to carbonate deposits. In successive "sedimentary cycles", from the bottom to the top of the complex, the amount of limestone increases and clastics decrease.

Marine sediments dominate in the "Treskelodden Beds". Clastics (conglomerates, and especially the Grey Conglomerate horizon in the 2nd "sedimentary cycles") all show features of rapid deposition (i.e. low degree of reworking of clasts). They may have originated as a result of erosion of nearby islands of short existence. Such a tectonically active area (being the source of clastic components) was located most probably east or south-east of the Treskelen-Hyrnefjellet basin (BIRKENMAJER 1964*a*), or west of Treskelen (HELLEM and WORSLEY 1978). SIEDLECKA (1968) considers the "Treskelodden Beds" as lagoonal or brackish water deposits. During carbonate deposition, this basin could have had a temporary marine connection. The opinion that the Hornsund area (and particularly Treskelen Peninsula) was during the Lower Permian part of Sakmarian Land (STEEL and WORSLEY 1984), seems not convincing according to the earlier investigations.

The entire coral fauna in all five Coral Horizons of the "Upper Treskelodden Beds" was redeposited, with the degree of reworking decreasing toward the top of the formation. At first, an opinion prevailed (BIRKENMAJER 1964*a*, SIEDLECKA 1968, CZARNIECKI 1969) that coral colonies occur *in situ* and as bioherms. More recent investigations (HEINZ in FEDOROWSKI 1967 and FEDOROWSKI, 1982) have shown that all corals, to a greater or lesser degree, were transported, redeposited and were derived from different original assemblages. Coral Horizon V shows only slight displacement of rugose colonies (FEDOROWSKI 1982) and of large tabulate colonies.

The overall character of the deposits as well as redeposited faunal assemblages indicates that the Hornsund area was located in a marginal part of the marine basin, during both clastic and carbonate deposition, very close to land, but below local wave base.

The "Upper Treskelodden Beds" contain, in addition to Tabulata (HOLTEDAHL 1913, FEDOROWSKI 1967, NOWIŃSKI 1982), abundant solitary and colonial rugose corals (HOLTEDAHL 1913, HERITSCH 1929, 1939, FEDOROWSKI 1964, 1965, 1967) of the genera *Caninophyllum*, *Timania*, *Bothrophyllum*, *Hornsundia*, *Svalbardphyllum*, *Heintzella*, *Tschussovskenia*, *Stylastraea*, *Protowentzella*, *Kleopatrina* (subgenera *Kleopatrina*, *Porfirievella*), *Lonsdaleiastrea*, and numerous brachiopods (GOBBET 1964, CZARNIECKI 1969) and crinoids (stem fragments). Less common are bryozoans (among others *Coscinium cyclops* KEYSERLING, mainly in the Coral Horizon V in Hyrnefjellet), gastropods (KARCZEWSKI 1982), bivalves and trilobites (OSMÓLSKA 1968), hydrozoans (among others *Palaeoaplysina laminaeformis* KROTOV, mainly in Coral Horizon IVc in Treskelen), foraminifers (LISZKA 1964), algae among others *Anthracoporella spectabilis* and plant detritus. These deposits, particularly in Coral Horizons IV and V in Treskelen, are rich in biogenic clasts.

Isfjorden area. — In the Isfjorden area the outcropping Permo-Carboniferous deposits with corals occur in a wide belt which extends from Tempelfjorden through Billefjorden to Oscar II Land, and are also present in the Kapp Starostin region (HOLTEDAHL 1912, 1913, HERITSCH 1939*a*, GEE *et al.* 1953, PADGET 1954, FORBES *et al.* 1958, HARLAND 1961, CUTBILL and CHALLINOR 1965, WATERHOUSE 1976, MAŁKOWSKI 1982, STEEL and WORSLEY 1984). In the Billefjorden region, Permo-Carboniferous deposits were distinguished as the Lower, Middle and Upper "Wordiekammen Limestones" (FORBES *et al.* 1958, HARLAND 1961, BIRKENMAJER 1964*a*, FEDOROWSKI 1964, 1965) or as "Wordiekammen Limestone" (FEDOROWSKI 1986), and also as *Cyathophyllum* Limestone ("Wordiekammen Limestones" + "Limestone B" + + Upper Gypsiferous series) (FORBES *et al.* 1958, HARLAND 1961). Resulting from the revision of a stratigraphical scheme based on numerous sections in this area (CUTBILL and CHALLINOR 1965), the whole complex of "Wordiekammen Limestones" has been divided into two series: the lower one — Cadellfjellet member, and the upper one — Tyrrellfjellet member. Together, both series form the upper part of the Nordenskjoldbreen Formation (CUTBILL and CHALLINOR 1965).

The deposits of the Cadellfjellet member consist mostly of limestones, and the Tyrrellfjellet member consists of limestones, dolomites, sandstones and shales with subordinate intercalations of gypsum. Both series show an uninterrupted sedimentary sequence about 470 meters thick, and include most probably a much larger stratigraphical interval than the "Treskelodden Beds" in the Hornsund area.

The age "Wordiekammen Limestone" is regarded as Upper Carboniferous to Lower Permian (FORBES *et al.* 1958, BIRKENMAJER 1964*a*, CUTBILL and CHALLINOR 1965, FEDOROWSKI 1965, 1986, STEEL and WORSLEY 1984). The "Lower Wordiekammen Limestone" (being and equivalent of the Cadellefjellet member), which contains *Triticites*, is included in the Gzhelian and Orenburgian. The "Middle Wordiekammen Limestone" (lower part of the Tyrrellfjellet member), containing in the lowermost part *Pseudoschwagerina*, is included in the Asselian (CUTBILL and CHALLINOR 1965, FEDOROWSKI 1986). The "Upper Wordiekammen Limestone" (upper part of Tyrrellfjellet member, up to the so-called "Limestone B"), which contains *Pseudoschwagerina*, is included in the Asselian (FEDOROWSKI 1986), but it may also be of Sakmarian age (CUTBILL and CHALLINOR 1965).

Tabulate and rugose corals so far described from the central part of Billefjorden area (Central Vestspitsbergen) have no stratigraphical dating (HOLTEDAHL 1912, 1913, HERITSCH 1929, 1939, PADGET 1954, TIDEN 1972) or are presented only as a faunal list (FORBES *et al.* 1958). FEDOROWSKI (1965, 1986), based on his comparative investigations, has found that rugose corals from the uppermost part of the Cadellfjellet member (and perhaps also from the lower part of the Tyrrellfjellet member) are Carboniferous in character (Upper or ?uppermost Carboniferous). In contrast, the assemblage of Rugosa from the upper part of the Tyrrellfjellet member ("Upper Wordiekammen Limestone") are Lower Permian (Asselian) in character, and could be correlated with the coral assemblage of the "Upper Treskelodden Beds" from Hornsund area.

Except for endemic species, tabulates so far described from the central part of the Isfjorden area (HOLTEDAHL 1912, 1913, HERITSCH 1939, PADGET 1954, FORBES *et al.* 1958, see also p. 15 and Table 2), are characterized by long stratigraphical ranges, and allow dating of these deposits only as Upper Carboniferous to Lower Permian. The Lower Permian age of the top of the "Wordiekammen Limestone" is supported by the presence of *Roemeripora wimani wimani* HERITSCH, which is also known from the Permian of Grinnell Peninsula [Canadian Arctic Archipelago (HARKER 1960)] as well as by the occurrence ot *Hayasakaia elegantula* (YABE and HAYASAKA) which is known trom the Lower Permian ot China (YABE and HAYASAKA 1915, 1920, YOH and HUANG 1932) and the Lower Permian of Viet-Nam (FONTAINE 1955, LIN BAO-YUI 1962*a*). On the other hand, the assemblage of tabulates from the "Wordiekammen Limestone" is comparable with the assemblage of the "Upper Treskelodden Beds" from the Hornsund area only at a generic level. Most of the species are different (see p. 17 and Table 2). The presence in both sections, of species of tabulates endemic for Vestspitsbergen such as *Roemeripora wimani* HERITSCH and *Roemeripora minor* HERITSCH also supports an opinion that these sections can be correlated. Common occurrence of such cosmopolitan, long ranging species as *Syringopora ramulosa* or *S. reticulata*, should also be considered.

SETTING AND MODE OF DISTRIBUTION OF TABULATA IN THE "TRESKELODDEN BEDS" AND "WORDIEKAMMEN LIMESTONE"

The investigated collection of tabulates comes from six areas of southern and central Spitsbergen (fig. 1): 1. Treskelen Peninsula — Coral Horizons: I (layers a, and b, total thickness 0.1—0.3 m), II (0.05 to 0.2 thick), III (about 1.6 m thick), IV (layers b and c, total thickness 1.5 to 4.8), V (layers a and c, total thickness 1.6 to 3.0 m). 2. Hyrnefjellet (SE slopes of Hyrnefjellet) — Coral Horizon V (layers: a_1, a_2, a_3, a_4, b_1, b_2, c — total thickness about 14.0 m). 3. Urnetoppen — Coral Horizons II and V. 4. Kruseryggen — Coral Horizon V. 5. Isfjorden

(Skanska Bukta) — "Wordiekammen Limestone". 6. Kapp Starostin region (Linnaeus Valley) — "*Cyathophyllum* Limestone". Detailed distribution of tabulate species from the Hornsund and Isfjorden areas, in particular Coral Horizons of the "Upper Treskelodden Beds", is presented in the Table 1.

Frequency of tabulate colonies in different coral horizons of the "Upper Treskelodden Beds" varies. At Treskelen Peninsula in Horizons I, II and III tabulates are rare, colonies are oval to hemispherical and rather small, not exceeding 200 mm in diameter. The assemblage is dominated by two genera — *Roemeripora* (various species) and *Multithecopora* (2 species). At both Treskelen Peninsula and SE slopes of Hyrnefjellet and Urnetoppen in Coral Horizons IV and particularly V, tabulates are very abundant and highly diversified at generic as well as species level (Table 1). Shapes are ellipsoidal, hemispherical, discoidal and platy; sometimes

Table 1

Distribution of the Tabulata in the Coral Horizons of the "Upper Treskelodden Beds" of Hornsund are
and of the "Wordiekammen Limestone" of Isfjorden region of Spitsbergen

LOCALITY	TRESKELEN								HYRNEFJELLET							URNETOPPEN		KRUSERYGGEN V CL	ISFJORDEN
Coral Limestone Horizons	I		II	III	IV		V		V							III	V		
SPECIES	A	B			B	C	A	C	A_1	A_2	A_3	A_4	B_1	B_2	C				
Roemeripora wimani HERITSCH	6	7	1		3		2	3	2							1			
Roemeripora minor HERITSCH		1	1				1	2		1	2							1	
Roemeripora media sp. n.	1						5	2											
Roemeripora aspinosa NOWIŃSKI							2	3					2	1					
Roemeripora hornsundensis sp. n.		5	1																
Syringopora quadriserialis SOKOLOV								8			2		1				1		
Syringopora subreticulata NOWIŃSKI								2				1	3	1					
Syringopora cf. *reticulata* GOLDFUSS								1					1						
Syringopora stuckenbergi sp. n.								1											
Syringopora kruseriggensis sp. n.																		1	
Neosyringopora spitsbergensis sp. n.														1	1				
Syringopora sp.													1						
Fuchungopora arctica NOWIŃSKI							1	3					2	3					
Roemerolites laminatus (NOWIŃSKI)							1			1	3		1	1					
Roemerolites sp. (= *Armalites* sp.)								1						1					
Multithecopora syrinx (ETHERIDGE)			1		3												3		1
Multithecopora tchernychevi SOKOLOV				1	1				1										
Multithecopora sp.																	1		
Hayasakaia compacta NOWIŃSKI							1	6			1								
Hayasakaia multispinosa sp. n.							2	1											
Hayasakaia birkenmajeri sp. n.											2								
Hayasakaia variabilis sp. n.														2					
Tetraporinus spitsbergensis sp. n.								2					1						
Tetraporinus spinosus sp. n.								2					1						
Tetraporinus kozlowskii sp. n.														2				1	
Neoroemeria permica sp. n.																			1
Neoroemeria spitsbergensis sp. n.	1						1												

they attain large size. Some colonies of *Roemeripora* and *Multithecopora* attain a diameter of 2.5 meters and occur as massive flat blocks 60 to 100 cm thick. The tabulates of these horizons are dominated by various species of *Roemeripora, Syringopora, Fuchungopora, Roemerolites, Hayasakaia* and *Tetraporinus*. At both Treskelen Peninsula section and SE slopes of Hyrnefjellet sections, the absence of colonies of *Multithecopora* (usually common in the lower Coral Horizons) is very characteristic. In the same Coral Horizon V in SE slopes of Hyrnefjellet sections, considerable decrease in numbers of *Roemeripora* has been noted, when compared to the same Coral Horizon on Treskelen Peninsula. In Kruseryggen sections, tabulates are less common.

The assemblage of Tabulata from the Hornsund area is rich and diverse at generic level (the following genera are represented: *Roemeripora, Syringopora, Neosyringopora, Fuchungopora, Roemerolites, Multithecopora, Hayasakaia, Tetraporinus, Neoroemeria*) as well as at species level (see Table 1). All tabulates in the "Upper Treskelodden Beds" are redeposited, variously oriented, and together with rugose corals common there form a rather chaotic mixture. In Coral Horizons I, II and partly III, particular colonies, or even broken fragments, are embedded in a clastic rock (coarse grained quartz sandstones, sometimes carbonate). The degree of redeposition of tabulate fauna decreases toward the top of the "Treskelodden Beds" complex. In Coral Horizon V they are nearly all in living position, but in Coral Horizon IV, some, even very large platy specimens of *Roemeripora* and *Multithecopora*, are overturned or strongly displaced in relation to the living position. Some other small colonies or their fragments show traces of mechanical reworking. Similar features are typical also for the assemblage of rugose corals from the same beds (FEDOROWSKI 1967, 1982).

Most tabulate colonies are diagenetically altered and recrystallized as a result of post-depositional processes. In effect, primary microstructure of corallite walls, septa and tabulae is changed. Some colonies, or their fragments, (from various Coral Horizons, especially from Horizon II at Treskelen Peninsula) are totally recrystallized, making identification impossible. Specimens of *Roemeripora, Hayasakaia, Multithecopora* and *Roemerolites* show the best state of preservation. Most poorly preserved are colonies of *Syringopora* and *Tetraporinus*.

Tabulates in the "Wordiekammen Limestone" (Billefjorden area) and in the "*Cyathophyllum* Limestone" (Kapp Starostin region) are very common and are much better preserved than in the "Upper Treskelodden Beds". In my collection from Skanska Bukta and Linnaeus Valley, I have only few colonies of *Multithecopora* and *Neoroemeria*, which does not allow for analysis of the whole assemblage.

PALEOGEOGRAPHICAL REMARKS

The fauna of Tabulata of Central Spitsbergen is clearly endemic, but endemism is much better expressed in the "Upper Treskelodden Beds" (about 75% of endemic species) than in the "Wordiekammen Limestone" (about 43% of endemic species) (see Table 2). Additionally, despite general similarity (common genera are *Roemeripora, Syringopora, Multithecopora, Hayasakaia,* partly *Michelinia*) at the generic level, the two assemblages differ considerably at the species level (see Table 2). Common to both areas (as well as such cosmopolitan and long ranging species as *Syringopora reticulata, S. ramolosa* and *Multithecopora syrinx*) are only two species of *Roemeripora* (*R. wimani* and *R. minor*). On the other hand, specimens of *Fuchungopora, Roemerolites, Tetraporinus* and *Neoroemeria*, numerous in the "Upper Treskelodden Beds", have not so far been found in the "Wordiekammen Limestone".

Similar, large differences in generic and species composition were observed between assemblages of rugose corals of both areas (FEDOROWSKI 1965). Assuming a similar age for both complexes (i.e. the "Upper Treskelodden Beds" and "Wordiekammen Limestone"), the above

Table 2

Tabulata from the Permo-Carboniferous strata of Central Spitsbergen and their distribution in NW Asia and China areas

LOCALITY / SPECIES	Central Spitsbergen						Asia	
	Isfjorden area "Wordiekammen Limestone"				Hornsund area "Upper Treskelodden Beds"		NW Asia	
	Heritsch 1939	Padget 1954	Forbes *et al.* 1958	Nowiński present	Fedorowski 1967	Nowiński 1982 and present	North Ural; Novaya Zemlya; Timan Taymyr	CHINA
Roemeripora aspinosa Nowiński						+		
Roemeripora hornsundensis sp. n.						+		
Roemeripora media sp. n.						+		
Roemeripora minor Heritsch	+	+			+	+		
Roemeripora wimani Heritsch	+	+	+		+	+		
Roemeripora wimani var. *fasciculata* Wang			+					
Roemeripora wimani var. nov. Wang			+					
Roemeripora wimani var. A			+					
Michelinia abnormis (Huang)					+			+
Michelinia tenuisepta (Phillips)	+						+	
Syringopora degeeri Heritsch	+							
Syringopora eichwaldi Stuckenberg	+						+	
Syringopora kruseryggensis sp. n.						+		
Syringopora multattenuata Mc Chesney	+		+					
Syringopora parallela (Fischer von Waldh.)	+		+				+	+
Syringopora quadriserialis Sokolov						+	+	
Syringopora ramulosa Goldfuss	+	+	+				+	
Syringopora cf. *ramulosa* Goldfuss					+			
Syringopora reticulata Goldfuss	+						+	+
Syringopora cf. *reticulata* Goldfuss		+				+		
Syringopora stuckenbergi sp. n.						+		
Syringopora subreticulata Nowiński						+		
Syringopora tchernychevi Stuckenberg	+	+	+				+	
Syringopora sp. A			+					
Syringopora sp. B			+					
Syringopora sp.						+		
Neosyringopora spitsbergensis sp. n.						+		
Fuchungopora arctica Nowiński						+		
Roemerolites laminatus (Nowiński)						+		
Roemerolites sp. (= *Armalites* sp. Nowiński)						+		
Multithecopora syrinx (Etheridge)				+		+		+
Multithecopora tchernychevi Sokolov						+		
Multithecopora yohi Chi	+							+
Multithecopora sp.						+		
Hayasakaia birkenmajeri sp. n.						+		
Hayasakaia compacta Nowiński						+		
Hayasakaia elegantula Yabe et Hayasaka	+		+					+
Hayasakaia multispinosa sp. n.						+		
Hayasakaia profunda Fedorowski					+			
Hayasakaia variabilis sp. n.						+		
Tetraporinus kozlowskii sp. n.						+		
Tetraporinus spinosus sp. n.						+		
Tetraporinus spitsbergensis sp. n.						+		
Thecostegites permicus sp.				+				
Neoroemeria spitsbergensis sp. n.						+		
Cladochonus bacillaris Mc Coy			+					

facts suggest separation of the two sedimentary basins during the Upper Carboniferous—Lower Permian (by a distance of about 150 km), or entirely different environmental conditions in both areas.

Most (14) species of Tabulata from the "Upper Treskelodden Beds", belonging to the genera: *Roemeripora* (*R. wimani, R. minor, R. media* sp. n., *R. hornsundensis* sp. n.), *Neoroemeria* (*N. spitsbergensis* sp. n.), *Roemerolites* (*R. laminatus*), *Hayasakaia* (*H. multispinosa* sp. n., *H. birkenmajeri* sp. n., *H. variabilis* sp. n.), *Tetraporinus* (*T. spitsbergensis* sp. n., *T. spinosus* sp. n., *T. kozlowskii* sp. n.), *Neosyringopora* (*N. spitsbergensis* sp. n.), as well as some others, do not display any relation to coeval (Carboniferous or Permian) species of Tabulata from other world's regions. Outside of Isfjorden area, *R. wimani* HERITSCH (HERITSCH 1939, PADGET 1954, FORBES *et al.* 1958) was noted only from the Permian of Grinnell Peninsula, Canadian Arctic Archipelago (HARKER 1960).

The remaining, smaller part of the studied assemblage of Tabulata from the "Upper Treskelodden Beds", comprising known species and species of only loose affinity to known species, displays some similarity to coeval Tabulata from various regions of Asia. This part of the assemblage is most closely related to the Middle and Upper Carboniferous assemblages of NW Asia, i.e. the North Ural Mts., Novaya Zemlya, Timan and Taymyr Peninsula. Common to the Hornsund area and NW Asia is the occurrence of *Syringopora quadriserialis* SOKOLOV and the related species. Species from the Hornsund area, such as *Roemeripora aspinosa* NOWIŃSKI, *Syringopora stuckenbergi* sp. n. and *S. kruseryggensis* sp. n., show marked affinity to (respectively): *Roemeripora terrae-novae* from the Tournaisian of the Novaya Zemlya (SMIRNOVA 1957), *Syringopora uralica* from the Lower Carboniferous of the Northern Ural Mts. and the Upper Carboniferous of Timan (STUCKENBERG 1895) and *S. polaris* from the Lower Carboniferous of the Taymyr Peninsula (SOKOLOV 1947).

The tabulate assemblage from the "Upper Treskelodden Beds" also display some similarity with the tabulate fauna of Southern China, mainly in the common occurrence of *Michelinia abnormis* (HUANG). The species *Fuchungopora arctica* and *Hayasakaia compacta* (NOWIŃSKI 1982) and *Haysakaia profunda* (FEDOROWSKI 1967) are closely related, respectively to the south Chinese *Fuchungopora syringoporoides* and *F. multispinosa* from the Visean (LIN BAO-YUI 1963), and *Hayasakaia tsengi* (SOKOLOV 1955) and *Hayasakaia elegantula* (= *Tetrapora elegantula*) (YABE and HAYASAKA 1915, 1916), both from the Lower Permian. Other than the above, the species common, to both areas, *Syringopora reticulata* and *Multithecopora syrinx*, are cosmopolitan.

The tabulate assemblage from Isfjorden sections reveals closer relations with those of NW Asia and China, than does assemblage from the Hornsund area (HERITSCH 1939, PADGET 1954, FORBES *et al.* 1958, see also Table 2).

Relations with faunas of the North Ural Mountains, Novaya Zemlya, Taymyr and Timan are indicated by the presence of such species as *Syringopora eichwaldi* STUCKENBERG, *S. paralella* (FISCHER von WALDHEIM) and *S. tchernychevi* STUCKENBERG. The relations with the Upper Carboniferous and Lower Permian tabulate assemblages of China are revealed by the occurrence of *Syringopora paralella* (FISCHER von WALDHEIM), *Hayasakaia elegantula* (YABE and HAYASAKAIA) and *Multithecopora yohi* CHI. Various species of *Roemeripora*, *Syringopora degeeri* and *Neoroemeria permica* sp. n. are endemic for the area; *Michelinia tenuiseptata, Syringopora ramulosa* and *S. reticulata* common to both areas are long ranging cosmopolitan species.

It follows from the above data, that in the Upper Carboniferous and Lower Permian a marine connection existed between Central Spitsbergen and the present areas of North Ural Mountains, Taymyr and Timan, which facilitated migration of the coral fauna. This opinion is also supported by investigations of distribution of rugose corals of that age by FEDOROWSKI (1981, 1986), and also FRAKES (1979), SMITH *et al.* (1982), SCOTESE *et al.* (1979), and many others.

Still disputable is the existence of a marine connection, between Vestspitsbergen and South China during this time. The existence of such a connection is supported by the occurrence of relatively numerous south-chinese species of tabulates (see Table 2) in central Spitsbergen. Migration could, however, have taken place only through the Uralian paleoocean.

This conclusion is contradictory to the opinion, that both discussed areas were relatively isolated during Permo-Carboniferous time (Briden *et al.* 1974, Ramsbottom 1978, Scotese *et al.* 1979 and others), and/or to the opinion that colonial Permo-Carboniferous Rugosa from China province have a Paleotethyan character (Fedorowski 1981, 1986).

However, it follows from other investigations (Frakes 1979, Smith *et al.* 1982, Zonenshain *et al.* 1985 and others), that isolation of both areas could not have been permanent. According to Zonenshain *et al.* (1985: 112) during the Upper Carboniferous, but also in the Lower Permian, the European Arctic still had a connection with Paleotethys through the rather narrow Uralian paleoocean. The area of present China existed as an island separated from just-forming Pangea by two branches of the Paleotethys ocean: a north-eastern branch and an equatorial branch. The marine connection between Spitsbergen and South China (as well as coral fauna migration) could have been possible through the area of the present Urals (inlet of the Uralian paleoocean) and the north-eastern branch of Paleotethys. The existence of such a marine connection between both discussed areas is also evident from the maps presented by Smith *et al.* (1982, maps. 57—59 and 61—63).

GROWTH PERIODICITY

General remarks

Growth periodicity in corals is a common, though still little studied phenomenon. It consist of repetitive, cyclic variations in internal structure of a colony (and its corallites) which occur during astogeny in both modern hermatypic corals (e.g. Whitfield 1898; Wood-Jones 1908; Ma 1933, 1934*a*, *b*, 1937; Abe 1940; Shinn 1966; Barnes 1972; Knutson *et al.* 1972; Knutson and Buddemeier 1973; Dodge and Thompson 1974; Dodge *et al.* 1974; Grigg 1974; Baker and Weber 1975; Dodge and Vaisnys 1975, 1980; Buddemeier and Kinzie 1975; Weber *et al.* 1975*a*, *b*; Poljakov and Krasnov 1976; Stearn *et al.* 1977; Scrutton 1978; Poljakov 1980, 1982; Wellington and Glynn 1983) and in fossil colonial corals — Tabulata, Heliolitida (e.g. Lindström 1899; Jones 1936; Sokolov 1951, 1952*a*, *b*, 1955; Ross 1953; Philip 1960; Fischer 1964; Sutton 1966; Bondarenko 1978*c*, 1980*c*, 1981, 1982, 1985*a*, *b*; Bondarenko and Minzhin 1981; Powell and Scrutton 1978; Stel 1978; Scrutton and Powell 1980).

The phenomenon of growth periodicity is expressed as rhythmic occurrence in a colony (and in its corallites) of zones differing in density of skeletal tissue so-called growth bands. Each growth band consists of two optically different (light and dark) layers, accompanied by more or less distinct changes in morphology and density of skeletal elements. Consequently, the growth periodicity is expressed in longitudinal sections through a colony as a sequence of alternating light and dark layers (with sparser and denser skeletal tissue, respectively).

The presence of a rhytmic sequence of layers, both in modern and fossil coral colonies, is commonly explained by cyclic variations of conditions in the external environment (water temperature, light intensity, water chemistry, activity of symbionts), dependent on cyclic alternation of seasons of the year (Ma 1933, 1934*a*, *b*, 1937; Sokolov 1955; Goreau 1959*a*, b, 1961; Knutson *et al.* 1972; Buddemeier *et al.* 1974; Dodge and Thompson 1975; Macintyre and Smith 1974; Baker and Weber 1975; Buddemeier and Kinzie 1975; Weber *et al.* 1975*a*, *b*; Hudson *et al.* 1976; Poljakov and Krasnov 1976; Goreau and Hayes 1977; Stearn *et al.*

1977; Bondarenko 1978*c*, 1985*a*, *b*; Scrutton 1978; Highsmith 1979; Beauvais and Chevalier 1980; Dodge and Vaisnys 1980; Scrutton and Powell 1980; Hudson 1981; Glynn and Wellington 1983; Wellington and Glynn 1983), variations in abundance of food, periods of reproduction (e.g. Bassler 1950; Preobrazhensky 1967; Bondarenko 1978*c*; Schneider and Smith 1982; Wellington and Glynn 1983), or seasonal variations in "vital rhythm", "metabolic rhythm", or "biological rhythm" (Fischer 1964).

It is generally accepted that a single band (light-and-dark couplet) in both fossil and modern corals originates in one year (Ma 1933, 1934*a*, *b*, 1937; Shinn 1966; Sokolov 1955; Fischer 1964; Knutson *et al.* 1972; Weber *et al.* 1975*a*, *b*; Poljakov and Krasnov 1976; Bondarenko 1978*c*, 1985*a*, *b*; Poljakov 1980, 1982; Scrutton and Powell 1980; Bondarenko and Minzhin 1981; Wellington and Glynn 1983). The annual nature of the growth bands is confirmed by French studies of modern colonial corals in New Caledonia, using radioactive isotopes ^{90}Sr and ^{90}Y (e.g. Beauvais and Chevalier 1980).

Observations by various authors indicate that growth periodicity is very common in skeletons of fossil corals, but its occurrence is largely random. It is neither related to individual taxa of any rank nor to any definite areas of the Earth. Within single, taxonomically diverse associations, some colonies of particular genera, families or higher taxa display growth periodicity, while others do not (Ma 1933, 1937; Flower 1961; Fischer 1964; Bondarenko 1985*b*). For instance, in many colonies of Heliolitida in North China the growth periodicity is present, while it is absent from colonies of Favositida of the same area (Fischer 1964). In an assemblage of Heliolitida from the Upper Silurian of Podolia, rich in species and genera, the growth periodicity occurs in skeletons *Paraheliolites*, *Pachyhelioplasma*, *Okopites* and *Dnestrites* (Bondarenko 1978*c*, 1985*a*). Similarly, in assemblages of Tabulata from the Ordovician and Silurian of the Peri-Baltic area, rich in genera and species, the growth periodicity occurs mainly in *Paleofavosites*, *Cryptolichenaria* and *Palaeohalysites* (Sokolov 1951, 1952*a*, *b*, 1955). The cause of this selective occurrence of growth periodicity is not yet known. Fischer (1964) supposes that seasonal changes of conditions in the environment of the corals stimulated the metabolic rhythm of the colonies and this rhythm, in turn, influenced skeleton formation, but it disappeared beneath a definite threshold (different for different species and genera), e.g. when the contrast of seasonal variations was small.

The numbers of growth bands in skeletons of various fossil corals permitted calculations of life-spans of 3—50 years for various colonies (e.g. Ma 1933; Fischer 1964; Bondarenko 1985*b*). The maximum life-span of a colony of Heliolitida is estimated as twenty years, but their average life-span was 3—10 years (Bondarenko 1985*b*; Bondarenko and Minzhin 1981). The thicknesses of linear annual increments for some colonies of Heliolitida are as follows *Paraheliolites skalinensis* 4.0—5.0 mm, *Pachyhelioplasma* 2.0—6.4 mm, *Dnestrites transitus* 3.0—6.5 mm (Bondarenko 1978*c*, 1985*a*, *b*).

In Tabulata, apart from general consideration based on knowledge of the phenomenon in other coral groups (e.g. Sokolov 1955, 1962; Preobrazhensky 1967) and relatively numerous observations (e.g. Jones 1936; Sokolov 1951, 1952*a*, 1955; Ross 1953; Philip 1960; Sutton 1966; Powell and Scrutton 1978; Stel 1978), detailed studies on growth periodicity were very rare (Fischer 1964; Scrutton and Powell 1980). For example Sokolov (1951, 1952*a*, 1955) observed distinct rhythmicity in skeletal increments in numerous massive colonies, including *Paleofavosites* (*P. hystrix*, *P. felix*, *P. mysticus*, *P. luhai*), *Palaeohalysites* (*P. compressus*) from the Ordovician and Silurian of the Peri-Baltic area, as well as *Cryptolichenaria* (*C. miranda*) from the Ordovician of Siberia and *Tyrganolites* (*T. obrutschevi*) from the Eifelian of China. In some colonies of Favositida from the Peri-Baltic area the number of growth bands attains ten (ten year old colonies).

Scrutton and Powell (1980) described rhythmic changes in the density of skeletal elements in colonies of *Favosites multipora* and *Paleofavosites rugosus* from the Wenlockian of England, as annual increments of skeletal tissue (analogous with modern Scleractinia). The growth periodicity in these species features rhythmical crowding and separation of skeletal elements of the colonies and rhytmic changes in corallite diameters. In dark, thin layers which constitute 1/3—2/5 of the growth band thickness, the corallites have tabulae most densely packed, thickened walls and strongly developed septal spines. Their diameters in transverse sections show strong dimorphism irregularly arranged corallites of small diameters among corallites of large diameters. In light, thick layers of the growth bands, the corallites have tabulae less closely spaced, thin walls and rare, feebly developed septal spines, and their diameters are approximately equal. The authors attribute the origin of the dark growth bands to cold periods (fall-winter). The average annual skeletal growth rate of *Paleofavosites rugosus* was 5—14 mm/year and of *Favosites multipora* — 8—18 mm/year.

Earlier observations (e.g. JONES 1936; SOKOLOV 1951, 1952*a*, 1955, 1962; ROSS 1953; PHILIP 1960; SUTTON 1966; PREOBRAZHENSKY 1967; FISCHER 1964; POWELL and SCRUTTON 1978; STEL 1978; SCRUTTON and POWELL 1980) and those made by the present author, indicate that growth periodicity occurs more or less clearly in massive colonies of the tabulate orders Favositida, Lichenariida, Halysitida and Tetradiida, in dendroid colonies of the order Syringoporida, and in thick-branched, finger-like, cylindrical and flat colonies of some genera of the suborder Alveolitina and others (e.g. *Natalphyllum*, *Scoliopora*, *Tyrganolites*). The periodicity is similar to that in other fossil colonial corals — Heliolitida, and also in Palaeozoic Sclerospongiae of the order Chaetetida (SOKOLOV 1950, 1955). This phenomenon has not been hithertho observed either in branched colonies of the suborder Thamnoporina or in dendroid and arborescent colonies of the order Auloporida.

In summary, the periodicity of linear skeletal growth in various colonies of Tabulata is expressed in rhytmic changes of the following characteristics:

1. density, thickness and morphology of tabulae,
2. lack of septa or number, length and degree of development, where present,
3. thickness of corallite walls and the type of their microstructure,
4. number, diameter and meaning of connecting pores,
5. density, diameter and morphology of connecting elements (tubes, bridges, blades),
6. presence or lack of spines on tabulae.

The light growth bands (which formed in periods of rapid colony growth, analogous with modern hermatypic corals) are typically characterized by thin corallite walls, thin and loosely distributed tabulae, rare and short spines or septal scales (or their absence), greater distances between small-dimension connecting pores, and greater distances between less developed connecting elements (tubes, bridges, plates). The dark layers of the growth bands (which formed in periods of slowed colony growth) are characterized by respectively converse morphological and biometric features, namely: thick corallite walls that may be additionally thickened by layer of stereoplasm of different microstructure, more frequent, morphologically complex and thicker tabulae, well developed septal apparatus, more crowded and better developed connecting elements (pores, tubes, bridges plates), and sometimes the appearance of spines on the tabulae. In periods of slower corallite (and colony) growth the polyps "had more time" for building more and better developed skeletal elements than in periods of accelerated growth.

Growth periodicity in Tabulata from the "Upper Treskelodden Beds"

In Permo-Carboniferous colonies of Tabulata from the "Upper Treskelodden Beds", growth periodicity is rather common, though not consistent, and its intensity is subject to variability. The annual skeletal increments are best marked in massive, large colonies of the species of *Roemeripora* (*R. wimani*, *R. minor*, *R. media* sp. n.) and *Neoroemeria* (*N. spitsbergensis* sp. n.) and in dendroid colonies of *Fuchungopora* (*F. arctica*). A poorly expressed

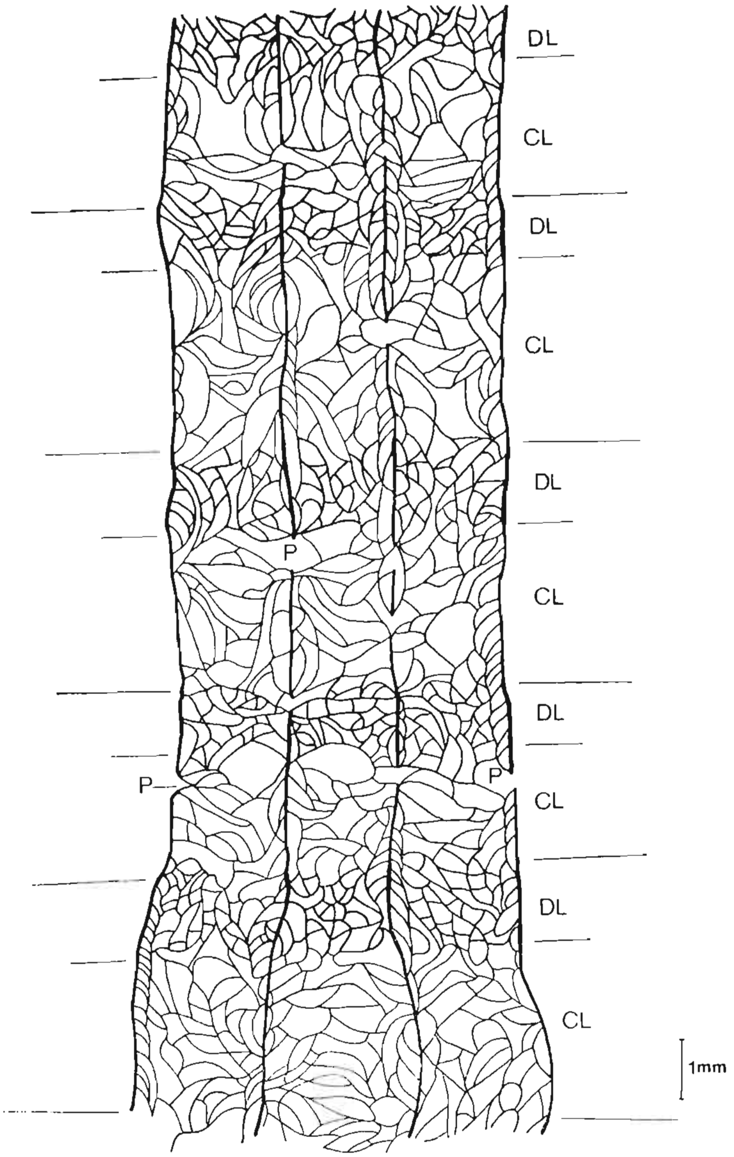


Fig. 2

Skeletal periodic growth (five bands of annual growth) of *Roemeripora wimani* Heritsch, Hyrnefjellet, Coral Horizon Va$_1$, (ZPAL T XIII/31); longitudinal section, × 7.5. For explanation of symbols see p. 8—9.

periodicity occurs also in colonies of *Roemeripora aspinosa*, *Syringopora quadriserialis* and *Hayasakaia compacta*. In colonies of *Syringopora* (except for *S. quadriserialis*), *Neosyringopora*, *Roemerolites*, *Multithecopora*, *Tetraporinus*, *Hayasakaia* (except for *H. compacta*) and *Roemeripora hornsundensis* sp. n., growth increments are invisible or weakly marked (only in some zones of some colonies).

The author's studies indicate that in individual colonies skeleton growth bands (if they are distinct) are usually manifested throughout vertical sections and usually show relatively constant rhythmicity. Growth periodicity phenomena in colonies of Tabulata from the "Upper Treskelodden Beds" are described below.

Colonies of *Roemeripora* (Table 3; pl. 3: 1, 2; pl. 5: 1; pl. 7: 1; fig. 2). — In most colonies of *Roemeripora wimani* and *R. minor* growth periodicity is well expressed. Colonies of these species were at different stages of development (astogeny) at their death. Their heights varied (based on reconstructed specimens) from 60 mm for young ones to 180 mm for older colonies. The number of identified growth bands in complete and reconstructed colonies varies from 4 to 38 (this corresponds to an age range of 4—38 years).

As the largest colonies of this genus (*R. wimani* and *R. media* from Coral Horizon IV) reaching a height of 1 meter, could not be collected whole, there was no possibility of studying annual growth bands in them. However, the annual growth bands studied in fragments of these colonies do not differ in thickness (5.0—10.0 mm) from those in other smaller colonies of the same species from the same coral horizon. Given the primary height of a colony one can estimate its age, which for the largest among them could be about 100 to 150 years.

In the colonies of *R. wimani* there are two types of growth bands. In almost all colonies that come from stratigraphically older coral horizons of the "Upper Treskelodden Beds", i.e. from Coral Horizons I and IV, there occur thick growth bands — 5.0—10.0 mm on average. In most colonies from the youngest, Coral Horizon V, growth band thickness is smaller by a half and is 2.5—6.0 mm on average. Of similarly small thickness are the growth bands in *R. minor* which occurs only in Coral Horizon V (see Table 3). In both types of growth bands, however, the thickness proportions of light and dark layer are constant (2/1 on average). The cause of these significant variations in thickness of growth bands is not known. In the colonies of *R. media* and *R. aspinosa* growth periodicity is weakly expressed. These colonies are usually 10—16 years old, and about 90 mm high. The thicknesses of their growth bands are 3.5—5.0 mm in *R. media* and 4.0—13.0 mm in *R. aspinosa*, and the proportions of light and dark layers are similar to those colonies of other species of this genus (2/1).

Morphological and biometric variability in the corallite skeletal elements in the light and dark layers, in the studied colonies of *Roemeripora*, is the following: the light layers are characterized by relatively thin corallite walls, thin, oblique and less dense tabulae of relatively simple shapes, a well developed vesicular zone near the corallite walls, and less densely distributed connecting pores which occur at different levels in neighbouring corallites. The dark layers — conversely — have thicker corallite walls, thick, short, closely spaced and strongly curved tabulae, less developed vesicular zones and connecting pores situated at one level in neighbouring corallites.

Colonies of *Syringopora* (only *S. quadriserialis* — Table 3; pl. 8: 1). — Growth bands are weakly expressed in colonies of *S. quadriserialis*. These are relatively young (5—6 years) colonies, about 50—70 mm high. The number of identified growth bands in complete and reconstructed colonies is 5—6, and their thicknesses are highly variable for various levels in colonies of the same species, from 6.0 to 15.0 mm. The thicknesses of the light layers equal approximately those of the dark layers and average 3.0—7.5 mm in various colonies. The differences in morphology and size of corallite skeletal elements between the light and dark layers in the colonies of *S. quadriserialis* display a variability similar to that in colonies of *Roemeripora*. Additionally, the light layers are characterized by a significantly greater separation of corallites and rare connecting tubes which occur at different levels in neighbouring corallites. Within the dark layers the corallites are densely spaced and communicate with numerous connecting tubes, distributed predominantly on the same levels in neighbouring corallites.

Colonies of *Fuchungopora arctica* (Table 3; pl. 12: 1). The growth periodicity in colonies of this species is very well expressed. These are young (4—5 years) dendroid colonies of syringoporidal type, about 50—60 mm high, composed of 4—5 growth bands strongly differentiated in thickness. The thicknesses of successive growth bands in astogeny are as follows: first growth band — 4.0—8.0 mm; second — 9.0—13.0 mm; third — 5.0—12.0 mm; fourth — 12.0—20.0 mm. The thicknesses of the light layers approximately equal those of dark layers and average 2.0—10.0 mm for the growth bands in different colonies. The light layer of each annual increment starts with a zone of intense budding in which young corallites are densely

Table 3

Quantitative and qualitative characterizations of annual growth bands in selected colonies of various species of Tabulata from the Lower-Permian ("Upper Treskelodden Beds") of Hornsund area of Spitsbergen

SPECIES	Number of specimen	Locality, Coral Horizon and layer	Height of complete colony or after reconstruction in mm.	Number of annual growth bands		Thickness of annual growth bands (measured as light/dark doublets)	Thickness of particular layers in annual growth bands; in mm.		Relation of thicknesses of layers: low density/high density
				before reconstruction	after reconstruction		low density (light)	high density (dark)	
Roemeripora wimani HERITSCH	ZPAL T XIII/10	Treskelen Ib CL	130	5	14	5.0—10.0	3.5—6.8	1.7—3.4	2/1
" " "	ZPAL T XIII/11	Treskelen Ib CL	60	4	6	6.0—10.0	3.8—6.6	2.0—3.5	2/1
" " "	ZPAL T XIII/16	Treskelen IVb CL	ca. 160	6	16	5.0—10.0	3.5—6.8	1.7—3.4	2/1
" " "	ZPAL T XIII/18	Treskelen Va CL	ca. 100	6	18	2.5—6.0	1.6—4.0	0.8—2.0	2/1
" " "	ZPAL T XIII/32	Hyrnefiellet Va_1 CL	ca. 150	24	35	2.5—5.5	1.6—3.8	0.8—1.9	2/1
Roemeripora minor HERITSCH	ZPAL T XIII/54	Hyrnefiellet Va_2 CL	ca. 120	20	38	2.0—3.0	1.4—2.0	0.7—1.0	2/1
Roemeripora media sp. n.	ZPAL T XIII/62	Treskelen Va CL	ca. 180	18	25	5.0—10.0	3.5—6.3	1.7—3.4	2/1
" " " "	ZPAL T XIII/63	Treskelen Vc CL	ca. 90	9	16	3.5—5.0	2.4—3.5	1.2—1.7	2/1
Roemeripora aspinosa NOWIŃSKI	ZPAL T XIII/21	Hyrnefiellet Vb_2 CL	90	8	10	4.0—13.0	3.0—9.5	1.0—3.5	2/1
Syringopora quadriserialis SOKOLOV	ZPAL T XIII/71	Treskelen Vc CL	70	5	6	6.0—11.0	3.0—5.5	3.0—5.5	1/1
" " "	ZPAL T XIII/81	Hyrnefiellet Vb_1 CL	65	5	6	10.0—15.0	5.0—7.5	5.0—7.5	1/1
Fuchungopora arctica NOWIŃSKI	ZPAL T XIII/48	Hyrnefiellet Vb_1 CL	60	4	4	4.0—20.0	2.0—10.0	2.0—10.0	1/1
Hayasakaia compacta NOWIŃSKI	ZPAL T XIII/117	Treskelen Vc CL	150	10	18	6.0—8.0	4.0—5.2	2.0—2.6	2/1
Neoroemeria spitsbergensis sp. n.	ZPAL T XIII/138	Treskelen Va CL	ca. 160	3	10	12.0—16.0	6.0—8.0	6.0—8.0	1/1

packed and connected with stolonal and connecting tubes, distributed at one level in neighbouring corallites. Higher up, the light layer is composed of loosely distributed corallites with less dense, thin tabulae, rarely connected with tubes. The dark layers are again characterized by greater concentration of corallites, connected with numerous tubes, distributed at the same levels in neighbouring corallites. The tabulae in corallites of these layers are widely spaced, and the septal spines are slightly better developed than in the light layers.

Colonies of *Hayasakaia compacta* (Table 3). — The growth periodicity is weakly expressed. These are large (10—18 years old) dendroid colonies, 130—200 mm high. The number of identified growth bands in complete and reconstructed colonies is 10—18. Their large thickness (6.0—8.0 mm) shows little variation during astogeny in different colonies of this species and indicates a high growth rate. The thickness proportions of light to dark layers in the growth bands are 2/1 on average. The variability of morphological elements and their sizes in the light and dark layers is relatively small and is similar to that in colonies of *Roemeripora*.

Colonies of *Neoroemeria spitsbergensis* (Table 3; pl. 20: 2; pl. 23: 2b). — In several colonies of this species the growth periodicity is very well expressed. These are large (6—12 years old) colonies, about 120—180 mm high. The number of identified growth bands in complete and reconstructed colonies is 8—10. The colonies of this species have very thick growth bands — 12.0—16.0 mm, indicating an exceptionally rapid skeleton growth rate. The thickness of the light layers equals approximately that of the dark layers and averages 6.0—8.0 mm for various double growth bands in different colonies. The light layers are characterized by wide spacing of corallites and very rare, randomly distributed connecting bridges. In the dark layers the corallites are densely distributed and connected by very numerous skeletal bridges which form stacked horizontal bands in the colonies. Other morphological elements of corallites in both light and dark layers display little variability.

The observations above show that thicknesses of particular annual growth bands in tabulates from the "Upper Treskelodden Beds" (average annual growth rate of skeletal tissue) vary widely from one taxon to another. Thicknesses vary from 2.0 mm in some colonies of *Roemeripora* to 20.0 mm in young colonies of *Fuchungopora* (see table 3). The differentiation is highest between different genera and/or species of the same genus. Much lower differentiation has been observed among colonies of the same species, from different strata of different Coral Horizons. The lowest differentiation of thickness of annual growth bands occurs in astogeny represented by different portions of a colony.

Apart from environmental influences, differentiation of thickness of annual growth bands among various species of the same genus seems to depend on different metabolic rhythms of different species and is probably of specific value.

Similar variation in thickness of growth bands of the skeleton (at the generic, specific and colonial level) occurs also, very often in Heliolitida (Bondarenko 1978*c*, 1985*a*, *b*) as well as in Palaeozoic sponges of the order Chaetetida (Sokolov 1950).

The ratio of the thicknesses of light and dark layers (independently of taxonomic position or colony) is stable in tabulates from the "Upper Treskelodden Beds", and amounts on average to 2 in one case or 1 in another.

Generally, growth periodicity in the studied colonies of Tabulata from the "Upper Treskelodden Beds" is expressed in the following way: the light layers of the annual skeleton increments originated during periods of accelerated colony growth, have thin walled, widely spaced, corallites thin tabulae of relatively simple shapes, and rarely distributed connecting elements that occur at different levels between neighbouring corallites. The dark layers, originated in periods of lowered colony growth rate, are characterized by thick corallite walls, densely packed, thickened tabulae of complex shapes, and more densely distributed connecting elements which occur at the same levels between neighbouring corallites.

In complete colonies and in those incomplete colonies that could be reconstructed (especially their heights), the colony age could be determined by counting the growth bands. The age, for different species and different colonies of Tabulata in the studied area, ranged from approximately 4 years for small, young colonies of the genera *Fuchungopora* and *Syringopora*, up to 38 years for large, platy colonies of the genus *Roemeripora* (see Table 3). The age of the largest, platy colonies of *Roemeripora* from the Coral Horizon IV, is estimated for 100—150 years.

The analysis of growth band thicknesses in different genera and species of Tabulata of the Hornsund area, as well as the proportions of light and dark layers in vertical sections of the colonies indicate that during the estimated life-span of these colonies relatively stable climatic conditions occurred that were subject to rhytmic seasonal variations similar to those of modern subtropical climates.

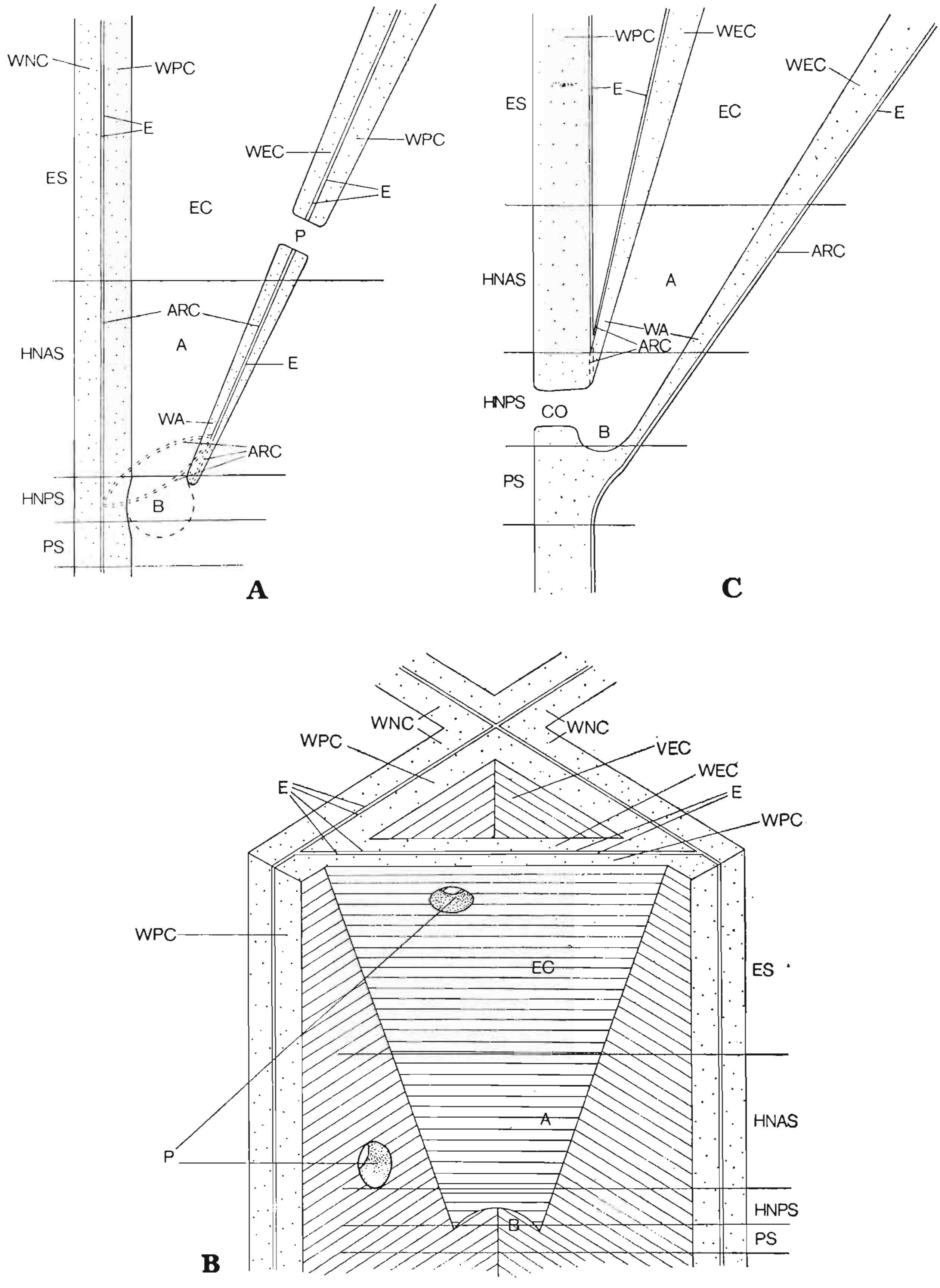
BLASTOGENY

General remarks

The history of studies on vegetative reproduction, and the classification of the main types of blastogeny in Tabulata have been presented by the author in an earlier paper (Nowiński 1976: 26—31, fig. 5; see also Sokolov 1955, 1962 and Hill 1981).

A new term "praecorallite" is introduced in the present paper for early growth stages (hystero-nepionic and hystero-neanic) ones of a hysterocorallite (offset). These stages include the development of hysterocorallite begining from the moment of formation of bud chamber of the moment of separation of a young polyp from the parent polyp with the first complete tabula (see below). The existing term "protocorallite" is used only for early stages of the first corallite skeleton development in a colony, which originates in the process of transformation of larvae (planula).

The investigated colonies of Tabulata from the "Upper Treskelodden Beds" show two types of budding: calicular budding and extracalicular budding. Calicular budding occurs within morphologically and functionally determined calices, where a calice is the terminal portion of a corallite skeleton containing a polyp and separated from other calices (or corallites) in a colony, or from the environment by an epitheca. In massive (compact) colonies, where corallites (and calices) are tightly packed, the boundary between calices (and corallites) is placed at the median line (of the double epitheca which belongs to two individuals). In a colony with widely spaced corallites (and calices), the individual epitheca is the most external part of a corallite (and a calice) separating it from the environment. Two types of calicular budding were distinguished in the investigated material: intravisceral budding and extravisceral budding. They differ in direction of growth of a wall and epitheca during the process of the formation of descendant individuals. Intravisceral budding which took place within the visceral chamber proper of the parent calice, occurred in colonies of the genus *Roemeripora*. The bud originated in an angle of the parent calice resulting from the joining of two wall processes, to form a kind of a wall swelling, which grew toward the interior of the visceral chamber (for schematic representation ofthis process in both transverse and longitudinal sections, see fig. 3A, B; 4, and Nowiński 1976). The bud after having been separated by its own wall and epitheca, was transformed into a young polyp, and a chamber into a praecorallite and subsequently into a young corallite. Extravisceral budding, which took place outside the visceral chamber proper of the parent calice, occurred in colonies of *Syringopora*, *Neosyringopora*, *Fuchungopora*, *Roemerolites*, *Multithecopora*, *Hayasakaia*, *Tetraporinus* and *Neoroemeria*. The bud originated in a convexity of the parent calice wall directed externally with respect to the parent calice wall directed externally with respect to the visceral chamber. After having become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separated with its own wall and epitheca, it diverged and, then, was transformed into a young polyp (schematic representation of this process shown in both transverse and longitudinal sections — see figs. 3C and 5 and Nowiński 1976). The bud chamber, as in intravisceral budding, was transformed into an praecorallite, and then into a young corallite.

These two calicular budding types (intra- and extravisceral) were achieved by invagination or evagination respectively, of the wall of a parent calice (inside or outside of its visceral chamber). The direction of development depends on the degree of compactness of a colony. In compact colonies, where there is no place for the forming bud, except in the parent calice space, blastogeny took place inside of its visceral chamber (in a corner of a calice). In branched colonies, with widely spaced corallites (and calices), where there is free space outside of the parent calice, a bud originated outside of the visceral chamber, by external evagination (a kind of visceral chamber pocket). Calicular budding proceeded in such a way that the newly forming individual occupied the smallest possible space of the parent calice. A similar type of calicular budding occurred also in Rugosa (with dissepimentarium), where it is called lateral budding.

Extracalicular budding in tabulate corals from the "Upper Treskelodden Beds" occurred but rarely. It was observed (together with calicular budding) in the following species: *Fuchungopora arctica* Nowiński, *Tetraporinus spinosus* sp. n., *Neoremeria spitsbergensis* sp. n., and *N. permica* sp. n. It was the stolonal type of budding. Young individuals bud off the connecting tubes or from horizontal stolonal tubes. When growing they turn up and become vertical (see pl. 12: 1, pl. 19: 4). Because of the poor state of preservation of the material it was not possible to observe details of this type of budding.

The blastogeny in all studied species of Tabulata of the "Upper Treskelodden Beds" occurred at random. There were no discrete budding zones within the colony (except for the zones of stolonal budding in *Fuchungopora arctica* and *Neoroemeria spitsbergensis*). The buds appeared in different places on each successive living surface of the colony. In the colonies of *Roemeripora* and *Hayasakaia*, composed of very long corallites, budding occurred rarely (praecoralites were rarely encountered), both in horizontal and vertical planes.

Budding and skeletal growth of young individuals in the investigated tabulate coral colonies proceeded in 4 successive growth stages: (fig. 3A, 3C; see also Nowiński 1976).

1. Preblastic stage — comprised morphological and structural changes of the corallite wall which occurred in the part of the parent calice in which the bud was to develop, and terminated with appearance of the bud.
2. Hystero-nepionic stage — began with bud appearance and comprised its development, its separation from the visceral chamber of the parent corallite and the formation of its own epitheca wall. This stage terminated as the bud became separated with its epitheca. The bud was transformed into a young polyp, and its chamber into a praecorallilte.
3. Hystero-neanics tage — began with complete separation of the young individual (praecorallite) from the parent calice, and terminated when it attained the features characteristic of the genus. At the end of this stage the praecorallite became a young corallite.
4. Ephebic stage — comprised the period of development, from attaining by the young of features diagnostic for the genus, to attaining by it features diagnostic of the species (especially to the attainment of a mean diameter, characteristic of a parent corallite). In the blastogeny of rugose corals the beginning of the ephebic stage is considered to be the mature stage of an individual, as a young corallite shows all features characteristic of the species. In tabulate

←

Fig. 3

Scheme of intracalicular budding and development of young corallites in Tabulata from Spitsbergen (in longitudinal section). *A* Intracalicular-intravisceral budding occurring by the formation of two wall processes and their fusion in the corner of a parent calice; *B* This same as visible from visceral chamber of parent calice; *C* Intracalicular-extravisceral budding, occurring in the lateral invagination on the wall of a parent calice. For explanation of symbols see p. 8—9.

corals, an individual in the ephebic stage does not show all species characters, and in particular diameters of corallites that is smaller than in mature corallites. They reach the terminal diameters only at the end of the ephebic stage.

Vegetative reproduction in Tabulata from the "Upper Treskelodden Beds"

a) Intravisceral budding

Intravisceral budding proceeded within the visceral chamber of the parent corallite, in any corner produced by two walls. The processes of this budding and the growth of young corallites were observed in colonies of *Roemeripora wimani* Heritsch, *R. minor* Heritsch, *R. media* sp. n., *R. aspinosa* Nowiński, and *R. hornsundensis* sp. n. The budding and growth of young corallites in these species was very similar to each other and reconstruction of these processes will be represented by the example of *Roemeripora wimani* Heritsch (figs. 3A, B; 4A—M).

1. Preblastic stage (fig. 4A—D). — Initially, in any wall corner of the parent corallite, in the place where a bud was to occur, two small swellings of the neighbouring calice walls occurred, and they were subsequently transformed into two wall processes. This way a hemispherical depression was formed in the corner of a calice. This was often preceded by the formation of a connecting pore in one of the walls of the parent calice. In the course of the further development the processes grew longer and approached one another, simultaneously shifting away from the calice corner. The growth of the processes was usually more or less asymmetrical.

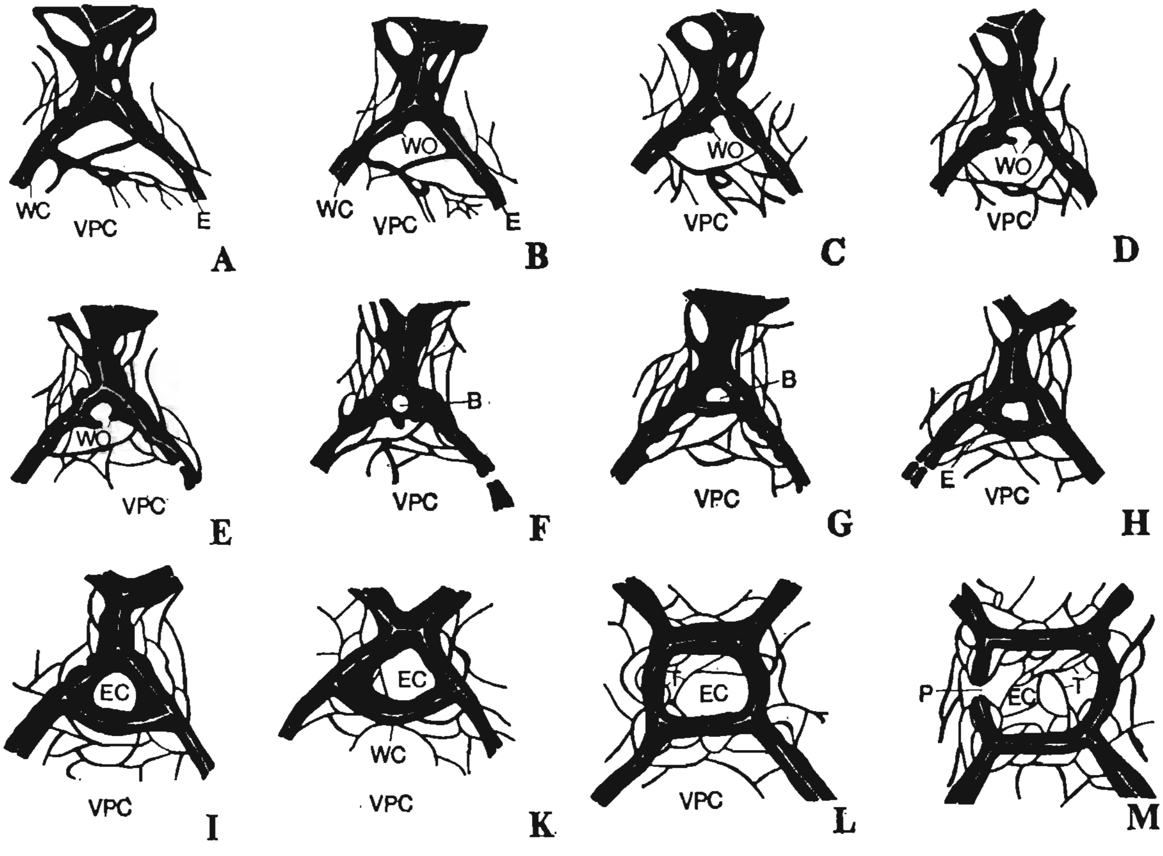

Fig. 4

Intracalicular-intravisceral budding occurring by the formation of wall processes in *Roemeripora wimani* Heritsch, Treskelen, Coral Horizon IVb, Creek II (ZPAL T XIII/16); transverse sections, × 15. *A—D* preblastic stage, *E—G* hysterd-nepionic stage, *H—K* hystero-neanic stage, *L—M* ephebic stage. For explanation of symbols see p. 8—9.

In *R. aspinosa* and *R. hornsundensis* the growth of processes was accompanied by the formation of a small invagination of the wall in the corner of the parent calice, in the direction of the neighbouring corallite. As a result of further growth during which the distal ends of the processes approached one another, a spherical or ovoid cyst originated, which communicated with the visceral chamber of the parent calice through a constricted passage — collum. It was in this cyst where the bud formed. In *R. wimani*, *R. minor* and *R. media* development of the preblastic stage was realised in a distance of ca. 0.08—0.25 mm (measured in the direction of corallite growth). In *R. aspinosa* and *R. hornsundensis* — over a somewhat longer distance (Table 4).

Table 4

Quantitative characterizations of growth of corallites in blastogeny in some species of Tabulata from the Permo-Carboniferous of Hornsund area and of Isfjorden region of Spitsbergen

SPECIES	Diameter of adult corallite in mm.	Diameter of bud chamber in mm.	Linear growth of skeletal tissue of corallites in blastogeny; in mm.		
			preblastic stage	hystero-nepionic stage	hystero-neanic stage
Roemeripora wimani Heritsch	2.3—2.6	0.12—0.15	0.12—0.25	0.15—0.25	0.40—0.60
Roemeripora minor Heritsch	1.8—2.0	0.10—0.15	0.08—0.20	0.13—0.22	0.35—0.50
Roemeripora media sp. n.	2.0—2.3	0.10—0.18	0.10—0.22	0.12—0.20	0.40—0.50
Roemeripora aspinosa Nowiński	1.5—1.8	0.10—0.14	0.08—0.18	0.12—0.20	0.30—0.45
Roemeripora hornsundensis sp. n.	2.0—2.4	0.12—0.16	0.10—0.19	0.15—0.20	0.40—0.55
Fuchungopora arctica Nowiński	1.5—2.8	0.40—0.60	0.25—0.50	0.35—0.55	0.40—0.60
Roemerolites laminatus (Nowiński)	1.8—2.2	0.30—0.60	0.35—0.45	0.40—0.50	0.40—0.60
Multithecopora syrinx (Etheridge)	2.0	0.35—0.60	0.40—0.50	0.45—0.55	0.50—0.70
Multithecopora tchernychevi Sokolov	1.5—1.7	0.30—0.55	0.30—0.45	0.35—0.50	0.40—0.50
Hayasakaia compacta Nowiński	1.3—1.6	0.30—0.50	0.20—0.40	0.30—0.50	0.35—0.60
Hayasakaia multispinosa sp. n.	1.2—1.6	0.25—0.40	0.30—0.40	0.30—0.45	0.35—0.55
Tetraporinus spinosus sp. n.	1.2—1.4	0.30—0.40	0.25—0.40	0.30—0.40	0.30—0.40
Tetraporinus kozlowskii sp. n.	1.2—1.8	0.30—0.45	0.30—0.40	0.30—0.45	0.35—0.65
Neoroemeria permica sp. n.	1.4—1.6	0.40—0.50	0.30—0.40	0.30—0.40	0.35—0.55
Neoroemeria spitsbergensis sp. n.	1.6—2.4	0.40—0.60	0.35—0.50	0.40—0.55	0.45—0.70

2. Hystero-nepionic stage (fig. 4E—G). — Further growth of such processes caused their approaching, and eventual joining, and final separation of a bud chamber from a visceral chamber of a parent calice. Elongation visible in successive transverse sections, and next, joining of wall processes, resulted from simultaneous and step by step growth of a corallite wall from two adjacent walls of a parent calice, as shown in longitudinal section (fig. 3A, B). The originating praeocorallite wall separated the bud and the parent polyp only laterally. In fact, at this developmental stage, the bud was still connected to the parent polyp below the margin of the praeocorallite wall. Total separation of both individuals occurred when the young polyp formed the first tabula, which took place only in the hystero-neanic stage.

The wall separating the bud chamber from the parent calice was probably produced simultaneously by the parent polyp and by the developing bud. The epitheca of the parent calice and the epitheca of the budding polyp (the median suture between both individuals of the newly formed wall) developed just before the junction of the processes or immediately after the junction. The accretion began at the bases of the processes (from the median suture of the parent calice walls forming the angle) and continued with their growth. After the junction of the processes into the wall separating the bud from the visceral chamber of the parent calice, the epithecas of both processes joined to form a double continuous suture line. After the formation of the epitheca, the bud was transformed into a young polyp, and its chamber, along with the new-formed wall and a fragment of the wall of the parent calice, into a praecorallite. The bud chambers and praecorallites have ovoid or irregularly rounded outlines in transverse sections, 0.1—0.2 mm in diameter, for different species studied here. The development in the hystero-nepionic stage was realised at a distance of ca. 0.08—0.2 mm of linear corallite growth.

3. Hystero-neanic stage (fig. 4H—K). — After their separation from the parent calice, the praecorallites were triangular in transverse section and had rounded visceral chambers. Their diameters were 0.15—0.35 mm in this stage, i.e. about 10% of the cross-sectional area of the parent calices. During their growth, the praecorallites gradually increased in diameters, while changing into young corallites. The number of walls and angles (four to five) and the wall thickness also increased. First, simple tabulae, and then connecting pores of normal diameters appeared at the beginning of this stage. Development in the hystero-neanic stage in the studied species of *Roemeripora* occurred in a distance of ca 0.35—0.55 mm of linear corallite growth, and at the end of this stage the young corallites already displayed all typical features of their genus.

4. Ephebic stage (fig. 4L—M). — It is characterized by continuing increase in the thickness and number of the corallite walls (five to six), increase in number and morphological complexity of the tabulae, and — at the end of this stage — the gradual appearance of the features characteristic of the given species, especially the increase in corallite diameter. Development in the ephebic stage was realised over relatively long vertical distances.

b) Extravisceral budding

Extravisceral budding proceeded outside the visceral chamber proper of the parent calice — in its evagination. The course of the budding and the development of the young corallites were observed in dendroid colonies of the following species: *Fuchungopora arctica* NOWIŃSKI, *Roemerolites laminatus* (NOWIŃSKI), *Multithecopora syrinx* (ETHERIDGE), *M. tchernychevi* SOKOLOV, *Hayasakaia compacta* NOWIŃSKI, *H. multispinosa* sp. n., *Tetraporinus spinosus* sp. n., *T. kozlowskii* sp. n., *Neoroemeria permica* sp. n., *N. spitsbergensis* sp. n., *Syringopora quadriserialis* SOKOLOV, *S. subreticulata* NOWIŃSKI.

Blastogeny and young corallite development in all these species were similar, and morphological and biometrical differences existing, in particular species and genera at different blastogenetic stages, are less important and could be omitted in description of the general pattern of these processes. The process of extravisceral budding will be represented by the example of *Roemerolites laminatus* (NOWIŃSKI) (figs. 3C and 5A—H).

1. Preblastic stage (fig. 5A—B). — At the initial stage, in any point of the calice wall where a bud was to appear, a local swelling appeared, later transformed into a mound-like evagination, directed outwards from the calice. At the same time, the adjacent part of the visceral chamber of the parent corallite lengthened in the direction of this evagination. Meanwhile, septal spines disappeared (species of the genus *Syringopora*, *Hayasakaia multispinosa*, *Fuchungopora arctica*) or were strongly reduced (*Roemerolites laminatus*, *Tetraporinus spinosus*) on the internal surface of the evaginated part of the parent calice wall, and the tabulae (visible in successive transverse sections across the corallites) moved laterally apart. At the next stage, a small protruberance appeared in the microstructure of the evaginated parent calice wall, and then an irregularly spherical or ellipsoidal cyst (bud chamber) was formed. The bud chamber communicated with the visceral chamber of the parent calice above the wall threshold (visible in the longitudinal section through the budding calice — see fig. 3C) that separated the chambers from each

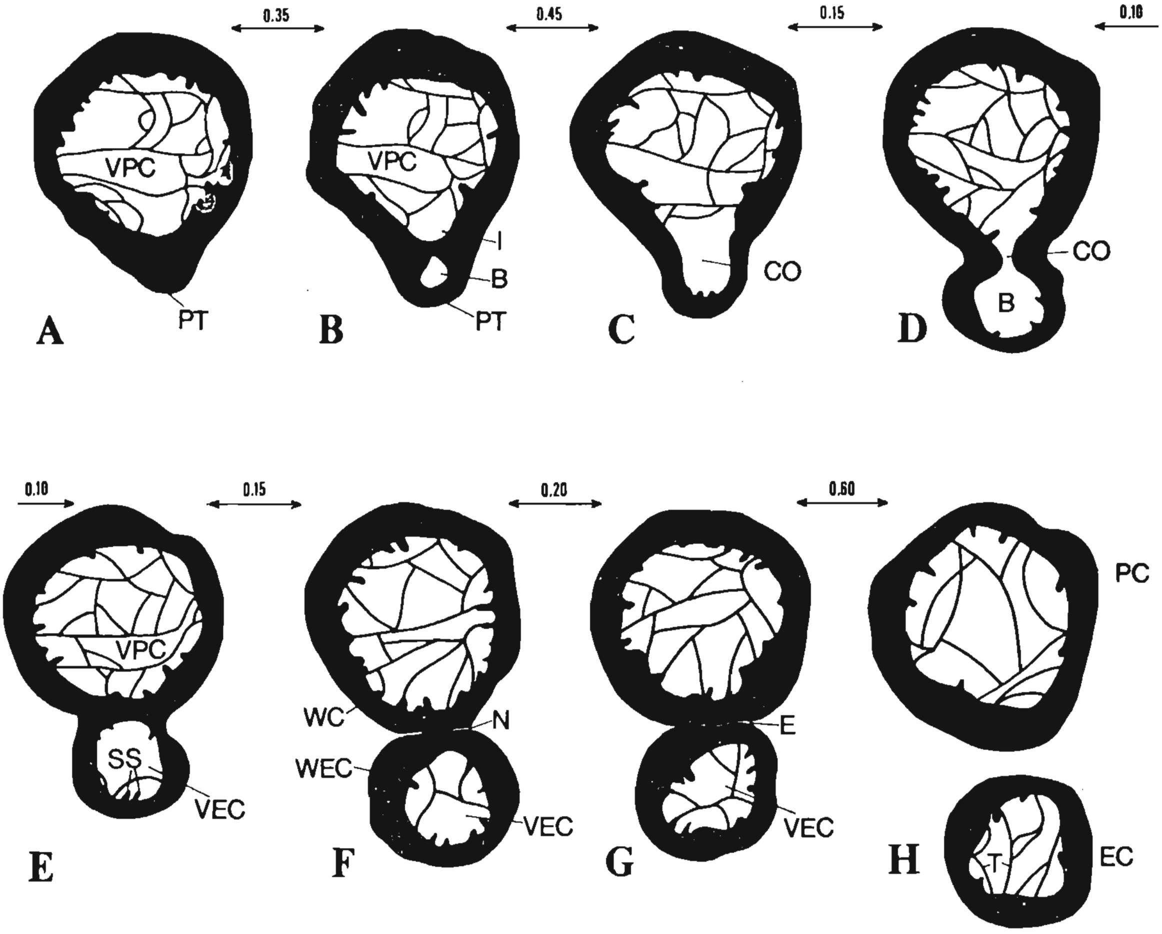

Fig. 5

Intracalicular-extravisceral budding occurring by the lateral invaginatin on the wall of a parent calice in *Roemerolites laminatus* (Nowiński), Hyrnefjellet, Coral Horizon Va_2, holotype (ZPAL T XIII/39); transverse sections, × 15. *A—B*— preblastic tage, *C—F*— hystero-nepionic stage, *G*— hystero-neanic stage, *H*— ephebic stage. For explanation of symbols see p. 8—9.

other in the horizontal plane (visible in transverse sections). In transverse sections the bud chamber is (in different studied species) irregularly round, oval, or rounded triangular (e.g. in *Hayasakaia compacta* and in species of *Tetraporinus*), and has diameters of 0.25 to 0.6 mm (see Table 4). Development in the preblastic stage occurred in a distance of ca 0.28—0.5 mm of linear corallite growth (see Table 4).

2. Hystero-nepionic stage (fig. 5C—F). — During bud development its chamber increased in size, and its horizontal connection with a visceral chamber of a parent calice widened, reaching maximum width, equal to the diameter of the opening of connecting tubes in this species. At the next stage, as a result of common building of the wall by the developing bud and the parent polyp, the horizontal junction between the bud chamber and the visceral chamber of the parent calice (visible in successive transverse sections) narrowed gradually and was eventually closed, separating both chambers and individuals. Connection between them existed only below the margin of a newly formed wall (fig. 3C). In the course of further development the wall separating both chambers in horizontal plane increased and thickened strongly, and the bud was transformed into a young polyp and its chamber into a praecorallite. The praecorallite shifted gradually away from the parent corallite and produced a wall construction

and an epitheca between itself and the parent corallite. The epitheca of the praecorallite directly adhered to the epitheca of the parent calice. In the narrowest part of the wall construction both thecae grew gradually and simultaneously on both sides towards the centre of the parent calice, up to the complete fusion into a continuous, double suture line. At this moment the praecorallite had its own wall and epitheca fully developed but it cannot be regarded as an independent individual (see fig. 3C). At the end of the hystero-nepionic stage, both individuals (as seen in transverse section, fig. 5G) touched one another only with their epithecae over a short distance. A quite similar formation of both epithecae has been observed during lateral budding in dendroidal Rugosa. In *Roemerolites laminatus* and other species of Tabulata studied, the development in the hystero-nepionic stage occurred over a distance of ca 0.3—0.55 mm of linear corallite growth (see Table 4).

3. Hystero-neanic stage (fig. 5G). — The praecorallite and a parent calice, their epithecae touching, grew side by side for a short vertical distance. Eventually the young polyp formed the first, whole (or more commonly several partial) tabulae, separating itself from the body of the parent polyp. Thus, it became a young individual, and its chamber — a young corallite. At this stage of development, young corallites show considerable similarity to mature ones. The area of transverse section amounts to 30—50% of that of parent calices (for different investigated species). At the next developmental stage, already formed young corallites separated from their parent calices, and increased in wall thickness and diameter.

At the end of the hystero-neanic stage, the young corallites already displayed most of the skeletal elements and other features typical of the genus. The sequence of development of structural elements in ontogeny roughly corresponding to the hystero-neanic stage was as follows: first, small septal spines were already formed (if present in adults) at the hystero-nepionic stage, before breaking of the horizontal communication between the bud chamber of the parent calice. First, thin tabulae appeared after the separation of the praecorallite from the parent calice with formation of its epitheca. Narrow poorly developed connecting tubes were last to appear, and formed only after the young corallites shifted away of the parent calices. The hystero-neanic stage of development corresponds to a distance of about 0.3—0.7 mm of corallite linear growth (see Table 4).

4. Ephebic stage (fig. 5H). — It is characterized by father thickening of the corallite walls, strong development of tabulae and septal spines (if they occur in parent individuals) and increase in corallite diameters. At this stage numerous connecting tubes of normal diameter (*Syringopora*, *Fuchungopora*, *Hayasakaia*, *Roemerolites*, *Tetraporinus*, *Neoroemeria*), or connecting bridges or pores (*Neoroemeria*) appeared. The connecting tubes and bridges originated either between a young corallite and the parent corallite from which the young individual budded away, or between the latter and other neighbouring young or mature corallites. At this stage the individualization of the axial canal also began (*Syringopora*, *Fuchungopora*, *Roemerolites*). The ephebic stage terminated when the young corallite attained the features diagnostic of its species especially corallite diameter, wall thickness and connecting tube diameter. The ephebic stage of development corresponds to a long section of vertical corallite growth.

SOME UNUSUAL MORPHOLOGICAL FEATURES OF THE TABULATA FROM SPITSBERGEN

Tabulata from the "Upper Treskelodden Beds" and "Wordiekammen Limestone" display several morphological features which do not occur in representatives of the same or related species and genera elsewhere, or occur only rarely. These features comprise: irregular structure of the colony, varying degree of corallite concentration in various parts of colonies, various types of connecting elements occurring in the same colony, two-layered corallite walls and others. These properties occur independently of the rhythmically repetitive changes in morphological elements of corallites related to growth periodicity (if this occurs). These features, used as diagnostic for genera, families and even orders in so called "normal" colonies, may when grouped together in the Spitsbergen colonies, introduce much chaos to the systematic of Tabulata in general.

In nearly all tabulate taxa from the "Upper Treskelodden Beds" a very variable degree of corallite concentration in colonies occurs (plates: 1: 2, 3; 2: 2, 3; 4: 3; 5: 1; 11: 1b, 2b; 12: 2; 13: 2a, b; 17: 2; 18: 1c; 19: 1, 2; 23: 2a). Within an individual colony, some corallites are localy close by crowded (corallite walls more or less closely in contact and connected by pores), and some corallites are more separated at very variable distances from one another. The loosely arranged corallites are interconnected by tubes, blades, bridges, irregular wall processes, or do not connect at all over relatively long vertical distances.

These aggregations of more loosely or closely arranged corallites vary in size and shape and do not display any regularity in their spatial distribution within a colony. They occur on different levels in both peripheral and central parts of the colony. Moreover, the variable degree of corallite concentration is directly related to changes in their morphology. In one colony, in zones of close crowding, the corallites are more or less prismatic, polygonal or rounded polygonal in transverse sections, while in less crowded they are tubular, or rounded or, more frequently, irregularly oval in transverse sections. In the Tabulata from Spitsbergen these morphological properties occur both in colonies of the genera for which this type of corallite distribution is considered diagnostic (*Roemerolites*, many species of *Roemeripora*) and in colonies of the genera known for their loose, dendroid arrangement of corallites (*Syringopora*, *Multithecopora*, *Tetraporinus*, *Hayasakaia* and others). Deviations in the relative regularity in the distances between corallites (or lack of separation) occur to some extent in almost all the genera of Tabulata which form dendroid colonies, and in many genera of close colony structure, but in the colonies from Spitsbergen these perturbations are exceptionally strongly manifested.

For this reason some features used as diagnostic for a species, such as distances between corallites (expressed quantitatively), or features considered diagnostic for a genus — such as the contacting of corallite walls or not (which is closely related to the rounded or polygonal outlines of their tranverse sections), or finally, the occurrence of connecting tubes, blades, bridges or pores, are invalidated for a majority of species and genera of Tabulata from the "Upper Treskelodden Beds" and "Wordiekammen Limestone". Variable corallite spacing similar to that in colonies of the Tabulata from Spitsbergen, is best known in *Neoroemeria* RADUGIN. This has resulted in some difficulties in determining the taxonomic position of this genus, even to it being included in different orders of Tabulata by different authors (RADUGIN 1938; SOKOLOV 1955, 1962; TCHUDINOVA 1964; CHEKHOVICH 1960; HILL and JELL 1970; HILL 1981; see also p. 00). However, in contrast to the species from Spitsbergen (*Neoroemeria spitsbergensis* sp. n. and *N. permica* sp. n.), colonies of *Neoroemeria* species known from Europe and Asia have two clearly distinct zones of corallite crowding. In the axial part of a colony, polygonal corallites connected by pores, adjoin one another closely, while in the peripheral zone corallites of rounded transverse sections, connected by regularly blades, processes or canals, are loosely distributed.

The varying degree of corallite crowding (massiveness) of the colonies of Tabulata from Spitsbergen is accompanied by significant changes in corallite wall thickness (plates: 3: 3; 5: 3; 12: 2; 13: 1; 20: 1a), changes in the vertical distances between connecting elements, and a great variability in corallite diameters. These morphological differences within one colony are sometimes so significant that neighbouring zones of different corallite spacing seem to belong to different species, sometimes even to different genera.

The above presented skeletal features peculiar to colonies of Tabulata from Spitsbergen are difficult to explain, and even more so because colonies from particular Coral Horizons are redeposited, and do not represent original life assemblages. Perhaps particular populations of tabulate corals, and associated fauna, inhabited strongly and irregularly changing local environments, for example with changing water circulation and supply of terrigenous material from land. The presence of numerous non skeletal commensals cannot be excluded. Their traces, however, have not been found. Rather stable growth periodicity also contradicts such a hypothesis.

A two-layered wall structure occurs very often in the studied colonies of Tabulata, especially in species of *Roemerolites* and *Multithecopora*. The inner layer of stereoplasm of the wall, directly surrounding the visceral chamber of the corallite, has fibro-normal microstructure, and the outer layer — lamellar, typical of *Syringopora*, *Multithecopora* and *Roemerolites* (fig. 15). The two layered structure of stereoplasm in the wall of corallites in Tabulata (except in representatives of the suborder Thamnoporina) occurs rarely and only in some dendroid colonies of the orders Syringoporida and Auloporida. The two-layered corallite wall was described among others in *Roemerolites novellus* (TCHUDINOVA) (= *Armalites novellus* TCHUDINOVA), *R. venustus* (TCHUDINOVA) (= *Armalites venustus* TCHUDINOVA) and *Grabaulites annexus* TCHUDINOVA — from the Eifelian of the Kuznetsk Basin (TCHUDINOVA 1964), and in *Sinopora polonica* NOWIŃSKI, from the Upper Visean of the Holy Cross (Świętokrzyskie) Mountains (NOWIŃSKI 1976). The origin of the double wall in corallites of Tabulata has not been hitherto explained. In the author's opinion, this phenomenon could possibly be related to secondary stereoplasmic thickening of corallite walls. The secondary (inner) layer of stereoplasm in the corallite wall in Tabulata of Spitsbergen, could be preserved in a form different from the structure of the original wall, resulting eventually in the secondary, fibrous structure. Regardless of the occurrence of two-layered structure, the corallite wall thickness in most of the studied Tabulata species is generally slightly greater than in the same or related species in Europe and Asia.

SYSTEMATIC PART

Order **Favositida** SOKOLOV, 1962
Suborder **Favositina** SOKOLOV, 1950
Family **Syringolitidae** WAAGEN et WENTZEL, 1886
Genus *Roemeripora* KRAICZ, 1934

Type species: Roemeria bohemica POČTA in BARRANDE, 1902 [= *Roemeripora bohemica* (POČTA) in KRAICZ, 1934]

Diagnosis. — See MIRONOVA 1974.

It should be added that in many species of *Roemeripora* (especially in Permo-Carboniferous ones) the corallite walls are very thin, and septal spines poorly developed or absent.

Remarks. — *Roemeripora* has been characterized and compared with related genera by: SOKOLOV (1955, 1962), DUBATOLOV (1959), VASSILJUK (1960), HILL and JELL (1970). HILL and JELL (1970) regard the following genera as synonymous with *Roemeripora* KRAICZ: *Vaughanites* PAUL 1937, *Bayhaium* LANGENHEIM and MC CUTHEON 1959, *Roemerolites* DUBATOLOV

1963, *Armalites* Tchudinova 1964, *Neoroemeria* Radugin 1938, *Pseudoroemeria* Chekhovich 1960, *Pseudoroemeripora* Koksharska 1965. Representatives of *Vaughanites* and *Bayhaium* are not well known to the author. The present studies demonstrate that *Roemerolites* Dubatolov is synonymous with *Armalites* Tchudinova (see also p. 49), and *Neoroemeria* Radugin is a separate genus belonging to the order *Syringoporida* (see also p. 64), *Pseudoroemeria* Chekhovich and *Pseudoroemeripora* Koksharska (with the present knowledge of their morphology) should be considered as separate genera within the family *Syringolitidae*.

So far eighteen species of *Roemeripora* from the Lower Devonian through the Lower Permian have been described.

Occurrence. — Lower Devonian: Czechoslovakia, USSR (Altai), Australia (Victoria, New South Wales), New Zealand; Lower through Middle Devonian: USSR (Salair), Australia (Queensland), Viet-Nam; Middle Devonian: USSR (Kuznetsk Basin); Lower Carboniferous: France, USSR (Donetsk Basin, Novaya Zemlya), China; Middle Carboniferous: USSR (South Ural, Novaya Zemlya); Upper Carboniferous through Lower Permian; Spitsbergen (Isfjorden, Hornsund); Permian: Canadian Arctic Archipelago.

Roemeripora wimani Heritsch, 1939

(pl. 1: 1—3; pl. 2: 1—3; pl. 3: 1—3; figs. 6A, B)

1939. *Roemeripora wimani* Heritsch; Heritsch: 109—116, pl. 8: 4, pl. 4, 5, pl. 21: 1—3.
1960. *Roemeripora wimani* Heritsch; Harker: 48—49, pl. 14: 6, 7.
1967. *Roemeripora wimani wimani* Heritsch; Fedorowski: 38—39, pl. 7: 1; fig. 20.

Diagnosis. — Corallites long, prismatic, 2.3—2.6 mm in diameter. Corallite walls 0.05—0.1 mm thick. Connecting pores 0.2—0.3 mm in diameter, with spaces of 2.5—3.5 mm. Tabulae very numerous, thin, densely spaced, bent, and funnel-shaped, in the peripheral zone of corallite form two or three layer vesicular tissue. Septal structures absent. Small spines present only on tabulae.

Material. — Large fragments of twenty five well-preserved colonies: ZPAL T XIII/1—20, 29—33 from Treskelen, Hyrnefjellet and Urnetoppen. 1. Treskelen: Nos. 1—6 in the Ia Coral Horizon, Creek IV. Nos. 7—13 in the Ib Coral Horizon, Creek IV. No. 14 in the II Coral Horizon, Creek IV. Nos. 15—17 in the IVb Coral Horizon, Creek II. Nos. 18, 19 in the Va Coral Horizon, Creek IV. Nos. 20, 29, 30 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: Nos. 31, 23 in the Va_1 Coral Horizon. 3. Urnetoppen: No. 33 in the III Coral Horizon.

Eighty nine transverse and longitudinal sections have been made as well as eight series of acetate peels for budding examinations.

Description. — Massive, platy and irregular colonies of various size, 20 cm — 2.5 m in diameter, with surfaces often eroded. Corallites very long, prismatic, straight, arranged in parallel, perpendicular to the surface of colony. In central parts of the colonies the corallites closely adhere to each other. In peripheral zones of colonies they are often arranged loosely and some of the walls are free. In transverse sections corallites polygonal (penta-, hexagonal) with diameters 2.0—2.8 mm, most commonly 2.3—2.6 mm. Corallite walls very thin, most often 0.05—0.1 mm, of fibro-normal microstructure. Median suture dark, thin, distinct. Connecting pores round, 0.2—0.3 mm in diameter, arranged in vertical rows at corallite angles or close to them, with vertical spaces of 2.5—3.5 mm. Occasionally the connecting pores widen into canals. Tabulae very numerous, thin, densely packed, bent, funnel-shaped, often incomplete, in the peripheral zone of corallites they form two-or three-layer vesicular tissue. Around pores and connecting canals, the tabulae form bunches characteristic of the genus *Roemeripora*. Axial canal indistinct, short, narrow. Septal structures absent. Spines very sparce, short, triangular, present on the tabulae. Vegetative reproduction by calicular, intravisceral budding. The bud appeared in any corner of the parent calice, within the visceral chamber.

Remarks. — The specimens discussed do not differ from the holotype, described from the Central Spitsbergen considered by HERITSCH (1939) to be of Upper Carboniferous age. Colonies from the "Upper Treskelodden Beds" have slightly smaller corallite diameters.

Roemeripora wimani differs from all species of the genus known so far in exceptionally large colonies, up to 2.5 m on diameter. The species shows certain similarities to *R. aisenvergi* VASSILJUK, *R. clara* KATCHANOV and *R. salairica* MIRONOVA.

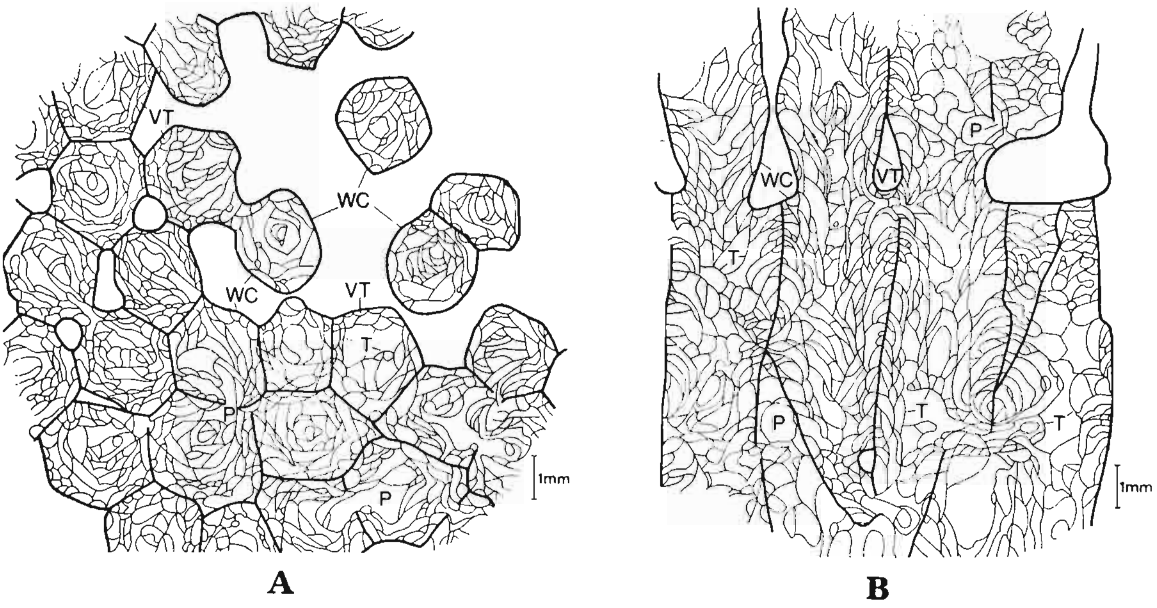

Fig. 6

Roemeripora wimani Heritsch, Treskelen, Coral Horizon IVb, Creek II, (ZPAL T XIII/16); *A* transverse section, × 6, longitudinal section, × 6. For explanation of symbols see p. 8—9.

R. wimani is close to *R. aisenvergi* from the Lower Carboniferous of Donetsk Basin (VASSILJUK 1960*a*, 1966) in lack of septal spines on corallites walls, sparse connecting pores as well as in indistinct axial canals. On the other hand it differs in much smaller diameters of corallites, much thinner corallite walls, better developed vesicular tissue of tabulae as well as in the presence of septal spines on the tabulae.

R. wimani is similar to *R. clara* from the Upper Visean of South Urals (KATCHANOV 1964) in the arrangement of corallites in the colony, diameters of connecting pores, shape and spacing of tabulae and the presence of septal spines on tabulae. It differs from the species in having smaller corallite diameters, smaller spaces between connecting pores, and in lacking both a distinct axial canal and septal spines on corallite walls.

It is close to *R. salairica* from the Lower Devonian of Salair (MIRONOVA 1974) in corallite diameters, sparse connecting pores with similar diameters as well as in morphology and arrangement of tabulae. It differs in having thinner corallite walls, and lacking both septal spines on corallite walls and a distinct axial canal.

Occurrence. — Upper Carboniferous through Lower Permian: Spitsbergen (Hornsund, Isfjorden); Permian: Canadian Arctic Archipelago (Grinnell Peninsula).

Roemeripora minor HERITSCH, 1939
(pl. 4: 1a, b, 2, 3; pl. 5: 1; figs. 7A, B)

1939. *Roemeripora wimani minor* HERITSCH; Heritsch: 116—117, pl. 15: 11.
1967. *Roemeripora wimani minor* HERITSCH; Fedorowski: 39, pl. 7: 2, 3.

Diagnosis. — Corallites long, prismatic, 1.5—2.2 mm in diameter, most often 1.8—2.0 mm. Corallite walls 0.05—0.1 mm thick. Connecting pores 0.2—0.25 mm in diameter, spaced every 2.0—3.0 mm. Tabulae numerous, very densely packed, forming two-layer, vesicular tissue at the corallite walls. Septal spines absent.

Material. — Large fragments of nine well-preserved colonies: ZPAL T XIII/34—38, 54—57 from Treskelen, Hyrnefjellet and Kruseryggen. 1. Treskelen: No. 34 in the Ib Coral Horizon, Creek IV; No. 35 in the II Coral Horizon, Creek IV; No. 36 in the Va Coral Horizon, Creek IV; Nos. 37, 38 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: Nos. 54—56 in the Va_{2-3} Coral Horizon. 3. Kruseryggen: No. 57 in the Coral Horizon V.

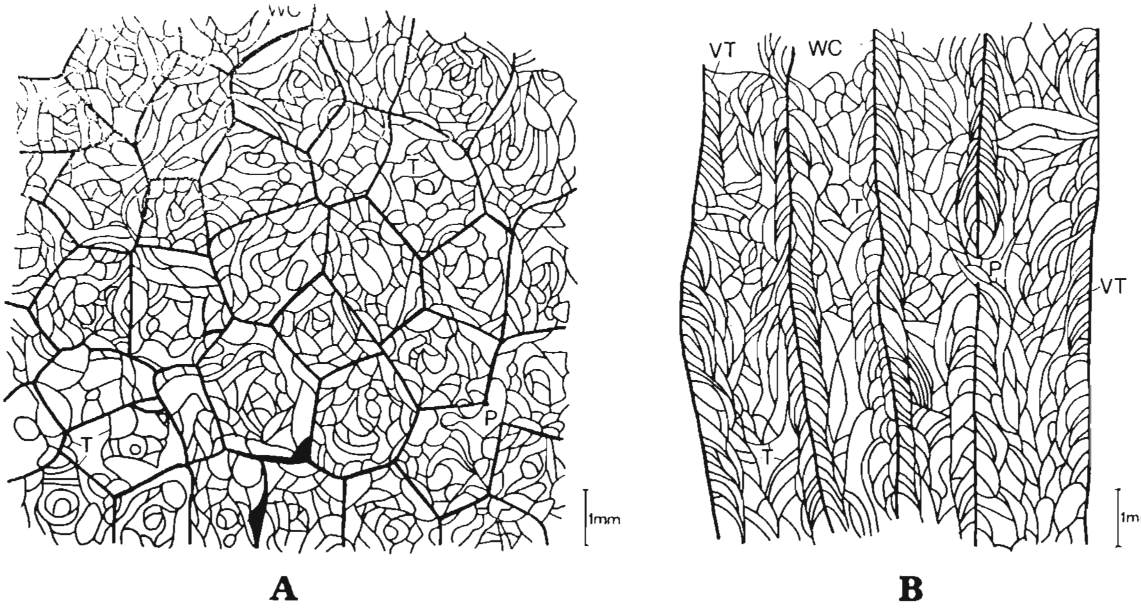

Fig. 7

Roemeripora minor Heritsch, Hyrnefjellet, Coral Horizon Va_3 (ZPAL T XIII/55); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Thirty one transverse and longitudinal sections have been made as well as two series of imprints on celluloid film for the study of budding.

Description. — Massive large, platy colonies from 15 cm to 2 m in diameter and up to 60 cm in height. Corallites long, straight, more or less prismatic, perpendicular to the colony surface. Corallites less crowded than in *R. wimani* and, in general, are not in contact with each other with all their walls. In transverse sections the corallites in less crowded parts of colonies are polygonal with rounded angles and oval, and in the more crowded parts of colonies — polygonal (penta-, heptagonal). They are 1.5—2.2 mm in diameter, most often 1.8—2.0 mm. Corallite walls thin, 0.05—0.15 mm, most often about 0.1 mm, with fibro-normal microstructure. Median suture thin, dark, distinct. Connecting pores numerous, round, ca. 0.3 mm in diameter, arranged irregularly at or near corallite angles, with vertical spaces of 1.0—3.0 mm. Occasionally the pores widen into connecting canals. Tabulae very numerous, thin, strongly crowded, bent, in the central parts of corallites funnel-shaped, in the peripheral zones of corallites they form a two-layer vesicular tissue. Around the pores and connecting canals tabulae form bunches. Axial canal indistinct. Septal spines absent from both tabulae and corallite walls. Vegetative reproduction as in *R. wimani*, by calicular and intravisceral budding.

Remarks. — *Roemeripora minor* differs from *R. wimani* in having more rounded corallites in transverse sections and more loosely spaced corallites with smaller diameters, slightly thicker corallite walls and more numerous connecting pores of smaller diameters. From colonies of the same species, described from the Permo-Carboniferous of Isfjorden area (HERITSCH 1939) and from the Lower Permian of Hornsund area (FEDOROWSKI 1967) it differs only in the lack of spines both on tabulae and corallite walls.

Occurrence. — Upper Carboniferous through Lower Permian: Central Spitsbergen (Isfjorden, Hornsund).

Roemeripora media sp. n.

(pl 5: 3; pl. 6: 1a, b; figs. 8A, B)

Holotype: Specimen ZPAL T XIII/62; pl. 5: 2; pl. 6: 1; figs. 8A, B.

Type horizon: Vth Coral Horizon, "Upper Treskelodden Beds", Lower Permian.

Type locality: Treskelen, Creek IV, Hornsund, Spitsbergen.

Derivation of the name: Lat. *medius* — diameters, media — size of corallite intermediate between *R. wimani* and *R. minor*.

Diagnosis. — Corallites long, prismatic, 2.0—2.3 mm in diameter. Corallite walls 0.05—0.1 mm thick. Connecting pores 0.2—0.3 mm in diameter with vertical spaces of 1.3—2.5 mm. Tabulae thin or thickened, not very numerous, of irregular morphology, form a single-layer vesicular tissue at corallite walls. Septal spines absent.

Material. — Large fragments of seven colonies: ZPAL T XIII/58—64 from Treskelen, Creek IV. No. 58 in the Ia Coral Horizon; Nos. 59—62 in the Va Coral Horizon and Nos. 63, 64 in the Vc Coral Horizon. Twenty seven transverse and longitudinal sections have been made as well as one series of imprints on celluloid film for the study of vegetative reproduction.

Description. — Large, massive colonies, 20 cm (plano-convex colonies) to 1 m in diameter (platy colonies) and up to 60 cm in height. Corallites long, straight, prismatic, perpendicular to the surface of colony. Corallites are in close contact with each other with all their walls, in both central and peripheral parts of colonies. In transverse sections corallites irregularly polygonal (penta- hexagonal) with sharp angles, 1.8—2.5 mm in diameter, most often 2.0—2.3 mm. Corallite walls thin, 0.05—0.1 mm, with indistinct fibro-normal microstructure. Median suture dark, continuous, thick. Connecting pores numerous, 0.2—0.3 mm in diameter, occur mainly near corallite angles, rarely in the middle of walls. They are spaced irregularly in vertical rows of 1.3—2.5 mm. The pores often widen into connecting canals with diameters up to 0.5 mm. Tabulae not very numerous, thin or secondarily thickened form a single vesicular layer at corallite walls. The central parts of corallites are filled with tabulae of irregular morphology, bent, funnel-shaped, concave and convex, sometimes horizontal. In longitudinal sections of colonies one can see zones of densely packed and sparse tabulae, occurring at the same levels in adjoining corallites, which form a pseudo-layered colony structure (growth periodicity phenomenon — see p. 22). In the zones with sparse tabulae, the corallites, especially in transverse sections, resemble colonies from the genus *Roemeria*. Axial canal absent. Septal spines not observed. Vegetative reproduction, as in the species described, through calicular intravisceral budding.

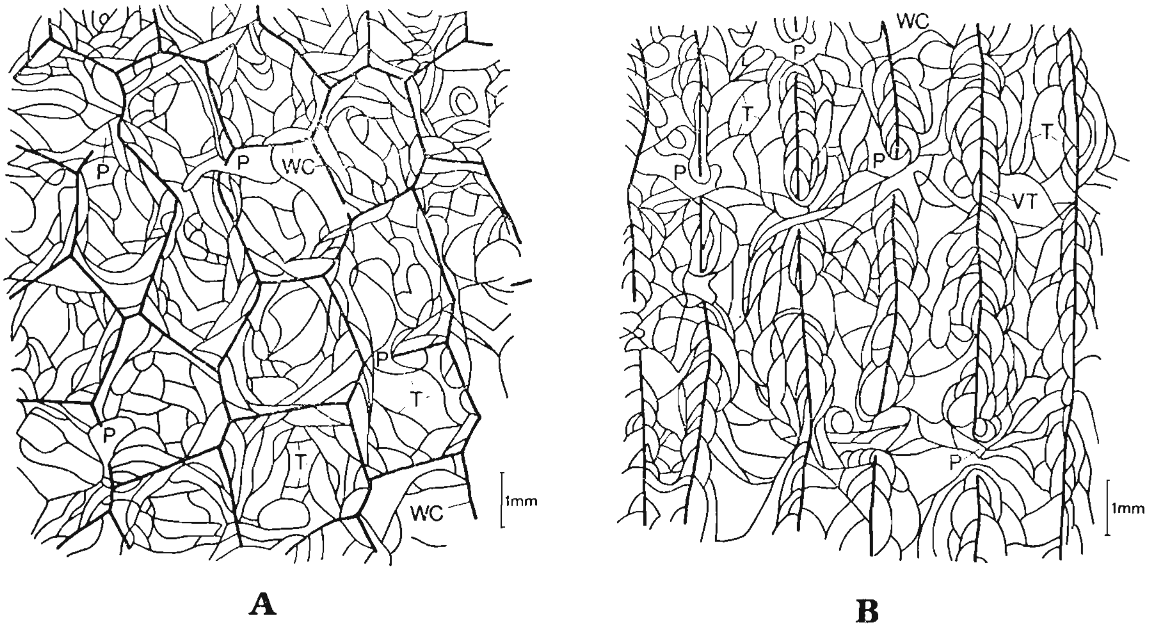

Fig. 8

Roemeripora media sp. n., Treskelen, Coral Horizon Va, Creek IV, holotype (ZPAL T XIII/62); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Remarks. — *Roemeripora media* sp. n. differs from both species described above in having prismatic corallites, in a close contact with each other in both central and peripheral parts of the colony, less densely packed tabulae, which form unilamellar vesicular tissue near corallite walls and thick epitheca. It differs also in having connecting pores outside of corallite corners, and in the absence of an axial canal. Moreover, it differs from *R. wimani* in having smaller corallite diameters, narrower spaces between connecting pores and in lacking of septal spines. From *R. minor* it differs in having larger corallite diameters as well as pores of slightly smaller diameters and smaller spaces between the pores.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Roemeripora aspinosa Nowiński, 1982

(pl. 7: 1)

1982. *Roemeripora aspinosa* Nowiński; Nowiński: 87—88, pl. 30: 1, 2; figs. 2A, B.

Diagnosis, description, remarks and **illustrations** — see Nowiński 1982.

Material. — Eight almost complete, well-preserved colonies: ZPAL T XIII/21—28 from Treskelen and Hyrnefjellet. 1. Treskelen: Nos. 24, 25 in the Va Coral Horizon, Creek IV and Nos. 26—28 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: Nos. 21 (holotype), 22, 23 in the Vb_1 Coral Horizon.

Thirty four transverse and longitudinal sections have been made as well as two series of imprints on celluloid film for the study of budding.

Remarks. — Growth periodicity of the skeleton in colonies of *Roemeripora aspinosa* s. poorly visible and expressed only in rhythmic changes of spacing and morphology of tabulae. The thickness of annual growth bands is from 4.0 to 13 mm (see Table III). Vegetative reproduction in this species was through calicular intravisceral budding (see p. 28 and Table 4).

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Roemeripora hornsundensis sp. n.

(pl. 6: 2a, b; figs. 9A, B)

Holotype: Specimen ZPAL T XIII/68; pl. 6: 2a, b.
Type horizon: Ib Coral Horizon, Upper Treskelodden Beds, Lower Permian.
Type locality: Treskelen, Creek IV, Hornsund, Spitsbergen.
Derivation of the name: hornsundensis — coming from the vicinity of Hornsund Fjord in Spitsbergen.

Diagnosis. — Corallites long, cylindrical, 0.1—0.5 mm distant from each other. In transverse sections corallites regularly round, 2.0—2.4 mm in diameter. Corallites walls 0.15—0.25 mm thick. Connecting pores sparse, 0.3—0.5 mm in diameter, pass into connecting canals and continue as an axial canal. Spaces between the pores 3.0—4.5 mm. Tabulae numerous, thin, funnel-shaped, form a one-or two-layer vesicular zone at corallite walls. No septal spines.

Material. — Six almost complete colonies: ZPAL T XIII/65—70 from Treskelen. Nos. 65—69 in the Ib Coral Horizon, Creek IV and No. 70 in the II Coral Horizon, Creek IV. Eighteen transverse and longitudinal sections have been made as well as two series of imprints on celluloid film for the study of budding.

Description. — Small, hemispherical and discoidal colonies, up to 80 mm in diameter and up to 50 mm in height. Corallites long, cylindrical, straight or slightly bent, spaced irregularly every 0.1—0.5 mm, or partly in contact with each other, arranged perpendicularly to the colony surface. In transverse sections corallites regularly round or suboval, in the zones where individuals are most densely packed — irregularly round or slightly polygonal. Their diameters are 1.8—2.5 mm, most often 2.0—2.4 mm. Calices deep, conical. Corallite walls vary in thickness from 0.1—0.3 mm, most often 0.15—0.25 mm, of indistinct, fibro-normal microstructure. Median suture and epitheca thin, dark. Connecting pores sparse, large, round, 0.3—0.5 mm in diameter, passing into connecting canals, which continue as an axial canal. Pores arranged irregularly in vertical rows, with spaces of 3.0—4.5 mm. Tabulae numerous,

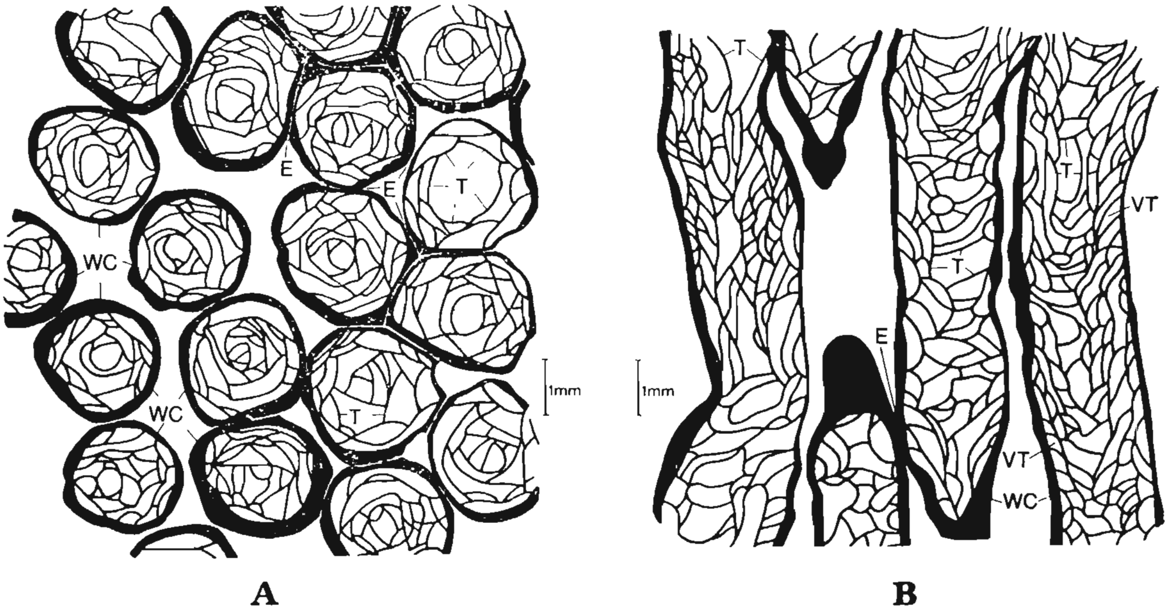

Fig. 9

Roemeripora hornsundensis sp. n., Treskelen, Coral Horizon Ib, Creek IV (ZPAL T XIII/67); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

thin, bent, strongly funnel-shaped, form one-or two-layer vesicular tissue at corallite walls. Axial canal most often situated centrally, wide, 0.3—0.6 mm in diameter, discontinuous, generally without tabulae. No septal spines. Vegetative reproduction as in *R. wimani.*

Remarks. — *Roemeripora hornsundensis* sp. n. most resembles *R. arctica* SMIRNOVA from the Visean and Namurian of Novaya Zemlya (SMIRNOVA 1957). There is a similarity in size and habit of colonies as well as in the presence of cylindrical (instead of prismatic) corallites, which in *R. arctica* occur only in some parts of colonies. Most of the corallites are distinctly prismatic in *R. arctica.* The new species differs from *R. arctica* in having larger corallite diameters, thicker corallite walls, sparse connecting pores, strongly funnel-shaped tabulae, the presence of an axial canal and a lack of septal spines.

From *R. wimani* HERITSCH, *R. minor* HERITSCH and *R. media* sp. n. (with similar arrangement and morphology of tabulae) the new species differs in having small, hemispherical colonies, smaller diameter cylindrical (instead of prismatic) corallites as well as in the presence of well-developed axial canals.

The new species is close to *R. progenitor* (CHAPMAN) from the Lower and Middle Devonian of Australia and New Zealand (CHAPMAN 1921; HILL 1950; 1955; HILL, PLAYFORD and WOODS 1967; HILL and JELL 1970) only in the presence of connecting pores-canals, passing into axial canals.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Order **Syringoporida** SOKOLOV, 1962
Family **Syringoporidae** NICHOLSON, 1897
Genus *Syringopora* GOLDFUSS, 1826

Type species: Syringopora ramulosa GOLDFUSS, 1826.

Diagnosis. — See TCHUDINOVA, 1971.

Occurrence. — Upper Ordovician: USSR (Ural); Silurian: Baltic Region, USSR (Podolia, Siberia); Wenlockian: Sweden (Gotland); Wenlockian through Ludlovian: Norway; Silurian through Carboniferous: USSR (Urals, Kuznetsk Basin, Kazakhstan, Kolyma Basin), Central Asia; Devonian: USSR (East-European Platform, Transcaucasia); Carboniferous: USSR (Moscow and Donetsk Basins, Novaya Zemlya), China, Viet-Nam; Lower Permian: USSR (Urals, Timan); Silurian through Carboniferous: Eastern and Western Europe, South and North America, China, Southeastern Asia, Australia; Upper Carboniferous through Lower Permian: Spitsbergen.

Syringopora quadriserialis SOKOLOV, 1950
(pl. 7: 2a, b, 3; pl. 8: 1, 2)

1950. *Syringopora quadriserialis* SOKOLOV; Sokolov: 25—27, pl. 2: 1—4.

Diagnosis. — See SOKOLOV, 1950.

Material. — Twelve almost complete, poorly preserved colonies: ZPAL T XIII/71—82 from Treskelen, Hyrnefjellet and Urnetoppen. 1. Treskelen: Nos. 71—78 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: Nos. 79 and 80 in the Va_3 Coral Horizon and No. 81 in the Vb_1 Coral Horizon. 3. Urnetoppen: No. 82 in the V Coral Horizon.

Fifty six transverse and longitudinal sections have been made as well as a number of serial sections to study the colony development.

Description. — Irregularly spherical and oval, sometimes hemisphaerical, dendroid colonies up to 150 mm in diameter. Corallites long, straight or slightly bent, arranged in parallel or radially with regular spaces of 0.1—1.0 mm, most often 0.2—0.6 mm. In some parts of the colony corallites walls are partly in contact, forming local crowded zones. Calices with sharp margins, deep, often with large septal spines. Corallites in transverse sections irregularly round, oval or slightly triangular, in the crowded zones polygonal, with rounded angles. Corallite diameters variable from 1.3—2.0 mm, most often 1.5—1.8 mm. Corallite walls 0.1—0.4 mm thick, most often 0.2—0.3 mm. Skeleton microstructure lamellar, poorly visible. Epitheca poorly marked. Connecting tubes numerous, short, 0.4—0.5 mm in diameter, irregularly arranged in four vertical rows with spaces of 1.4—2.0 mm, sometimes even 0.8 mm. In the case of corallites partially in contact the tubes pass into connecting canals with inner diameters of 0.1—0.2 mm. Both connecting tubes and canals often occur at one level in adjacent corallites. Tabulae numerous, thin, long, funnel-shaped, strongly oblique, localy form a short and wide axial canal. Septal spines very numerous, long (up to one-third of corallite diameter), thin and sharp, arranged slightly obliquely to corallite walls and directed distally towards the calice. Septal spines often pierce tabulae and reach the axial canal. Isolated spines occur also on tabulae.

Remarks. — *Syringopora quadriserialis* from the Hornsund area differs from the same species described from the Visean of the Ukraine (SOKOLOV 1950) in having considerably larger colonies, greater variability of corallite diameters, corallites arranged at smaller distances from each other as well as thinner corallite walls.

The corallite interior structures of this species resemble those of *S. conferta* KEYSERLING from the Lower Carboniferous of Novaya Zemlya and the Urals (KEYSERLING 1846; STUCKENBERG 1895; IVANOV 1938; GORSKY 1935; VASSILJUK 1950, 1960), *S. gracilis* KEYSERLING from the Lower Carboniferous of the USSR, Novaya Zemlya and China (KEYSERLING 1846; EICHWALD 1861; STUCKENBERG 1895, 1904; IVANOV 1938; CHI 1933; GORSKY 1935; VASSILJUK 1950) and *S. hoffmani* STUCKENBERG from the Lower Carboniferous of the Urals (STUCKENBERG 1895). It differs, however, from these species in having much smaller corallite diameters.

From *S. reticulata* it differs in having numerous, more densely packed connecting tubes and better developed septal apparatus.

Occurrence. — Visean: USSR (Ukraine); Lower Permian: Spitsbergen (Hornsund).

Syringopora subreticulata NOWIŃSKI, 1976

(pl. 8: 3a, b; pl. 9: 1, 2)

1976. *Syringopora subreticulata* NOWIŃSKI; Nowiński, 89—91, pl. 19: 3, figs. 21A, B.

Revised diagnosis. — Corallites cylindrical, 1.3—1.8 mm in diameter, arranged with spaces of 0.1—0.8 mm. Corallite walls 0.2—0.35 mm thick. Connecting tubes numerous, 0.5—0.7 mm in diameter, with spaces of 1.0—2.5 mm. Tabulae funnel-shaped, numerous. Axial canal straight, with variable diameter. Septal spines very numerous on tabulae and walls.

Material. — Seven almost complete, well-preserved colonies: ZPAL T XIII/83—89 from Treskelen and Hyrnefjellet. 1. Treskelen: Nos. 83 and 84 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: No. 85 in the Va_4 coral Horizon and Nos. 86—89 in the Vb_1 Coral Horizon.

Thirty six transverse and longitudinal sections have been made as well as a number of serial sections to study colony development.

Description. — Colonies large, dendroid, irregularly oval, sometimes flat and encrusting, up to 250 mm in diameter. Corallites long, cylindrical, straight or slightly bent, arranged in parallel or radially with spaces of 0.1—1.0 mm, most often 0.2—0.5 mm. Occasionally they form small, local assemblages of individuals in contact with their walls. In transverse sections corallites irregularly round, oval, sometimes slightly triangular, 1.0—2.0 mm in diameter, most often 1.3—1.8 mm. Calices deep, conical, with sharp edges. Corallite walls 0.1—0.35 mm thick, most often 0.2—0.3 mm with lameller microstructure, locally secondarily changed into fibro-normal. Epitheca thin. Connecting tubes numerous, well developed, 0.4—0.8 mm in diameter, most often 0.5—0.6 mm, arranged with vertical spaces of 1.0—2.5 mm, in the adjacent corallites often occurring at the same level. Tabulae numerous, funnel-shaped, thin or secondarily thickened due to recrystallisation, sometimes straight and strongly oblique, locally form a thin vesicular zone at corallite walls. Straight, horizontal or slightly oblique tabulae occur also in the axial canal. Axial canal in places well developed, 0.2—0.4 mm in diameter. Septal spines very numerous, long, thick, densely arranged in vertical rows, often pierce the tabulae. Spines occur on tabulae as well.

Remarks. — *Syringopora subreticulata* from Hornsund vicinity differs from specimens of the Middle Visean of Poland (Nowiński 1976) in having larger colonies, slightly smaller diameters of corallites, thicker walls, more densely packed connecting tubes and better developed septal apparatus.

Comparison with closely related species such as: *S. reticulata* Goldfuss, *S. parallela* (Fischer von Waldheim), *S. permiana* Stuckenberg, *S. uralica* Stuckenberg (Fischer von Waldheim 1828; Stuckenberg 1895; Chi 1933) — see Nowiński 1976 (p. 90—91).

Occurrence. — Visean: Poland (Cracow Region); Lower Permian: Spitsbergen (Hornsund).

Syringopora cf. *reticulata* Goldfuss, 1826

(pl. 9: 3a, b, 4)

1826. *Syringopora reticulata* Goldfuss; Goldfuss: 76, pl. 26: 6.
1933. *Syringopora* cf. *reticulata* Goldfuss; Chi: 8—10, pl. 1: 1, 2a, b.

Material. — Large fragments of two poorly preserved colonies: ZPAL T XIII/90, 91 from Treskelen: No. 90 in the Vc Coral Horizon, Creek IV and No. 91 in the Vb Coral Horizon, Creek IV.

Ten transverse and longitudinal sections have been made.

Description. — Hemispherical or irregularly oval, dendroid colonies, up to 150 mm in diameter. Corallites tube-like, short, slightly bent, arranged in parallel or radially, with irregular spaces of 0.1—0.8 mm, or in contact. In transverse sections corallites irregularly oval, elongate, slightly triangular or quadrangular in outline, rarely round, 1.3—2.0 mm in diameter, most often 1.5—1.8 mm. Calices shallow, with sharp margins, funnel-shaped. Corallite walls 0.2—0.3 mm thick with undiscernible microstructure. Epitheca not isolated. Connecting tubes scarce, short, thick, 0.4—0.7 mm in diameter, with irregular spaces of 1.5—2.5 mm, locally more closely spaced vertically and often situated at the same level in adjoining corallites. Tabulae numerous, thin or secondarily thickened, long, strongly funnel-shaped. Axial canal not isolated. Septal spines numerous, thick, long, arranged in about a dozen vertical rows. Spines occur also on tabulae.

Remarks. — Due to the poor preservation state of the specimens it is impossible to determine the species. *Syringopora* cf. *reticulata* from Treskelen is most similar to *S.* cf. *reticulata* from the Lower Carboniferous of China (Chi 1933), from which it differs in having shorter corallites, wider spaces between them, narrower spaces between the connecting tubes as well as no isolated axial canal. From *S. reticulata* Goldfuss it differs in having slightly longer corallite diameters, much smaller spaces between the connecting tubes and in lacking an axial canal.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Syringopora stuckenbergi sp. n.

(pl. 10: 1a, b; figs. 10A, b)

Holotype: Specimen ZPAL T XIII/92; pl. 10: 1a, b.
Type horizon: Vc Coral Horizon, "Upper Treskelodden Beds", Lower Permian.
Type locality: Treskelen, Creek IV, Hornsund, Spitsbergen.
Derivation of the name: stuckenbergi — in honour of A. A. STUCKENBERG.

Diagnosis. — Corallites short, tube-like, with spaces of 0.2—0.7 mm, or in contact, 1.4—2.2 mm in diameter, most often 1.6—2.0 mm. Corallite walls 0.2—0.4 mm thick. Connecting tubes short, numerous, 0.3—0.5 mm in diameter, with spaces of 0.7—1.0 mm. Tabulae numerous, funnel-shaped and oblique. Axial canal short, rarely present. Septal spines very numerous, long, thick. Spines also occur on tabulae.

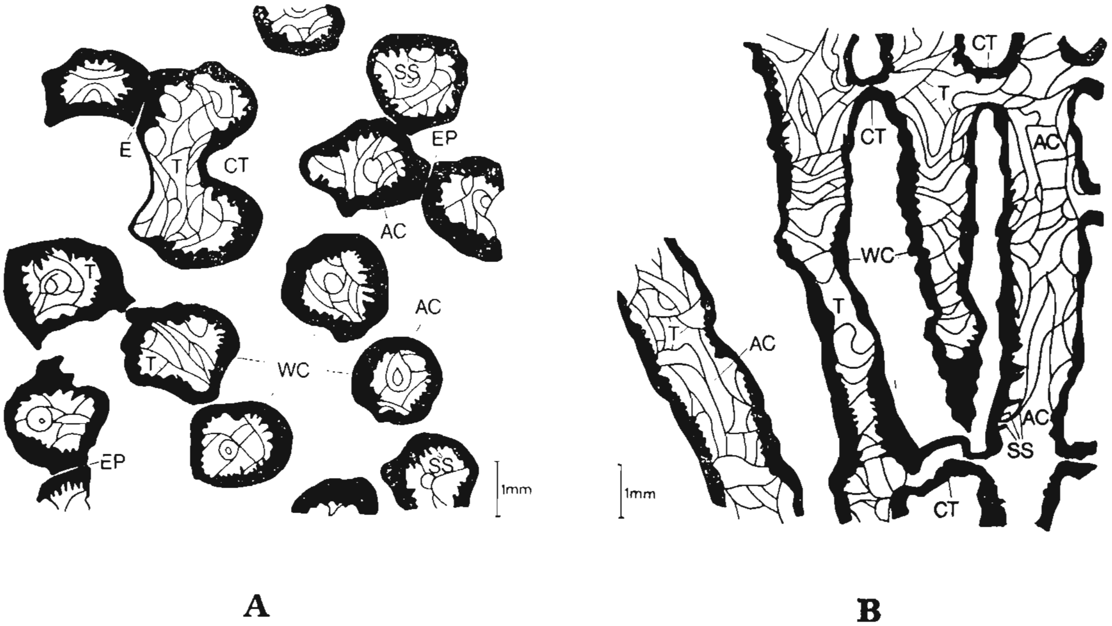

Fig. 10

Syringopora stuckenbergi sp. n., Treskelen, Coral Horizon Vc, Creek IV, holotype (ZPAL T XIII/92); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Material. — One, almost complete, well preserved colony from Treskelen: ZPAL T XIII/92 in the Vc Coral Horizon, Creek IV. Six longitudinal and transverse sections have been made.

Description. — Hemispherical, flattened, dendroid colony about 100 mm in diameter. Corallites short, tube-like, slightly bent, arranged in parallel, in some parts of the colony radial, irregularly spaced of 0.1—1.0 mm, most often 0.2—0.7 mm or in contact. In transverse sections corallites round or oval, often slightly triangular or quadrangular, 1.4—2.2 mm in diameter, most often 1.6—2.0 mm. Corallite walls thick, 0.1—0.5 mm, most often 0.2—0.4 mm, with indistinct lamellar microstructure. Ephitheca not isolated. Calices deep, conical or irregular, with rounded margins. Connecting tubes numerous, short, 0.2—0.6 mm in diameter, most often 0.3—0.5 mm, irregularly arranged with vertical spaces of 0.5—1.2 mm, most often 0.7—1.0 mm. In some parts of the colony they occur at the same level in adjacent corallites. Tabulae numerous, thin, funnel-shaped and oblique, often slightly inclined. Axial canal short, discontinuous, poorly developed. Septal spines very numerous, large, long, thick and occupying about 1/3 of lumen diameter of a corallite tube. Spines present also on tabulae.

Remarks. — *Syringopora stuckenbergi* sp. n. is most similar to *S. uralica* STUCKENBERG from the Lower Carboniferous of Ural and Upper Carboniferous of Timan (STUCKENBERG 1895). Similar features are habit and diameter of corallites and thickness of corallite walls. However, the new species differs from *S. uralica* in having wider spaces between the corallites, more numerous connecting tubes with much narrower vertical spaces as well as very numerous, well developed septal spines.

From *S. quadriserialis* SOKOLOV (1950), which has equally strongly developed septal spines and similar habit of corallites, equally thick corallites walls and similar diameters of connecting tubes, the new species differs in having much shorter corallites with larger diameters, rounded calice margins as well as narrower spaces between the connecting tubes.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Syringopora kruseryggensis sp. n.

(pl. 10: 2a, b; figs. 11A, B)

Holotype: Specimen ZPAL T XIII/93; pl. 10: 2a, b.
Type horizon: Vth Coral Horizon, "Upper Treskelodden Beds", Lower Permian.
Type locality: Kruseryggen, Hornsund, Spitsbergen.
Derivation of the name: kruseryggensis — from the locality of Kruseryggen.

Diagnosis. — Corallites straight, with spaces of 0.1—0.7 mm or in contact. In transverse sections corallites round, 1.5—2.2 mm diameter, most often 1.6—2.0 mm, or irregularly oval, with measurements of 1.5—2.0 × 2.0—2.5 mm. Corallite walls 0.1—0.15 mm thick. Connecting tubes very sparse, short, 0.3—0.6 mm in diameter, with irregular spaces in between. Tabulae sparse, strongly funnel-shaped. Axial canal short, 0.2—0.5 mm in diameter. Septal spines very sparse, long.

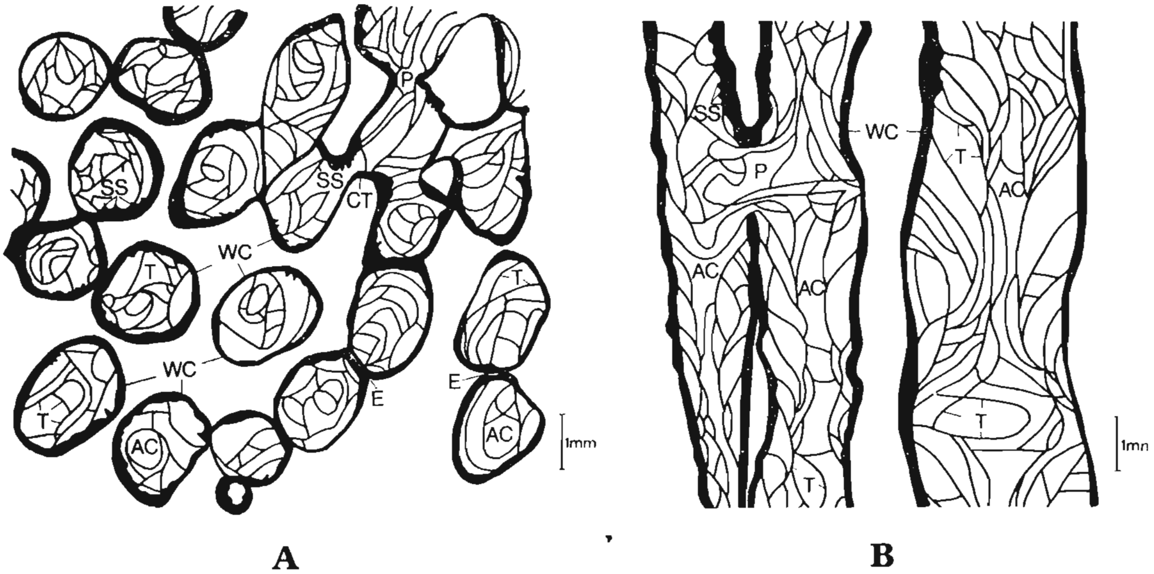

Fig. 11

Syringopora kruseryggensis sp. n., Kruseryggen, Coral Horizon V, holotype (ZPAL T XIII/93); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Material. — One complete, well preserved colony from Kruseryggen: ZPAL T XIII/93 in the V Coral Horizon. Six longitudinal and transverse sections have been made.

Description. — Irregular, dendroid colony, about 150 mm in diameter. Corallites long, straight or slightly bent, parallel, with irregular spaces of 0.1—0.7 mm, most often 0.2—0.5 mm. Most often the corallites are in contact with each other over most of their walls. In transverse sections the corallites are irregularly round, with very variable diameters of 1.2—2.2 mm, most often 1.4—2.0 mm, as well as irregularly elliptical, oval and elongated, with measurements 1.5—2.0 × 2.0—2.4 mm. Corallites walls thin 0.1—0.15 mm, with indistinct microstructure. Epitheca thin, dark, discontinuous. Connecting tubes sparse, thick, short with variable diameter 0.3—1.0 mm, most often 0.5—0.8 mm, scattered. In the corallites adhering to each other, connecting pores 0.3—0.4 mm in diameter occur. Tabulae relatively sparse, thin, strongly funnel-shaped. Locally at the centre of the tube, they form and axial canal 0.2—0.5 mm in diameter. Septal spines very sparse, long, large.

Remarks. — *Syringopora kruseryggensis* sp. n. most resembles *S. polaris* SOKOLOV from the Lower Carboniferous of Taymyr (SOKOLOV 1947) in the following features: corallite diameters, thickness of corallite walls, habit and morphology of tabulae as well as lack of septal spines. It differs, however, from *S. polaris* in having smaller spaces between the corallites, greater variability of diameters, oval transverse sections of corallites, which are often in contact thicker, sparser and scattered connecting tubes as well as sparser tabulae, sporadically forming an axial canal at the centre of the tube.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Genus *Neosyringopora* SOKOLOV, 1955

Type species: Neosyringopora bulloides SOKOLOV, 1955.

Diagnosis. — Colonies dendroid. Corallites syringoporoidal, cylindrical or irregular, in transverse sections round or angular, tightly in contact or arranged loosely in the colony. Corallites are joined by short and sparse tubes or pore-canals. Corallite walls thin. Tabulae form a system of smaller or larger vesiculae, some are funnel-shaped, arranged obliquely along the corallite walls. Septal spines poorly developed or absent.

REMARKS. — According to SOKOLOV (1955, 1962) and the present author *Neosyringopora* differs from *Syringopora* in: (1) presence of dense zones (corallites in contact and sparse zones separated corallites) in the same colony, and, related to this, the occurrence of connecting pore-canals and connecting tubes, respectively. Both tubes and pores are sparse. (2) tabulae most often not funnel-shaped, irregularly bent and oblique, form a system of smaller and larger vesiculae filling the whole interior of corallite tubes. The vesicular system of tabulae is characteristic of many late Paleozoic genera in the order *Syringoporida* (also Permo-Carboniferous species of *Roemeripora*). (3) septal apparatus poorly developed or absent. On the basis of these features some late Paleozoic species of various genera of the order Syringoporida should be included in *Neosyringopora*, e.g. Upper Carboniferous *Syringopora multattenuata* MC CHESNEY (MC CHESNEY 1860).

Occurrence. — Permian: USSR (Urals), Western Europe; Upper Carboniferous through Lower Permian: Spitsbergen (Hornsund).

Neosyringopora spitsbergensis sp. n.

(pl. 11: 1a, b, 2a, b; figs. 12A, B)

Holotype: Specimen ZPAL T XIII/96; pl. 11: 1a, b.
Type horizon: Vc Coral Horizon, "Upper Treskelodden Beds", Lower Permian.

Type locality: S slope of Hyrnefjellet, Hornsund, Spitsbergen.
Derivation of the name: spitsbergensis — coming from Spitsbergen.

Diagnosis. — Corallites long with spaces 0.2—0.5 mm or in contact. In transverse sections corallites irregularly round and angular, 1.5—1.8 mm in diameter, and oval, 1.4—1.6 × 1.8—2.1 mm. Corallites walls 0.1—0.2 mm thick. Connecting tubes sparse, short, 0.4—0.6 mm in diameter. Connecting pores sparse, 0.3—0.4 mm in diameter, locally with spaces of 1.5—3.5 mm. Tabulae thin, not numerous, vesicular. No septal spines.

Material. — Two almost complete, rather not well-preserved colonies from S slope of Hyrnefjellet: ZPAL T XIII/95, 96. No. 95 in the Vb_2 Coral Horizon. No. 96 (holotype) in the Vc Coral Horizon. Five transverse and longitudinal sections have been made.

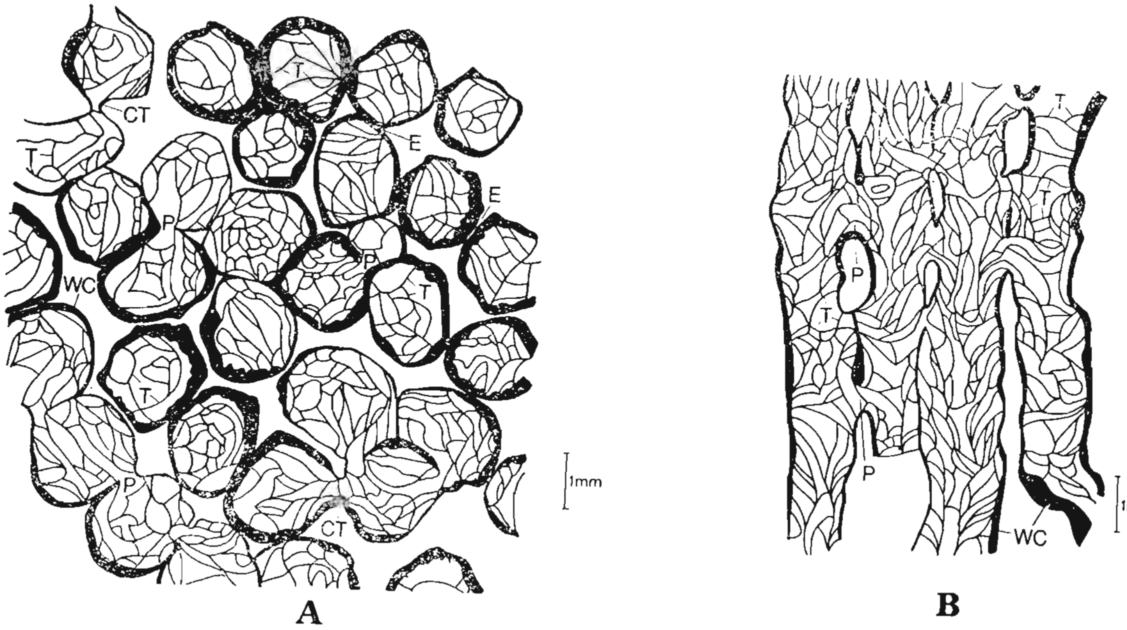

Fig. 12

Neosyringopora spitsbergensis sp. n., Hyrnefjellet, Coral Horizon Vc, holotype (ZPAL T XIII/96); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Description. — Small, irregular and bulbous, dendroid colonies about 100 mm in diameter. Corallites long, straight, unequal, arranged in parallel, in contact in some parts of the colony, in others arranged irregularly with spaces of 0.1—0.8 mm, most often 0.2—0.5 mm. In transverse sections corallites irregularly round and slightly angular, 1.2—2.0 mm in diameter, most often 1.5—1.8 mm, or oval and elongate, with measurements 1.4—1.6 × 1.8—2.1 mm. Corallite walls 0.1—0.2 mm thick, with no traces of microstructure. Epitheca thin, dark, locally disappears. Connecting tubes sparse, very short, thick, 0.3—0.8 mm in diameter, most often 0.4—0.6 mm, scattered. Connecting pore-canals 0.3—0.4 mm in diameter, locally with spaces of 1.5—3.5 mm. Tabulae thin, not very numerous, vesicular, bent, rarely funnel-shaped, strongly oblique. No septal spines.

Remarks. — From the type species — *Neosyringopora bulloides* SOKOLOV, described from the Upper Carboniferous of the Western slope of the Urals (SOKOLOV 1955), the new species differs in having much smaller corallite diameters, the presence of corallites with oval and elongate cross-sections, larger spaces between the corallites, smaller diameters of connecting tubes as well as sparser tabulae, sometimes funnel-shaped.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Genus *Fuchungopora* LIN BAO-YUI, 1963

Type species: Fuchungopora multispinosa LIN BAO-YUI, 1963.

Diagnosis. — See NOWIŃSKI 1982.

Remarks. — LIN BAO-YUI (1963b) and NOWIŃSKI (1982) included *Fuchungopora* in the order Sarcinulida. However, more recent studies by the author conducted on rich material as well as observations of blastogeny and the development of a colony, suggest that the genus *Fuchungopora* should be included in the order Syringoporida, family Syringoporidae. *Fuchungopora* has all features typical of the family Syringoporidae, such as: habit of corallites, typical connecting tubes, habit and arrangement of tabulae, and septal spines of syringoporoidal type. Apart from connecting tubes, *Fuchungopora* has connecting platforms or bridges (characteristic of the order Sarcinulida), which are also present in genera *Thecostegites* and *Chonostegites* (Syringoporidae). Representatives of *Fuchungopora* lack such features characteristic of the order Sarcinulida as: (1) connecting pores forming a wreath between the trabecular septa and tabulae running through connecting pores to the spaces in connecting platforms or connecting bridges, (2) and having spines. Connecting bridges and platforms of Sarcinulida have a different structure than those of *Fuchungopora*. These elements are a uniform tissue resembling coenenchyme. Moreover, the genus *Fuchungopora* shows calicular extravisceral budding (the bud appears on an external evagination of the parent calice wall), as in the genus *Syringopora*.

Occurrence. — Lower Carboniferous (Visean): South China; Upper Carboniferous through Lower Permian: Spitsbergen (Hornsund).

Fuchungopora arctica NOWIŃSKI, 1982

(pl. 12: 1—3; pl. 13: 1)

1982. *Fuchungopora arctica* NOWIŃSKI; Nowiński: 92—93, pl. 33: 5a—c; figs. 5A, B.

Diagnosis, description, remarks and illustrations — See NOWIŃSKI 1982.

Material. — Nine almost complete, well preserved colonies ZPAL T XIII/47—49, 97—102, from Treskelen and Hyrnefjellet. 1. Treskelen: No. 97 in the Va Coral Horizon, Creek IV and Nos.: 98, 99, 100 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet (S slope): Nos.: 47 (holotype), 48, 49, 101, 102 in the Vb_{1-2} Coral Horizon.

Twenty nine longitudinal and transverse sections have been made as well as three series of imprints on celluloid film for the study of budding and colony development.

Remarks. — Young (4—5 years old) colonies of *Fuchungopora arctica* show rather clear growth periodicity. The thickness of particular growth bands varies from 4.0 to 20.0 mm. The thickness ratio of dark to light layers within growth bands is equal to 1. The light layers of the annual growth bands started with intensive budding. Vegetative reproduction in this species proceeded by calicular and extracalicular budding. During calicular budding, a bud originated by evagination of the parent corallite wall, as in *Syringopora*. In extracalicular budding young individuals bud off from connecting tubes, or from horizontal stolonal tubes (stolonal budding).

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Genus *Roemerolites* DUBATOLOV, 1963
(= *Armalites* TCHUDINOVA, 1964)

Type species: Roemerolites batschatensis DUBATOLOV, 1963.

Diagnosis. — See DUBATOLOV 1963.

Remarks. — According to the present author, *Armalites* TCHUDINOVA, 1964 (see also NOWIŃSKI 1982) is synonymous or very close to *Roemerolites* DUBATOLOV, 1963 From earlier descriptions and illustrations, and the present author's investigations (see also. *Roemerolites lublinensis* STASIŃSKA et NOWIŃSKI, 1978), the two genera seem to have no important diagnostic features that would distinguish one from the other, apart from the number and size of septal spines. This feature is very variable even in different species of the same genus. Despite such clear analogy, the two genera have not so far been compared. Thus, *Roemerolites* should be removed from the family Syringolitidae and placed into the family Syringoporidae. *Armalites* (which is already in the family Syringoporidae) should be regarded as synonymous with *Roemerolites* or as a very closely related genus. Both genera, included in the Syringoporidae on the basis of the thorough studies by TCHUDINOVA (1964) have features much more typical of Syringoporidae than of Syringolitidae.

HILL and JELL (1970) consider *Armalites* and *Roemerolites* as synonymous with *Roemeripora* KRAICZ but this does not seem well substantiated. However, such diagnostic features of *Roemerolites* (also *Armalites*) as: cylindrical corallites with very thick walls with lamellar microstructure of multithecoporoidal type, very strongly developed septal apparatus, relatively sparce tabulae of syringoporoidal type forming no vesicular zone in the peripheral part of the corallites, show that *Roemerolites* (and *Armalites*) differs in important characters from *Roemeripora* and should be considered a separate genus of the family Syringolitidae. Two species were so far described under the generic name of *Roemerolites* [(*R. batschatensis* DUBATOLOV from the Eifel of Kuznetsk Basin (DUBATOLOV 1963) and *R. lublinensis* from the Frasnian of Poland, Lublin region (STASIŃSKA and NOWIŃSKI 1978)]. Five other species were described under the name of *Armalites* (DUBATOLOV 1963, TCHUDINOVA 1964, MIRONOVA 1974, see also NOWIŃSKI 1982).

Occurrence. — Lower Devonian (Siegenian, Emsian): USSR (Altai, Salair); Middle Devonian (Eifelian): USSR (Kuznetsk Basin); Upper Devonian (Frasnian): Poland (Lublin Region); Lower Permian: Spitsbergen (Hornsund).

Roemerolites laminatus (NOWIŃSKI, 1982)
(pl. 13: 2a, b)

1982. *Armalites laminatus* NOWIŃSKI; Nowiński: 88—89, pl. 31: 1a, b, 2, 3; figs. 3A, B.

Diagnosis, description, remarks and illustrations — See NOWIŃSKI 1982.

Material. — Seven large, almost complete, very well preserved colonies: ZPAL T XIII/39—45 from Treskelen and Hyrnefjellet. 1. Treskelen: No. 40 in the Va Coral Horizon, Creek IV. 2. Hyrnefjellet: Nos.: 39 (holotype), 42, 43, 44 in the Va Coral Horizon and Nos.: 41, 45 in the Vb Coral Horizon.

Thirty three transverse and longitudinal sections have been made as well as four series of imprints on celluloid film for the study of budding and colony development.

Remarks. — Earlier, NOWIŃSKI (1982) described *Roemerolites laminatus* as *Armalites laminatus*. The reasons for changing the generic name are summarized above (see above). The author's studies of a new material have revealed new characteristics of this species, which are as follows: some colonies or their fragments consist of corallites which are triangular or quadrangular in outline in transverse section; corallites show clearly and ordered pattern of distribution i.e. they occur in small circlets or short chains. In particular, tabulae occur in two different manners. Horizontal or slightly oblique, densely spaced tabulae occur near connecting elements such as tubes and pores, and cause pseudolamination of a colony as visible in longitudinal sections. In spaces between connecting elements occur rare, long and arcuate or funnel-shaped tabulae.

Vegetative reproduction occurred by calicular extravisceral budding in *Roemerolites laminatus* (the bud appeared on the external bulge of the parent calice wall), similarly to those in representatives of *Syringopora.*

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Family **Multithecoporidae** SOKOLOV, 1950

Genus *Multithecopora* YOH, 1927

Type species: Multithecopora penchiensis YOH, 1927.

Diagnosis. — See WILSON 1963.

Remarks. — Some species of *Multithecopora* exhibit considerable septal development and geniculate corallites (connected directly with the type of budding), resembling corallites of *Cladochonus.* Due to this same species of *Multithecopora* have been wrongly described as representatives of *Cladochonus.*

In Spitsbergen species of *Multithecopora* the stereoplasm of corallite walls has a non-uniform (pseudo-two-layered structure) (see p. 34)).

Multithecopora has been characterized and compared to related genera by: YOH (1927), SOKOLOV (1950, 1962), VASSILJUK (1960), WILSON (1963), OEKENTORP and KAEVER (1970), NOWIŃSKI (1976).

Occurrence. — Lower Silurian (Llandoverian): Norway; Lower Carboniferous: Poland (Holy Cross Mts.), USSR (Taymyr), Australia; Lower through Upper Carboniferous: USSR (Moscow and Donetsk Basins, Urals, Timan), Central Asia; Middle through Upper Carboniferous: Southern Europe, North America; Upper Carboniferous through Lower Permian: China, Spitsbergen; Middle Permian: Iran, Afghanistan.

Multithecopora syrinx (ETHERIDGE, 1900)

(pl. 13: 3; pl. 14: 1a, b, 2—4; figs. 13A, B)

1900. *Syringopora syrinx* ETHERIDGE; Etheridge, 6, pl. 1: 6—9; pl. 2: 11.
1934. *Syringopora syrinx* ETHERIDGE; HILL, 99, pl. 11: 37—39.
1960. *Multithecopora levensteini* VASSILJUK; Vassiljuk, 208, pl. 40: 7.
1963. *Multithecopora levensteini* VASSILJUK; Vassiljuk, 79—80, pl. 3: 1.
1966. *Syringopora syrinx* ETHERIDGE; Pickett, 35, pl. 17: 1—4.
1970. *Multithecopora syrinx* (ETHERIDGE); Oekentorp and Kaever, 292—294, pl. 2: 8; pl. 3: 11; pl. 4: 14; pl. 5: 20, 24; Text-fig. 3.

Diagnosis. — Corallites cylindrical, slightly bent, about 2 mm in diameter. Corallite walls 0.5—0.7 mm thick. The lumen of visceral chamber 1/3—1/4 of the corallite diameter. Few septal spines. Connecting tubes scarce. Tabulae of variable thickness, bent, concave, oblique, sometimes vesicular, scarce.

Material. — Large fragments of eight well preserved colonies: ZPAL T XIII/104—111 from Treskelen, Urnetoppen and Isfjorden area (Linneus Valley). 1. Treskelen: No. 104 in the II Coral Horizon, Creek IV, and Nos.: 105, 106, 107 in the IVb Coral Horizon, Creek IV. 2. Urnetoppen: Nos.: 108, 109, 110 in the V Coral Horizon. 3. Isfjorden: No. 111.

Twenty nine longitudinal and transverse sections have been made as well as three series of imprints on celluloid film for the study of budding.

Description. — Large, oval, irregular, sometimes platy, dendroid colonies, up to 1 m in diameter. Corallites relatively short, cylindrical or slightly bent, scattered all over the colony with irregular spaces, frequently budding. Corallites in transverse sections regularly round or slightly

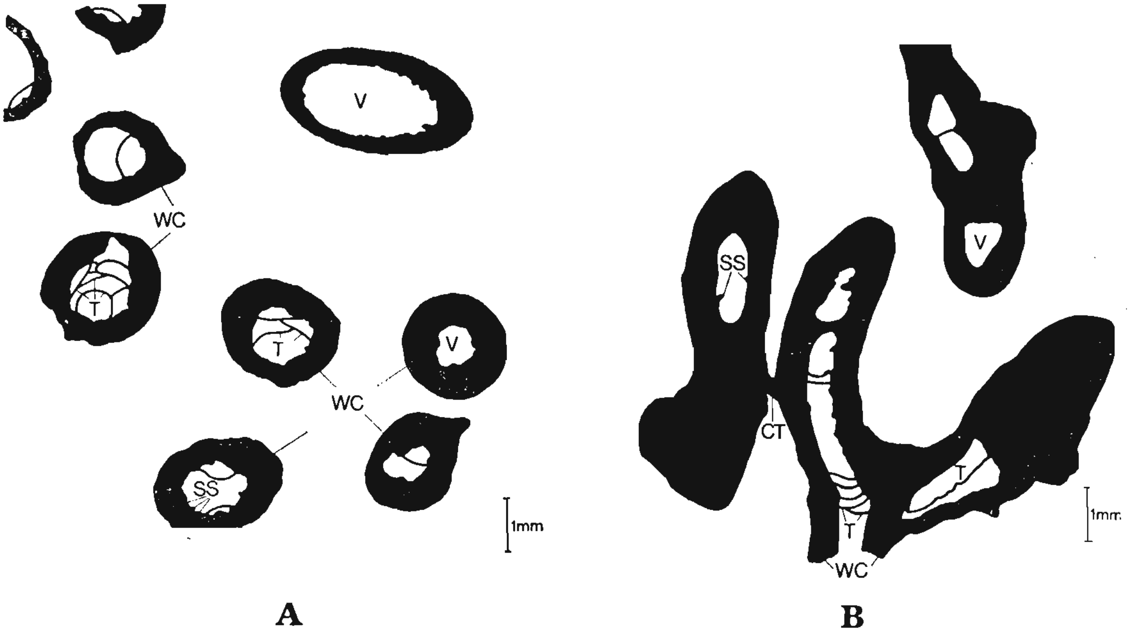

Fig. 13

Multithecopora syrinx (Etheridge), Treskelen, Coral Horizon IVb, Creek IV (ZPAL T XIII/106); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

oval, 1.8—2.2 mm in diameter, most often 2.0 mm. Corallite walls 0.4—0.8 mm thick, most often 0.5—0.7 mm, i.e. 1/2—1/4, most often about 1/3 of the corallite diameter. The stereoplasm of corallite walls is two layered. The inner layer, directly enclosing the visceral chamber, has a fibro-normal microstructure. The external layer has an indistinct lamellar microstructure. Epitheca very thin, poorly preserved, with fibro-normal microstructure. The lumen of visceral chamber round, oval or irregular. Tabulae very sparse, thick, horizontal, concave or convex, arranged in groups of two or three with spaces of 0.3—0.8 mm, or very long and strongly oblique (almost parallel to the corallite walls). Septal spines sparse, thick, sharp, slightly embedded in the stereoplasm of corallite walls. Connecting tubes very scarce. Calices very deep, with sharp margins.

Vegetative reproduction occurred by calicular extravisceral budding as in *Roemerolites laminatus* (p. 30).

Remarks. — Colonies of *Multithecopora syrinx* from the Upper Treskelodden Beds and from the Isfjorden area differ from the colonies of *M. levensteini* (considered by Oekentorp and Kaever 1970 as a synonym of *M. syrinx*) from the Upper Carboniferous of Donetsk Basin (Vassiljuk 1960, 1963) in having irregular spaces between the corallites, a two-layered structure of stereoplasm in the corallite wall, and less numerous tabulae. From specimens of *M. syrinx* from the Permian of Afghanistan (Oekentorp and Kaever 1970) they differ in having very sparse connecting tubes as well as scarce septal spines and tabulae.

Multithecopora syrinx is most similar to *M. sokolovi* Vassiljuk from the Upper Namurian of the Donetsk Basin (Vassiljuk 1960*a*, *b*). It differs, however, in having slightly smaller corallite diameters and in the presence of septal spines. From the similar species *M. huanglungensis* from the Upper Carboniferous of South China (Lee and Chen 1930), *M. syrinx* differs only in having a more compact colony structure and straight, cylindrical corallites.

Occurrence. — Lower Carboniferous (Visean): Australia (New South Wales, Queensland); Lower Carboniferous: USSR (Donetsk Basin); Upper Carboniferous through Lower Permian: Spitsbergen (Hornsund, Isfjorden); ?Upper Permian: SE-Afghanistan (Paktia Province).

Multithecopora tchernychevi Sokolov, 1950

(pl. 15: 1a—c, 2; figs. 14A, B; 15)

1950. *Multithecopora tchernychevi* Sokolov; Sokolov, 20—31, pl. 3: 1, 2.
1963. *Multithecopora tchernychevi* Sokolov; Vassiljuk, 77—79, pl. 2: 1.

Diagnosis. — Corallites long, bent in different directions, 1.5—1.7 mm in diameter. Corallite walls 0.3—0.5 mm thick. The lumen of visceral chamber about 1/3 corallite diameter. Septal spines quite numerous. Tabulae of various thickness, straight or concave and/or convex, horizontal or oblique, scarce. Connecting tubes very scarce.

Material. — Large fragments of three, well preserved colonies: ZPAL T XIII/112—114 from Treskelen and Hyrnefjellet. 1. Treskelen: Nos.: 112 in the III Coral Horizon, Creek IV and 113 in the IVb Coral Horizon, Creek IV. 2. Hyrnefjellet: No. 114 in the Va Coral Horizon.

Twenty one longitudinal and transverse sections have been made as well as two series of imprints on celluloid film for the study of budding.

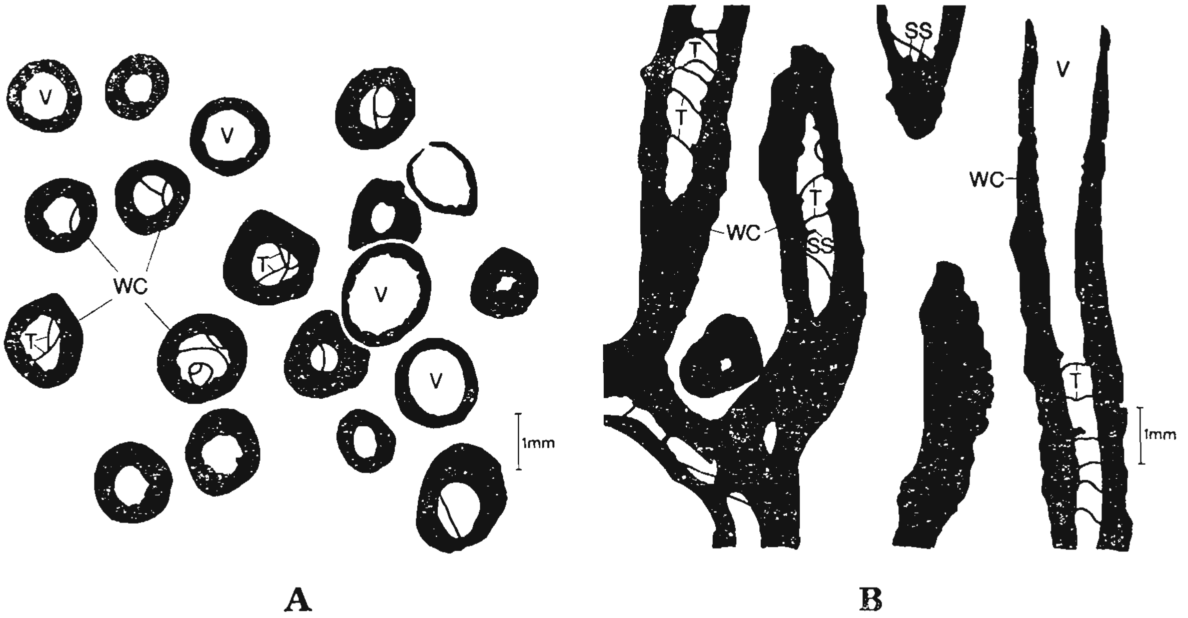

Fig. 14

Multithecopora tchernychevi Sokolov; *A* transverse section, × 7.5, Hyrnefjellet, Coral Horizon Va (ZPAL T XIII/114); *B* longitudinal section, × 7.5, Treskelen, Coral Horizon IVb, Creek IV (ZPAL T XIII/113). For explanation of symbols see p. 8—9.

Description. — Very large, platy, dendroid colonies, up to 2 m in diameter and up to 50 cm in height (thickness). In vertical sections some parts of the colonies exhibit a multilayer structure, connected with the sequence of successive corallite generations.

In these parts of a colony, young individuals budded simultaneously and on the same level in successive stages of colony growth, forming layers of densely spaced corallites. This feature has no relationship to growth periodicity, as the morphological changes in elements of corallites are not cyclic. Corallites long, cylindrical or slightly flattened, strongly bent, spaced irregularly every 0.2—0.7 mm, most often 0.4—0.6 mm. Calices slightly conical, very deep, with sharp margins. In transverse sections corallites round, 1.3—1.8 mm in diameter, most often 1.4—1.6 mm, or oval, with measurements 1.2—1.4 × 1.6—2.0 mm. Corallite walls 0.3—0.7 mm thick, most often 0.4—0.5 mm, i.e. about 1/3 corallite diameter. Microstructure of corallite walls two-layered (Fig. 15). The external layer (thicker) has concentric-lamellar microstructure. The inner layer, enclosing the visceral chamber (thinner) has fibronormal microstructure. In the stereoplasm of corallite walls, at various depths, one can see concentric growth rings marked by dark iron oxide pigmentation. The lumen of visceral chamber round, oval rarely irregular. Tabulae sparse, of various thickness, straight, horizontal, concave up, sometimes oblique, groupped in small assemblages, with spaces inbetween of 0.5—0.8 mm. Septal spines numerous, large, thick, sharp. No connecting tubes have been found. Vegetative reproduction by calicular extravisceral budding (the bud appeared in the external bulge of the parent calice wall).

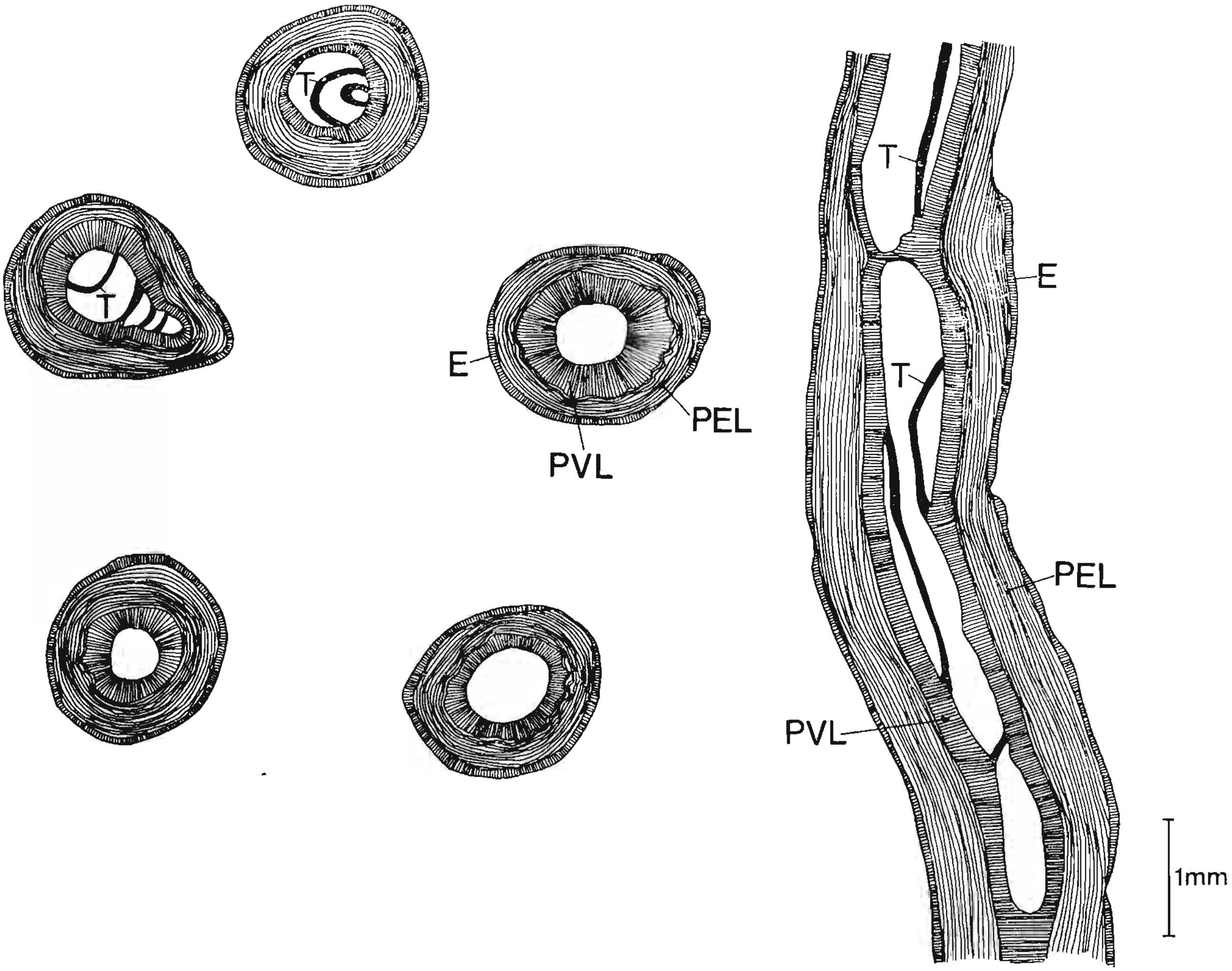

Fig. 15

Bilayered stereoplasm in corallites walls of *Multithecopora tchernychevi* Sokolov; Transverse and longitudinal sections, × 10; Hyrnefjelled, Coral Horizon Va (ZPAL T XIII/114). For explanation of symbols see p. 8—9.

Remarks. — *Multithecopora tchernychevi* from the "Upper Treskelodden Beds" differs from known specimen of the species in having exceptionally large colonies (sometimes over 2 m in diameter) of multilayer structure. From the colonies described from the Lower Namurian of Donetsk Basin (Sokolov 1950; Vassiljuk 1963) it differs in having corallites of slightly smaller diameters, strongly bent and much more densely packed, sparser tabulae and connecting tubes as well as better developed septal apparatus.

Occurrence. — Upper Carboniferous (Namurian): USSR (Donetsk Basin); Lower Permian: Spitsbergen (Hornsund).

Multithecopora sp.

(pl. 5: 4)

Material. — A fragment of one, poorly preserved colony: ZPAL T XIII/115 from Urnetoppen in the V Coral Horizon. Three transverse and longitudinal sections have been made.

Description. — Size and shape of the colony unknown. Corallites long, cylindrical, straight or slightly bent, irregularly spaced. In transverse sections corallites round and oval, 0.8—1.4 mm in diameter, most often 1.0—1.2 mm. Visceral chamber round and oval, strongly narrowed due to considerable thickness of the corallite walls. Their diameters are 0.4—0.6 mm, i.e. 1/2—1/3 of corallite diameter. Calices very deep, sharply conical, with sharp margins. Corallite walls 0.3—0.5 mm thick. Wall microstructure concentric-lamellar, indistinct. Epitheca thin, dark, uneven, sometimes discontinuous as a consequence of damage. Tabulae very sparse, thin, horizontal, straight or slightly bent, sometimes strongly oblique. No septal spines. Connecting tubes undiscernible.

Remarks. — Due to poor preservation and the fragmentary nature of the colony it is impossible to determine the species. *Multithecopora* sp. from Hornsund differs from all known species of the genus in having very small corallite diameters and very thick corallite walls in relation to their diameters. It is most similar to *M. tanaica* VASSILJUK from the Lower Carboniferous of the Donetsk Basin (VASSILJUK 1963), first of all in absolute thickness of corallite walls, morphology and arrangement of tabulae, and lack of septal spines. It differs, however, from *M. tanaica* in having larger corallite diameters and closer spaced corallites walls in relation to their diameters.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Family **Tetraporellidae** SOKOLOV, 1950
Genus *Hayasakaia* LANG, SMITH et THOMAS, 1940
(= *Tetrapora* YABE et HAYASAKA, 1915)

Type species: Tetrapora elegantula YABE et HAYASAKA, 1915.

Diagnosis. — See LIN BAO-YUI 1958.

Remarks and **occurrence.** — See NOWIŃSKI 1982.

Hayasakaia compacta NOWIŃSKI, 1982

(pl. 16: 3; pl. 23: 3)

1982. *Hayasakaia compacta* NOWIŃSKI; Nowiński: 90—91, pl. 32: 1, 2; figs. 4A, B.

Diagnosis, description, remarks and illustration. — See NOWIŃSKI 1982.

Material. — Large fragments of eight well preserved colonies: ZPAL T XIII/50—53, 116—119 from Treskelen and Hyrnefjellet. 1. Treskelen: No. 51 in the Va Coral Horizon, Creek IV and Nos.: 50 (holotype), 52, 53, 116, 117, 118 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: No. 119 in the Va_3 Coral Horizon.

Twenty seven longitudinal and transverse sections have been made as well as three series of imprints on celluloid film for the study of budding and colony development.

Remarks. — In *Hayasakaia compacta* connecting elements are rare and reveal the transitional character between pores and true connecting tubes. Corallites are connected by these pores, which cut small evagination of the wall margins of neighbour corallites. Typical connecting tubes are short and very rare. Tabulae are thickened secondarily by stereoplasm, straight, relatively rare and nonsyringoporoidal.

This species differs from *Hayasakaia profunda* FEDOROWSKI from the Lower Permian. „Treskelodden Beds" (FEDOROWSKI 1967) in having smaller diameters of corallites, poorly developed vesicular zones near the corallite wall, more simple construction of tabulae, no axial canals and very rare true connecting tubes.

In *Hayasakaia compacta* vegetative reproduction occurred by calicular extravisceral budding. The bud developed in an evagination of the wall of the parent calice.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Hayasakaia multispinosa sp. n.

(pl. 16: 1a, b, 2; figs. 16A, B)

Holotype: Specimen ZPAL T XIII/121; pl. 16: 1a, b.
Type horizon: Va Coral Horizon, "Upper Treskelodden Beds", Lower Permian.
Type locality: Treskelen, Creek IV, Hornsund, Spitsbergen.
Derivation of the name: multispinosa — with numerous, well developed septal spines.

Diagnosis. — Corallites long, straight, grouped in short chains of *Halysites* type or in circular rings. In transverse sections corallites irregularly round and polygonal, 1.2—1.6 mm in diameter. Corallite walls 0.2—0.3 mm thick. Connecting tubes short thick, 0.5—0.7 mm in diameter arranged in 2—4 vertical rows, spaced every 1.3—2.3 mm, often at one level in adjacent corallites. Tabulae thick, straight and oblique, concave and convex, incomplete, spaced every 0.2—0.6 mm. Vesicular zone poorly marked. Septal spines numerous, thick long.

Material. — Three almost complete, well preserved colonies: ZPAL T XIII/120—122 from Treskelen, Creek IV. Nos.: 120, 121 in the Va Coral Horizon and No. 122 in the Vc Coral Horizon.

Eleven longitudinal and transverse sections have been made as well as two series of imprints on celluloid film for the study of budding and colony development.

Description. — Irregularly hemispherical and oval dendroid colonies about 80 mm in diameter. Corallites long, straight or slightly bent, arranged in parallel or slightly radially, emerging perpendicular to the colony surface. In transverse sections of the colony, corallites are grouped in short (three-five corallites), slightly curved chains of *Halysites* type, or in circular and oval rings formed by four-eight corallites. In these aggregates corallites are connected by short tubes or touch at their margins, without wall perforations. In transverse sections corallites irregularly round and oval, often polygonal (triangular or quadrangular), 1.0—1.8 mm in diameter, most often 1.2—1.6 mm. Corallite walls 0.2—0.3 mm thick, uneven, with indistinct concentric-lamellar microstructure, locally changed into fibro-normal, perhaps due to diagenetic processes. Epitheca very thin, vestigial. Connecting tubes numerous, very short, 0.5—0.7 mm thick, arranged in two-four vertical rows on corallite margins, with irregular spaces of 1.3—2.3 mm. Occasionally, the tubes occur at the same level in several adjacent corallites. Tabulae not very numerous, thick, straight or concave and convex, often oblique and incomplete, occupy the central part of the corallite tube. Strongly oblique, sparse tabulae form a discontinuous vesicular zone at corallite walls. Septal spines very numerous, thick, long, in vertical rows. Single spines occur also on tabulae.

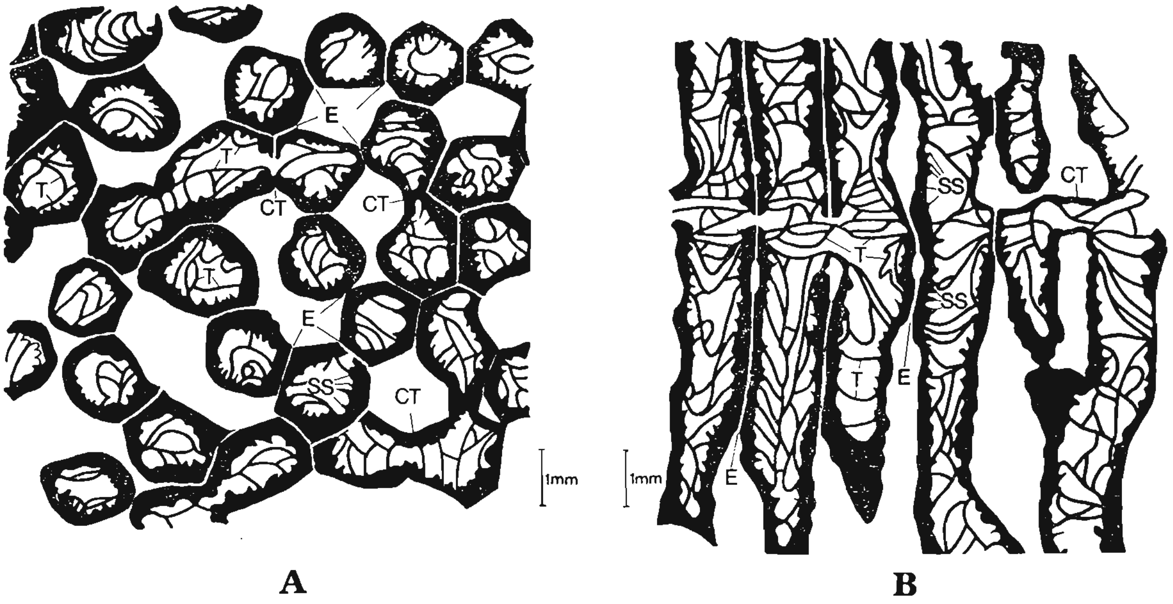

Fig. 16

Hayasakaia multispinosa sp. n., Treskelen, Coral Horizon Va, Creek IV, holotype (ZPAL T XIII/121); *A* transverse section, *B* longitudinal section, × 7.5. For explanation of symbols see p. 8—9.

Vegetative reproduction in *Hayasakaia multispinosa* by calicular extravisceral budding (the bud appeared on the external bulge of the parent calice wall), just as in the genus *Syringopora.*

Remarks. — *Hayasakaia multispinosa* sp. n. differs from the known species of the genus in having exceptionally strongly developed septal apparatus, a poorly marked vesicular zone at the corallite walls as well as halysitoid arrangement of trangular and quadrangular corallites in the colony. Similar arrangement of corallites occurs also in *H. yunnanensis* Lin Bao-yui and *H. halysitoides* (Huang) from the Lower Permian of South China (Huang 1932; Lin Bao-yui 1958), as well as in *H. septentrionalis* (Gorsky) from the Lower Carboniferous of Novaya Zemlya (Gorsky 1935), however, it is not as distinct as in *H. multispinosa* sp. n. The new species is most similar to *H. irregularis* Lin Bao-yui from the Lower Permian of South-West China (Lin Bao-yui 1958). The similar features are: spaces between connecting tubes, arrangement and habit of tabulae and poorly developed vesicular zones. It differs from *H. irregularis* in having less differentiated diameters of triangular and quadrangular corallites arranged halysitoidally, thicker corallite walls and well developed septal spines.

H. multispinosa sp. n. is similar to the type species *H. elegantula* (Yabe et Hayasaka) from the Lower Permian of South China and from the Permian of Viet-Nam (Yabe and Hayasaka 1915, 1920; Yoh and Huang 1932; Huang 1932; Fontaine 1955; Lin Bao-yui 1962) only in corallite diameters, and in the case of the colonies described by Fontaine (1955) from the Permian of Viet-Nam in the halysitoid arrangement of corallites as well.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Hayasakaia birkenmajeri sp. n.

(pl. 17: 1a, b, 2; figs. 17A, B)

Holotype: Specimen ZPAL T XIII/123; pl. 17: 1a, b.

Type horizon: Va$_3$ Coral Horizon, "Upper Treskelodden Beds", Lower Permian.

Type locality: S slope of Hyrnefjellet, Hornsund, Spitsbergen.

Derivation of the name: birkenmajeri — in honour of Professor Krzysztof Birkenmajer.

Diagnosis. — Corallites short, straight, with spaces of 0.2—1.0 mm or in contact. They form irregular groups of a few individuals or short chains. In transverse sections corallites round and oval, in the little chains and in the groups triangular or quadrangular, 1.2—1.6 mm in diameter. Corallite walls 0.1—0.3 mm thick. Connecting tubes very sparse, short, thick, 0.3—0.5 mm in diameter, scattered. Tabulae not very numerous, straight and concave, oblique and incomplete, no vesicular zone. Septal spines numerous, thick.

Material. — Two almost complete, poorly preserved colonies: ZPAL T XIII/123, 124 from Hyrnefjellet (S slope) in the Va_3 Coral Horizon. Thirteen transverse and longitudinal sections have been made.

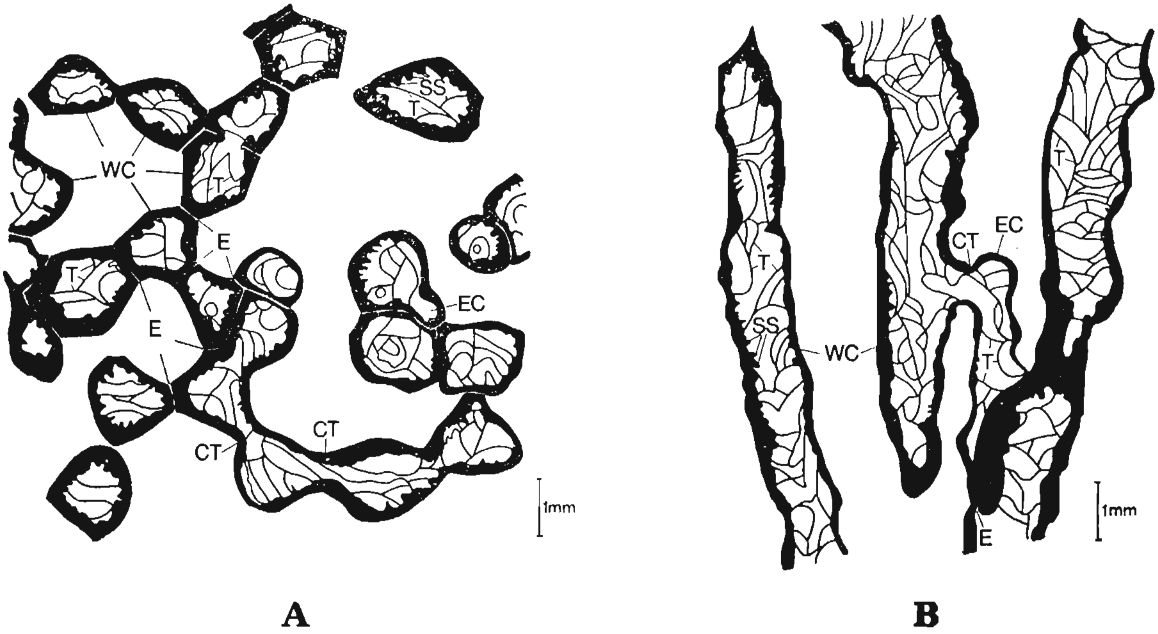

Fig. 17

Hayasakaia birkenmajeri sp. n., Hyrnefjellet, Coral Horizon Va_3, holotype (ZPAL T XIII/123); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Description. — Oval and irregular, dendroid colonies, about 100 mm in diameter. Corallites short, straight, unequal, arranged in parallel or slightly radially, emerge perpendicular to the colony surface. In transverse sections through the colony one can see irregular arrangement of corallites spaced every 0.1—1.2 mm, most often 0.2—1.0 mm. In some parts of the colonies, the corallites touch each other forming irregular groups (a few individuals each) or little chains. In transverse sections corallites less or more regularly round and oval, in groups triangular or quadrangular, with irregular diameters of 1.0—1.8 mm, most often 1.2—1.6 mm. Corallite walls 0.1—0.3 mm thick, with fibro-normal microstructure. Epitheca undiscernible. Connecting tubes very sparse, short, thick, 0.3—0.5 mm in diameter, scattered. Corallites exhibit frequent budding, usually occurring at the same level in adjacent corallites, which gives rise to a definite layering in the colonies. Tabulae not very numerous, straight and concave, horizontal and oblique, incomplete, sometimes funnel-shaped, no vesicular zone at corallite walls. Septal spines numerous, thick, long, poorly preserved.

Remarks. — *Hayasakaia birkenmajeri* sp. n. is most similar to *H. multispinosa* sp. n. (described above). The similar features are: corallite diameters, the morphology and arrangement of tabulae as well as well developed septal spines. It differs, however, from *H. multispinosa* sp. n. in having short, unequal corallites of round and oval transverse section (rarely angular), arranged in irregular groups (rarely in little chains), more sparse and scattered connecting tubes as well as lacking vesicular zones.

The new species has also some features similar to those of *H. syringoporoides* (YOH) from the Lower Permian of South-West China (YOH 1932; HUANG 1932; LIN BAO-YUI 1958, 1962). Both species have short corallites, round or oval in transverse section, similar wall thicknesses, habit and arrangement of scarce tabulae as well as sparse connecting tubes. *H. birkenmajeri* sp. n., however, differs from *H. syringoporoides* in having smaller spaces between the corallites, corallites arranged in irregular groups, larger corallite diameters, well developed septal spines and in lacking vesicular tissue at corallite walls.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Hayasakaia variabilis sp. n.

(pl. 18: 1a—c; pl. 19: 1, 2; figs. 18A, B)

Holotype: Specimen ZPAL T XIII/125; pl. 18: 1a—c.
Type horizon: Vb_2 Coral Horizon, "Upper Treskelodden Beds", Lower Permian.
Type locality: S slope of Hyrnefjellet, Hornsund, Spitsbergen.
Derivation of the name: variabilis — from large individual variability.

Diagnosis. — Corallites long, straight, irregularly arranged every 0.2—3.5 mm, partly or closely in contact. Diameters of the loosely arranged corallites 1.0—1.5 mm, and of the closely spaced ones — 1.6—2.0 mm, occasionally up to 2.1 mm. Corallite walls 0.1—0.2 mm thick, uneven. Connecting elements very sparse, occur as short tubes, 0.3—0.4 mm in diameter, or as pores, about 0.2 mm in diameter. Tabulae sparse, thin, of syringoporoidal-type, forming no vesicular zone at corallite walls. No septal spines.

Material. — Two almost complete, poorly preserved colonies: ZPAL T XIII/125, 126 from Hyrnefjellet in the Vb_2 Coral Horizon. Nine transverse and longitudinal sections have been made.

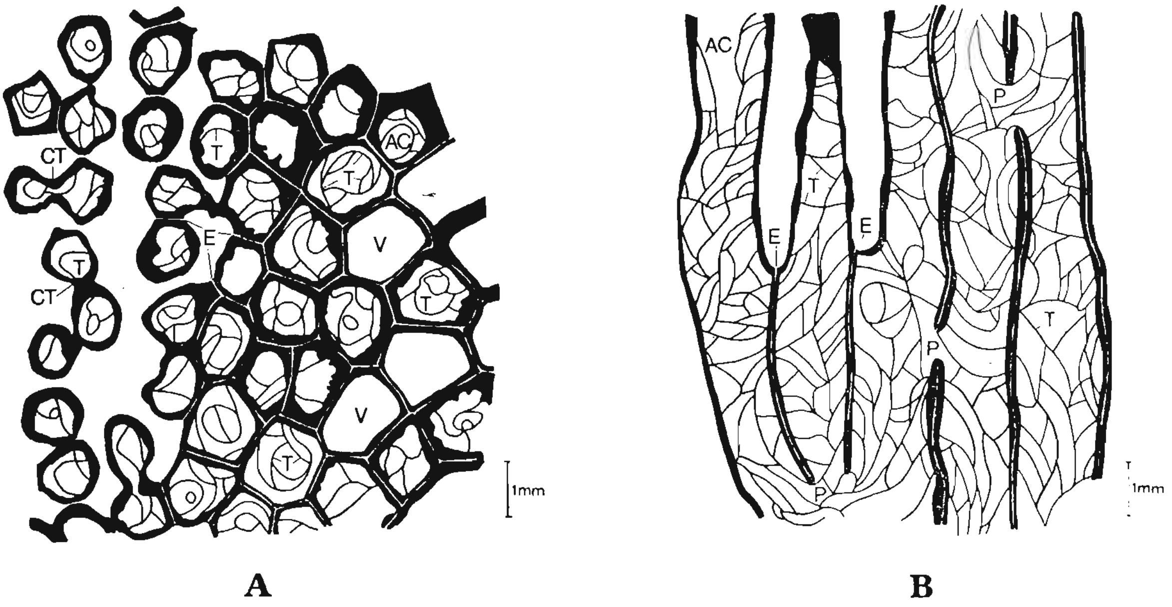

Fig. 18

Hayasakaia variabilis sp. n., Hyrrnefjellet, Coral Horizon Vb_2; *A* transverse section (ZPAL T XIII/126), *B* longitudinal section, holotype (ZPAL T XIII/125); × 7.5. For explanation of symbols see p. 8—9.

Description. — Irregularly hemispherical and flattened, dendroid colonies, about 100 mm in diameter and up to 70 mm in height, consisting of long, nearly straight corallites of diverse sizes and with uneven walls. Corallites in the central portion of a colony are parallel to each other, and in marginal parts are radially oriented and perpendicular to the surface of the colony.

Corallites occur either in local groups, where they are completely in contact with each other, or are loosely spaced and only partly touch with some of the walls or do not touch at all. In loose colony zones, spaces between the corallites are very irregular from 0.2—3.5 mm. Transverse sections of corallites from such parts of the colony are irregularly round and oval, 1.0—1.5 mm in diameter. In the zones where the corallites partly touch to each other their transverse sections are irregularly polygonal, 1.3—1.6 mm in diameter. In the zones of more closely packed corallites they are more or less regularly polygonal (penta-, hexagonal), 1.6—2.0 mm in diameter. Corallite walls relatively thin, 0.1—0.2 mm, very uneven and jagged, with poorly visible fibro-normal microstructure. Epitheca dark, thin. Connecting elements very sparse, occur as tubes and pores. Connecting tubes short, irregular, poorly marked, 0.3—0.4 mm in diameter, scattered, occur in loosely arranged corallites. Connecting pores rare, about 0.2 mm in diameter, occur only in the zones with densely packed corallites. Tabulae sparse (especially in loosely arranged corallites), thin or thickened by the secondary layer of stereoplasm, long, of syringoporoidal-type, often incomplete, sometimes forming a short, asymmetrically placed axial canal. No vesicular zone at the walls of corallites. Septal spines undiscernible.

Remarks. — *Hayasakaia variabilis* sp. n. differs from all known species of the genus in its not uniform colony structure, in which, in addition to closely packed polygonal corallites with large diameters, there are round and oval, loosely arranged corallites, with small diameters, very sparse, scattered connecting pores and tubes as well as long tabulae forming no vesicular zone at the corallite walls.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Genus *Tetraporinus* Sokolov, 1947

Type species: Tetraporinus singularis Sokolov, 1947.

Diagnosis. — Small, irregular, dendroid colonies. Corallites triangular, quadrangular or rounded in transverse sections, regularly spaced within the colony. Connecting tubes numerous, in four vertical rows on corallite margins. Tabulae numerous, incomplete, oblique, form no vesicular ring at the corallite walls. Septal spines absent or poorly developed.

Remarks. — The genus has been characterized and compared with the similar genera — *Tetraporella* and *Hayasakaia* — by Sokolov (1947, 1955, 1962) and Vassiljuk (1966). Seven species of the genus have been described so far: *T. singularis* Sokolov, *T. nankingensis* (Yoh), *T. carbonica* (Chu), *T. septentrionalis* (Gorsky), *T. septentrionalis intermedia* (Gorsky), *T. gilungshanensis* Lin Bao-yui, *T. grandis* Lin Bao-yui, all from the Carboniferous and Lower Permian as well as a few species from the Silurian.

Occurrence. — Upper Silurian: USSR (Vaygach Island, North Urals); Lower Carboniferous: USSR (Taymyr, Novaya Zemlya, Donetsk Basin), Southern China (Yunnan); Lower Permian: Southern China (Sechuan); Lower Permian; Spitsbergen (Hornsund).

Tetraporinus spitsbergensis sp. n.

(pl. 19: 3a, b; pl. 20: 1a, b; figs. 19A, B)

Holotype: Specimen ZPAL T XIII/127; pl. 19: 3a, b.
Type horizon: Vc Coral Horizon, "Upper Treskelodden Beds", Lower Permian.

Type locality: Treskelen, Creek IV, Hornsund, Spitsbergen.
Derivation of the name: spitsbergensis — coming from Spitsbergen.

Diagnosis. — Corallites long, straight, with spaces of 0.1—0.5 mm or touching each other, with diameters of 1.0—1.5 mm. Corallite walls 0.2—0.3 mm thick. Connecting tubes numerous, 0.3—0.4 mm in diameter, arranged in three-four vertical rows with spaces of 1.4—2.0 mm. Apart from connecting tubes are numerous, blind wall outgrowth. Tabulae numerous, thin, vesicular, oblique, bent and funnel-shaped, often incomplete. No septal spines.

Material. — Three almost complete, fairly well preserved colonies: ZPAL T XIII/127—129 from Treskelen and Hyrnefjellet. 1. Treskelen: Nos.: 127 and 128 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: No. 129 in the Vb Coral Horizon.

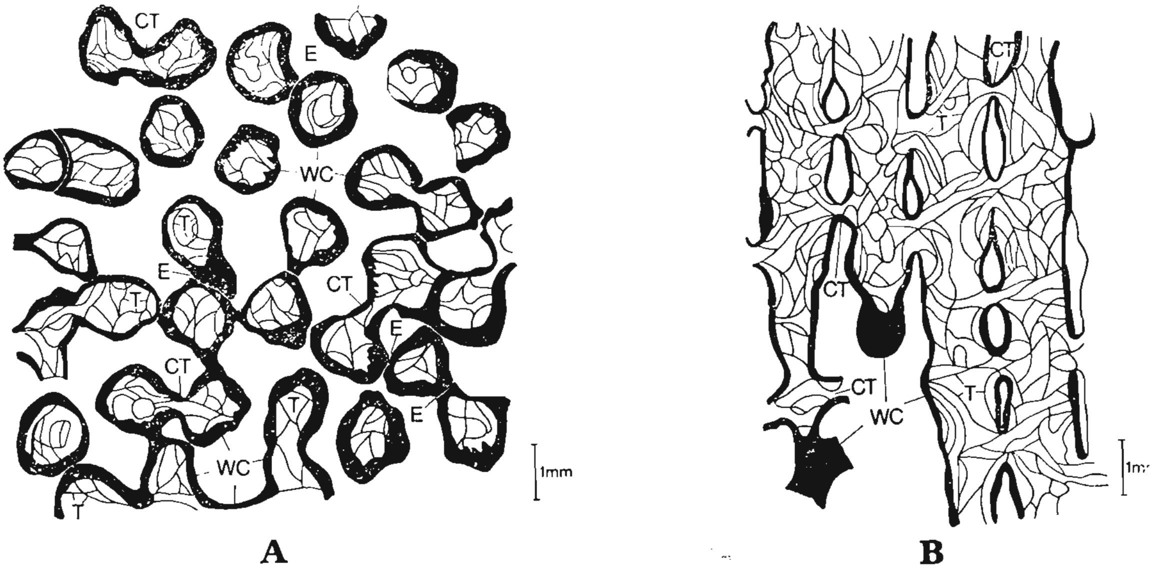

Fig. 19

Tetraporinis spitsbergensis sp. n., Treskelen, Coral Horizon Vc, Creek IV; *A* transverse section (ZPAL T XIII/128), *B* longitudinal section, holotype (ZPAL T XIII/127); × 5. For explanation of symbols see p. 8—9.

Ten longitudinal and transverse sections have been made.

Description. — Small, irregularly oval, dendroid colonies up to 80 mm in diameter, consisting of long or short, straight corallites with uneven jagged walls. Corallites arranged in parallel in the colony, with spaces 0.1—0.7 mm, most often 0.1—0.5 mm, or touching one another with walls or their margins. In transverse sections corallites irregularly round and oval, often triangular or quadrangular in outline, sometimes form short zigzag chains. Their diameters are 1.2—1.5 mm. Corallite walls uneven, 0.1—0.3 mm thick, most often 0.2—0.3 mm, with indistinct, concentric-lamellar microstructure. Epitheca undiscernible. Connecting tubes numerous, not very long, 0.25—0.6 mm in diameter, most often 0.3—0.4 mm, arranged in three-four vertical rows on corallite margins, spaced every 1.4—2.0 mm. Apart from connecting tubes there are blind, side wall outgrowths, resembling incipient connecting tubes. Tabulae quite numerous, thin, vesicular, oblique, bent and funnel-shaped, often incomplete. No septal spines.

Remarks. — Due to its morphology and arrangement of tabulae (resembling representatives of the genus *Hayasakaia*) as well as the presence of blind outgrowths on corallite walls, *Tetraporinus spitsbergensis* sp. n. is most similar to the type species — *T. singularis* SOKOLOV from the Lower Carboniferous of Taymyr (SOKOLOV 1947). However, it differs from it in having considerably smaller diameters, more angular corallites, wider spaces between them, much thicker corallite walls as well as smaller diameters of connecting tubes and larger vertical distans between the tubes.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Tetraporinus spinosus sp. n.

(pl. 19: 4; pl. 20: 2; figs. 20A, B)

Holotype: Specimen ZPAL T XIII/132; pl. 19: 4; pl. 20: 2.
Type horizon: Vb_1 Coral Horizon, "Upper Treskelodden Beds", Lower Permian.
Type locality: S slope of Hyrnefjellet, Hornsund, Spitsbergen.
Derivation of the name: spinosus — having septal spines.

Diagnosis. — Corallites short, arranged radially in circular whorls or chains of *Halysites*-type, with spaces 0.1—0.8 mm. In transverse sections corallites round, triangular, 1.2—1.4 mm in diameter, and oval, and quadrangular with measurements of 1.0—1.5 × 1.4—2.0 mm. Corallite walls 0.15—0.3 mm thick. Connecting tubes numerous, short, 0.4—0.6 mm in diameter, with spaces about 1.0 mm. Tabulae scarce, horizontal and oblique, concave and funnel-shaped, incomplete. Septal spines numerous, short, thick.

Material. — Three almost complete, well preserved colonies: ZPAL T XIII/130—132 from Treskelen and Hyrnefjellet. 1. Treskelen: Nos.: 130 and 131 in the Vc Coral Horizon, Creek IV. 2. Hyrnefjellet: No. 132 in the Vb_1 Coral Horizon.

Nine longitudinal and transverse sections have been made as well as three series of imprints on celluloid film for the study of budding and colony development.

Description. — Small, flat and flat-convex, dendroid colonies, up to 50 mm in diameter and up to 20 mm in height. Corallites short, tube-like, unequal, arranged radially, parallel only in early stages of colony development, extend perpendicularly to the colony surface. Calices deep, straight or slightly conical, with blunt, rounded margins. In transverse sections corallites irregularly round and oval, with more or less distinct triangular or quadrangular

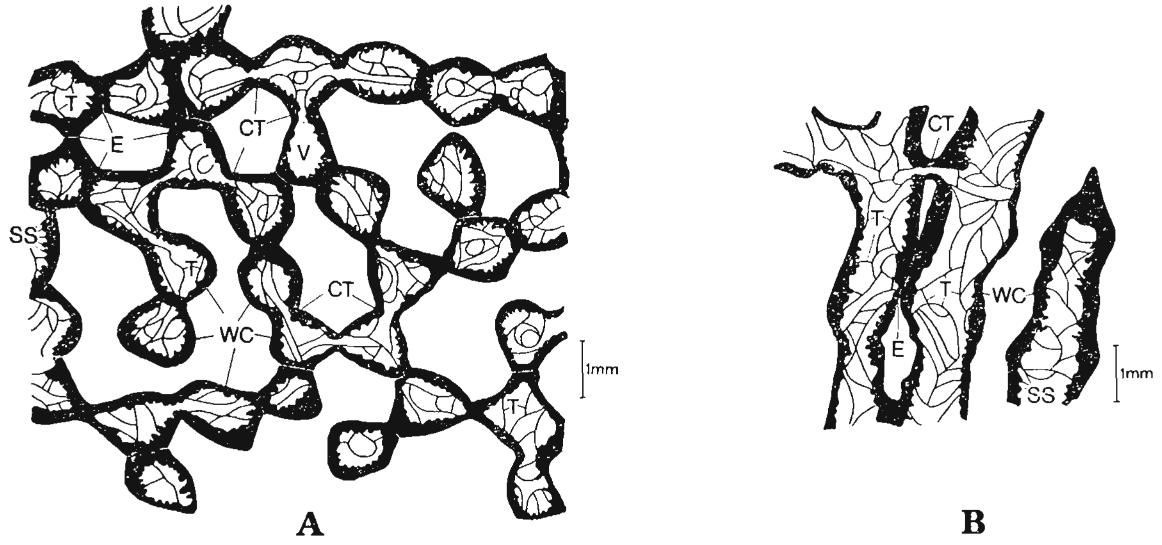

Fig. 20

Tetraporinus spinosus sp. n.; *A* transverse section, Hyrnefjellet, Coral Horizon Vb_1, holotype (ZPAL T XIII/132), *B* longitudinal section, Treskelen, Coral Horizon Vc, Creek IV (ZPAL T XIII/130); × 7.5. For explanation of symbols see p. 8—9.

outlines, grouped in circular whorls (four—six corallites in each) or chains (five—ten corallites in each), resembling colonies of *Halysites*. In whorls and chains the corallites are connected by tubes or touching of the wall margins. Spaces between sparse, single corallites are 0.1—0.8 mm. Triangular and quadrangular corallites are 0.9—1.5 mm in diameter, most often 1.2—1.4 mm, and the oval ones, rectangular in outline with measurements, 1.0—1.5 × 1.4—2.0 mm in cross sections. Corallite walls 0.1—0.4 mm thick, most often 0.15—0.3 mm, with indistinct concentriclamellar microstructure. The walls of the corallites, in some parts of the colony, show pseudofibro-normal microstructure, which may be the effect of later processes of recrystalization. Epitheca very thin, dark. Connecting tubes numerous, short, thick, with unequal diameters of 0.3—0.8 mm, most often 0.4—0.6 mm, often irregularly bent, arranged in three—four vertical rows on corallite margins, with spaces of about 1.0 mm. The lumen of connecting tubes 0.1—0.3 mm in diameter. Tabulae not numerous, thin, concave, rarely straight, oglique, funnel-shaped, incomplete. Septal spines numerous, long, in vertical rows.

Vegetative reproduction in *Tetraporinus spinosus* sp. n. proceeded by calicular and extracalicular budding. In calicular budding, a bud originated by external evagination of a parent calice wall, similarly as in *Syringopora* and *Roemerolites* (see p. 30). During extracalicular budding, young individuals budded off from short stolonal tubes (stolonal budding), lying horizontally on a substrate. Young corallites, were growing arcuately, in early stages, from the stolonal tubes, and later on vertically and parallel to each other. In later stages of a colony development, corallites grew in radial pattern. Stolonal budding was not studied in details because of the poor state of preservation of the investigated colonies.

Remarks. — *Tetraporinus spinosus* sp. n. differs from all known Permo-Carboniferous species of the genus in the presence of well-developed septal spines, distinct, halysitoidal arrangement of the corallites as well as larger corallite diameters [(except *T. grandis* LIN BAO-YUI from the Lower Permian of Southern China (LIN BAO-YUI 1962) which has much larger diameters]. In the arrangement and morphology of tabulae the species resembles *T. singularis* SOKOLOV from the Lower Carboniferous of Taymyr (SOKOLOV 1947). All its remaining features, however, are different.

Tetraporinus spinosus sp. n. is similar to *T. spitsbergensis* sp. n., described above, in corallite diameters, the thickness of corallite walls as well as in the morphology and arrangement of tabulae. It differs, however, in the presence of round and elongated corallites in transverse sections, of distinct halysitoid corallite arrangement and closer spacing, in thicker connecting tubes with wider spaces inbetween, and well-developed septal spines.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Tetraporinus kozlowskii sp. n.

(pl. 21: 1a, b, 2a, b; figs. 21A, B)

Holotype: Specimen ZPAL T XIII/134; pl. 21: 1a, b.
Type horizon: Vb$_2$ Coral Horizon, "Upper Treskelodden Beds", Lower Permian.
Type locality: S slope of Hyrnefjellet, Hornsund, Spitsbergen.
Derivation of the name: kozlowskii — in honour to the late Prof. ROMAN KOZŁOWSKI.

Diagnosis. — Corallites long, spaced every 0.2—0.5 mm. The diameters of triangular and quadrangular corallites in transverse sections variable — 0.8—1.8 mm, most often 1.2—1.8 mm. Measurements of cross-sections oval and rectangular corallites — 1.3—1.6 × 1.8—2.4 mm. Connecting tubes numerous, short, 0.4—0.5 mm in diameter, in three—four rows, spaced every 1.4—2.0 mm. Tabulae numerous, thin, with morphology and arrangement intermediate between *Syringopora* and *Hayasakaia*. Septal spines sparse, long. Spines present also on tabulae.

Material. — Three almost complete, well preserved colonies: ZPAL T XIII/133—135 from Hyrnefjellet and Kruseryggen. 1. Hyrnefjellet: Nos.: 133 and 134 in the Vb_2 Coral Horizon. 2. Kruseryggen: No. 135 in the V Coral Horizon.

Twelve longitudinal and transverse sections have been made as well as two series of imprints on celluloid film for the study of budding and colony development.

Description. — Small, flat and flat-convex, dendroid colonies, up to 80 mm in diameter and up to 30 mm in height. Corallites long, tube-like, straight or slightly bent, arranged radially and perpendicular to the colony surface. In transverse sections corallites irregularly round and oval, triangular and quadrangular in outline, sometimes grouped in short chains (three—five corallites each), where they are connected by tubes or the touching of their walls. Spaces between the isolated corallites unequal, 0.1—0.7 mm, most often 0.2—0.5 mm. The round corallites, triangular and quadrangular in outline are unequal, 0.8—1.8 mm in diameter, most often 1.2—1.8 mm. A few oval corallites, rectangular in outline are 1.3—1.6×1.8—2.4 mm in cross-section. Corallite walls unequal, of variable thickness 0.15—0.3 mm, occasionally 0.05 mm and 0.4 mm, most often 0.2—0.3 mm, of indistinct, concentric-lamellar microstructure. Walls of some corallites have pseudo-fibro-normal microstructure. In colony No. 133 the corallite walls have a two-layer structure. The inner layer of stereoplasm, enclosing the visceral chamber of corallite has a concentric-lamellar microstructure. In the external layer the fibres are arranged radially. Epitheca very thin, dark, discontinuously preserved. Connecting tubes numerous, short, thick, 0.3—0.6 mm in diameter, most often 0.4—0.5 mm, arranged in three—four vertical rows on the wall margins, with spaces of 1.4—2.0 mm. At places where the connecting tubes become very short and the corallites touch one another over large area of walls, there occur connecting pores 0.2— 0.4 mm in diameter. Tabulae numerous, thin, bent, long, strongly oblique and funnel-shaped, sometimes short and incomplete, with no vesicular zone at the walls of corallites. In morphology and arrangement the tabulae expose

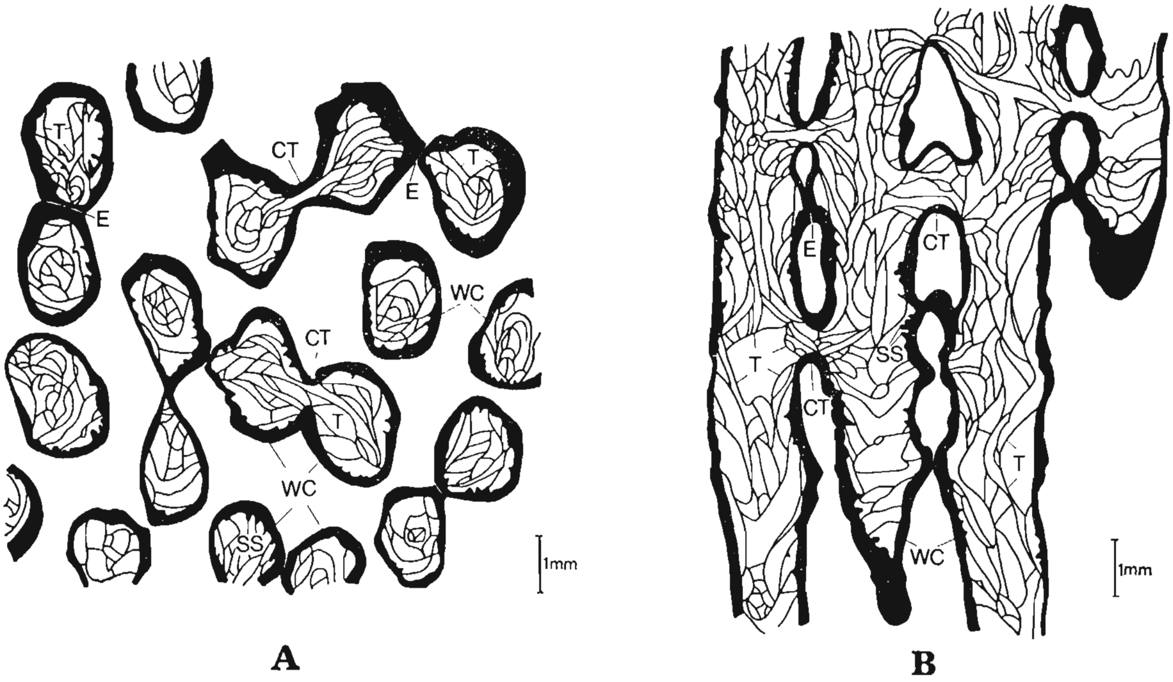

Fig. 21

Tetraporinus kozlowskii sp. n., Hyrnefjellet, Coral Horizon Vb_2, holotype (ZPAL T XIII/134); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

features intermediate between these in *Syringopora* and *Hayasakaia*. Septal spines sparse, large, long, arranged in vertical rows. Single spines occur also on tabulae.

Vegetative reproduction proceeded by calicular extravisceral budding (bud originated in external evagination of the parent calice wall), similarly to *Syringopora*.

Remarks. — *Tetraporinus kozlowskii* sp. n. is most similar to *T. spinosus* sp. n., described above, in spaces between the corallites, the thickness of corallite walls, the diameters of connecting tubes, the morphology and arrangement of tabulae as well as in the presence of septal spines. *T. kozlowskii* sp. n. differs from *T. spinosus* sp. n. in its chaotic (not halysitid) arrangement of corallites with poorly marked triangular and quadrangular sections, larger corallite diameters, much wider spaces between the connecting tubes, more syringoporoid arrangement of tabulae as well as in less developed septal apparatus and presence of spines on the tabulae.

Some similarity to the type species — *T. singularis* SOKOLOV from the Lower Carboniferous of Taymyr (SOKOLOV 1947), can be found only in morphology and the arrangement of the tabulae.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Family **Thecostegitidae** SOKOLOV, 1950
Genus *Neoroemeria* RADUGIN, 1938

Type species: Neoroemeria westsibirica RADUGIN, 1938.

Diagnosis. — See TCHUDINOVA 1964.

Remarks. — Desciiption and comparison with related genera such as: *Syringopora*, *Thecostegites*, *Chonostegites*, *Armalites* and *Roemerolites* were presented by RADUGIN (1938), SOKOLOV (1955, 1962), DUBATOLOV (1959, 1972), CHEKHOVICH (1960), TCHUDINOVA (1964), HILL and JELL (1970), HILL (1981).

According to the authors mentioned above *Neoroemeria* has a number of features similar to both family Syringolitidae and the order Syringoporida (especially the family Thecostegitidae). This makes it difficult to determine its place in the taxonomy. The features mentioned are: 1. Prismatic corallites (polygonal in cross-section), in closely contact with each other, connected by pores occur in the axial zone of the colony. 2. Tube-like (round in cross-section), single corallites, connected by short shapeless tubes or connecting flats (bridges), arranged in tiers. 3. Thick corallites walls, of *Roemerolites* type, with concentric-lamellar microstructure. 4. The presence of large, numerous septal spines, arranged in vertical rows. 5. Tabulae concave and convex, oblique, bent and funnel-shaped (syringoporoidal type) locally vesicular, near the connecting pores they form characteristic bunches as in *Roemeripora*.

According to the present author in representatives of *Neoroemeria* the features of Syringoposida (especially the family Thecostegitidae) dominate over the features of Syringolitidae. It is quite common in representatives of Syringolitidae (e.g. *Roemeria*, *Roemeripora*) and of Syringoporida (e.g. *Roemerolites*, *Neoroemeria*, *Haysakaia*, see also p. 49) that polygonal corallites, closely in contact with one another and connected by pores occur together with single, tube-like (round in cross-section) ones in one colony. This is common also in Spitsbergen colonies as well. In Syringolitidae, however, when single corallites are present, short tubes or pore-canals (solenia) appear instead of connecting flats (or bridges), arranged in tiers. Sometimes, on short, vertical segments the corallites are not connected at all. The presence of connecting flats or bridges in *Neoroemeria* seems to be the feature decisive for the inclusion of the genus in Syringoporida (family Thecostegitidae), all the more because connecting elements of similar morphology have been observed locally (most often at the initial growth stages of colonies) in some of the Spitsbergen colonies of *Syringopora* and *Hayasakaia*.

Very thick corallite walls (especially single corallites) with rows of strongly developed septal spines in *Neoroemeria* are more characteristic of Syringoporida (e.g. *Roemerolites*) than Syringolitidae, which have thinner walls and smaller septal spines. Also morphology and the arrangement of relatively sparse tabulae in *Neoroemeria* resembles more the representatives of *Thecostegites*, *Syringopora* or *Roemerolites* than Syringolitidae. The bunches of tabulae near connecting pores, characteristic of the genus *Roemeripora*, occur also in some *Syringopora* species and do not seem to be a diagnostic feature of Syringolitidae.

Four species of *Neoromeria* have been described so far: *N. westsibirica* RADUGIN, *N. parasitica* RADUGIN, *N. gibbosa* TCHUDINOVA, *N. soshkinae* TCHUDINOVA.

Occurrence. — Givetian: USSR (North-East periphery of Kuznetsk Basin); Upper Carboniferous through Lower Permian: Spitsbergen (Hornsund, Isfjorden).

Neoroemeria spitsbergensis sp. n.

(pl. 20: 3, 4; pl. 23: 1, 2a, b; figs. 22A, B)

Holotype: Specimen ZPAL T XIII/137; pl. 20: 4; pl. 23: 1.
Type horizon: Ia Coral Horizon, "Upper Treskelodden Beds", Lower Permian.
Type locality: Treskelen, Creek IV, Hornsund, Spitsbergen.
Derivation of the name: spitsbergensis — coming from Spitsbergen.

Diagnosis. — Corallites long, tube-like spaced every 0.2—0.8 mm, touching one another or connected by bridges. In transverse sections corallites round, 1.6—2.0 mm in diameters and slightly oval, with measurements 1.5—2.0 × 2.0—2.6 mm. Corallite walls very thick 0.3—0.7 mm, with two-layer microstructure. Connecting bridges of flats 0.3—0.5 mm thick, densely spaced, with spaces of 0.2—0.6 mm, with an internal canal about 0.3 mm in diameter. Tabulae sparse, thick, of two types: 1. very long, strongly oblique — form a short axial canal, and 2. short, concave and convex, horizontal, spaced every 0.1—0.5 mm. Septal spines widely spaced, long.

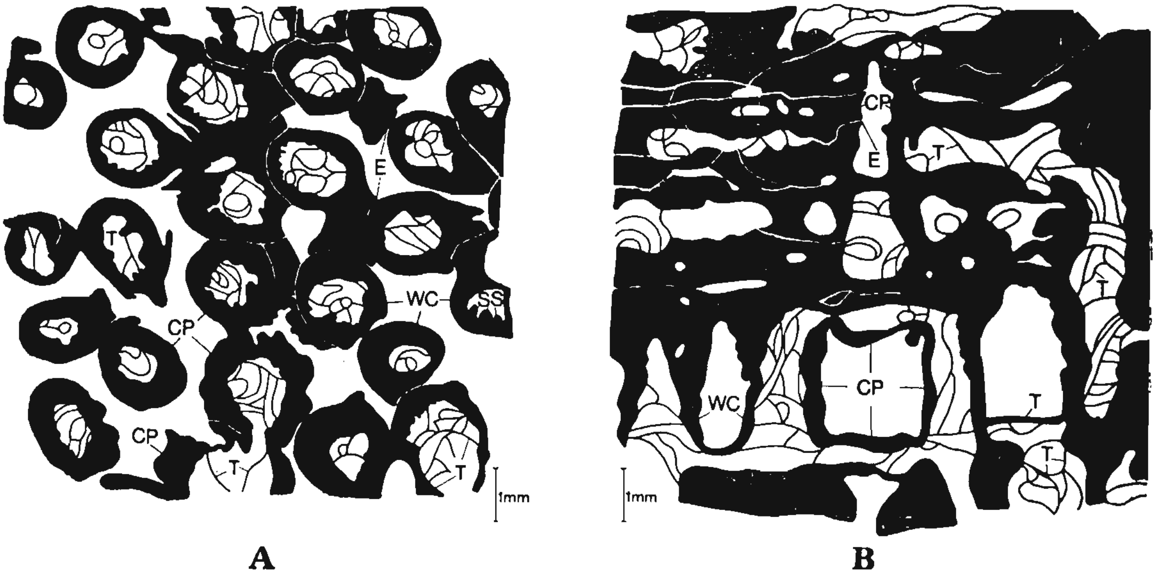

Fig. 22

Neoroemeria spitsbergensis sp. n., Treskelen, Coral Horizon Ia, Creek IV, holotype (ZPAL T XIII/137); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Material. — Two almost complete, well preserved colonies: ZPAL T XIII/137, 138 from Treskelen. No. 137 in the Ia Coral Horizon, Creek IV, and No. 138 in the Va Coral Horizon, Creek IV.

Seven longitudinal and transverse sections have been made as well as three series of imprints on celluloid film for the study of colony development.

Description. — Colonies irregularly flat-convex, up to 180 mm in diameter and about 70 mm in height, without axial zone with densely spaced corallites. Corallites long, tube-like, bent, arranged in parallel, with irregular spaces of 0.1—1.2 mm, often 0.2—0.8 mm touching with their walls or connected by very irregular connecting bridges or flats. In transverse sections corallites more or less regularly round (not polygonal), with variable diameters of 1.4—2.4 mm most often 1.6—2.0 mm, and slightly oval, with dimensions 1.5—2.0 × 1.0—2.6 mm. Corallite walls (uneven?), very thick — 0.3—0.7 mm, most often 0.3—0.5 mm — of *Roemerolites* or *Multithecopora* type, with two-layer microstructure. The inner layer, enclosing the visceral chamber is thick and has indistinct, concentric-lamellar microstructure. The thin outer layer has fibro-normal microstructure. Epitheca thin, dark, poorly developed Visceral chamber strongly compressed, oval and irregular in cross-section. Connecting elements in the form of very irregular, bent, swelled bridges, 0.3—0.5 mm thick. In longitudinal sections of the colony they are in the form of bent or convex irregular tubes, densely arranged tiers, with spaces of 0.2—0.6 mm. Inside the connecting bridges there are bent canals, round or oval in cross-section, about 0.3 mm in diameter, sometimes with single, sparse, bent tabulae. In longitudinal sections, in the vertical sequence of the colony, the connecting bridges arranged in tiers, are grouped in thick zones, separated by thin, up to 10 mm, ones, almost completely lacking connections between the corallites. Tabulae sparse, thick, of two types: 1. very long, strongly oblique, arched, funnel-shaped (not vesicular), often forming a short, and wide axial canal, about 0.2—0.5 mm in diameter, and 2. short, concave and convex, horizontal and oblique, incomplete, spaced every 0.1—0.5 mm. Groups of long and strongly oblique tabulae most often alternate with groups of short, horizontal tabulae. Septal spines numerous, sparsely spaced in vertical rows, very large, thick, deeply embedded in the stereoplasm of corallite walls.

Vegetative reproduction in this species proceeded by calicular extravisceral budding — similarly to that in *Roemerolites laminatus.*

Remarks. — *Neoroemeria spitsbergensis* sp. n. differs from all known species of the genus in the colony habbit (irregularly flat-convex, and not cylindrical), the presence of long, strongly oblique and bent tabulae, resembling representatives of *Syringopora,* which locally form a short axial canal, as well as the absence of polygonal corallites, closely in contact with one another and connected by pores.

From the type species, *Neoroemeria westsibirica* RADUGIN, from the Givetian of the North-East periphery of Kuznetsk Basin (RADUGIN 1938; DUBATOLOV 1972), the new species, moreover, differs in having larger corallite diameters, thinner connecting bridges and better developed septal spines. Only the thickness of corallite walls is similar in the two species.

Occurrence. — Lower Permian: Spitsbergen (Hornsund).

Neoroemeria permica sp. n.

(pl. 22: 1a—e; figs. 23A, B)

Holotype: Specimen ZPAL T XIII/136; pl. 22: 1a—e.

Type horizon: "Wordiekammen Limestone", Upper Carboniferous through Lower Permian.

Type locality: Skanska Bukta, Isfjorden, Spitsbergen.

Derivation of the name: permica — coming from the Permian (the first species of the genus described from the Permian).

Diagnosis. — Flat-convex colony with internal structure of *Tubipora* type. Corallites straight, long, spaced every 0.2—0.7 mm, in transverse section regularly round, 1.4—1.6 mm in diameter. Corallite walls 0.2—0.4 mm thick. Connections between the corallites of three types: connecting bridges 1.4—3.0 mm thick, with vertical spaces of 3.0—6.0 mm, connecting tubes short, about 0.5 mm in diameter, and connecting pores about 0.2 mm in diameter. Tabulae not numerous, very long, thick, strongly oblique and funnel-shaped, near the connecting elements concave and horizontal. Septal spines strongly developed in 22—26 vertical rows. Spines occur on the tabulae.

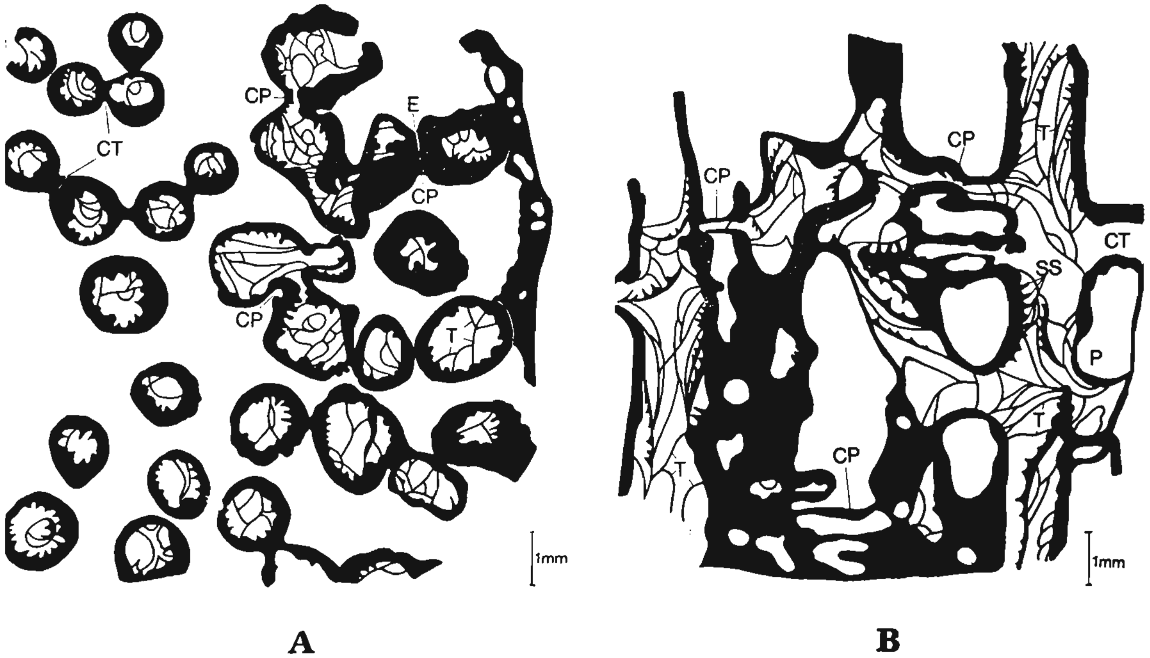

Fig. 23

Neoroemeria permica sp. n., Isfjorden (Skanska Bukta), "Wordiekammen Limestone", holotype (ZPAL T XIII/136); *A* transverse section, *B* longitudinal section; × 7.5. For explanation of symbols see p. 8—9.

Material. — One complete, very well-preserved colony from Isfjorden (Skanska Bukta): No. ZPAL T XIII/136 in the "Wordiekammen Limestone". Five longitudinal and transverse sections have been made as well as two series of imprints on celluloid film for the study of budding and colony development.

Description. — Flat-convex, hemispherical, dendroid colony, about 150 mm in diameter and about 70 mm in height, in its internal structure resembling colonies of the genus *Tubipora*. Corallites long, tube-like, straight, arranged in parallel, with irregular spaces of 0.1—1.2 mm, most often 0.2—0.7 mm or touching one another. Corallites arranged perpendicularly to the colony surface. In transverse section, corallites regularly round, rarely slightly oval, 1.4—1.6 mm in diameter, very rarely 1.0—1.3 mm and 1.7—2.0 mm in diameter. Calices very deep, strongly conical, with sharp margins, and with numerous septal spines. Corallite walls thick, 0.1—0.5 mm, most often 0.2—0.4 mm, with indistinct concentric-lamellar microstructure. Epitheca relatively thick, 0.02—0.1 mm, dark, well developed, with numerous vertical septal furrows, similar to those in Rugosa. There are three kinds of connections between the corallites: 1. Irregular, horizontal, large outgrowths of corallite walls in the form of connecting bridges, 1.4—3.0 mm in diameter (thickness), placed most often at the same level in all observed corallites of the colony, arranged in tiers, with irregular vertical spaces of 3.0—6.0 mm. Irregular zones of more or less dense packing of these elements are visible in transverse sections. 2. Connecting bridges are locally reduced to irregular, short connecting tubes, often swollen and bulb-like, about 0.5 mm in diameter, arranged in irregular vertical rows, with spaces close to those of connecting bridges. 3. Where corallites touch with their walls there occur connecting pores about 0.2 mm in diameter. Both connecting bridges and tubes have the same type of wall microstructure as the corallite walls. Inside the canals and chambers in connecting bridges occur single, bent tabulae. Tabulae in corallites not very numerous, thick, very long, strongly oblique and funnel-shaped, of the syringoporoidal type, near the connecting elements concave and straight, horizontal, often passing through the connecting tubes and pores to the neighbouring corallites. Septal spines very numerous, strongly developed, thick, long, blunt or sharp ending, arranged in 22—26 regular vertical rows. Single spines occur also on the tabulae.

Vegetative reproduction in *Neoroemeria permica* sp. n. proceeded by calicular and extracalicular budding.

Calicular extravisceral budding proceeded in a similar way to that in *Syringopora* and *Roemerolites* (bud originated in external evagination of a parent calice wall). Details of this process could not be observed. Development of the colony by extracalicular budding proceeded by budding of young corallites from horizontally lying, short stolonal tubes or from bridges connecting corallites.

Numerous spherical or irregular, structureless, light yellow patches of skeletal tissue (diameter 0.4—0.6 mm) occur in the corallite walls, especially in the walls of the connecting bridges, which may represent traces of some internal organisms, maybe symbionts.

Remarks. — *Neoroemeria permica* sp. n., similarly to *N. spitsbergensis* sp. n., differs from previously described species of this genus in the absence of polygonal corallites which form an axial zone of a colony, as well as in the presence of long syringoporoidal tabulae.

Neoroemeria permica, sp. n., having in common with *N. spitsbergensis* sp. n. the general colony form and morphology and pattern of tabulae, differs from it in having more regular, rounded corallites in transverse section with smaller diameters and thinner corallite walls with homogeneous, concentric-lamellar (not bilamellar) microstructure. *N. permica* sp. n. also has a more strongly developed epitheca with septal furrows, and much thicker connecting bridges which are more widely spaced vertically. It differs also in much stronger development of septal apparatus and in the presence of large spines on tabulae.

Occurrence. — Upper Carboniferous through Lower Permian: Spitsbergen (Isfjorden).

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PLATES

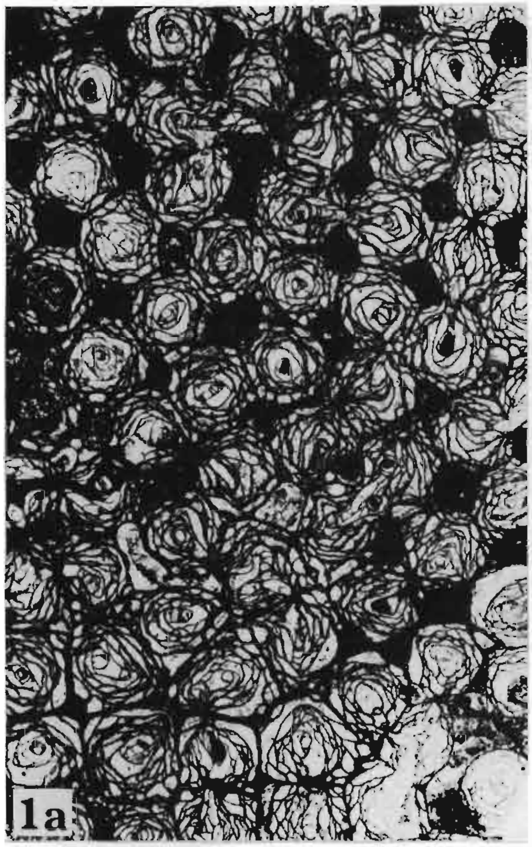
A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 1

Fig. 1. *a* Transverse section, × 5; *b* longitudinal section, × 5; ZPAL T XIII/16; Colony with a typical structure; Treskelen, Coral Horizon IVb, Creek II.

Fig. 2. Longitudinal section through a fragment of a colony with densely spaced corallites, × 5; ZPAL T XIII/20; Treskelen, Coral Horizon Vc, Creek IV.

Fig. 3. Transverse section through a fragment of a colony with densely spaced corallites, × 5; ZPAL T XIII/31; Hyrnefjellet, Coral Horizon Va_1.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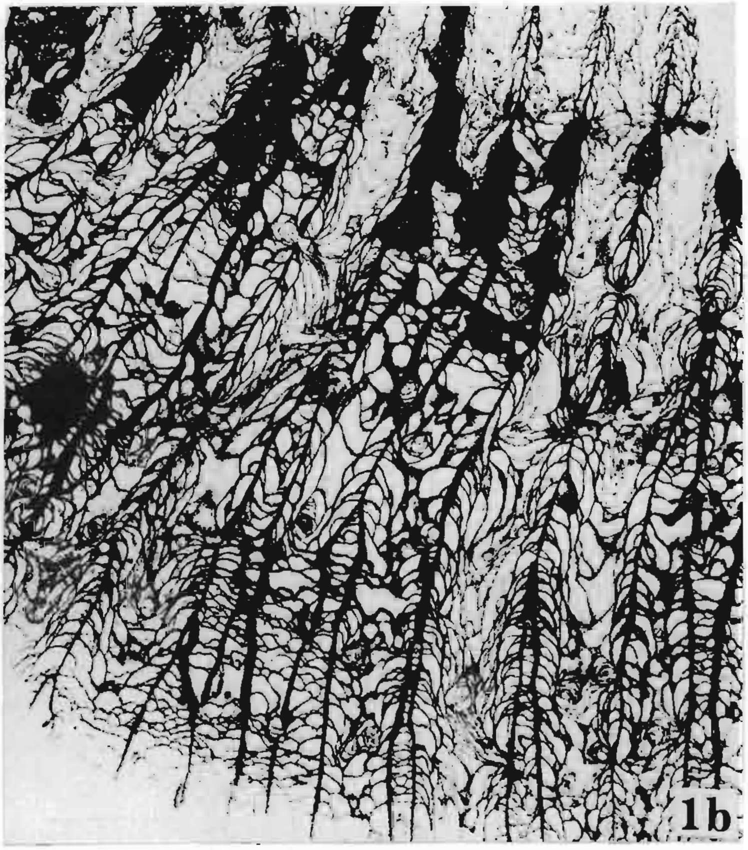
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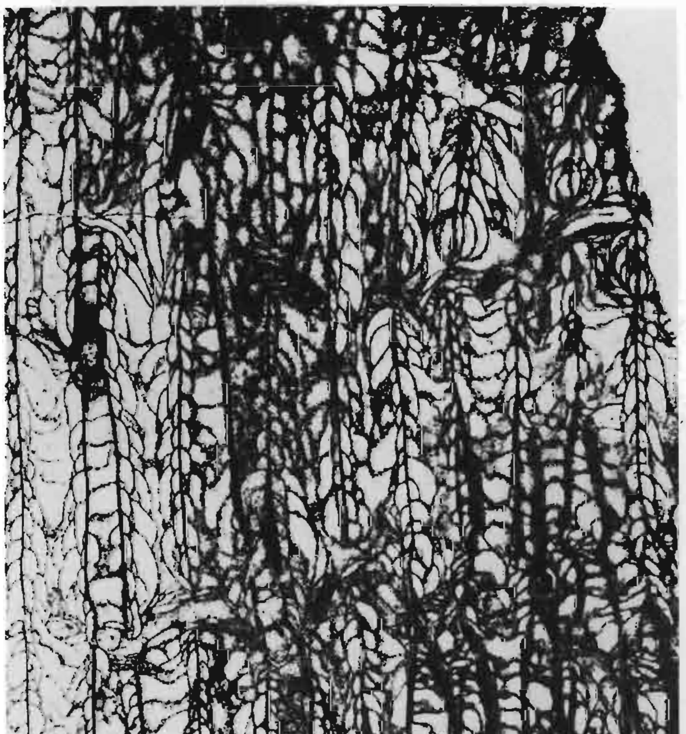
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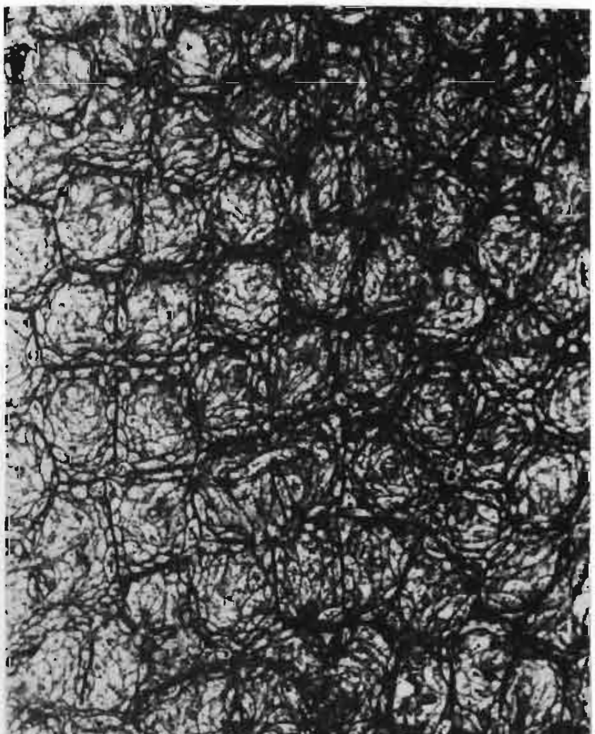
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 2

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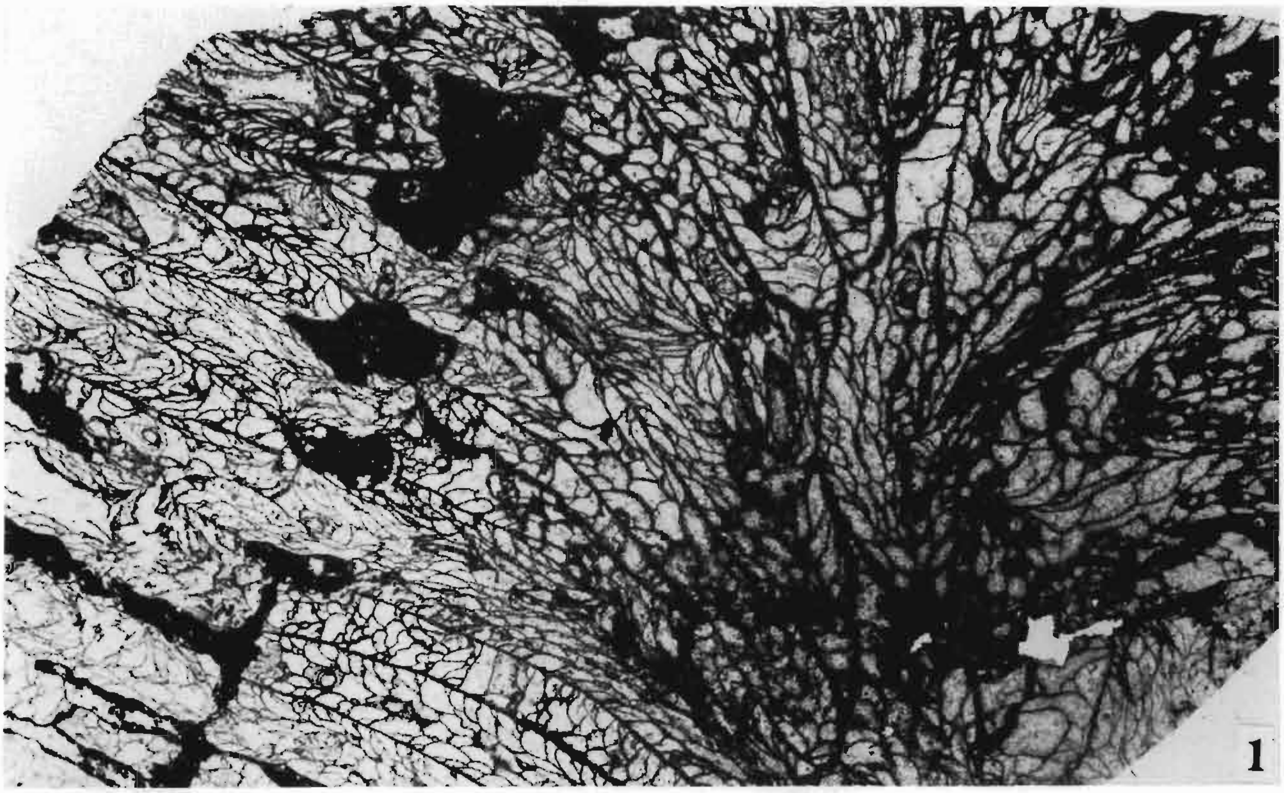
Roemeripora wimani HERITSCH, 1939	35

Fig. 1. Longitudinal section through a fragment of a colony, showing budding zone and radial orientation of corallites, × 5; ZPAL T XIII/17; Treskelen, Coral Horizon IVb, Creek II.

Fig. 2. Transverse section through a fragment of a colony with loosely spaced corallites, × 5; ZPAL T XIII/16; Treskelen, Coral Horizon IVb, Creek II.

Fig. 3. Longitudinal section through a fragment of a colony with loosely spaced corallites, × 5; ZPAL T XIII/32; Hyrnefjellet, Coral Horizon Va_1.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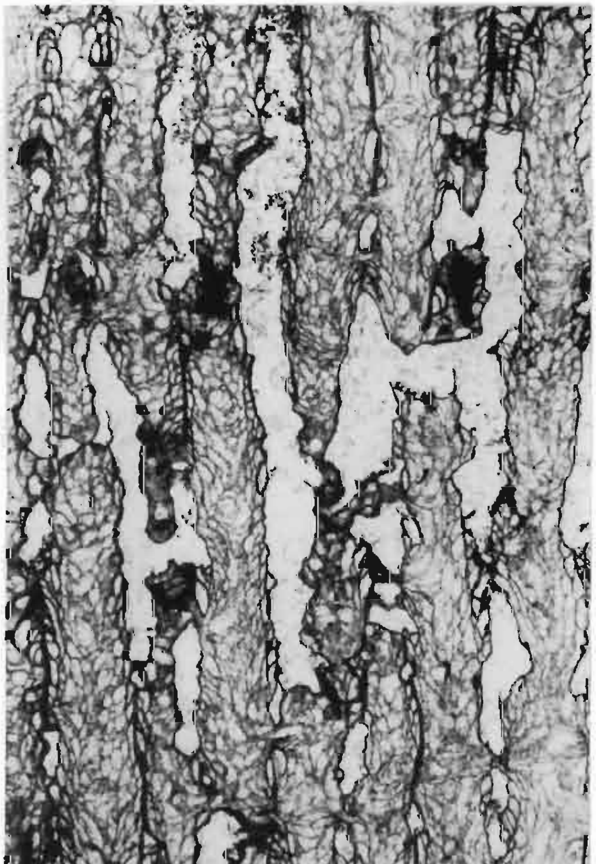
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 3

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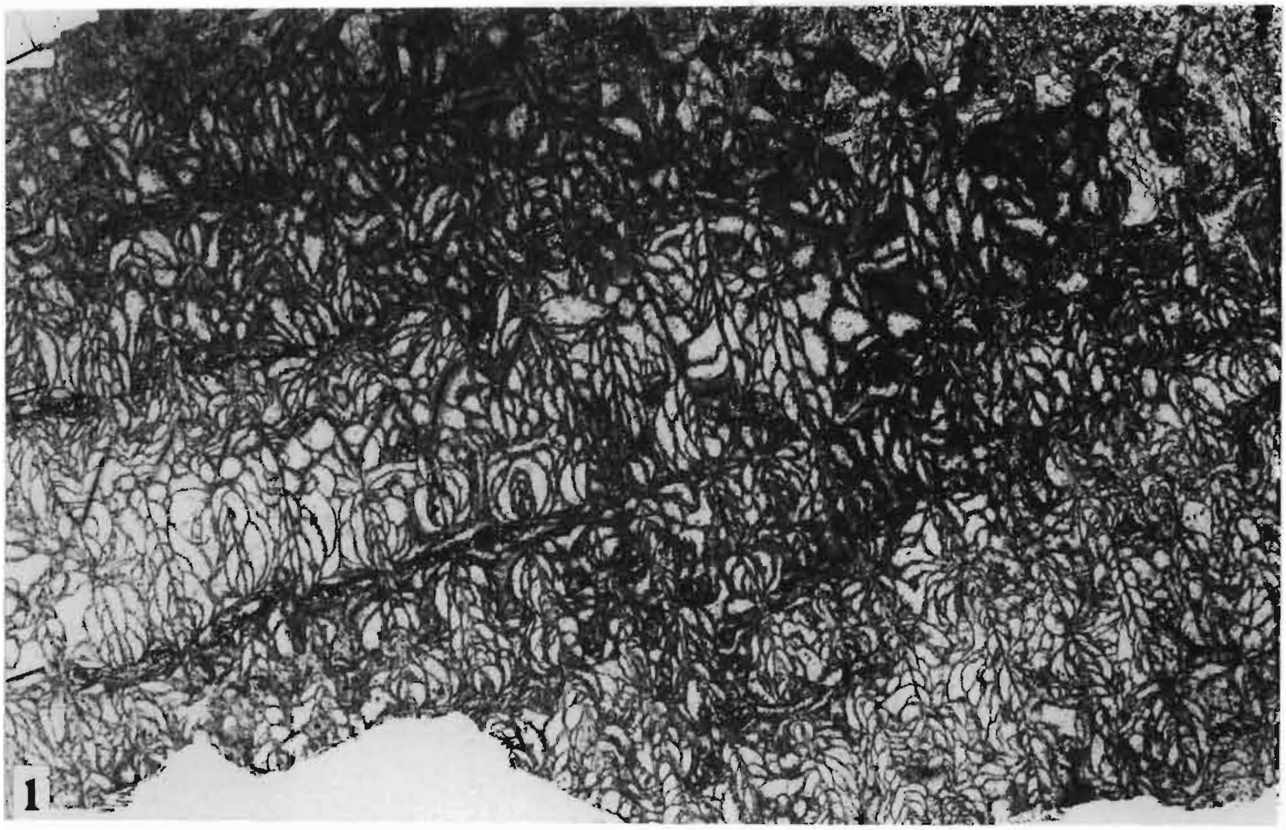
Roemeripora wimani HERITSCH, 1939	35

Fig. 1. Longitudinal section through the near surface part of 18 year old colony with 6 growth bands visible, × 5; ZPAL T XIII/18; Treskelen, Coral Horizon Va, Creek IV.

Fig. 2. Longitudinal section through a central part of a dozen years old colony with seven growth bands visible, × 5; ZPAL T XIII/31; Hyrnefjellet, Coral Horizon Va_1.

Fig. 3. Transverse section through a fragment of a colony with thick walled corallites, × 5; ZPAL T XIII/1; Treskelen, Coral Horizon Ia, Creek IV.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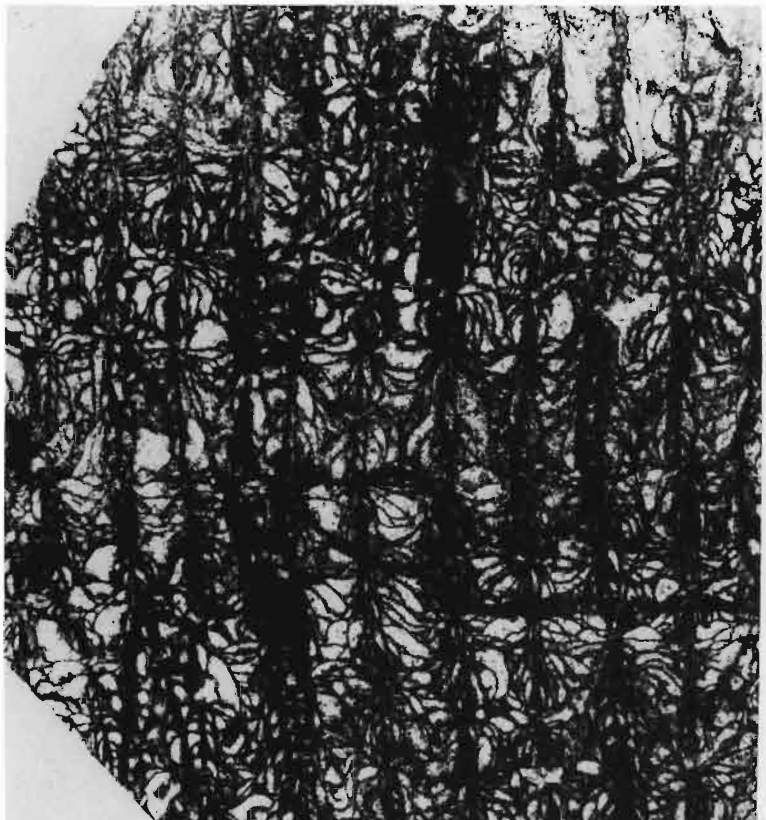
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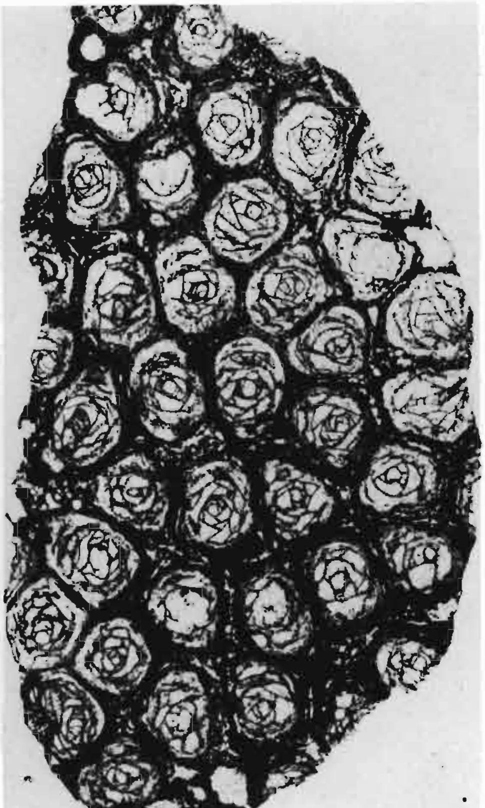
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 4

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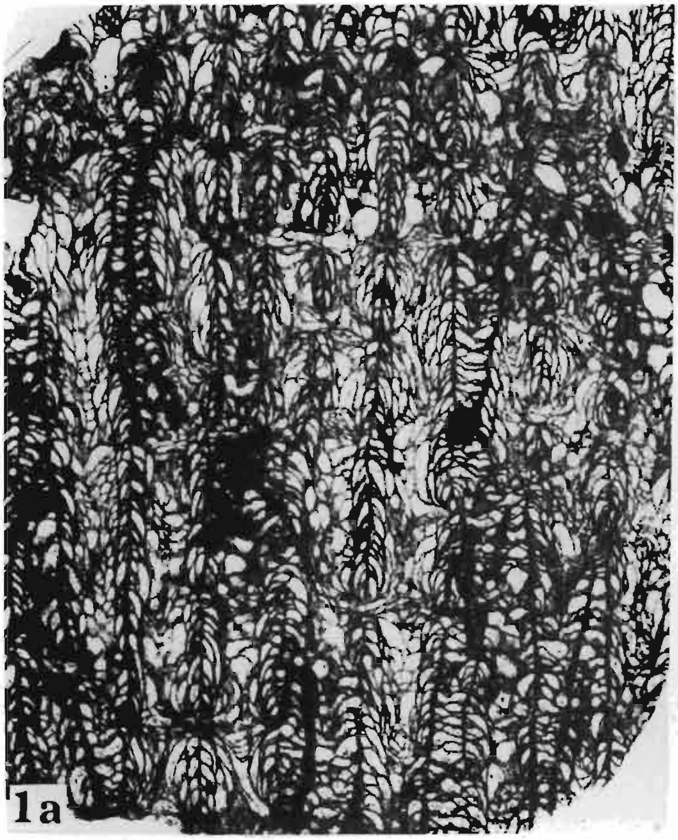
Roemeripora minor HERITSCH, 1939 37

Fig. 1. Colony with a typical structure. a longitudinal section, × 5; *b* transverse section, × 5; ZPAL T XIII/54; Hyrnefjellet, Coral Horizon Va_2.

Fig. 2. Transverse section through a fragment of a colony with corallites having loosely spaced tabulae, × 5; ZPAL T XIII/55; Hyrnefjellet, Coral Horizon Va_3.

Fig. 3. Transverse section through a fragment of a colony with loosely spaced corallites, × 5; ZPAL T XIII/38; Treskelen, Coral Horizon Vc, Creek IV.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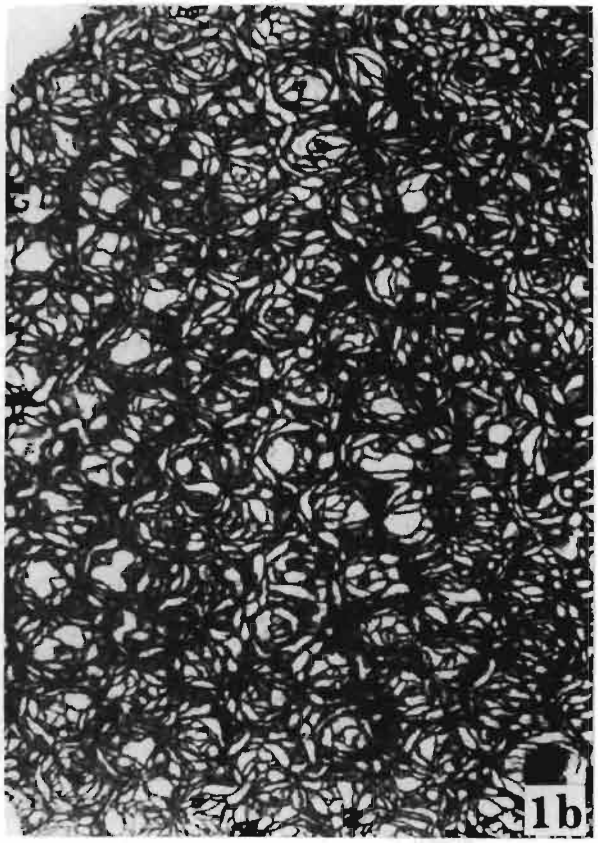
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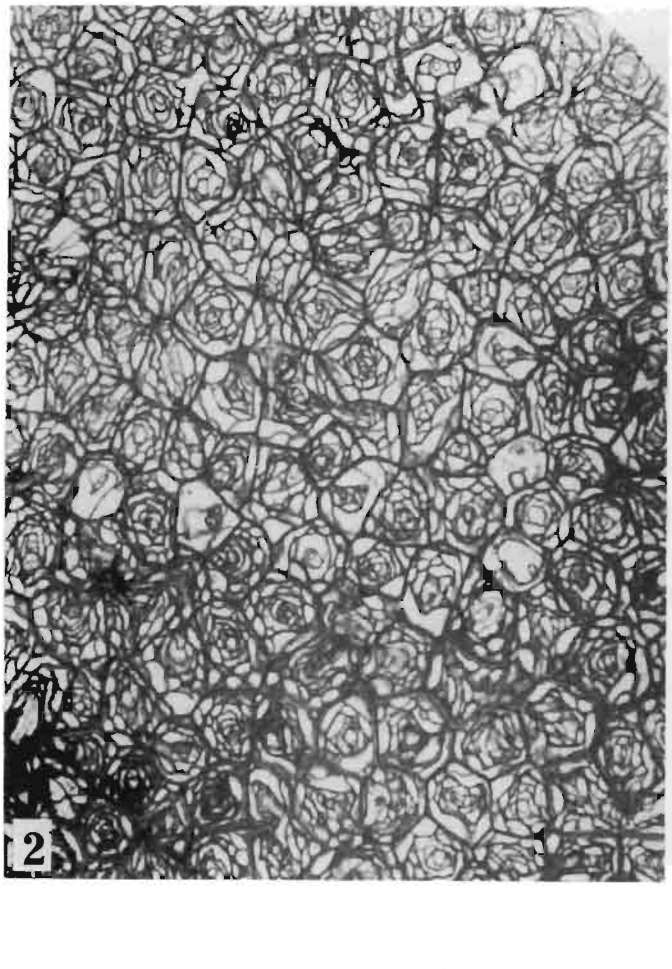
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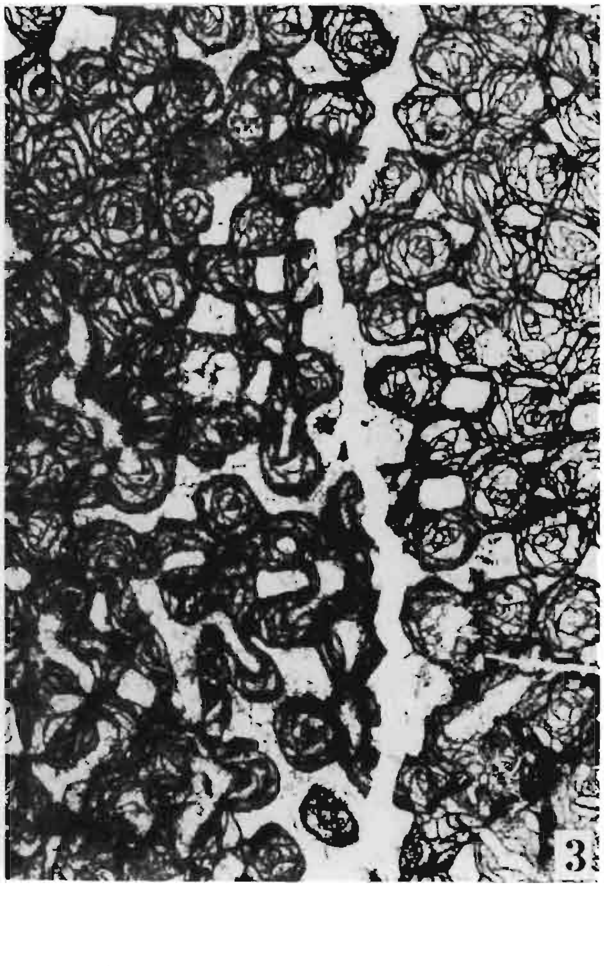
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 5

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Roemeripora minor HERITSCH, 1939 37

Fig. 1. Longitudinal section through the central part of a dozen years old colony with loosely spaced corallites — eight growth bands visible, × 5; ZPAL T XIII/55; Hyrnefjellet, Coral Horizon Va_3.

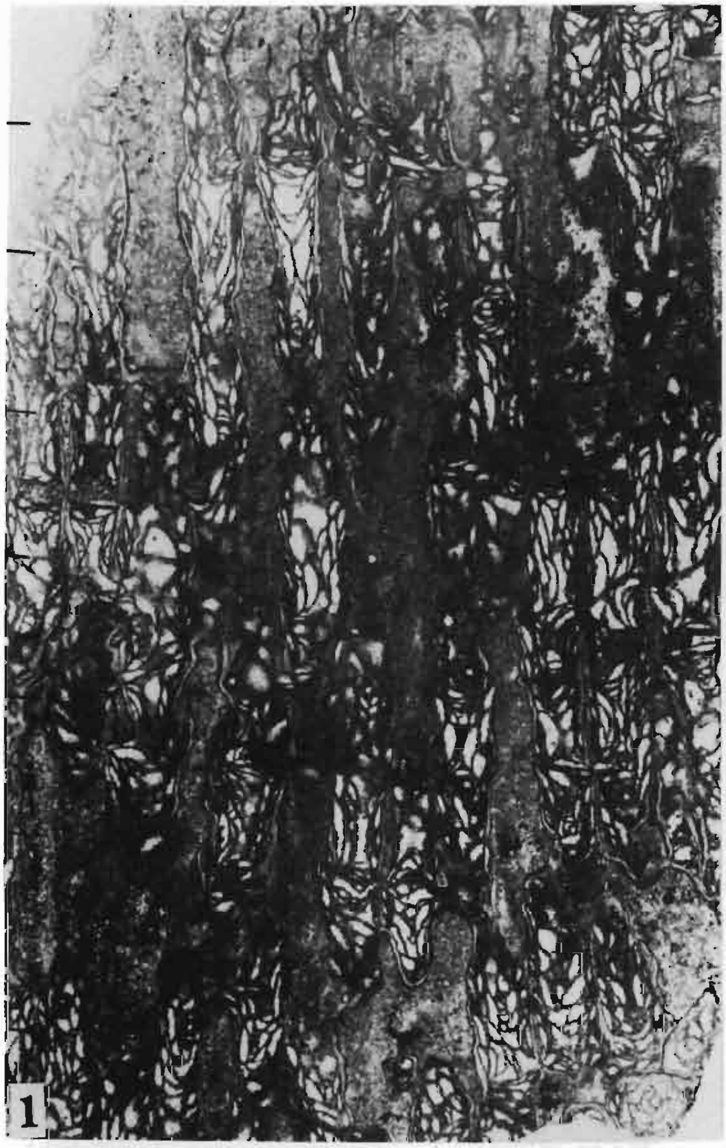
Roemeripora media sp. n. 38

Fig. 2. Longitudinal section through a colony with eroded surface — holotype ZPAL T XIII/62, which is in turn overgrown by a colony of *Hayasakaia multispinosa* sp. n. — holotype ZPAL T XIII/121, × 5; Treskelen, Coral Horizon Va, Creek IV.

Fig. 3. Transverse section through a fragment of a colony with thick walled corallites and simple tabulae, × 5; ZPAL T XIII/59; Treskelen, Coral Horizon Va, Creek IV.

Multithecopora sp. 54

Fig. 4 Longitudinal section through a fragment of a colony, × 5; ZPAL T XIII/115; Urnetoppen, Coral Horizon V.



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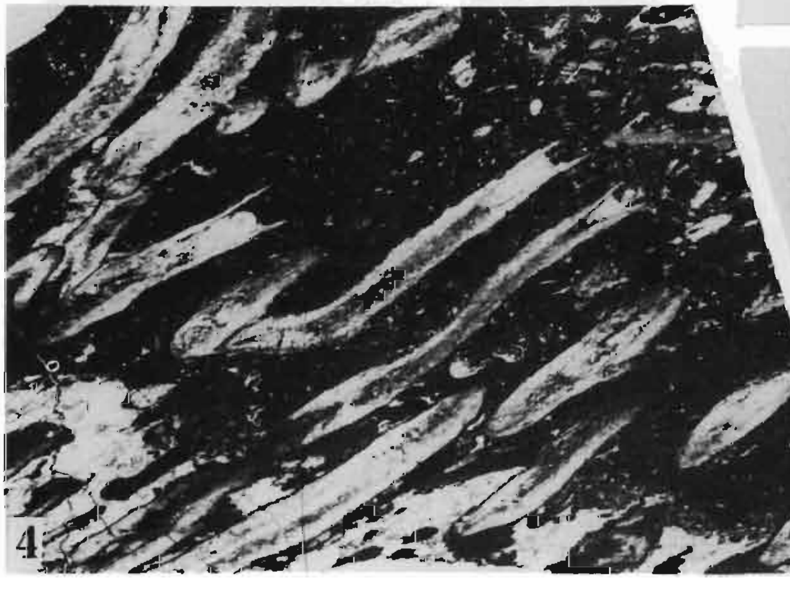

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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 6

Page

Roemeripora media sp. n. 38

Fig. 1. *a* longitudinal section, × 5; *b* transverse section, × 5; holotype ZPAL T XIII/62; Treskelen, Coral Horizon Va, Creek IV.

Roemeripora hornsundensis sp. n. 40

Fig. 2. *a* longitudinal section, × 5; *b* transverse section, × 5; holotype ZPAL T XIII/68; Treskelen, Coral Horizon Ib, Creek IV.


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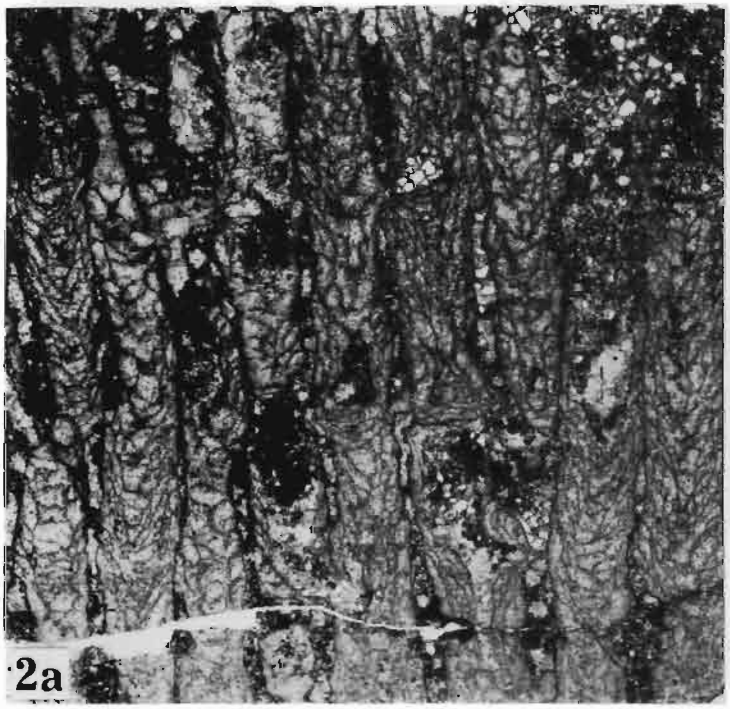
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 7

Page

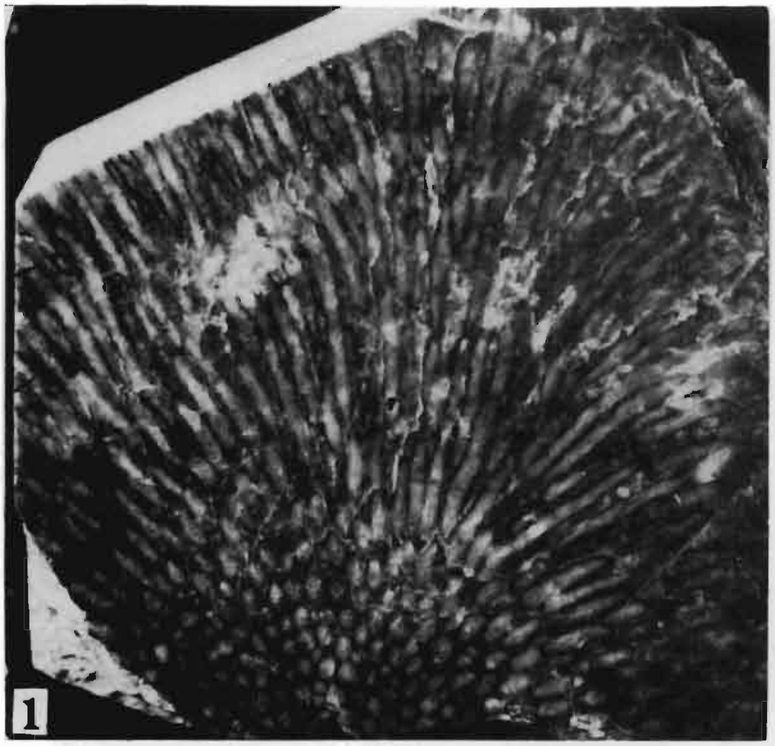
Roemeripora aspinosa NOWIŃSKI, 1982 39

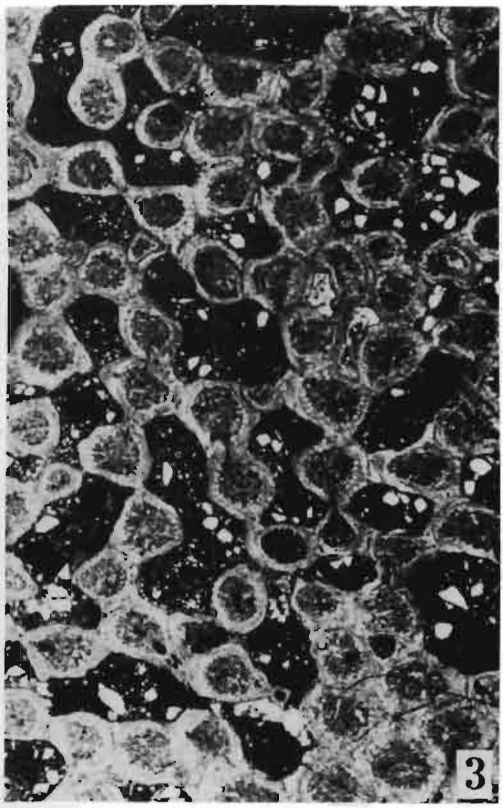
Fig. 1. Longitudinal section through ten year old colony with growth bands visible, × 1.5; holotype ZPAL T XIII/21; Hyrnefjellet, Coral Horizon Vb_2.

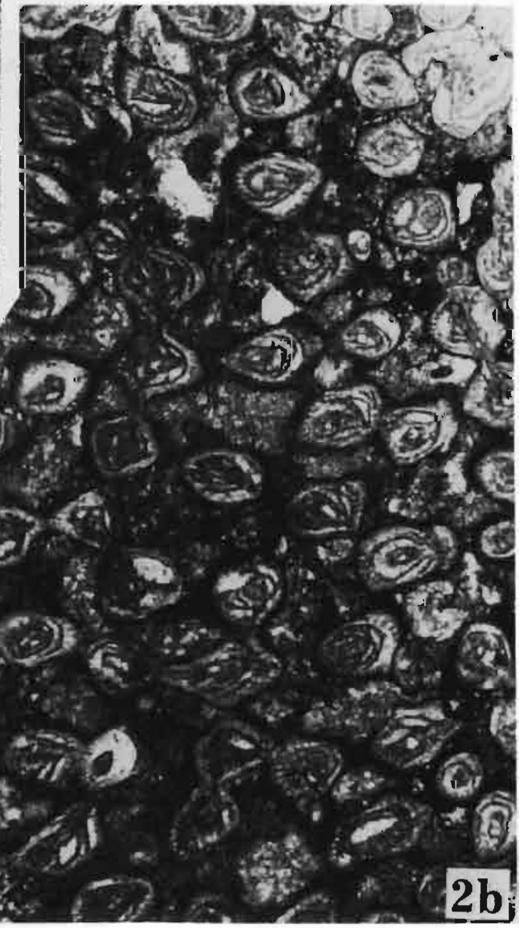
Syringopora quadriserialis SOKOLOV, 1950 41

Fig. 2. *a* longitudinal section, × 5; *b* transverse section, × 5; ZPAL T XIII/81; Hyrnefjellet, Coral Horizon Vb_1.

Fig. 3. Transverse section through a fragment of a colony with corallites arranged in a chain-whorl pattern and strongly developed septal spines, × 5; ZPAL T XIII/73; Treskelen, Coral Horizon Vc, Creek IV.







A. NOWIŃSKI: LATE PALAEOZOIC TABULATA from SPITSBERGEN

A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 8

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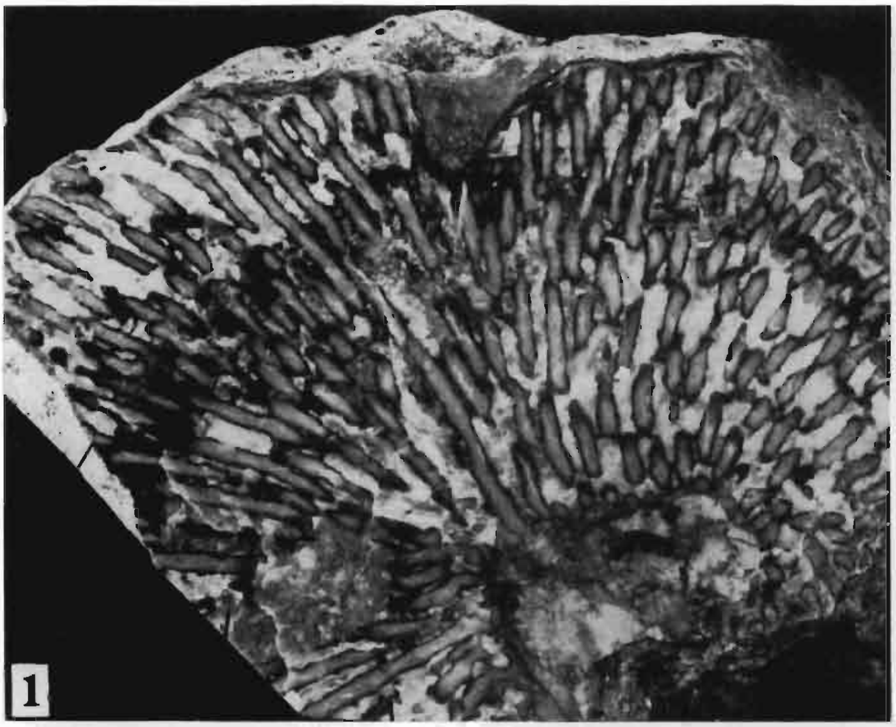
Syringopora quadriserialis SOKOLOV, 1950	41

Fig. 1. Longitudinal section through a six year old colony with growth bands visible, × 1.5; ZPAL T XIII/81; Hyrnefjellet, Coral Horizon Vb_1.

Fig. 2. Longitudinal section through corallites with strongly developed septal spines, × 5; ZPAL T XIII/73; Treskelen, Coral Horizon Vc, Creek IV.

Syringopora subreticulata NOWIŃSKI, 1976	42

Fig. 3. *a* longitudinal section, × 5; *b* transverse section, × 5; ZPAL T XIII/89; Hyrnefjellet, Coral Horizon Vb_2.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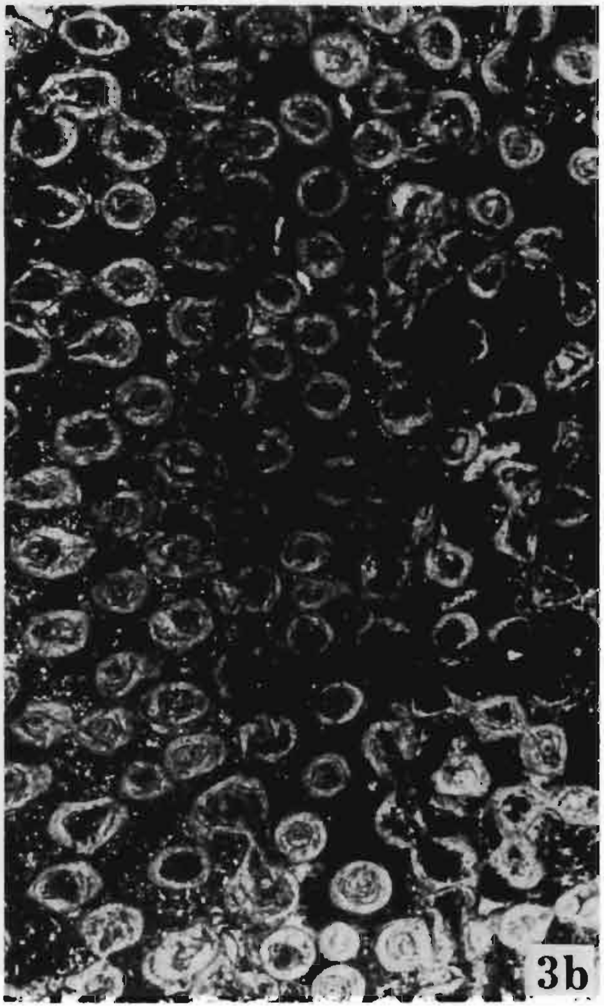
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PLATE 9

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Syringopora subreticulata NOWIŃSKI, 1976 42

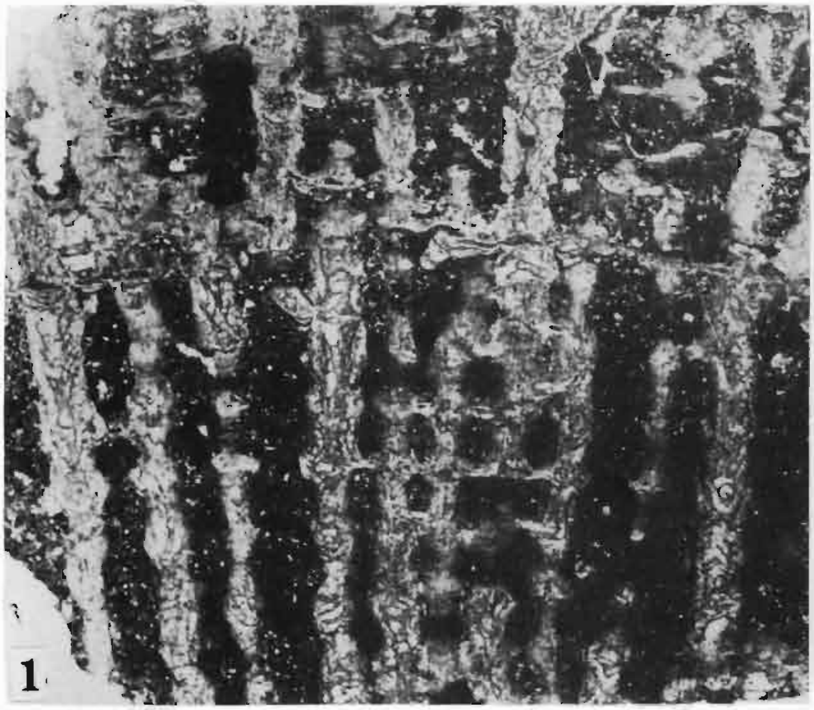
Fig. 1. Longitudinal section through a fragment of a colony with densely spaced connecting tubes, × 5; ZPAL T XIII/85; Hyrnefjellet, Coral Horizon Va_4.

Fig. 2. Transverse section through corallites with strongly developed septal spines, × 5; ZPAL T XIII/87; Hyrnefjellet, Coral Horizon Vb_1.

Syringopora cf. *reticulata* GOLDFUSS, 1826 43

Fig. 3. *a* longitudinal section, × 5; *b* transverse section, × 5; ZPAL T XIII/91; Hyrnefjellet, Coral Horizon Vb_1.

Fig. 4. Longitudinal section through a fragment of a colony with corallites having strongly thickened tabulae, × 5; ZPAL T XIII/90; Treskelen, Coral Horizon Vc, Creek IV.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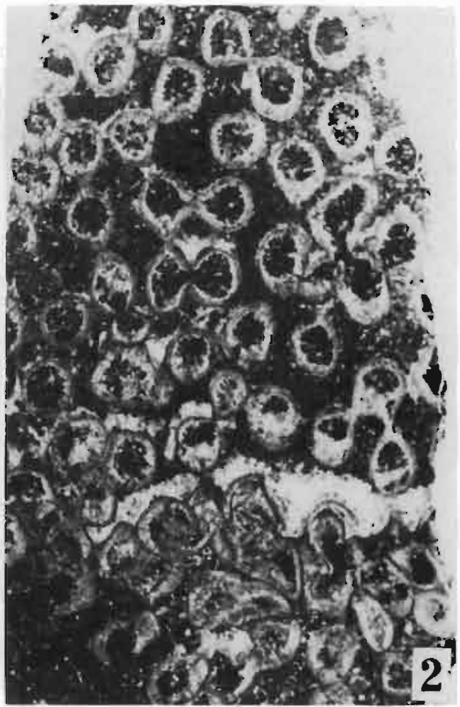
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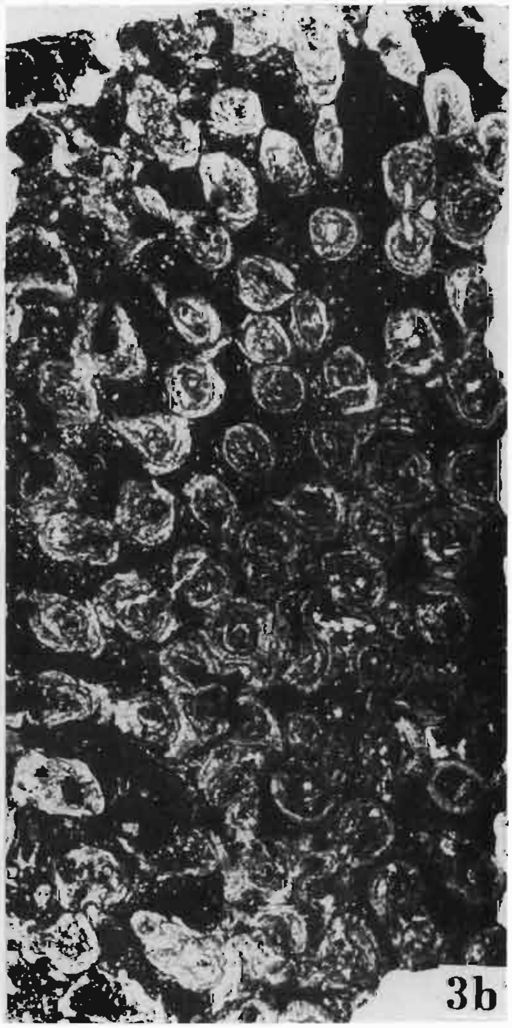
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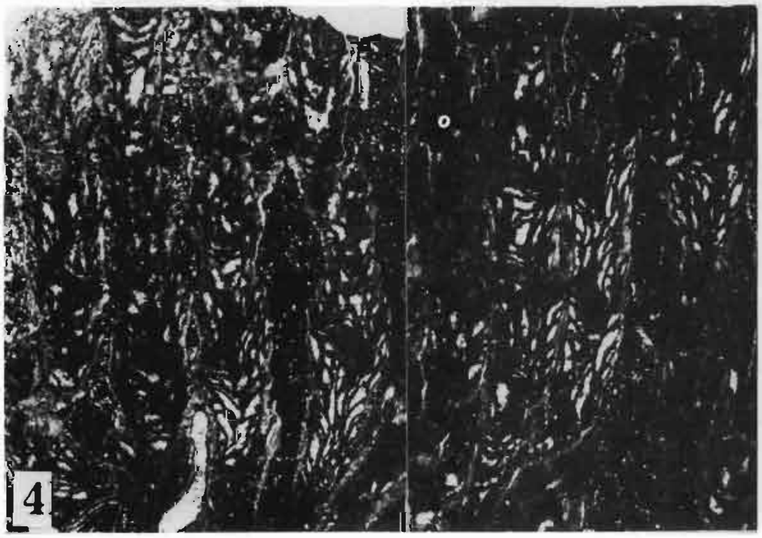
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 10

Page

Syringopora stuckenbergi sp. n. 44

Fig. 1. *a* longitudinal section, × 5; *b* transverse section, × 5; holotype ZPAL T XIII/92; Treskelen, Coral Horizon Vc, Creek IV.

Syringopora kruseryggensis sp. n. 45

Fig. 2. *a* transverse section, × 5; *b* longitudinal section, × 5; holotype ZPAL T XIII/93; Kruseryggen, Coral Horizon V.


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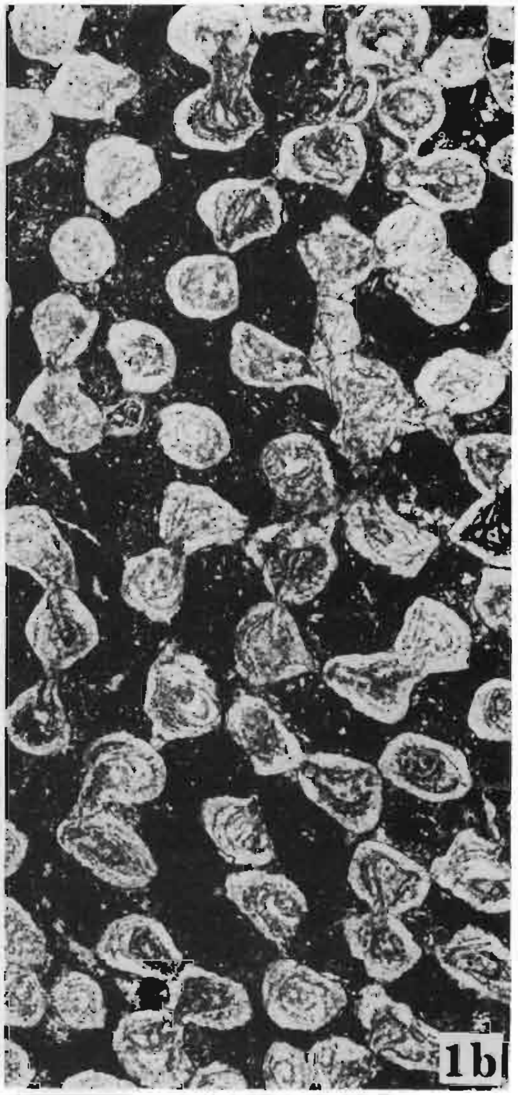
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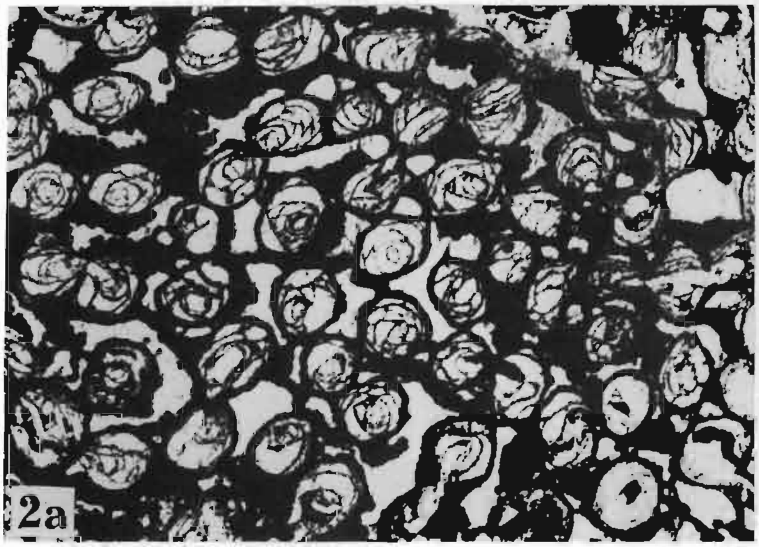
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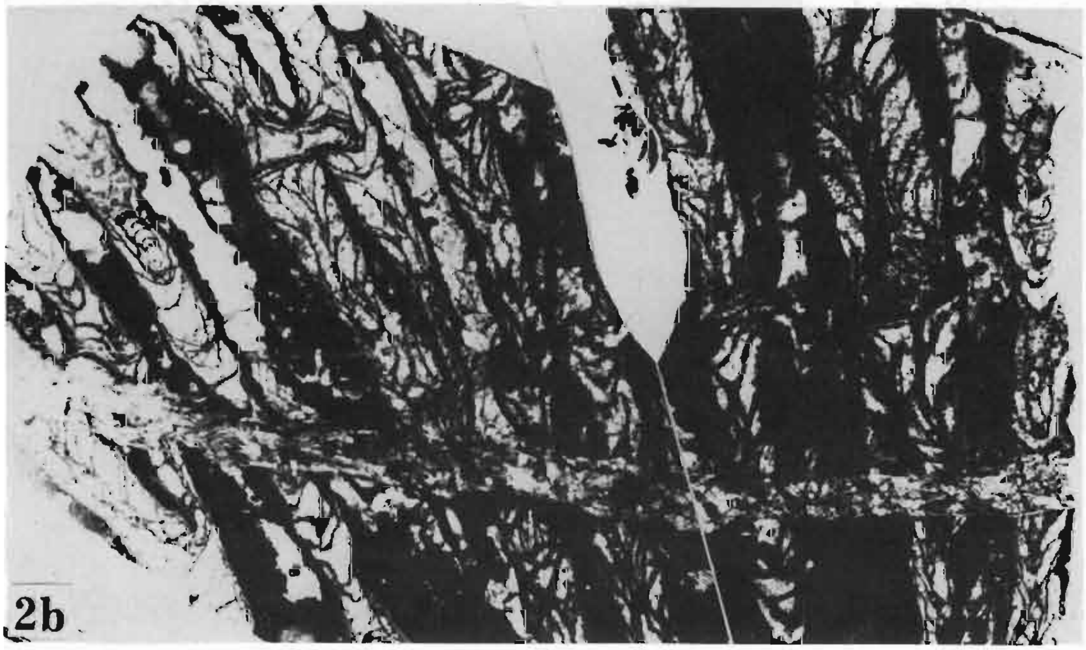
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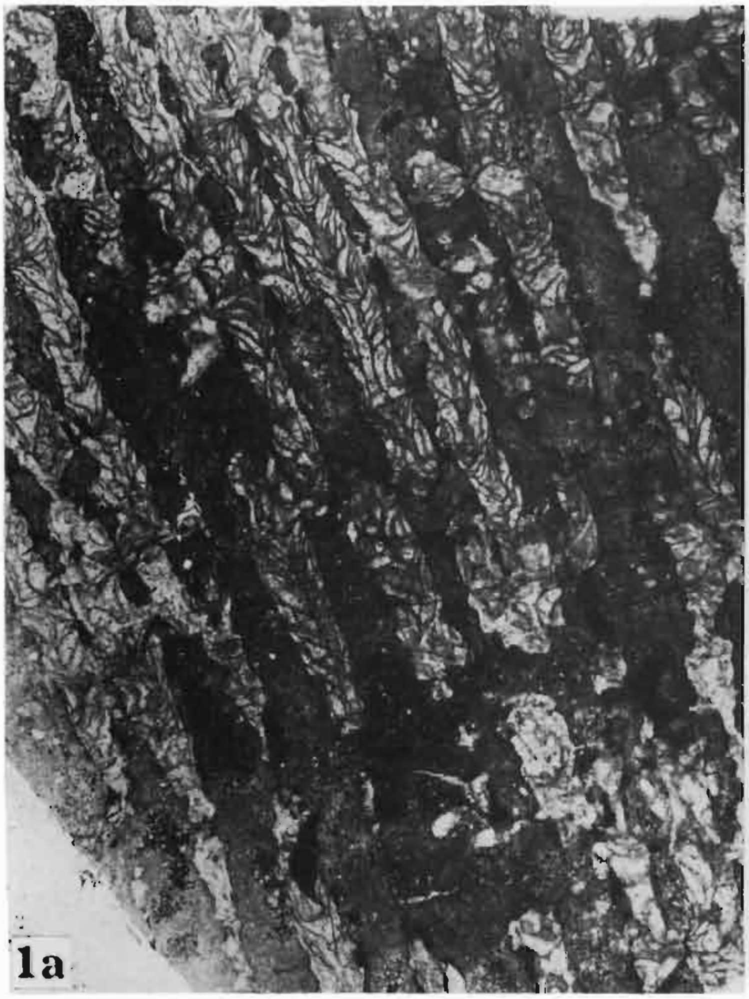
A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 11

Fig. 1. *a* longitudinal section, × 5; *b* transverse section through a fragment of a colony with densely packed corallites which are connected by pores, × 5; holotype ZPAL T XIII/96; Hyrnefjellet, Coral Horizon Vc.

Fig. 2. *a* longitudinal section through a fragment of a colony in which some corallites are connected by pores and others by tubes, × 5; *b* transverse section through a fragment of a colony with loosely spaced corallites, × 5; ZPAL T XIII/95; Hyrnefjellet, Coral Horizon Vb_2.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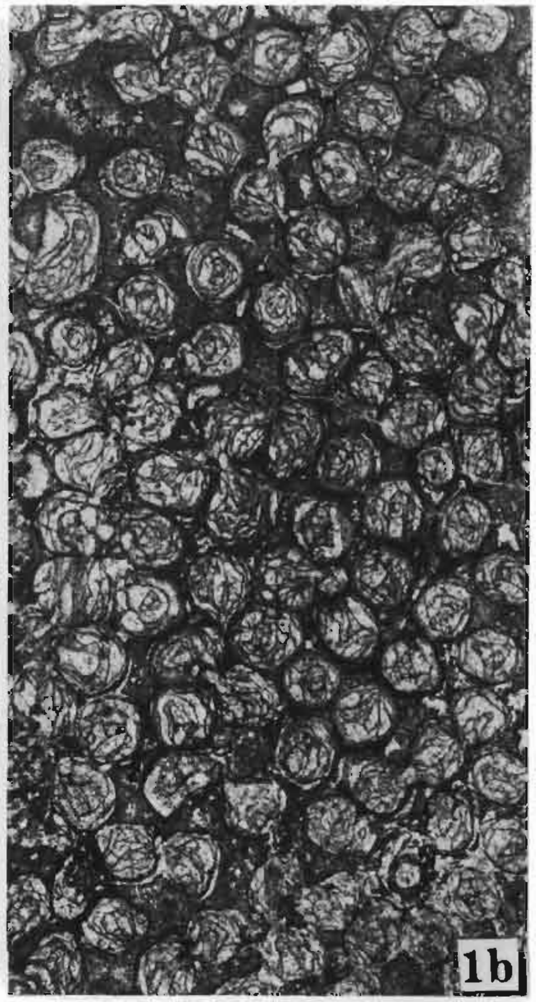
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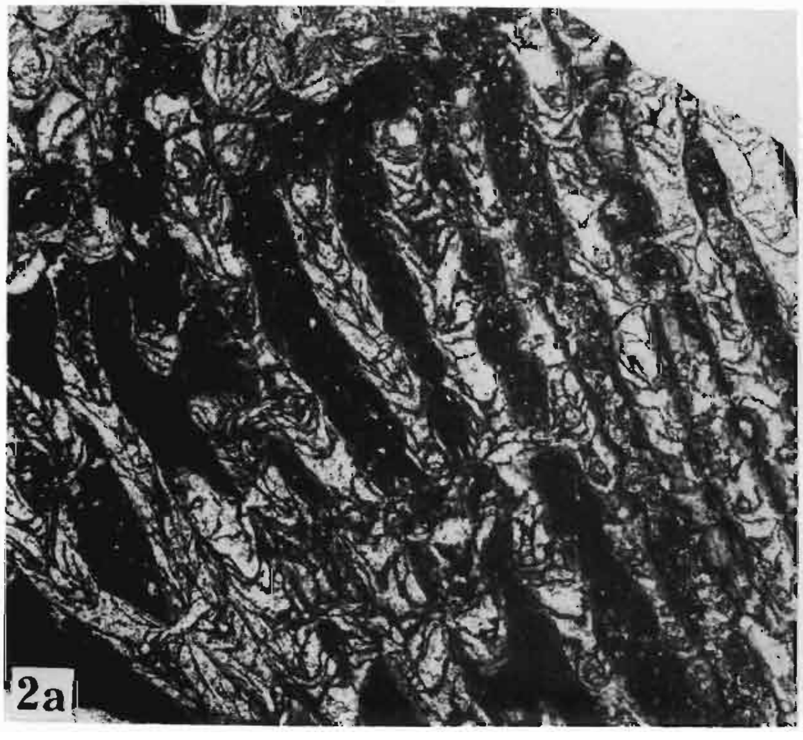
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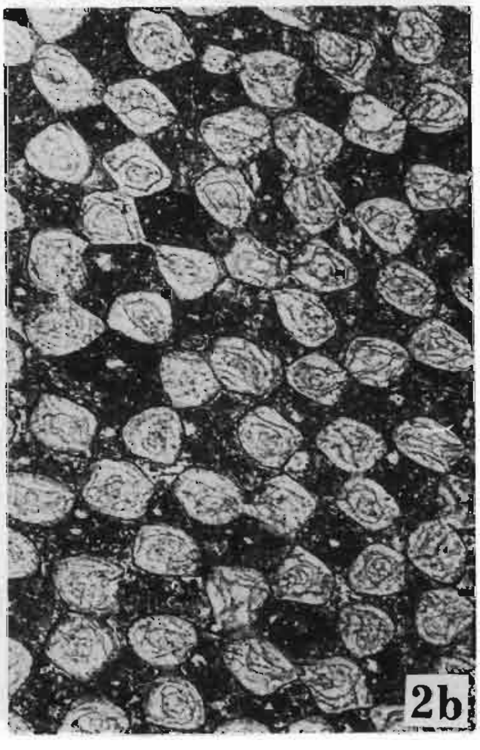
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

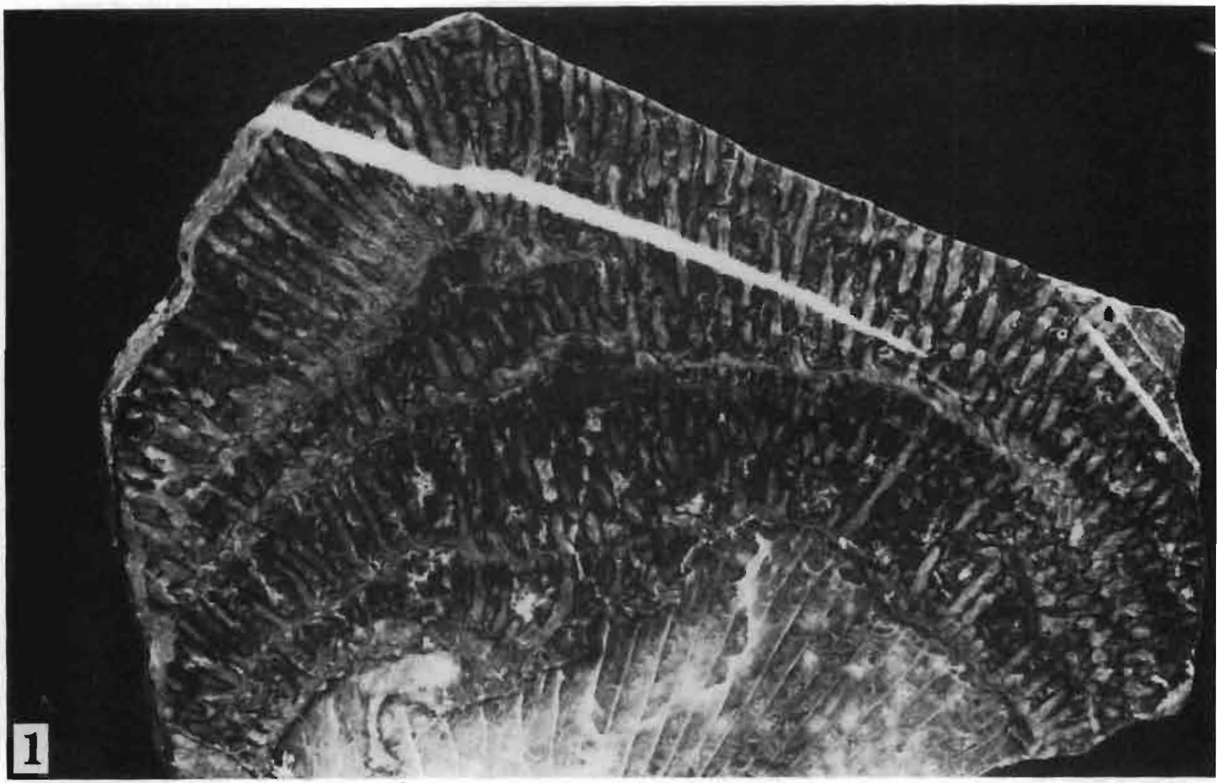
PLATE 12

	Page
Fuchungopora arctica Nowiński, 1982	48

Fig. 1. Longitudinal section through a four year old colony encrusting the lateral surface of a solitary rugose coral. Four growth bands visible where young corallites branch off from stolonal or connecting tubes, × 1.5; ZPAL T XIII/48; S slope of Hyrnefjellet, Coral Horizon Vb_1.

Fig. 2. Transverse section through a fragment of a colony with thick walled, densely spaced corallites, × 5; ZPAL T XIII/49; S slope of Hyrnefjellet, Coral Horizon Vb_2.

Fig. 3. Transverse section through a fragment of a colony with corallites arranged in a chain-whorl pattern, × 5; ZPAL T XIII/102; S slope of Hyrnefjellet, Coral Horizon Vb_2.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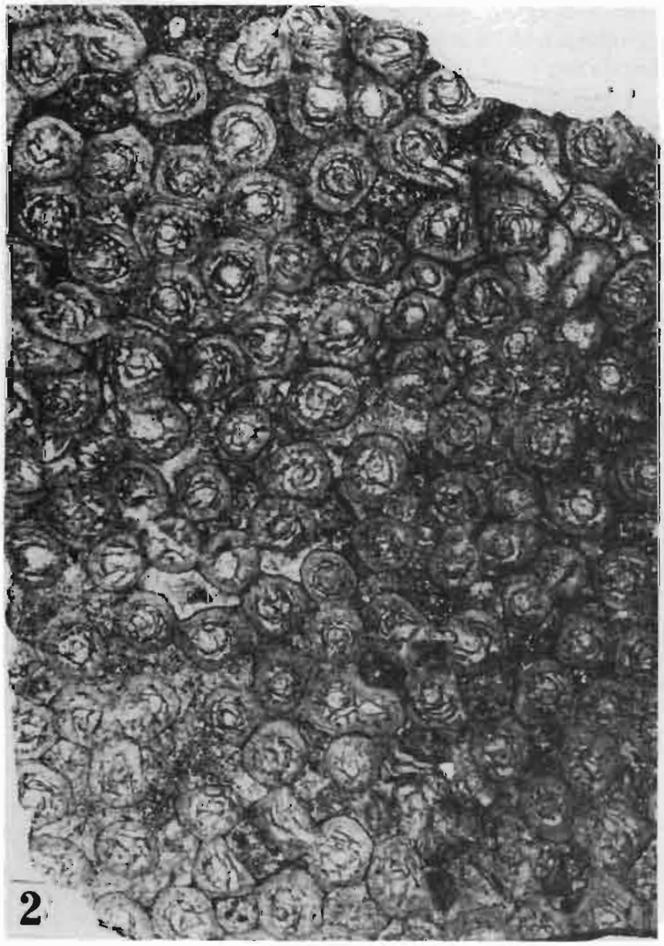
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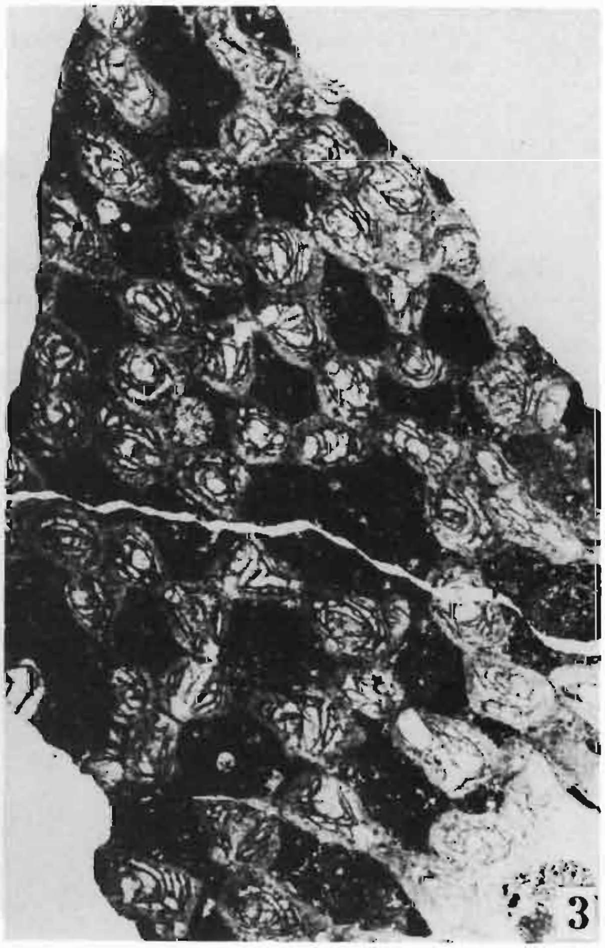
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 13

Page

Fuchungopora arctica NOWIŃSKI, 1982 48

Fig. 1. Longitudinal section through a fragment of a colony with thick walled corallites having strongly developed septal spines, × 5; ZPAL T XIII/49; S slope of Hyrnefjellet, Coral Horizon Vb_2.

Roemerolites laminatus (NOWIŃSKI, 1982) 49

Fig. 2. *a* longitudinal section through a fragment of a colony with loosely spaced corallites, connected by rare tubes, × 5; *b* transverse section through a fragment of a colony with loosely spaced corallites which are arranged in chains and whorls, × 5; ZPAL T XIII/42; Hyrnefjellet, Coral Horizon Va_3.

Multithecopora syrinx (ETHERIDGE, 1900) 50

Fig. 3. Section through a fragment of a colony with budding off corallites; corallites with densely spaced tabulae also visible, × 5; ZPAL T XIII/106; Treskelen, Coral Horizon IVb, Creek IV.


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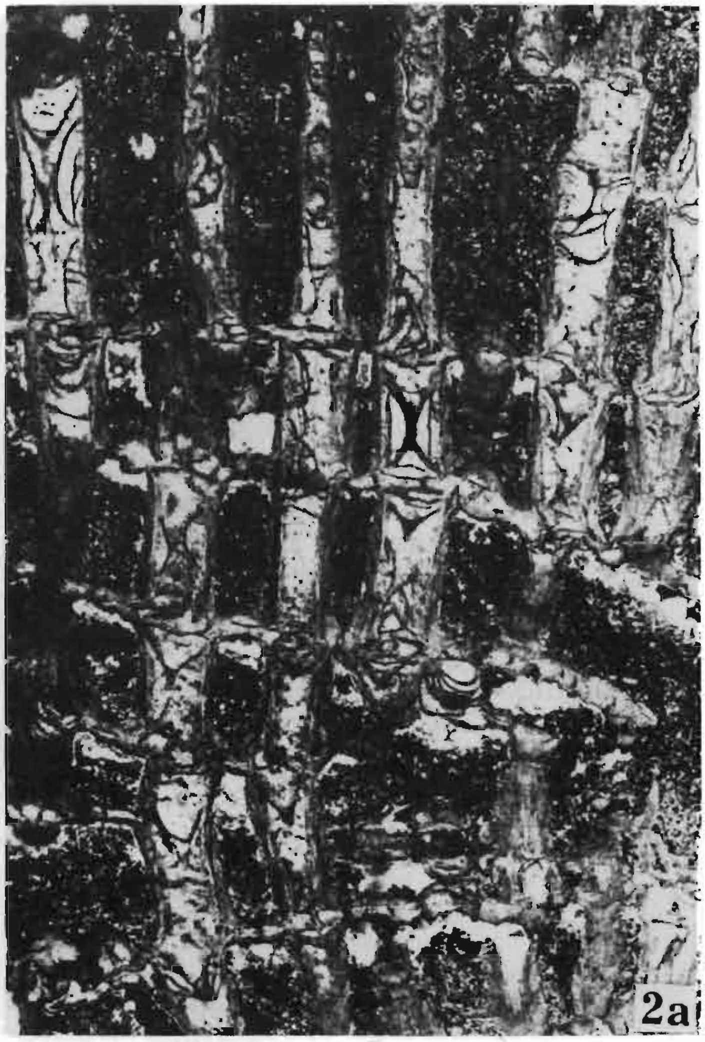
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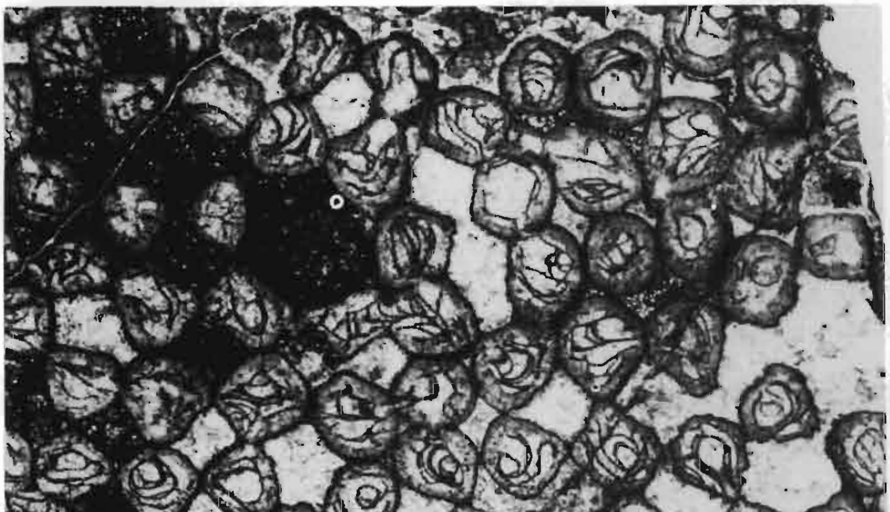
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

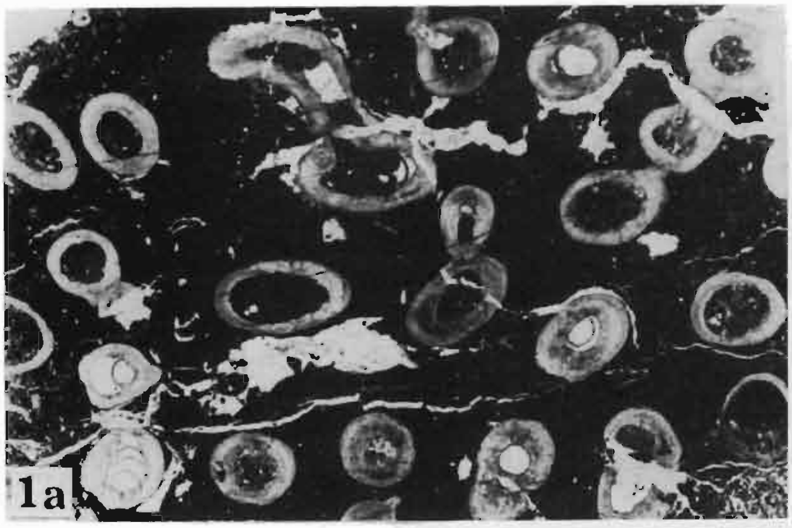
PLATE 14

Fig. 1. *a* transverse section through a fragment of a colony, × 5; *b* longitudinal section through corallites with strongly oblique tabulae, × 5; ZPAL T XIII/106; Treskelen, Coral Horizon IVb, Creek IV.

Fig. 2. Longitudinal section through a fragment of a colony, × 5; ZPAL T XIII/105; Treskelen, Coral Horizon IVb, Creek IV.

Fig. 3. Longitudinal section through long corallites, × 5; ZPAL T XIII/107; Treskelen, Coral Horizon IVb, Creek IV.

Fig. 4. Longitudinal section through a fragment of a colony with short corallites having strongly densely spaced tabulae, × 5; ZPAL T XIII/104; Treskelen, Coral Horizon II, Creek IV.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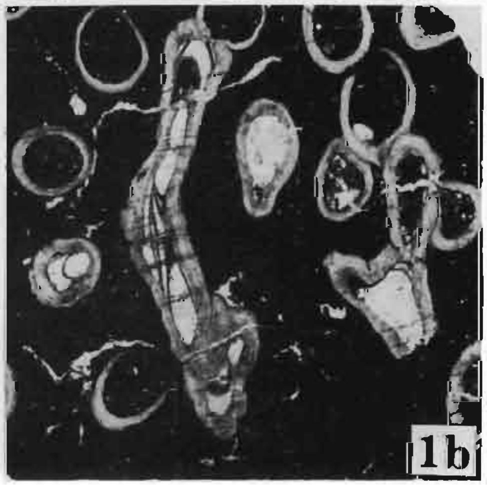
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PLATE 15

Page

Multithecopora tchernychevi SOKOLOV, 1950 52

Fig. 1. *a* longitudinal section through a fragment of a colony, × 5; *b* transverse section through a fragment of a colony, × 5; *c* longitudinal section through corallites with strongly developed septal spines, × 10; ZPAL T XIII/113; Treskelen, Coral Horizon IVb, Creek IV.

Fig. 2. Longitudinal section through the near-surface portion of a colony showing deep calices, × 5; ZPAL T XIII/112; Treskelen, Coral Horizon III, Creek IV.


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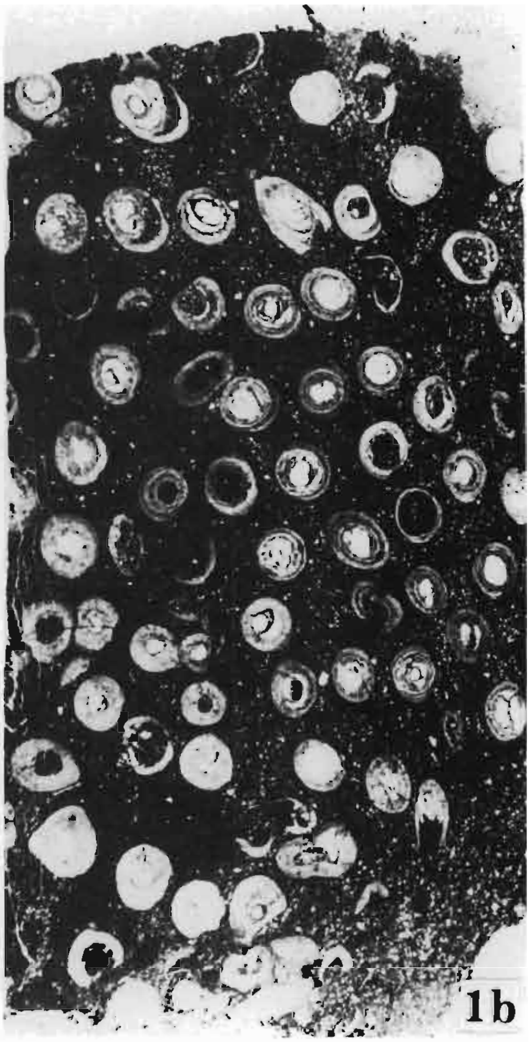
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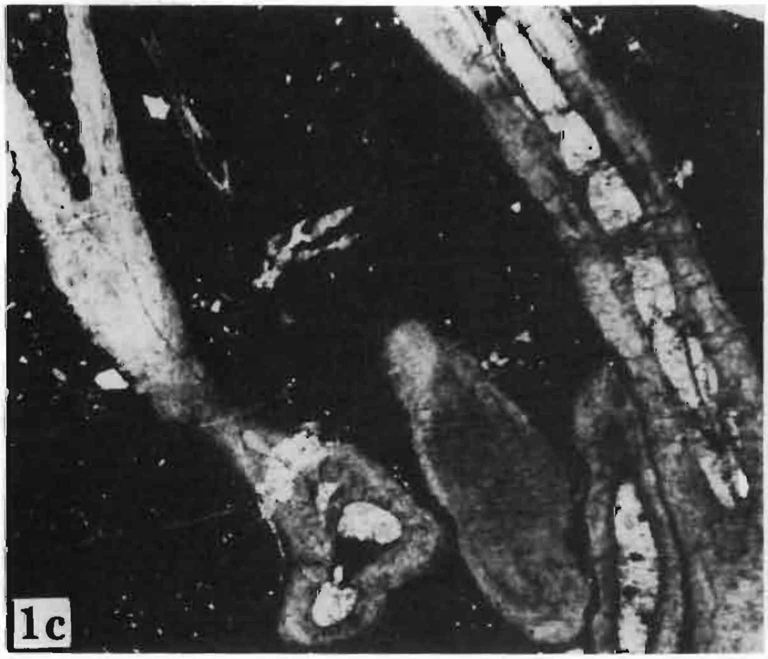
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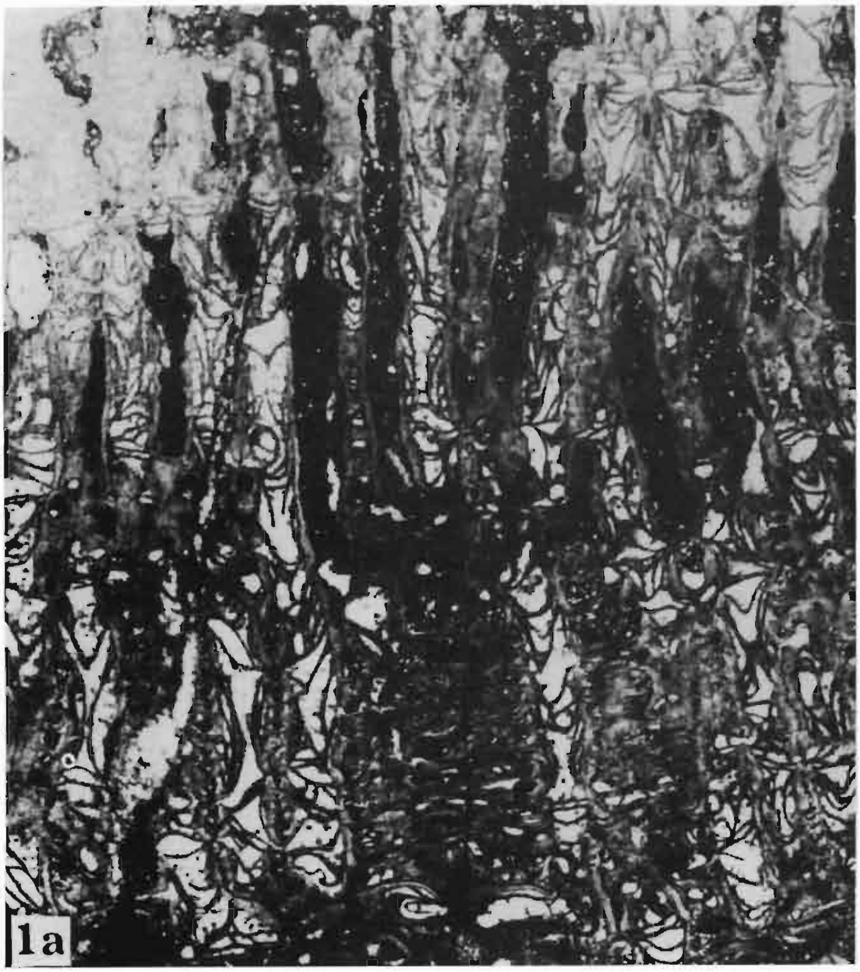
A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 16

Fig. 1. *a* longitudinal section, × 5; *b* transverse section, × 5; holotype ZPAL T XIII/121; Treskelen, Coral Horizon Va, Creek IV.

Fig. 2. Transverse section through a fragment of a colony with corallites arranged in a chain-whorl pattern, × 5; ZPAL T XIII/120; Treskelen, Coral Horizon Va, Creek IV.

Fig. 3. Transverse section through a fragment of a colony, × 5; ZPAL T XIII/53; Treskelen, Coral Horizon Vc, Creek IV.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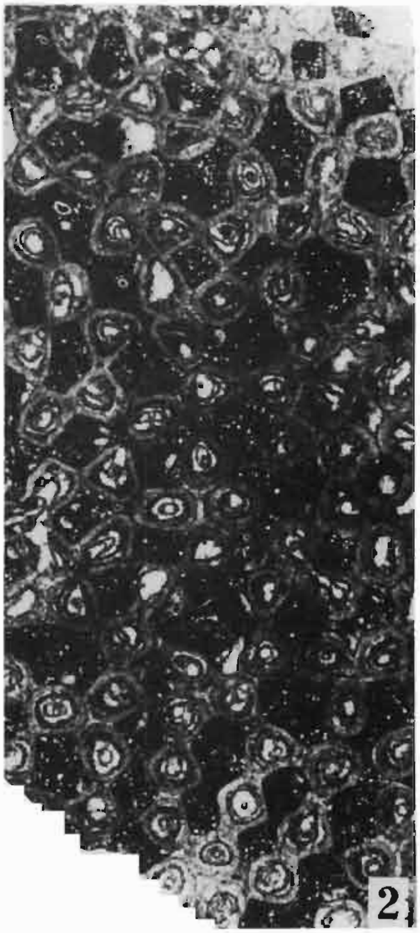
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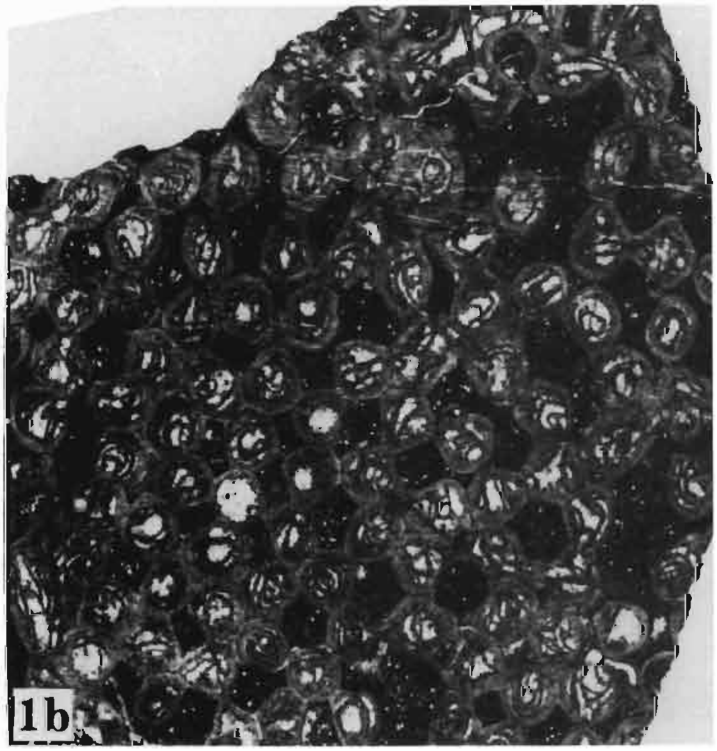
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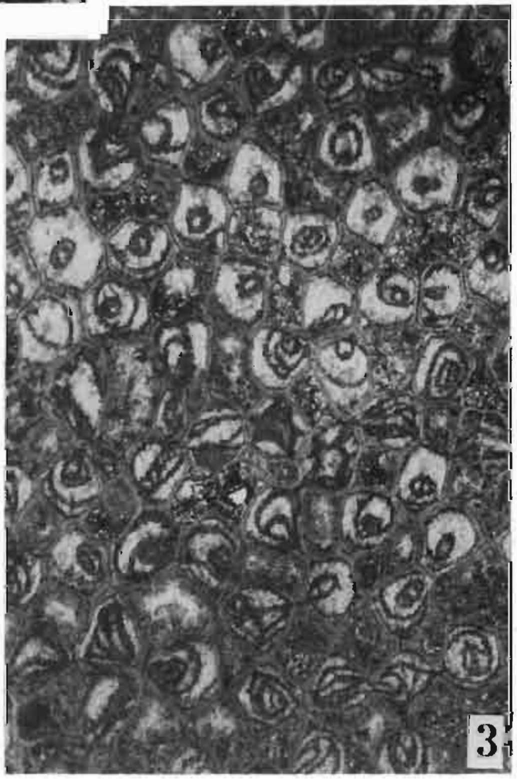
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PLATE 17

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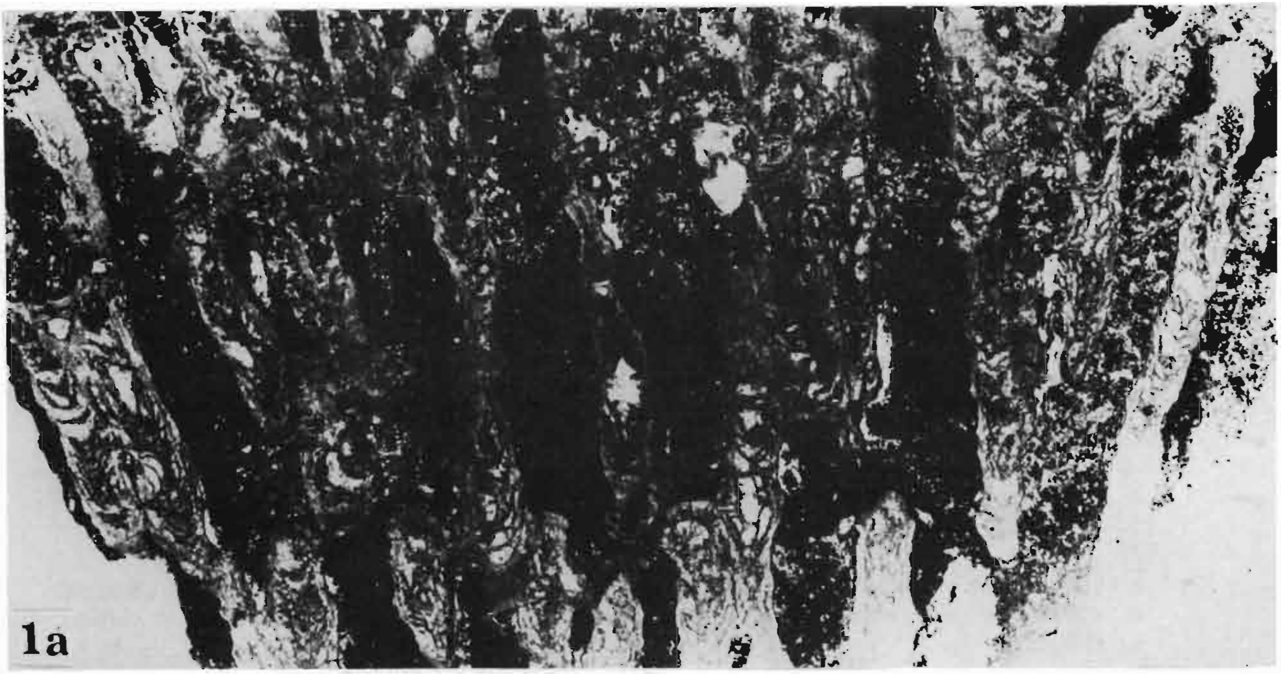
Hayasakaia birkenmajeri sp. n.	56

Fig. 1. *a* longitudinal section, × 5; *b* transverse section, × 5; holotype ZPAL T XIII/123; Hyrnefjellet, Coral Horizon Va_3.

Fig. 2. Transverse section through a fragment of a colony with densely spaced corallites, × 5; ZPAL T XIII/124; Hyrnefjellet, Coral Horizon Va_3.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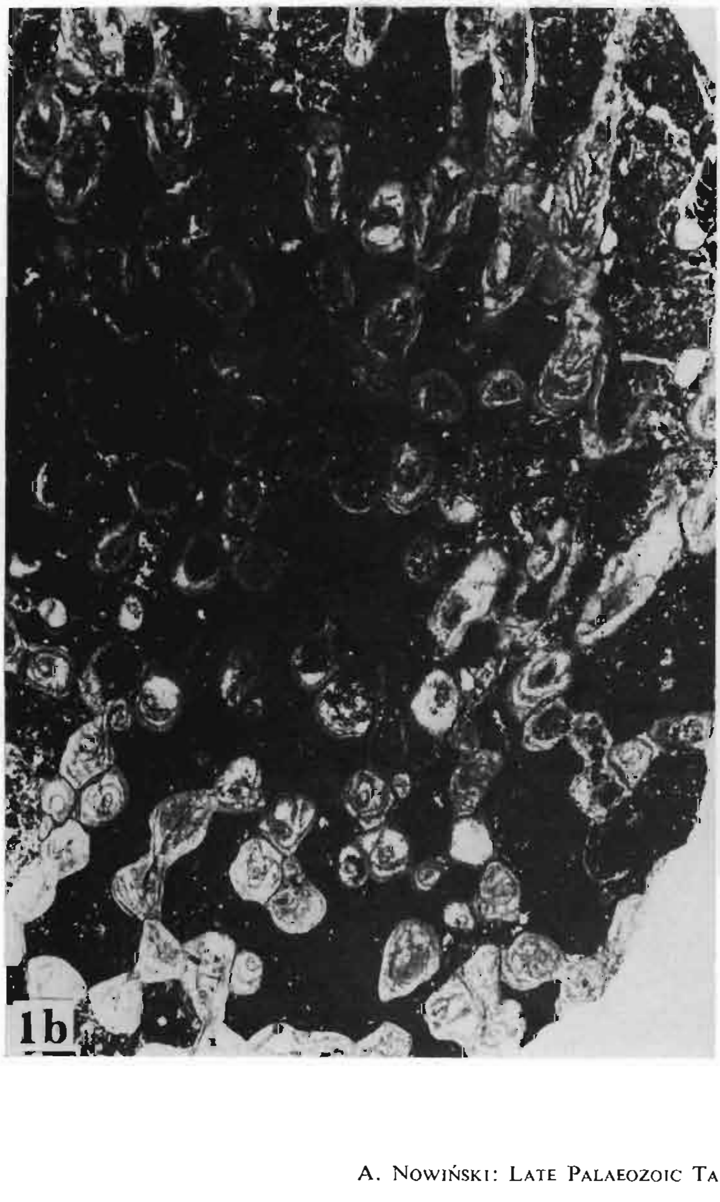
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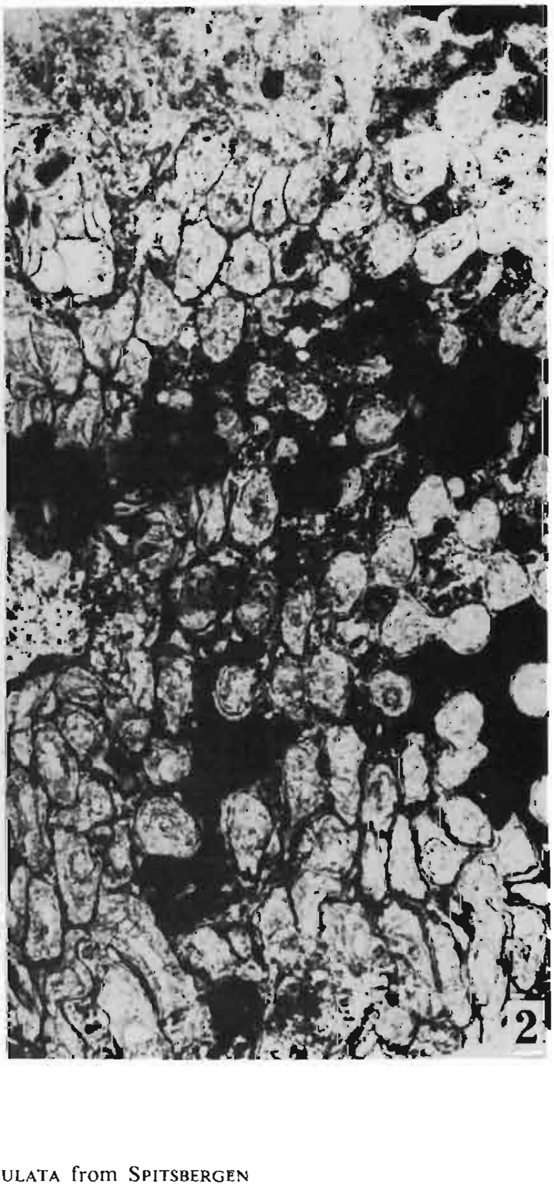
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A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 18

Fig. 1. *a* longitudinal section, × 5; *b* transverse section, × 5; *c* longitudinal and transverse sections through a fragment of a colony showing zones of densely and loosely spaced corallites, × 3; holotype ZPAL T XIII/125; Hyrnefjellet, Coral Horizon Vb_2.


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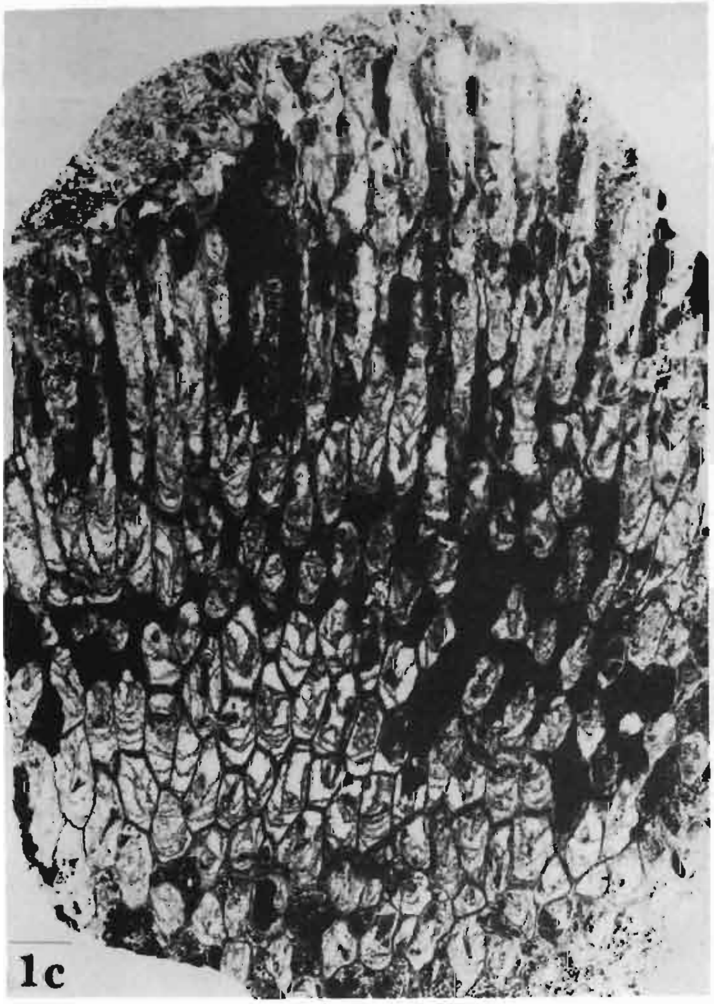
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PLATE 19

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Hayasakaia variabilis sp. n.	58

Fig. 1. Transverse section through a fragment of a colony with loosely spaced corallites having circular cross-sections and small diameters, × 5; ZPAL T XIII/126; Hyrnefjellet, Coral Horizon Vb_2.

Fig. 2. Transverse section through a fragment of a colony consisting of loosely distributed multiangular corallites having small diameters and arranged in a chain-whorl pattern, × 5; holotype ZPAL T XIII/125; Hyrnefjellet, Coral Horizon Vb_2.

Tetraporinus spitsbergensis sp. n.	59

Fig. 3. *a* transverse section, × 5; *b* longitudinal section, × 5; holotype ZPAL T XIII/127; Treskelen, Coral Horizon Vc, Creek IV.

Tetraporinus spinosus sp. n.	61

Fig. 4. Longitudinal section through a fragment of a young colony. The basal portion shows corallites budding off stolonal tubes, × 5; holotype ZPAL T XIII/132; Hyrnefjellet, Coral Horizon Vb_1.


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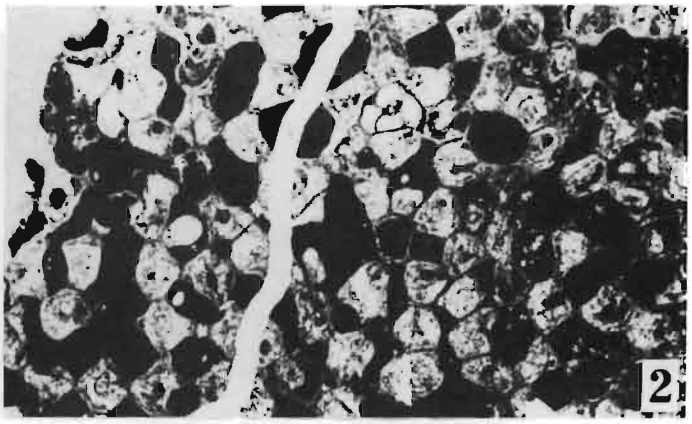
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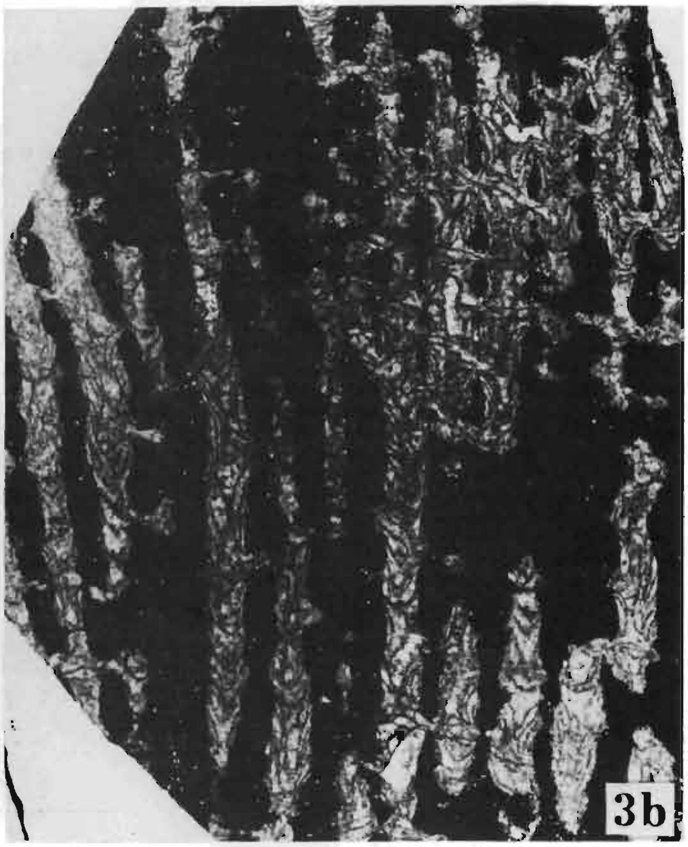
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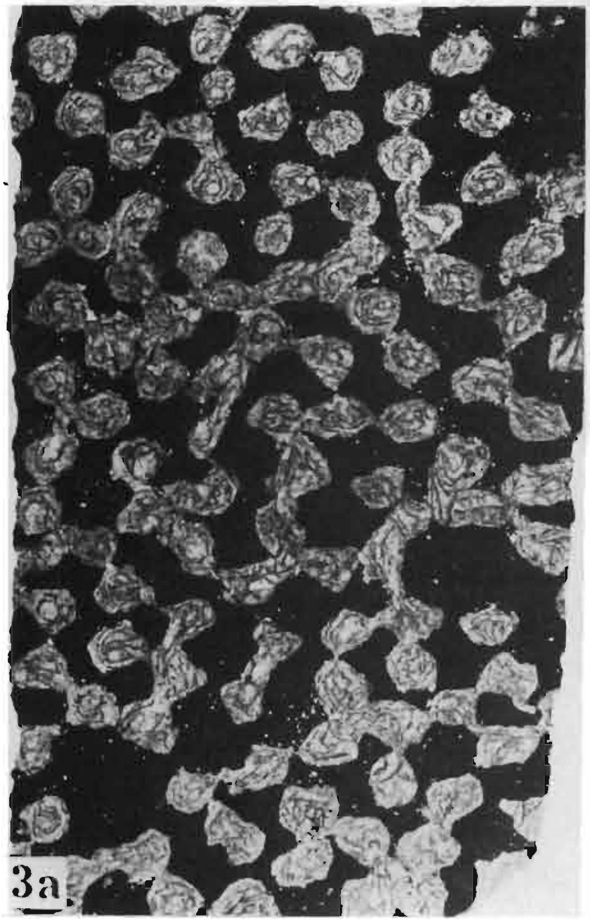
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PLATE 20

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Tetraporinus spitsbergensis sp. n. 59

Fig. 1. *a* transverse section through a fragment of a colony with thick walled corallites, × 5; *b* longitudinal section through a fragment of a colony with corallites which are connected by thin tubes, × 5; ZPAL T XIII/129; Hyrnefjellet, Coral Horizon Vb_1.

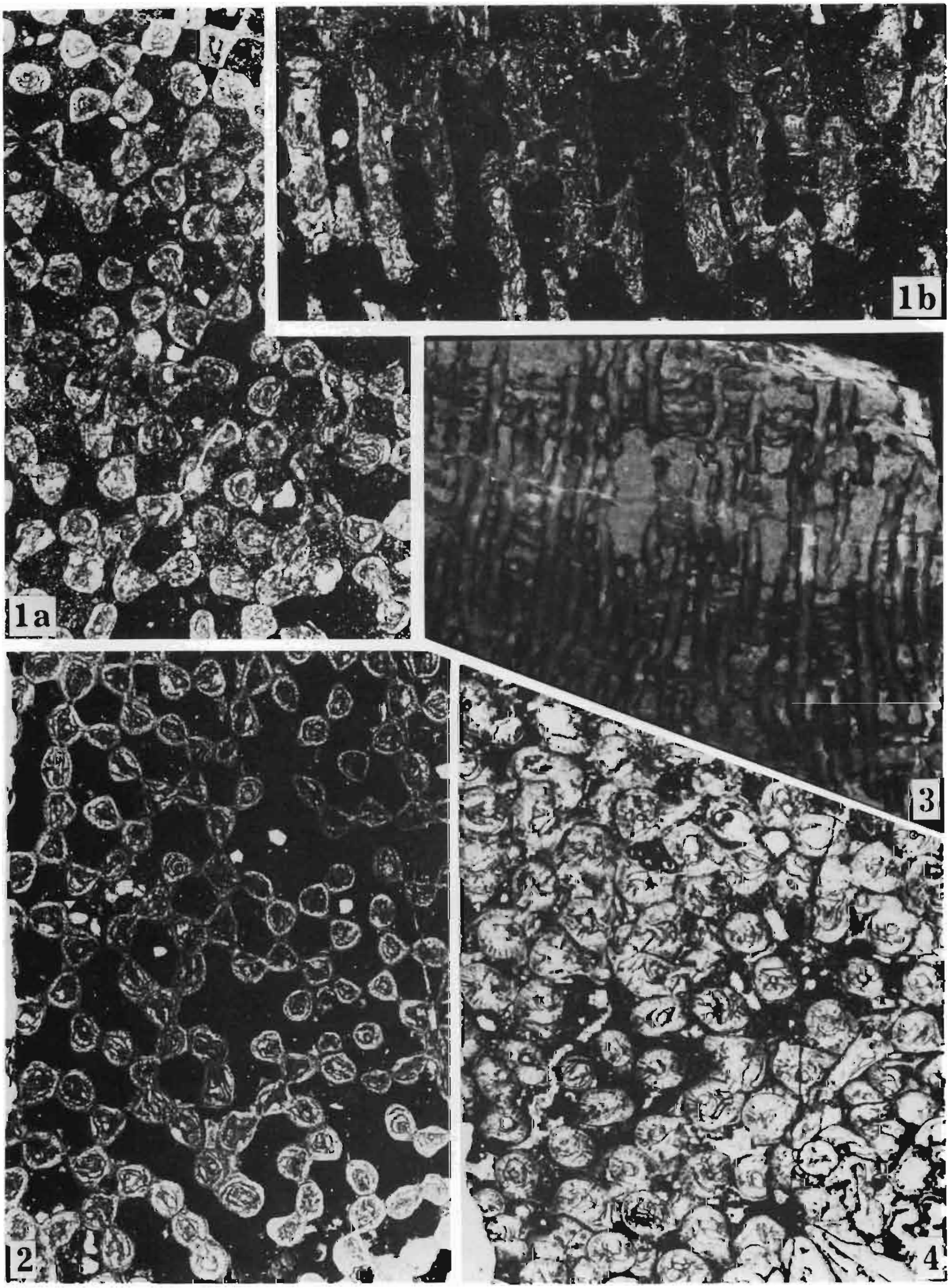
Tetraporinus spinosus sp. n. 61

Fig. 2. Transverse section through a fragment of a colony with corallites arranged in a chain-whorl pattern, × 5; holotype ZPAL T XIII/132; Hyrnefjellet, Coral Horizon Vb_1.

Neoroemeria spitsbergensis sp. n. 65

Fig. 3. Longitudinal section through a fragment of a ten year old colony; three growth bands and corallites budding off connecting bridges visible, × 1.5; ZPAL T XIII/138; Treskelen, Coral Horizon Va, Creek IV.

Fig. 4. Transverse section through a fragment of a colony with densely spaced corallites, × 5; holotype ZPAL T XIII/137; Treskelen, Coral Horizon Ia, Creek IV.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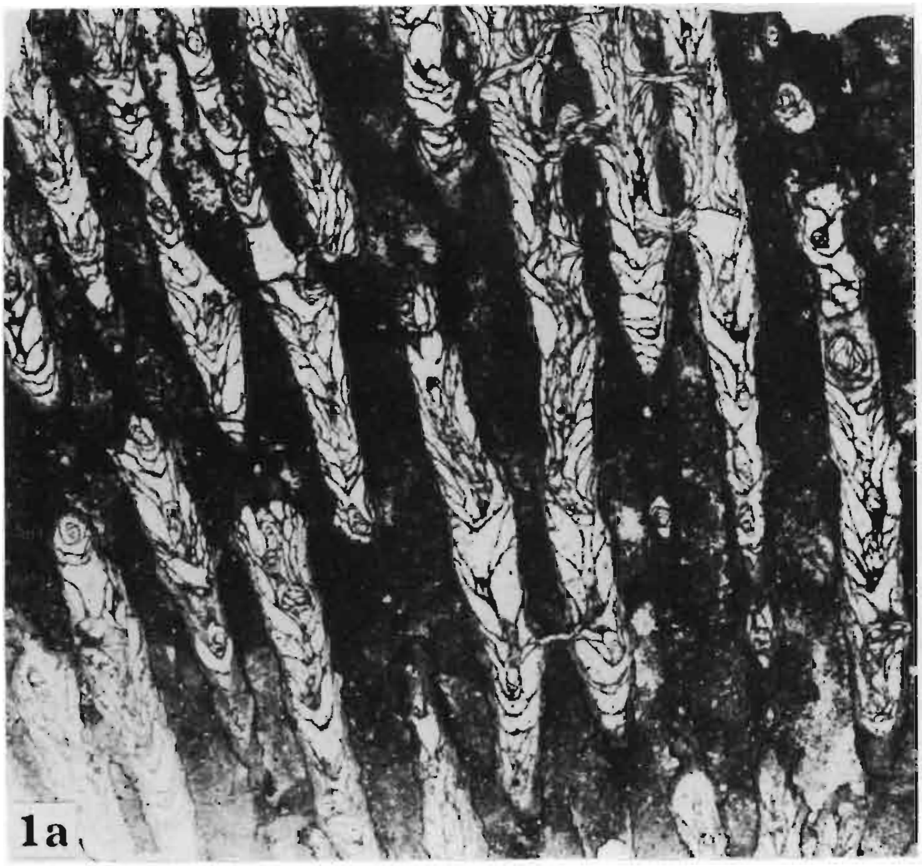
A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 21

Fig. 1. *a* longitudinal section, × 5; *b* transverse section, × 5; holotype ZPAL T XIII/134; Hyrnefjellet, Coral Horizon Vb_2.

Fig. 2. *a* longitudinal section through a fragment of a young colony, × 5; *b* transverse section through a fragment of a young colony with quadrangular corallites, × 5; ZPAL T XIII/133; Hyrnefjellet, Coral Horizon Vb_2.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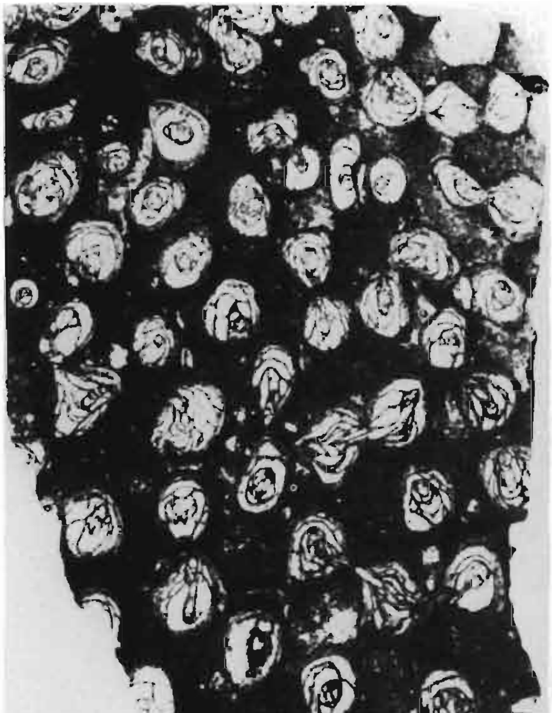
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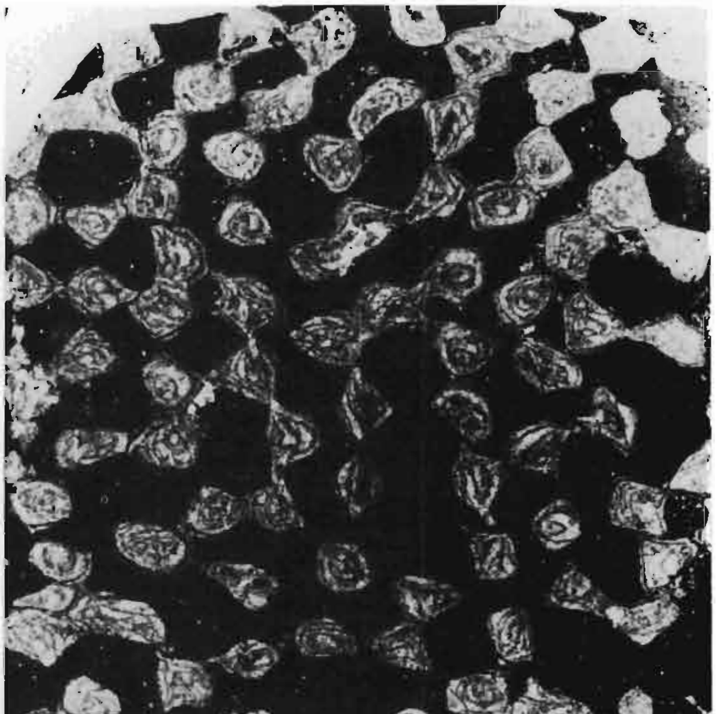
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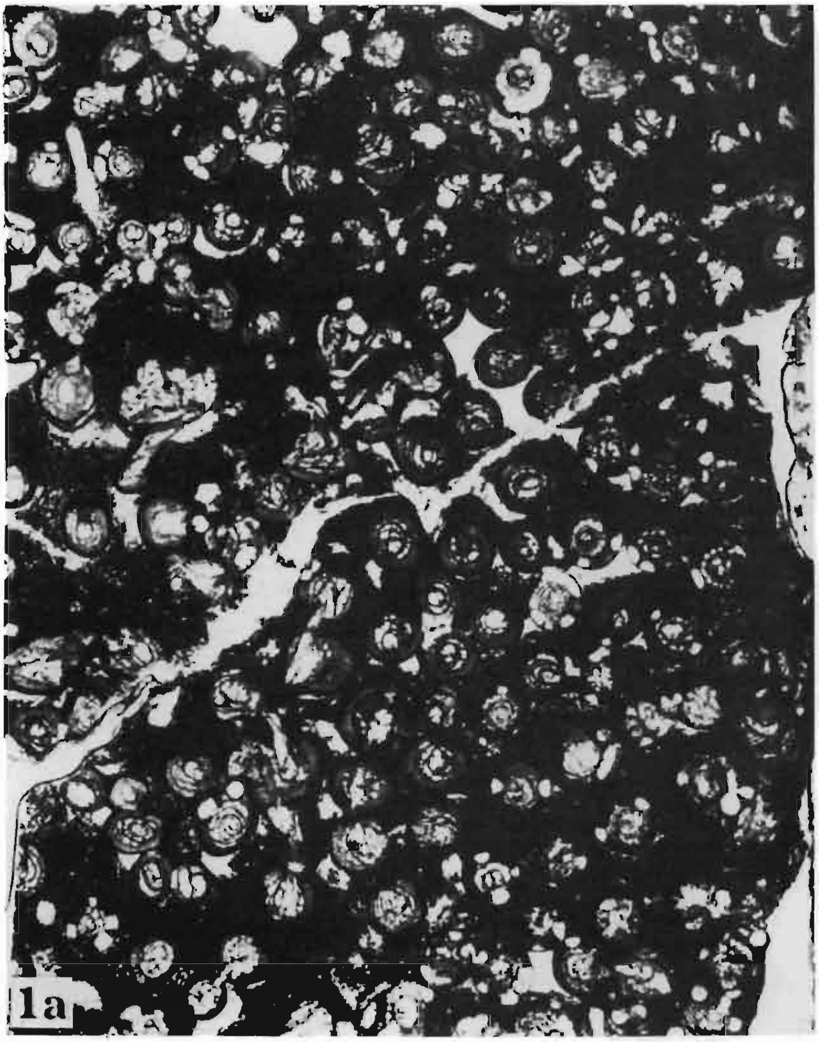
A. NOWIŃSKI: LATE PALAEOZOIC TABULATA FROM SPITSBERGEN

PLATE 22

Fig. 1. *a* transverse section through a fragment of a colony, × 5; *b* longitudinal section through a fragment of a colony, × 5; *c* transverse section through a fragment of a colony with strongly developed and irregular connecting bridges, × 5; *d* longitudinal section through corallites with strongly developed septal spines, × 5; *e* longitudinal section through a basal zone of a colony with corallites budding off basal tubes, × 5; holotype ZPAL T XIII/136; Isfjorden (Skanska Bukta), "Wordiekammen Limestone".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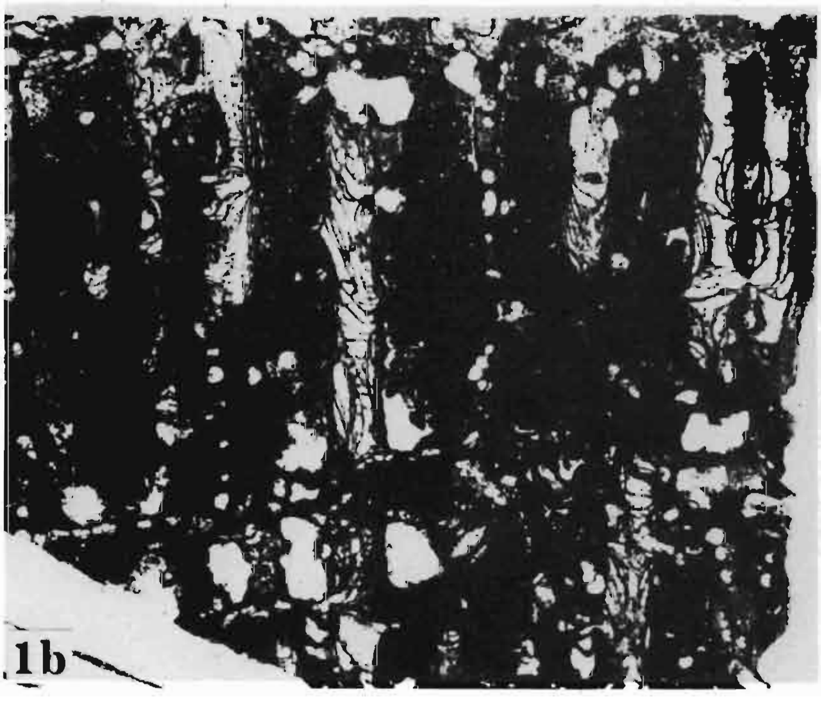
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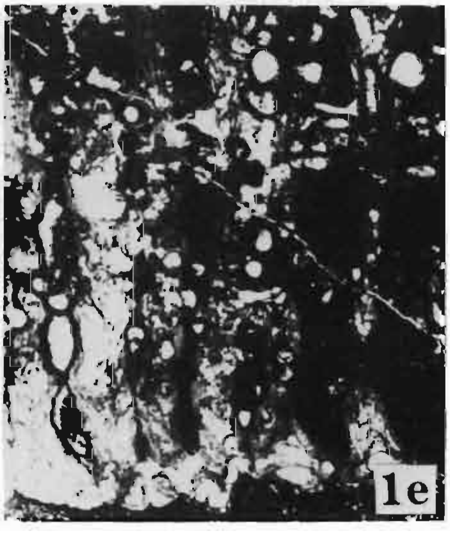
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PLATE 23

Page

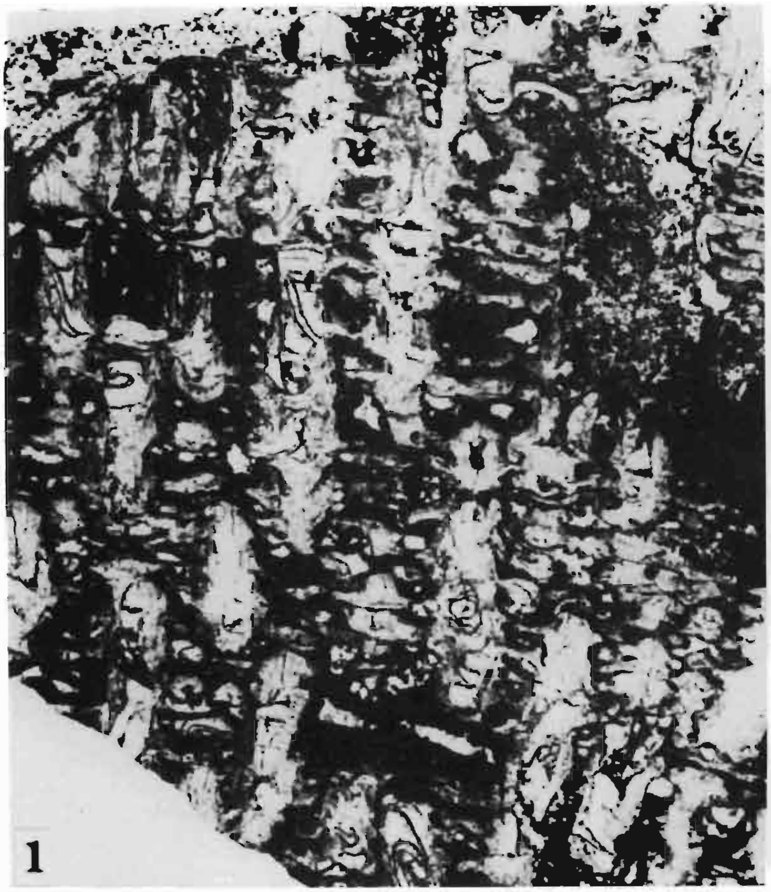
Neoroemeria spitsbergensis sp. n. 65

Fig. 1. Longitudinal section through a fragment of a colony with corallites linked by densely distributed connecting bridges, × 5; holotype ZPAL T XIII/137; Treskelen, Coral Horizon Ia, Creek IV.

Fig. 2. *a* transverse section through a fragment of a colony showing variation between densely and loosely spaced corallites, × 5; *b* longitudinal section through a fragment of a ten year old colony with growth bands visible, × 3; ZPAL T XIII/138; Treskelen, Coral Horizon Va, Creek IV.

Hayasakaia compacta NOWIŃSKI, 1982 54

Fig. 3. Longitudinal section, × 5; ZPAL T XIII/119; Hyrnefjellet, Coral Horizon Va_3.



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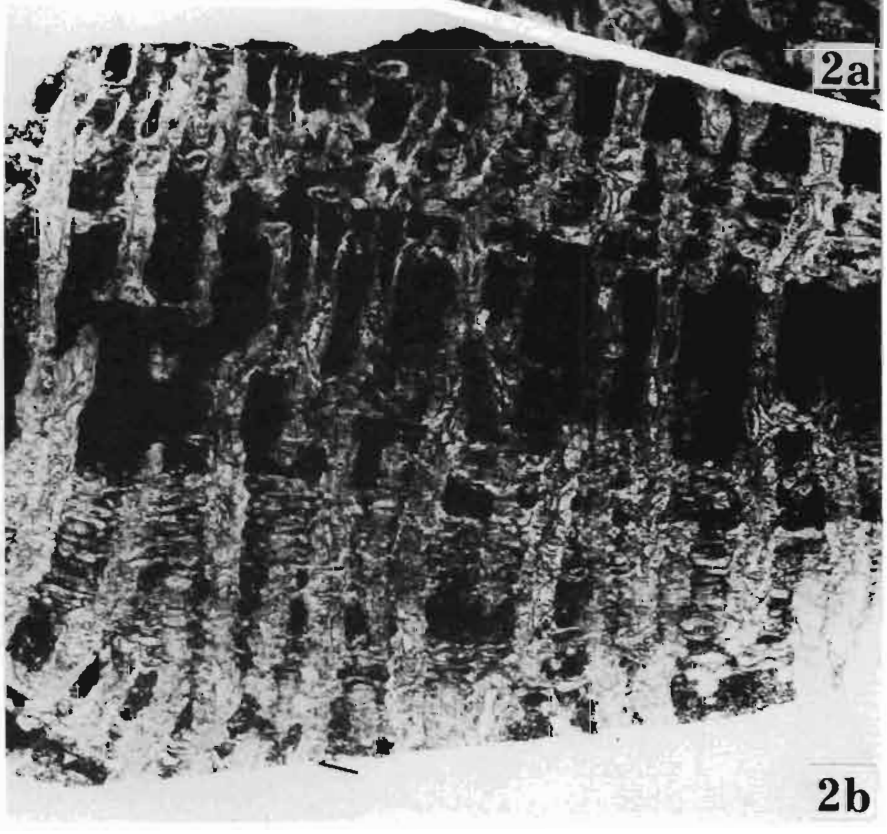

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