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# A new trachypsammiid cnidarian from the Late Permian of Spitsbergen

ABSTRACT: *Starostinella nordica* gen. et sp. n. is described from the uppermost Permian (Kapp Starostin Formation) of the Kapp Starostin (Isfjorden) in West Spitsbergen. The new genus is attributed to Trachypsammiidae Gerth – a family *incertae sedis* among Cnidaria. Members of the Trachypsammiidae have been previously associated with different higher rank taxa within the Cnidaria, or their skeletons were interpreted as a result of symbiosis of a cladochonoidal organism (Tabulata) with an indeterminate hydroid or stromatoporoid. *S. nordica* gen. et sp. n. seems to support the latter assumption. Hydrocoralla of *S. nordica* have a simpler structure than those of other Trachypsammiidae and are branching like those of *Cladochonus*. Their thick-walled, horn-shaped hydrocorallites are surrounded with a very thick cortical zone of sclerenchyme organized into trabecular microstructure. The proper corallite wall is fibro-radial in structure, sharply distinct from the outer cortical zone.

Key words: Arctic, Permian, Cnidaria (Trachypsammiidae).

## Introduction

The family Trachypsammiidae Gerth, to which the new genus *Starostinella* is here assigned, occupies an *incertae sedis* position among the Cnidaria. Its representatives have been variously included into Tabulata (Favositida, Auloporida), Octocorallia (Trachypsammiacea), or simply to Cnidaria without further indication of class nor order. A hypothesis was also put forward that the hydrocoralla of Trachypsammiidae result from symbiosis of two skeletal organisms: a cladochonoidal organism (Tabulata) and an indeterminate stromatoporoid or a hydroid. The enigmatic taxonomic placement of the family is due to the peculiar, complicated skeletal structure of its representatives, especially those representing the type genus *Trachypsammia*.

The Trachypsammiidae have small, branching or digitate colonies, consisting of few short, horn-shaped hydrocorallites with *Cladochonus*-like morphology

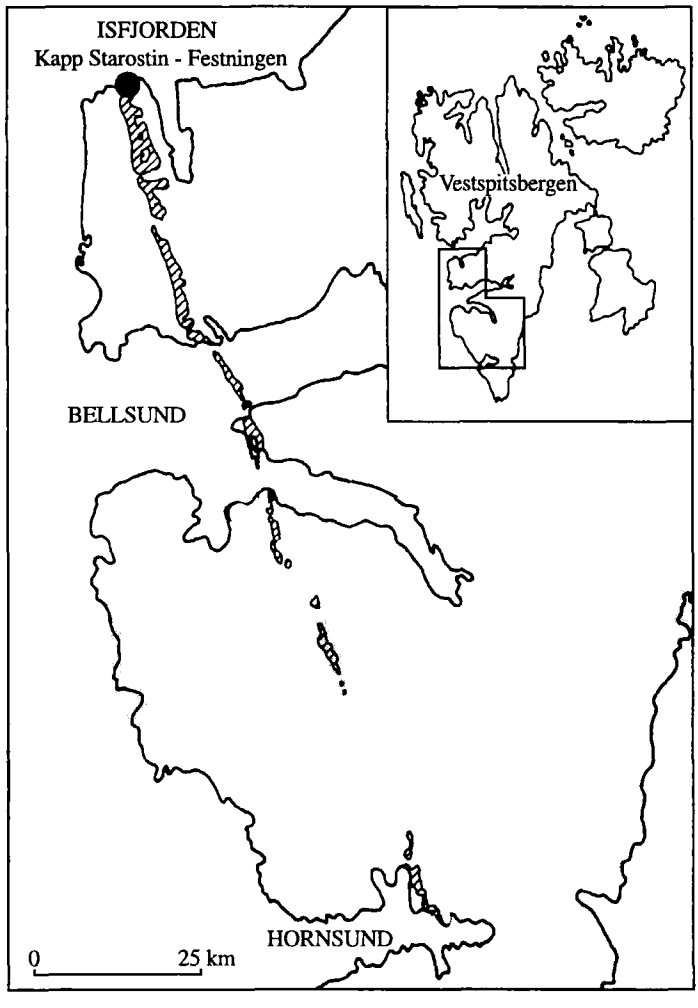


Fig. 1. Outline map of West Spitsbergen, showing the location of the Kapp Starostin – Festningen section, from where the *Starostinella nordica* gen. et sp. n. has been collected.

and arrangement. The hydrocorallites are surrounded with a very thick and microstructurally diverse sclerenchyme layer. The internal walls of their shallow calices are smooth or covered with septal ribs arranged like in the Rugosa.

The new genus is atributed to the Trachypsammiidae because of the presence of a zigzag (*i.e.* alternating in two opposing rows) arrangement of *Cladochonus*-like corallites, and the presence of a very thick cortical zone of sclerenchyme with trabecular microstructure around the corallites. The structural and morphological studies on *Starostinella nordica* gen. et sp. n. do not resolve the taxonomic position of the Trachypsammiidae. They seem, however, to support the

assumption that their skeletons may have resulted of symbiosis of two different organisms growing together.

The fossil colonies of *Starostinella nordica* gen. et sp. n. come from the uppermost Permian – the Kapp Starostin Formation (uppermost part of Festningen section – see Małkowski 1982, Fig. 2) – at the Kapp Starostin (Isfjorden) in West Spitsbergen (Fig. 1). Numerous colonies have been preserved in black marls and marly shales, containing also a rich fauna of brachiopods (e.g. *Kochinoproductus, Cancrinella, Spiriferella, Paeckelmanella, Camarophoria*; see Małkowski 1982 for a faunal list), bryozoans (e.g. *Tabulipora*), and rare bivalves, solitary Rugosa, sponges and foraminifers. The colonies of *Starostinella nordica* gen. et sp. n. have been collected by Dr. Krzysztof Małkowski during the Polish Paleontological Expedition to the West Spitsbergen in 1976.

Thirty five thin sections have been made for morphological studies. The ultra- and microstructure has been studied with SEM.

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

## Paleontology

### Trachypsammiidae Gerth, 1921

The Trachypsammiidae Gerth, is a Permian family of Cnidaria, with as yet undetermined position within the subphylum. The family has been erected by Gerth (1921), for the single monotypic genus *Trachypsammia* Gerth, with *T. dendroides* Gerth, described from a classic Permian profile of Timor (Basleo, Bitanui) in Indonesia (Gerth 1921,1922)

The Trachypsammiidae have little, branching, digitate, columnar or seldom encrusting colonies, consisting of a small number of short, horn-shaped or subconical corallites (hydrocorallites) with *Cladochonus* or *Palaeacis* type. The hydrocorallites are surrounded with a very thick and microstructurally diverse layer of sclerenchyme, resembling the coenenchyme of hydroids or stromatoporoids. The sclerenchyme is perforated with numerous tiny canals, often anastomosing; their openings at the hydrocorallum surface form pores irregularly placed between the calices. The calices are crater-like or cupule-like, with internal walls either smooth or covered with numerous septal ribs.

The Trachypsammiidae includes three genera: (1) *Trachypsammia* Gerth, 1921 (Gerth 1921, 1922; Hehenwarter 1951; Lecompte 1952; Sokolov 1950, 1955, 1962; Yakovlev 1939; Montanaro-Gallitelli 1954, 1955, 1956a, b; Hill 1981; Tourneur, Lafuste and Plusquellec 1993), (2) *Oculinella* Yakovlev (Yakovlev 1939; Sokolov 1955, 1962; Hill 1981), (3) A poorly known *Dictyopora*

Gerth, 1921 (non *Dictyopora* Steininger, 1849; non *Dictyopora* McGillivray, 1869) has been provisionally included to the family by Hill (1981).

The genus best known so far, *Trachypsammia*, is represented by four species: *T. dendroides* Gerth, 1921, from the Permian of Timor, *T. monoseptata* Gerth, 1921, also from the Permian of Timor, *T. mediterranea* Montanaro-Gallitelli, 1954, from the Permian of Sicily and *T. xiangensis* Lin, 1983, from the Permian of Tibet. Previous studies (*e.g.* Hehenwarter 1951, Montanaro-Gallitelli 1956, Plusquellec and Tourneur 1992), and a recent revision by Tourneur, Lafuste and Plusquellec (1993), show that all these species are very similar structurally and morphologically, differing only in quantitative traits and degree of development of particular specific characters. Members of the genus *Trachypsammia* have little, columnar or thick ramose colonies, often dichotomously branching. A small number of short, horn-shaped hydrocorallites of *Cladochonus* type arranged in one plane in a zigzag pattern. They do not have a clearly structurally separated wall, and are filled with a stereoplasm or (rarely) have a very irregular and discontinuous vertical axial canal. The lumen of the canal is surrounded by three concentric layers of sclerenchyme of different microstructure merging into each other: these are, medullar, annular and canalicural layers. The hydrocoralla and spaces between hydrocorallites are filled with a very thick layer of sclerenchyme – the cortical zone with trabecular microstructure and radial arrangement (see also Tourneur, Lafuste and Plusquellec 1993). The sclerenchyme is perforated with numerous tiny vertical, horizontal and oblique canals opening as pores at the hydrocorallum surface and between the calices. The calices are shallow, crater-like, round in cross section, arranged obliquely to the hydrocorallum surface in two opposing rows; their outer rim forms a sharp edge, protruding above the branch surface. The internal walls of calices bear numerous thick septal ribs.

The genus *Oculinella* Yakovlev is known from a single species *O. gerthi* Yakovlev (Yakovlev 1939; Sokolov 1955, 1962; Hill 1981), and differs from *Trachypsammia* in having more or less evenly spaced calices over the hydrocorallum surface. The calices do not protrude above the hydrocorallum surface and do not have any septal structures.

Another genus, *Dictyopora* Gerth, 1921 (Gerth 1921, Hill 1981) is poorly known and represented by a single species *D. incrustans* Gerth. Its inclusion into the Trachypsammiidae seems problematical. Members of the genus form flat colonies encrusting skeletons of other animals. Short, tubular hydrocorallites terminate with calices, whose rims protrude above the hydrocorallum surface. The internal walls of calices bear numerous septal ribs. The intercalicular spaces are filled with a skeletal tissue of poorly known microstructure. The tissue is pierced with numerous tiny canals with open in the form of pores dispersed at the hydrocorallum surface.

The unresolved position of the family Trachypsammiidae Gerth among the Cnidaria is due to the peculiar, complicated structure of its representatives,

especially of the type genus *Trachypsammia*. Other, as yet non-revised genera (*Oculinella* and *Dictyopora*) are not important in this regard.

Not taking into account the peculiarity of the skeletal structure of *Trachypsammia*, and some resemblances to the post-Paleozoic Hexacorallia (*e.g.* Dendrophillidae) and Octocorallia, Gerth (1921, 1922), Yakovlev (1939), Hehenwarter (1951) and other authors included it into the subclass Tabulata, namely to Pachyporidae Gerth, 1921. Montanaro-Gallitelli (1954), describing a new species, *T. mediterranea* from the Permian of Sicily, presented a new interpretation of the trachypsammiid corallum. Her microstructural studies revealed the presence of a medullar system, generally resembling that of the Octocorallia. Thus, she classified the type genus *Trachypsammia*, and the whole family Trachypsammiidae, to Octocorallia, erecting for them a new order – Trachypsammiacea (Montanaro-Gallitelli 1955, 1956a, b). The studies by Plusquellec and Tourneur (1994) on vegetative reproduction and growth of *Trachypsammia dendroides* colonies have proven that in this species an intracanalicular budding occurred, unknown in the Tabulata, but very similar to that in the Octocorallia.

Hill and Stumm (1956), on the basis of calice morphology, included *Trachypsammia* to the Tabulata (into the subfamily Palaeacinae Počta, 1902). Later, Hill (1960, 1981) classified this genus, together with *Oculinella* and *Dictyopora* within the order Auloporida (Tabulata), interpreting its skeletons as a possible result of symbiosis of *Cladochonus* or a cladochonoidal organism with an indeterminate stromatoporoid or hydroid.

A study by Plusquellec and Tourneur (1992) has shown that the calices of *T. monoseptata* and *T. dendroides* have a bilateral symmetry, and that in their septal apparatus two larger septa can be discerned, that could be interpreted as the cardinale septum and connter septum. This pattern of septal apparatus, typical of the Rugosa, has been also described in a Devonian member of the Tabulata, *Kerforneidictyum* (Lafuste and Plusquellec 1976), and in some species of *Palaeacis* (Plusquellec *et al.* 1990). There are also similarities in the microstucture of the sclerenchyme among the three above genera, especially between *Trachypsammia* and branching *Palaeacis* (see Plusquellec *et al.* 1990; Webb 1989, 1990; Tourneur, Lafuste and Plusquellec 1993). Plusquellec and Tourneur (1992) included *Trachypsammia* to the Tabulata.

A recent revision of all Trachypsammiidae and very detailed studies on their skeletal microstructure and submicrostructure (Tourneur, Lafuste and Plusquellec 1993) revealed a complicated structure of sclerenchyme, *i.e.* four concentric layers mentioned above, which surround the lumen of their axial canals. The studies have not, however, resolved the taxonomic position of the *Trachypsammia*. The authors classified the genus *Trachypsammia* to Cnidaria. Also the new genus *Starostinella* described below does not allow to solve the problem.

## Family Trachypsammiidae Gerth, 1921
## Genus *Starostinella* gen. n.

Type species: *Starostinella nordica* gen. et sp. n.
Derivation of the name: *Starostinella* – from the name of Kapp Starostin in West Spitsbergen.

Diagnosis. — Branching mono- or biserial hydrocorallum with *Cladochonus*-like morphology and arrangement of hydrocorallites. The hydrocorallites lacking tabulae nor septal apparatus, not connected with visceral chambers in places of budding. Hydrocorallite walls very thick, with two layers: internal with fibrous microstructure and surrounded with a thin "epitheca", and external, with a trabecular microstructure, resembling that of cortical layer in *Trachypsammia*. Calices deep, cupule-like, without septal apparatus.

Remarks. — The main criterion allowing for the assignment of the new genus to the Trachypsammiidae is the presence of a very thick, trabecular cortical layer surrounding the *Starostinella* hydrocorallites, a feature typical of the family (Pl. 1, Fig. 2).

*Starostinella* shares with *Trachypsammia* the following characters: (1) dichotomous branching; (2) zigzag arrangement of hydrocorallites in a single plane; (3) alternating arrangement of the calices in two opposing rows, resulting in the bilateral symmetry of the hydrocorallum; (4) presence of a very thick external cortical zone of sclerenchyme with trabecular microstructure; (5) visceral chambers of the parent and offspring individual not connected.

*Starostinella* n. gen. differs from *Trachypsammia* in having the following characters: (1) Thin, branching colonies, with *Cladochonus*-like hydrocorallite morphology and arrangement; (2) Only epithecal contact of the proper hydrocorallite walls in budding places, without connections between the visceral chambers of the parent and offspring individuals. *Trachypsammia* lacks the epithecal layer and hydrocorallites are joined by tiny canals perforating the sclerenchyma. Some *Trachypsammia* corallites are totally embedded in the sclerenchyma of the cortical layer and do not extend onto the branch surface. (3) Thick, tubular and thick-walled hydrocorallites. The hydrocorallites of *Trachypsammia* are horn-shaped, with thin walls, structurally fuzzy and poorly delimited; (4) Funnel-shaped or cupule-like calices, not protruding above the hydrocorallum surface and having no septal apparatus; (5) Presence of only two sclerenchyme layers: the internal one with fibrous microstructure (proper hydrocorallite wall, surrounded with "an epitheca") and the external one, with trabecular microstructure (equivalent to the cortical layer in *Trachypsammia*). In *Trachypsammia*, there are three more sclerenchyme layers, absent in *Starostinella*, with different microstructure: medullar layer – filling partially or entirely the hydrocorallite interior, as well as the annular and canalicular layers, participating in the hydrocorallite wall; (6) Central location of the hydrocorallites within a branch. In *Trachypsammia*, the hydrocorallites are situated centrally with respect to the cortical zone only in the thin, young branches. In the thick, adult branches, the hydrocorallites

occupy subcentral or peripheral locations, and the cortical layer fills the entire space of the branch, including the intercorallite spaces. It looks like a *Trachypsammia* branch were embedded within a cylindrical cortical structure. In *Starostinella*, to the contrary, the cortical layer seems to depend fully on the hydrocorallites, and expands proportionally to the their growth, and follows their shapes. (7) Lack of canals within the sclerenchyme nor pores on the hydrocorallum surface.

*Starostinella* n. gen. differs from *Oculinella* Yakovlev in having thin-branching colonies with bilateral symmetry; a zigzag arrangement of the hydrocorallites; alternating arrangement of the calices in two opposing rows, in *Oculinella*, the calices are evenly distributed over the hydrocorallum surface, and the branches do not exhibit any symmetry. The new genus approaches the character states in *Oculinella* by the lack of septal apparatus in its calices.

An analysis of the internal structure of the *Starostinella* hydrocorallum suggests, that perhaps we deal here with two organisms growing and forming their skeletons together, possibly in a commensal relationship. A branching corallum of a member of the genus *Cladochonus* or a skeleton of a similar organism could have been overgrown by another organism secreting its own skeletal tissue (forming here the cortical layer). This encrusting organism could perhaps been a stromatoporoid or hydroid. Such a possibility has been proposed by Hill (1981) for *Trachypsammia* and *Oculinella*. A simultaneous growth of skeletons of two different organisms is supported by the following observations: (1) The cortical layer in *Starostinella* does not fill calices of the cladochonoidal hydrocorallum, but rather gets thiner near their edges, thus naturally widening their outlets. (2) The microstructure of the hydrocorallite wall of the cladochonoidal organism shows no structural continuity into the surrounding cortical layer of the encrusting organism. Both microstructures (fibrous and trabecular) are different, with a sharply delimited boundary, further enhanced by a strongly reduced epitheca of the cladochonoidal organism. Interestingly, in *Trachypsammia* all four microstructurally different layers of sclerenchyme merge into one another without clear boundaries.

## *Starostinella nordica* sp. n.
(Pl. 1, Figs 1–2; Pl. 2, Figs 1–2; Text-fig. 2)

Syntype: specimen ZPAL V. XXV/1; Pl. 1, Fig. 1
Type horizon: Kapp Starostin Formation, Upper Permian
Type locality: Kapp Starostin, Isfjorden, West Spitsbergen.
Derivation of the name: *nordica* – from the North.

Diagnosis. — Cladochonoidal hydrocorallum, consisting of few to a dozen of short hydrocorallites (8.0–10.5 mm) with a proximal and medial diameter of 4.0 to 6.0 mm, and distal diameter of 4.5 to 6.5 mm. The calices are deep, funnel-shaped or cupule-like. The internal (fibrous) layer of hydrocorallite

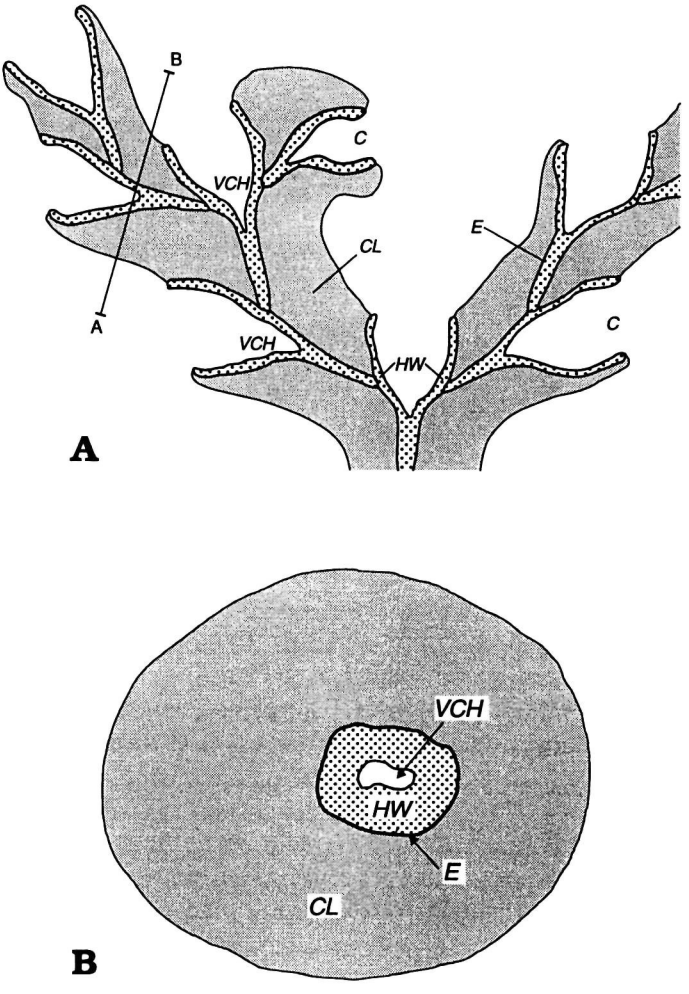


Fig. 2A–B. *Starostinella nordica* gen. et sp. n., Kapp Starostin, Kapp Starostin Formation (Upper Permian), semi-diagramatic restoration, syntype ZPAL V.XXV/1. A – Longitudinal section through hydrocorallum showing morphology and hydrocorallite arrangement, × 3.5. B – Transverse section through hydrocorallum in the plane marked see A–B on Fig. 2A. C – calice, CL – cortical layer with trabecular microstructure, E – "epitheca", HW – proper hydrocorallite wall, with fibro-radial microstructure, VCH – visceral chamber of hydrocorallite, × 15.

0.3 to 0.8 mm thick. The epitheca 0.02 to 0.03 mm thick. The cortical (trabecular) layer 1.6 to 4.3 mm thick. The angle between hydrocorallites growh axes 118 to 138°.

M a t e r i a l . — Very numerous, well preserved whole branching colonies or their large fragments, arranged along the bedding planes of the rock. Individual hydrocorallites and whole branches often strongly flattened, probably due to the sediment compaction.

Description. — External characters: Branching colonies. Branches long, thin, single or bifurcating, consisting of few to a dozen hydrocorallites (Fig. 2A). In particular branches (also those orginated by bifurcafion), the hydrocorallites are arranged in a zigzag pattern (alternating in two opposing rows) most often in a single plane, stressing the bilateral symmetry of the branches, like in the members of the genus *Cladochonus*. Budding and growth of the juvenile individuals was sympodial. They bedded from the dorsal side of the parent individuals. The internal angle between hydrocorallites growth axes ranges from 118 to 138°. The hydrocorallites are short (8.0–10.5 mm), slightly curved, very-thick-walled tubes, rarely slightly horn-shaped, with a proximal and medial diameter of 2.0 to 3.5 mm, and distal (calice) diameter of 2.5 to 4.0 mm in juvenile individuals; and a proximal and medial diameter of 4.0 to 6.0 mm, and distal diameter of 4.5 to 6.5 mm in adult individuals. The hydrocorallites are arranged strongly obliquely to the growh axis of the branch. The calices are deep, funnel-shaped or cupule-like, round or oval in cross-section, without a sharp rim and not protruding above the branch surface without tabulae nor septal apparatus (Fig. 2A; Pl. 2, Fig. 2). Their internal walls are smooth. The external surface of hydrocorallum is smooth, without visible growth rings, and without pores.

Internal characters: Hydrocorallite walls very thick in transverse sections, with two macro- and microstructurally different layers (Fig. 2B). The sections reveal a centrally or slightly subcentrally located hollow, being a section of the hydrocorallites visceral chamber, with 0.2 to 1.2 mm in diameter, elliptical (0.2 by 0.5 mm) or irregular. In longitudinal section, the visceral chamber is smooth-walled, without tabulae nor septal apparatus. The visceral chambers of the hydrocorallites lack connection, and the hydrocorallites contact one another only with their epithecae in budding places (Fig. 2A). The internal layer of the hydrocorallite wall, directly adjacent to the visceral chamber, about 0.3 to 0.8 mm thick, with uniform fibro-radial microstructure (Pl. 1, Fig. 2) similar to that of the epithecal layer of *Cladochonus* corallites. The proper wall is surrounded with a very thin (0.02 to 0.03 mm), darker layer of sclerenchyme with unclear microstructure, resembling the "epitheca" of the Tabulata. The "epitheca" distinctly separates the proper walls of the individual hydrocorallites from each other, even in budding places , as well as separates proper walls of the individual hydrocorallites from the thick cortical layer. This high degree of autonomy of the individual hydrocorallites is further expressed by the lack of connections between their visceral chambers in budding places. The extremely thick (1.6 to 4.3 mm) external, cortical layer, has a trabecular microstructure (Pl. 1, Fig. 2), closely resembling that of cortical layer in members of the genus *Trachypsammia* (see Tourneur, Lafuste and Plusquellec 1993). The layer is built of plates, arranged radially in transverse section, and parallel or subparallel in longitudinal section. The individual plates of sclerenchyme consist of trabeculae. In the cortical layer, clearly visible are concentric growth rings of sclerenchyme,

marked with darker pigmentation. Within this zone, there occur also numerous canals of variable thickness, arranged vertically or obliquely – recognized as traces of boring or comensal organisms (Pl. 1, Fig. 2).

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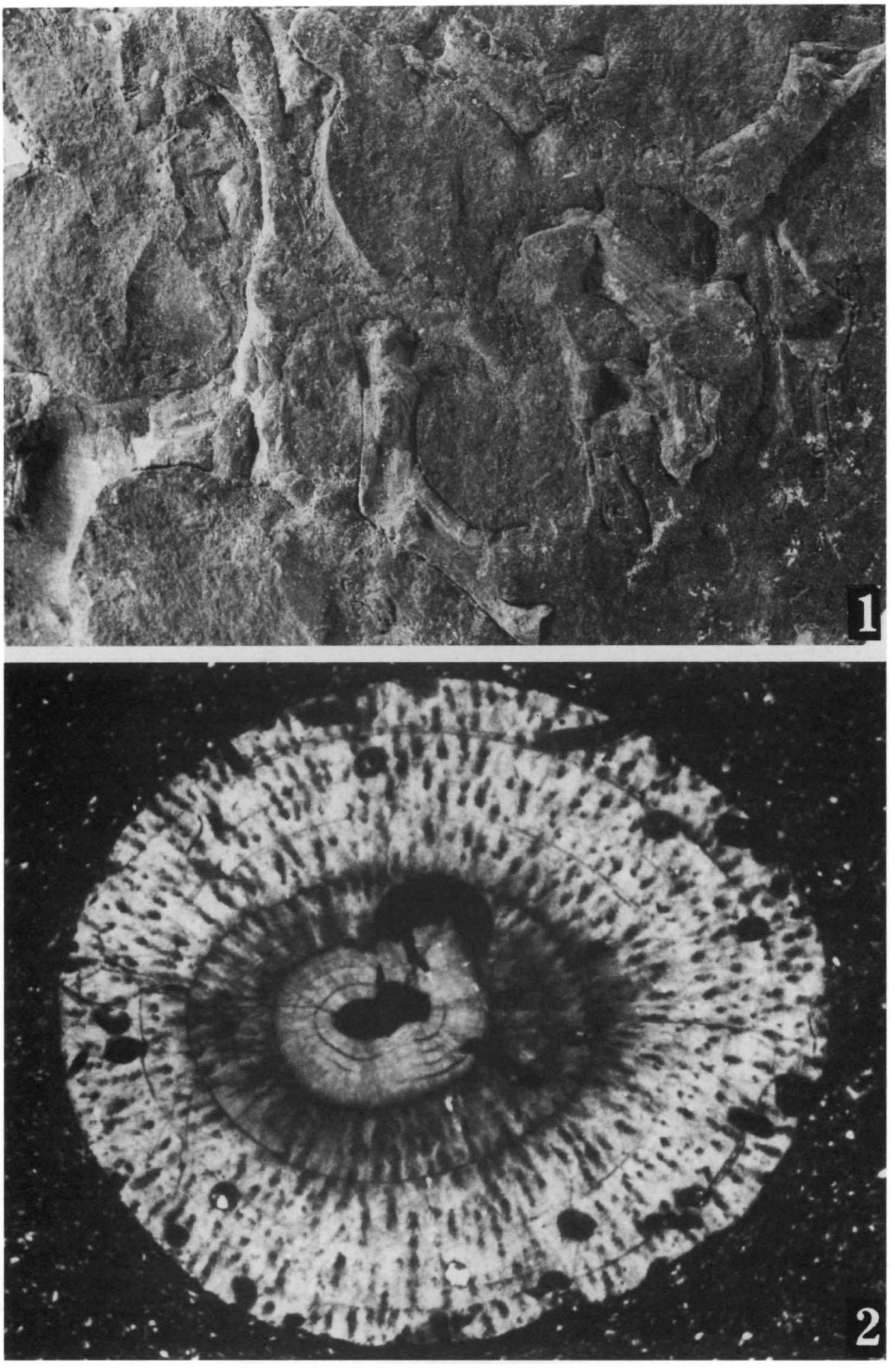


PLATE 1

*Starostinella nordica* gen. et sp. n. 1. Single and dichotomous branches at the surface of black marly shale, × 3; ZPAL V.XXV/1. 2. Transverse section through a hydrocorallite in mid-length, showing the two-layered wall structure, × 23; syntype ZPAL V.XXV/1b. Kapp Starostin Formation (Upper Permian), Kapp Starostin, Isfjorden, West Spitsbergen.

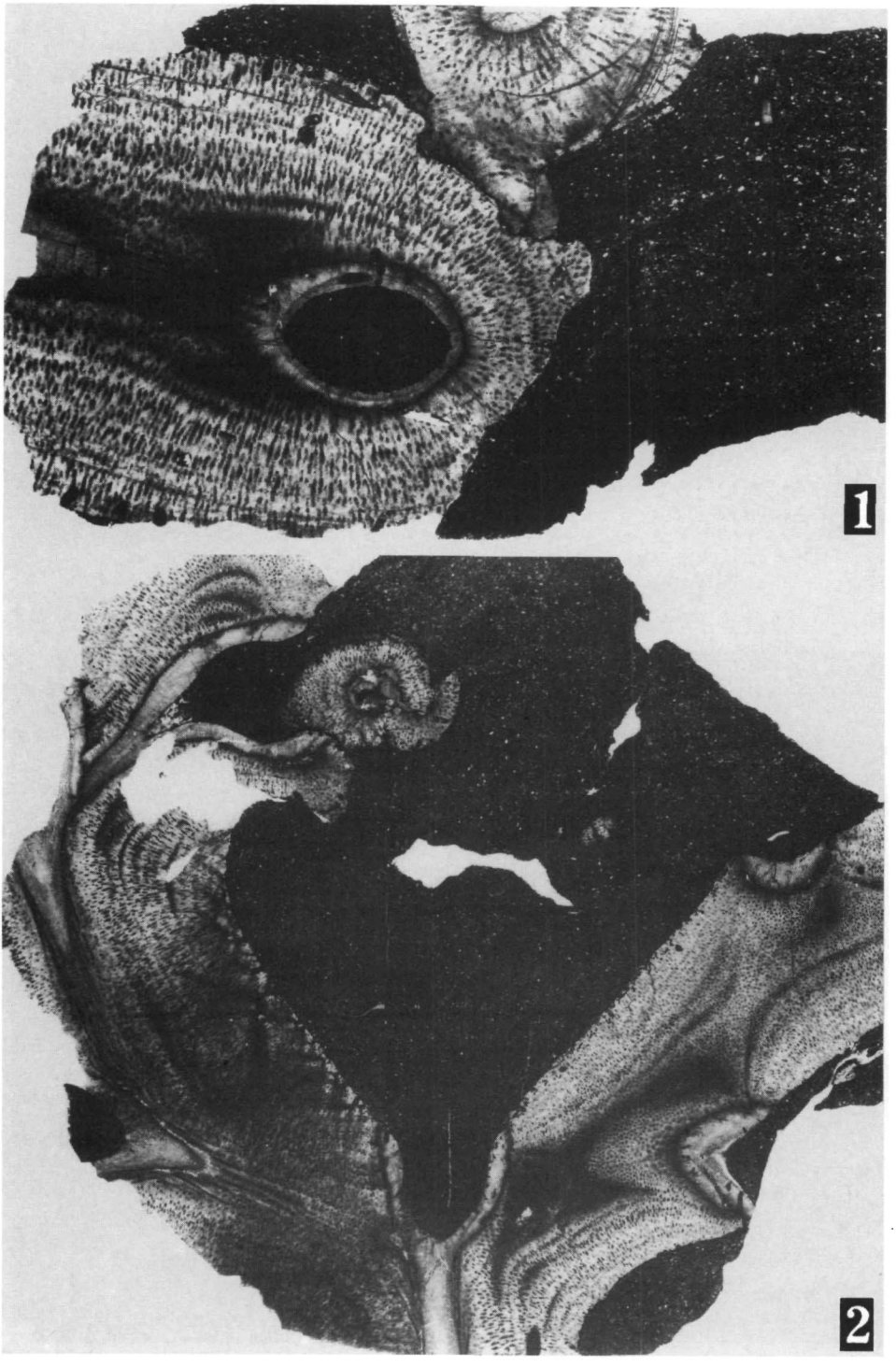


PLATE 2

*Starostinella nordica* gen. et sp. n. 1. Oblique section through a hydrocorallite in the area of new budding individual (left), × 10; syntype ZPAL V.XXV/1c. 2. Longitudinal section through a fragment of a dichotomous branch, × 5; syntype ZPAL V.XXV/1a. Kapp Starostin Formation (Upper Permian), Kapp Starostin, Isfjorden, West Spitsbergen.

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## Streszczenie

Z utworów permskiej formacji Kapp Starostin odsłaniających się w rejonie Isfjordu (Spitsbergen Zachodni) opisano i zilustrowano nowy rodzaj i gatunek hydroida kolonijnego *Starostinella nordica* (fig. 1–2, pl. 1–2). Nowy rodzaj zaliczono do Trachypsammiidae Gerth – rodziny o nieustalonej dotychczas pozycji systematycznej w obrębie Cnidaria. Szkielety kolonii Trachypsammiidae zaliczane były albo do różnych wyższych taksonów w obrębie parzydełkowców, albo uważano je za efekt symbiozy organizmu podobnego do koralowca *Cladochonus* (Tabulata) z bliżej nieokreślonym hydroidem lub stromatoporoidem. Nowy takson *Starostinella nordica* zdaje się potwierdzać to ostatnie przypuszczenie. Szkielety kolonii *Starostinella nordica* mają prostszą budowę niż inni przedstawiciele Trachypsammiidae i charakteryzują się gałązkową formą morfologiczną zbliżoną do *Cladochonus*. Ich grubościenne, rożkowate hydrokorality otoczone są bardzo grubą kortykalną warstwą sklerenchymy o mikrostrukturze trabekularnej. Mikrostruktura ścianki właściwej hydrokoralitów posiada fibro-radialną mikrostrukturę, ostro odcinającą się od zewnętrznej warstwy kortykalnej. Złożoność problemu przynależności systematycznej Trachypsammiidae, przedstawiono w oparciu o charakterystyki wszystkich rodzajów wchodzących w skład tej rodziny. Przedstawiono także krótki rys historii badań nad morfologią i strukturą szkieletów jej przedstawicieli.