

# Confirmation of the poriferan status of favositid tabulates

JÓZEF KAŻMIERCZAK



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Reported are findings of calcitic pseudomorphs of monaxonic sclerites (heloclones and ophirhabds) occurring as highly ordered vertical tracts and subhorizontal strands in the midwall of calcareous skeletal tubes of a common Silurian favositid species, *Favosites hisingeri*, from Gotland. The discovery ends conclusively the current controversy about the nature of favositids and related tabulomorphs in favour of the neglected early suggestion of Kirkpatrick (1911) that these fossils can be basal calcareous secretions of siliceous sponges similar to those in living *Merlia normani*. The type of sclerites found in *F. hisingeri* and other favositids indicate that favositids are closely related to fossil and extant sponges classified within the order Lithistida (class Demospongia) as the so-called sublithistids.

**Key words:** favositids, tabulomorphs, sclerites, affinity, sponges, Silurian.

*Józef Kaźmierczak, Institute of Paleobiology, Polish Academy of Sciences, Aleja Żwirki i Wigury 93, 02-089, Warszawa, Poland.*

## Introduction

From the first descriptions favositids have been considered remains of colonial organisms unquestionably related to zoantharian corals. Although it has never been clearly elucidated to which group of Anthozoa they should actually be classified, such an affinity was praised freely by all specialists and great authorities of invertebrate paleontology of the 19th and early 20th centuries, authors of generally accepted compendia and textbooks. No wonder, therefore, that when in 1911, a little known British zoologist-spongiologist, Randolph Kirkpatrick, suggested that some of the tabulate corals might be products of siliceous sponges, the proposal was ignored as the fling of an outsider, and, in fact, forgotten for almost sixty years.

This passive neglect is, however, somewhat puzzling, taking into account the fact that Kirkpatrick (1910) arrived at his conclusion after careful examination of peculiar living sponges dredged near the shores of Madeira and described by him formally as *Merlia normani* Kirkpatrick 1908. The peculiarity of *M. normani* concerns the bimineral character of its skeleton. In addition to typical siliceous sclerites, the sponge at the basal pinacoderm simultaneously produces a calcareous (calcitic) skeleton composed of vertical tubes crossed more or less regularly by horizontal partitions (tabulae). It was this skeleton which, in Kirkpatrick's opinion, closely resembles the skeletal organization of some tabulate fossils. There are two probable reasons as to why the idea was not taken up by contemporary and later workers. On one hand, judging retrospectively, Kirkpatrick's discovery was apparently *postmature* since at that time the conviction of the zoantharian nature of favositids was too firm and supported by too many authorities to be swayed by the suggestion of an 'obscure' author. On the other hand, however, the idea was clearly *premature* because the simultaneous secretion of siliceous and calcareous skeletal parts reported by Kirkpatrick in *M. normani* was incompatible with contemporary empirical evidence and conceptual schemes stating such secretion of bimineral skeletons to be thermodynamically impossible.

The revival of Kirkpatrick's suggestion concerning possible poriferan affinity of Tabulata began in the early seventies after rediscoveries of *Merlia* and findings of other similarly bimineral living sponges (Vacelet 1967; Hartman 1969, 1979; Hartman & Goreau 1970, 1972, 1975) named by some workers sclerosponges or coralline sponges (Hartman 1969; Hartman & Goreau 1972) and by others ischyrosponges or hypercalcified sponges (Termier & Termier 1973).

The possibility of the sclerosponge affinity of tabulomorph fossils, particularly of favositids, has been pondered by both zoologists (Hartman & Goreau 1970, 1972, 1975) and palaeontologists (Flügel 1976; Scruton 1987) who, however, did not find enough evidence for their conclusive transfer from corals to sponges. Strangely, the position of those opting for cnidarian affinities of favositids has been changed neither by discoveries of well-preserved spicules in Mesozoic and Palaeozoic chaetetids (Kaźmierczak 1979; Gray 1980), tabulomorph fossils which for a long time have been by many specialists classified within Tabulata, nor by occasional findings (Kaźmierczak 1984, 1989, 1991, 1993) of structures resembling sclerites of monaxial and sublithistid sponges in calcareous skeletons of typical representatives of Favositida such as *Thamnopora*, *Favosites*, *Palaeofavosites*, *Mesofavosites* or *Quepora*. Some workers (Oekentorp 1985; Finks 1986; Wood *et al.* 1990; Elias & Lee 1993) regard the morphology of these bodies as inadequate evidence to accept them as sponge sclerites and claim they can be equally interpreted as traces of filamentous endolithic microbiota. Moreover, the position of specialists opting for cnidarian affinity of favositids has been further strengthened after the report (Copper 1985) on radially lobated calcareous structures

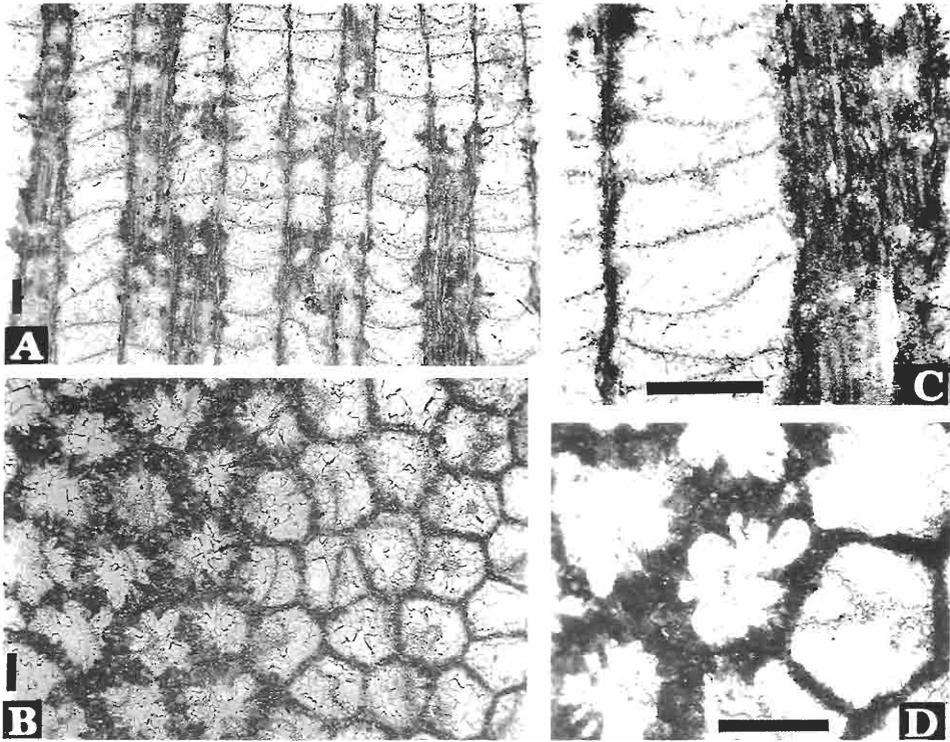


Fig. 1. *Favosites hisingeri* Edwards & Haime 1851; Visby Formation (Ygne Member, Ireviken bioherms), Early Wenlock, locality Ireviken 3 of Laufeld (1974), Gotland; specimen ZPAL T/XIX/1. □A–B. General structure of the calcareous skeleton in longitudinal and transversal section under standard magnification. Distinct striation visible on longitudinal sections of skeletal tubes in (A) represents remnants of predominantly vertically arranged monaxonic spicular tracts. Slightly oblique transversal section (B) shows two skeletal zones built of two strikingly different kinds of tubes passing continuously into each other: (1) thick-walled cylindrical tubes with short septa inside, and (2) thin-walled prismatic tubes without septa. Strangely enough, but according to the currently accepted and widely used taxonomy of Tabulata (Hill 1980), the skeletal structure on the left side of the section should be classified to the order Sarcinulida Sokolov 1950 whereas the right one to the order Favositida Wedekind 1937. □C–D. Magnified fragments of longitudinal (C) and transversal (D) thin sections from the same specimen showing the details of the skeletal structure. As visible in (D), the sudden change in the mode of skeletal growth may even result in the formation of tubes sharing morphological features of high (ordinal) taxonomic rank. All transmitted light micrographs; scale bars equal 500  $\mu\text{m}$ .

covering the surface of some *Favosites* specimens from the Silurian deposits of Anticosti Island, interpreted (Copper 1985; Copper & Plusquellec 1993) as almost instantaneous post-mortem calcification of favositid polyps. Although this interpretation has been criticized (Kaźmierczak 1991, 1993) as a misjudgement since structures similar to the alleged 'polyps' have been described by earlier authors (Dunbar 1927; Swan 1947; Flügel 1986) as skeletal elements named opercula and pseudopercula, many authors took it for granted. Overall, a rather paradoxical situation

developed, where both sides of the debate presented suggestive evidence for the correctness of their interpretation, with neither acceptable as the crucial one.

The reported below finding of extraordinarily preserved remains of sclerites within walls of the calcareous tubes of Silurian specimens of *Favosites*, definitely turns the balance of the debate in favour of the poriferan affinity of Favositida.

## Material

The studied material, enclosing three discoid specimens of favositids identified as *F. hisingeri* Edwards & Haime 1851, was collected by myself in the Silurian limestones of Gotland. According to Laufeld's (1974) reference localities for palaeontology and geology in the Silurian of Gotland, the collecting site corresponds with the locality Ireviken 3. It represents a cliff section comprising a few large bioherms rich in *F. hisingeri*. In the new lithostratigraphic scheme of the Silurian of Gotland (Riding & Watts 1991), these bioherms are formally included as Ireviken bioherms within the Ygne Member of the early Wenlock Visby Formation.

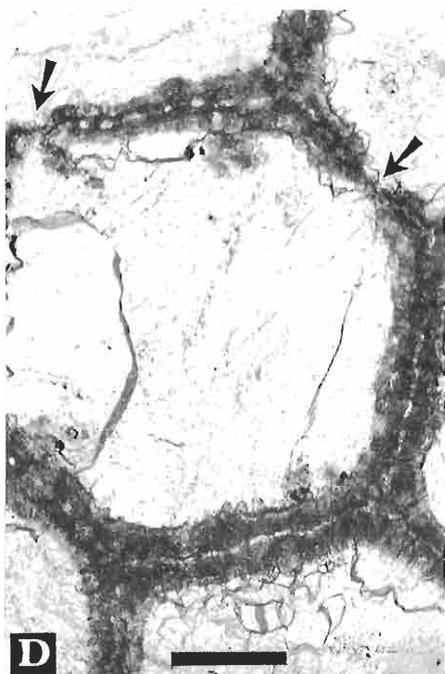
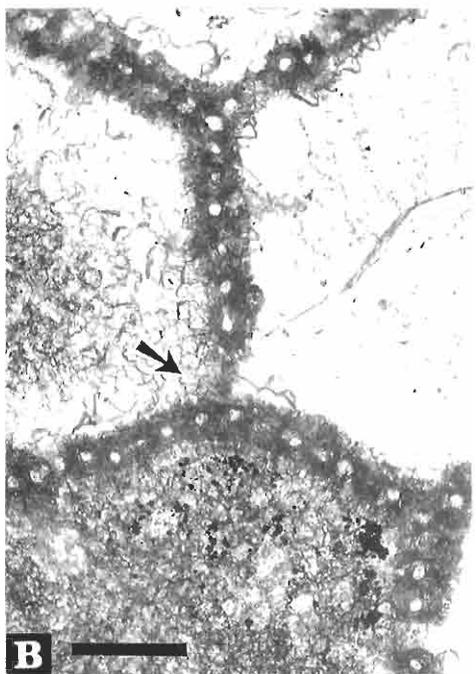
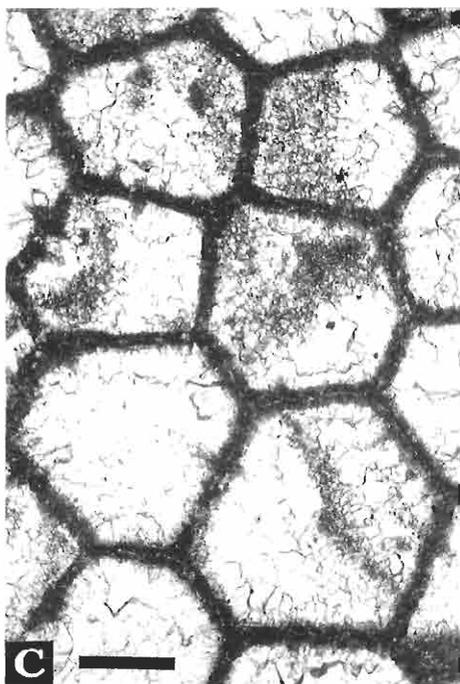
*F. hisingeri*, known also as *Angopora hisingeri*, is a well-studied favositid species described by several authors (Jones 1936; Stasińska 1967; Klaamann 1970; Stel 1978). The most detailed recent studies (Stel 1978) presenting the morphology, taxonomy and palaeoecology of *F. hisingeri* have been based on Gotland specimens derived largely from the same site as those presented in this report.

## Calcareous skeleton

The calcareous skeleton of *F. hisingeri* shows typical favositid traits: it is composed of tightly adhering tubes, averaging 0.8–1.2 mm in diameter, crossed by roughly evenly spaced subhorizontal tabulae (Fig. 1A–B). The

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Fig. 2. *Favosites hisingeri* Edwards & Haime 1851; Visby Formation (Ygne Member, Ireviken bioherms), early Wenlock, locality Ireviken 3 of Laufeld (1974), Gotland; specimen ZPAL T/XIX/2. □A. Transversal section through the prismatic portion of the calcareous skeleton showing almost equidistant distribution of the calcitic pseudomorphs (white roundish spots) of originally siliceous monaxonic sclerites arranged vertically along the midwall of skeletal tubes; scale bar equals 500  $\mu\text{m}$ . □B. Magnified portion of the same section showing distribution of sclerite pseudomorphs (white spots in the midwall of skeletal tubes) and of mural pores (arrowed) located at the edges and on the faces of prisms; scale bar equals 250  $\mu\text{m}$ . □C. Another portion of the same thin section as in A showing almost homogenous structure of the calcareous skeleton with remnants of subhorizontally located strands of sclerite pseudomorphs visible as very indistinct white lines in the middle of the tube walls; scale bar equals 500  $\mu\text{m}$ . □D. Transversal section through a magnified fragment of a skeletal tube showing a few cross sections of vertically arranged sclerites visible as white spots in the tube mid-wall (left and upper side of the figure), and longitudinal sections of subhorizontally



located strands of sclerites visible as an uneven white band ('median suture' of previous authors) in the middle of the tube wall (lower and right side of the figure). Scale bar equals 250  $\mu\text{m}$ : arrows indicate location of mural pores. All transmitted light micrographs.

tubes communicate with rare mural pores, about 100  $\mu\text{m}$  in diameter, distributed in irregular rows on the tube faces or rarely at the tube corners. An unusual feature of *F. hisingeri*, noted also by previous authors (Klaamann 1970; Stel 1978) is the presence of alternating skeletal zones built of two radically different types of skeletal tubes vertically passing continuously into each other (Fig. 1A–B). One type are polygonal (prismatic) tubes with relatively thin, smooth walls, whereas the other are cylindrical tubes with much thicker walls bearing discontinuous septa and septal spines. The transition between the two may be so sudden that some may share their walls (Fig. 1D). The phenomenon of such radical zonal changes in tube morphology remains largely unexplained. The suggestion (Klaamann 1970) that it may reflect cyclic growth rejuvenation of favositid zooids is inconsistent with the sponge nature of *F. hisingeri*, demonstrated below.

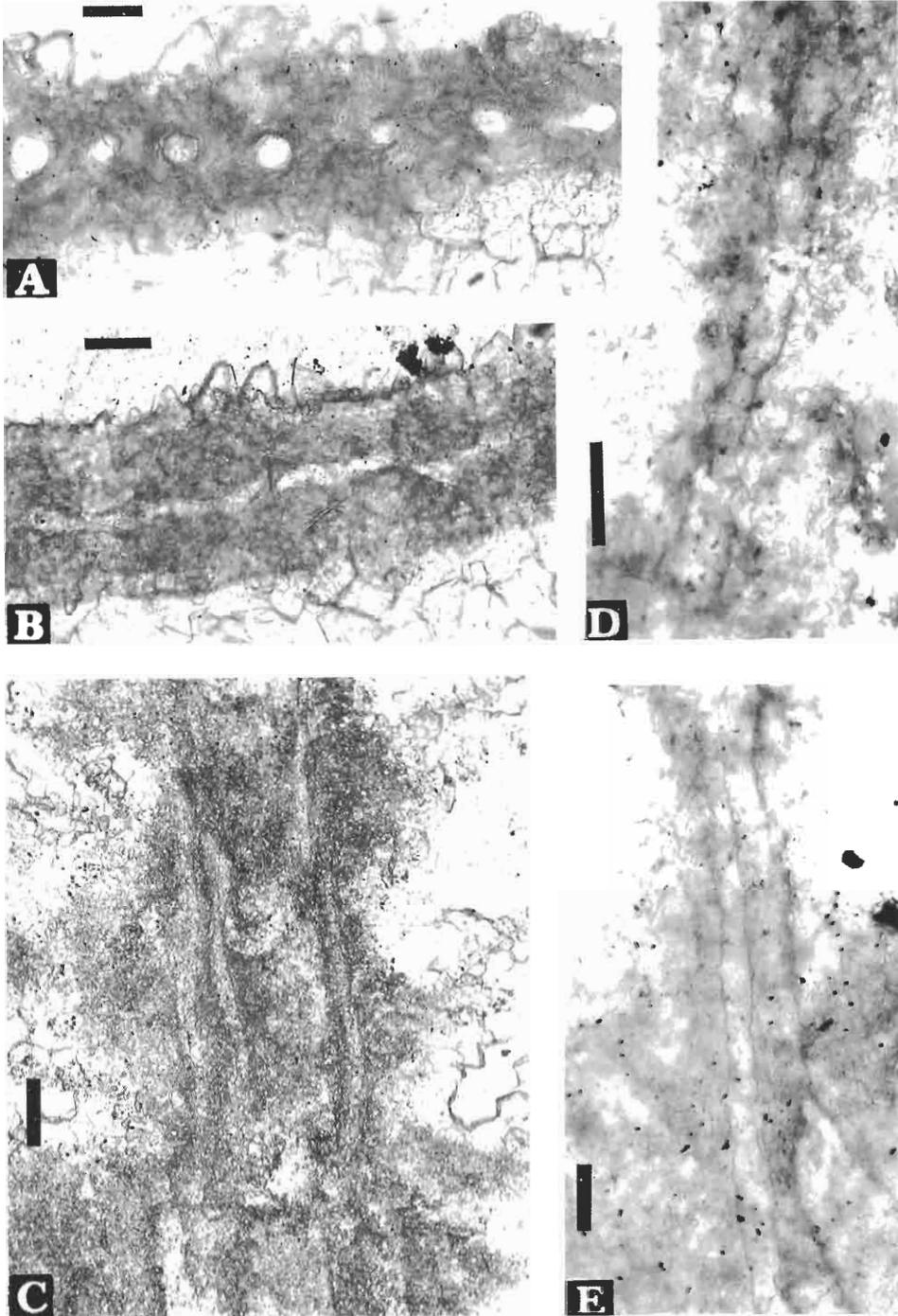
## Sclerites

The crucial evidence for the sponge nature of *F. hisingeri* is the remnants of originally siliceous sclerites preserved as calcitic pseudomorphs incorporated in the walls of the calcareous skeletal tubes. As in the case of other fossil and living sclerosponges (e.g., Kaźmierczak 1974; Kaźmierczak & Hillmer 1974; Hartman 1979) such pseudomorphs are products of diagenetic dissolution of the primary silica and subsequent replacement of the sclerite volume by calcium carbonate. The replacement is not always perfect and the pseudomorphs do not precisely reflect the original shape of sclerites.

The spicular system is composed of vertical tracts and subhorizontal strands located in the midwall of the calcareous tubes. The tracts are built predominantly of monaxial sclerites resembling monorepid desmas known as heloclones (Fig 3D), and of much less abundant, thinner, almost smooth monaxial sclerites resembling ophirhabds (Fig. 3E). The sclerites in the tracts are arranged in the form of a loose, regular palisade. In transversal section of the calcareous tubes the palisade is visible as a single row of roundish white spots distributed almost equidistantly along

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Fig. 3. *Favosites hisingeri* Edwards & Haime 1851; Visby Formation (Ygne Member, Ireviken bioherms), Early Wenlock, locality Ireviken 3 of Laufeld (1974), Gotland; specimen ZPAL T/XIX/2. □A. Transversal section of a fragment of skeletal tube wall crossing spicular tract composed of monaxial sclerites distributed equidistantly in the midwall and vertically oriented; scale bar equals 50  $\mu\text{m}$ . □B. Transversal section of skeletal tube wall passing through the level of spicular meshwork composed of subhorizontally located strands of irregularly bent monaxonic sclerites giving an impression of a midwall fissure (= 'median suture' of previous authors); scale bar equals 50  $\mu\text{m}$ . □C. A fragment of longitudinal section of skeletal tube showing vertically oriented pseudomorphs of heloclone- and ophirhabd-like sclerites; scale bar equals 100  $\mu\text{m}$ . □D–E. Examples of calcitic pseudomorphs of monaxonic sclerites from vertical tract in the midwall of a skeletal tube. The irregularly tuberculated scler-



rite shown in B can be classified as a heloclone-like monorepid desma whereas the almost smooth one illustrated in B is more reminiscent of an ophirhabd monaxon. All transmitted light photomicrographs.

the middle of the tube walls (Fig. 2A–B). In longitudinal sections of skeletal tubes the palisade is visible as distinct vertical striation of the tube walls (Figs 1A, C; 3C). Interestingly, such a striation was also observed and illustrated in *F. hisingeri* by previous students (Jones 1936; Klaamann 1970) without, however, any significance being ascribed to it. The subhorizontal spicular strands are also composed of monaxial sclerites (ophirhabds) which are somewhat thinner and shorter than those from tracts, more densely distributed and often irregularly bent. They are easily recognizable in transversal sections of skeletal tubes as white, slightly wavy and irregularly interrupted streaks located along the midwall of skeletal tubes (Figs 2C–D and 3B). In longitudinal sections of tube walls they are less obvious, due to their somewhat intermingled arrangement. Both spicular systems are more clearly visible in the walls of prismatic tubes; in the much thicker walls of the cylindrical tubes, the spicules are less regularly distributed and less conspicuous.

A diagrammatic reconstruction of the spicular meshwork in *F. hisingeri* (Fig. 4) based on the above observations shows that in transversal thin sections, depending on the skeletal level sectioned, either streak-like or dotted white zones can be observed in the midwall of skeletal tubes. These patterns were apparently very confusing to previous students of *F. hisingeri* who tried to interpret the more continuous median lines as recrystallized sutures separating walls of individual 'corallites' (Klaamann 1979; Stel 1978), and the dots, in turn, as traces left by some kind of commensal organisms (Klaamann 1970) or simply as recrystallization patterns (Stel 1978). Similar midwall tracts composed of less regular palisades of subvertically distributed heloclone-like sclerites corresponding with the so-called median line or median suture of typical favositids have been recently described in Devonian alveolitid favositids (Kaźmierczak 1993).

## Discussion and conclusions

Spicule morphology and spatial arrangement closely relate *F. hisingeri* to sponges classified within the order Lithistida as the so-called sublithistids. These are fossil and living sponges characterized by sclerites ranging from simple monaxons through ophirhabds and heloclones to fully developed desmas, which in particular species may occur in various proportions (Reid 1968). Examples of fossil sponges with sclerite systems particularly closely resembling the one described above from *F. hisingeri* are forms assigned to the rhizomorinid families Haplistidae De Laubenfels 1955 (*Chaunactis* Finks 1960, *Haplistion* Young & Young 1877, and *Kazania* Stuckenberg 1895) and Saccospongidae Rigby & Dixon 1979 (*Saccospongia* Ulrich 1889, *Eochaunactis* Rigby & Dixon 1979, and *Haplistionella* Rigby & Dixon 1979). The spicular system occurring in *F. hisingeri* show greatest similarity to spicular meshworks described in the Silurian *Haplistionella minitraba* and *H. garnieri* (Rigby & Dixon 1979), Carboniferous

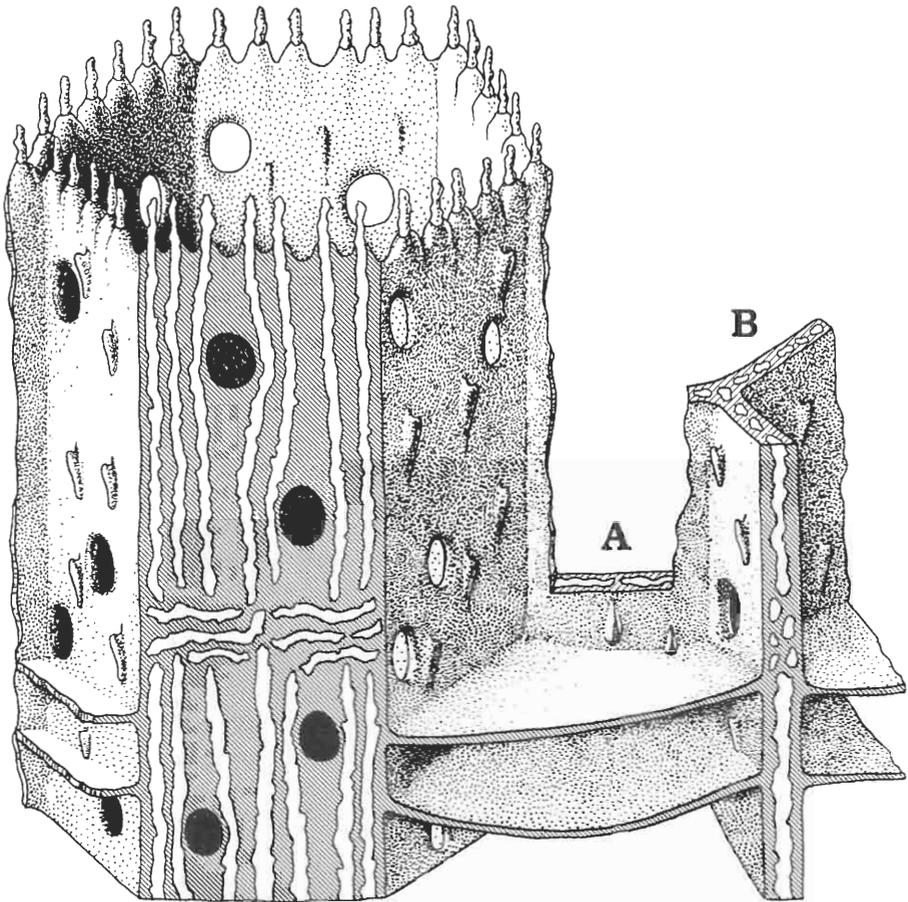


Fig. 4. Diagram showing the distribution of sclerites in the wall of a prismatic calcareous skeletal tube of *Favosites hisingeri* in median longitudinal and transversal sections. Depending on the skeletal level sectioned, the sclerites can be visible in transmitted light thin sections either as a somewhat discontinuous median white zone (A) or as a row of more or less equidistantly distributed white spots (B).

*Kazania elegantissima* (Tschernyschew 1898), and Permian *Haplistion arcticum* (Siedlecka 1970; Rigby & Terrell 1973; Hurcewicz 1982). Recent examples of sponges with spicular skeletons somewhat similar to that of *F. hisingeri* are members of the sublithistid genera *Desmatiderma* Topsent 1928 and *Monanthus* Kirkpatrick 1903. However, neither of these sponges has so elegantly regularly developed vertical sclerite tracts as *F. hisingeri*.

It should be stressed that the sclerites incorporated in the calcareous skeleton of *F. hisingeri* probably represent only part of the sponge sclerite system. Similarly as in living sclerosponges (Kirkpatrick 1911; Hartman & Goreau 1970; Willenz & Hartman 1989), the secretion of calcium carbonate was in *F. hisingeri* limited presumably to the basal pinacoderm. Therefore, only the spicules could be entrapped and incidentally preserved

in the calcareous skeleton, which during sponge growth were close enough the living tissue secreting the calcareous substance. The sclerites occurring in the mesohyl or the dermal layer had no chance for preservation. This precludes, unfortunately, the usage of spicules in the low rank favositid taxonomy since in lithistid and sublithistid sponges dermal sclerites, for instance, are important for specific and generic assignments. The few sclerite findings made thus far in various favositids (Kaźmierczak 1984, 1989, 1993) indicate that in spite of great differences in the morphology of their calcareous skeletons, the spicules are rather monotonous and practically limited to ophirhabds, heloclones, and simple rhizoclones. This may indicate that favositids are phylogenetically a rather coherent group and, in the absence of taxonomically reliable sclerites, the present finding will not remarkably change the taxonomic schemes proposed so far. It cannot also be excluded that as in the recent sclerosponges, *Merlia* (Kirkpatrick 1911) or *Acanthochaetetes* (Hartman & Goreau 1975), the spicules in some favositids might have never been incorporated in the calcareous skeleton.

Conversely, the concurrence in the studied specimens of *F. hisingeri* of the two above mentioned extremely different kinds of skeletal tubes demonstrates in a rather dramatic manner the basic problems and weakness of the taxonomy of the two core groups of Tabulata. One (the prismatic), according to the currently used taxonomic criteria in Tabulata (Hill 1981), should be classified to the order Favositida Wedekind 1937, and the other (the cylindrical with septa) to the order Sarcinulida Sokolov 1950. It seems that the morphological features used so far in Tabulata for designation of taxonomic categories at all levels require serious re-evaluation.

Moreover, the facultative character of the calcareous skeleton noticed in some *Merlia* (Vacelet 1980; Van Soest 1984) gave rise to speculations that the origin and appearance of extant and fossil sclerosponges may be strongly environmentally controlled. It has been suggested (Kaźmierczak *et al.* 1985; Kaźmierczak 1989) that increased  $\text{Ca}^{2+}$  concentration and/or increased alkalinity in the environment may have amplified uptake of this cation by the sponges, which must have been ameliorated by its increased extrusion resulting in deposition of skeletal calcium carbonate.

Whatever the reason causing siliceous sponges to produce the excessive calcareous skeletons, the favositids and probably other tabulomorph fossils seem to represent no more than mineral products of the basal pinacoderm carrying little information about the biological organization of the organisms secreting them.

## Acknowledgements

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## Streszczenie

W wapiennym szkielecie denkowców (Tabulata), *Favosites hisingeri* Edwards & Haim 1851, z osadów wczesnego wenloku Gotlandii, odkryto inkorporowane liczne kalcytowe pseudomorfozy sklerytów zbliżonych do heloklonów i ofirabdów krzemionkowych gąbek (Demospongia). Skleryty te występują w środkowej strefie ścian wapiennych rurek szkieletowych w postaci uporządkowanych systemów (tzw. traktów), złożonych z pojedynczych szeregów w prawie równych odstępach rozmieszczonych heloklonów i ofirabdów, poprzedzielanych krótszymi i cieńszymi, nieregularnie powyginanymi monaksonami, zebranymi w subhoryzontalnie ułożone pasma. Odkrycie to stanowi krytyczny dowód na słuszność ignorowanej przez wiele lat sugestii Kirkpatricka (1911), według której denkowce byłyby bazalnymi szkieletami wapiennymi gąbek krzemionkowych zbliżonych do dzisiejszych *Merlia normani* Kirkpatrick 1908. Typ sklerytów występujących u *F. hisingeri* i innych fawozytidów wskazuje, że są one blisko spokrewnione z niektórymi kopalnymi i dzisiejszymi gąbkami z rzędu Lithistida, szczególnie z tzw. sublitistidami, charakteryzującymi się sklerytami o cechach budowy przejściowych pomiędzy monaksonami i ryzoklonami.