A C T A P A L A E O N T O L O G I C A P O L O N I C A
Vol. XIV 1969 No. 4

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A NEW INTERPRETATION OF ASTRORHIZAE IN THE STROMATOPOROIDEA

Abstract. — The results of the author's studies on the morphology, function and taxonomic value of astrorhizae in the Palaeozoic Stromatoporoidea are presented. In contradistinction to previous views according to which astrorhizae were considered as structure formed by stolons or zooids of the Stromatoporoidea, the author concludes that they are traces of foreign organisms associated with the Stromatoporoidea. The relationships between both organisms were probably commensal or mutualistic in character. On the basis of associations observed in Recent sponges and coelenterates, the author has discussed the possibility of a plant (algae) or animal (non-skeletal coelenterates) nature of the organisms which were associated with the Stromatoporoidea. Depending on the manner of connecting astrorhizae with the skeletal tissue of the coenosteum, two types of these structures, i.e. a) *integrated* and b) *separated*, have been distinguished and their morphological and growth interpretation attempted. The new interpretation of astrorhizae allows one to eliminate these structures as diagnostic features of the Stromatoporoidea which may to a considerable extent simplify the taxonomy of this group.

INTRODUCTION

In the course of a taxonomic elaboration of the Devonian Stromatoporoidea of Poland (mostly from the area of the Holy Cross Mountains — Góry Świętokrzyskie), the present writer encountered certain difficulties in establishing taxonomic categories based on previously accepted diagnostic features on specific and, in many cases, generic level. A considerable arbitrariness of the diagnostic features so far accepted is the main reason why more and more species have been erected, a phenomenon particularly frequent in works published over the last two decades. New taxa are described without a critical estimation of the taxonomic value of fundamental morphological elements of coenosteum which were mostly determined as early as the late 19th century. With a negligible number of revisory works, the number of the species described has already exceeded 1700 (Flügel & Flügel-Kahler, 1968). It has been only recently that several specialists of the Stromatoporoidea have begun to pay attention to the importance of ecological and microstructural studies for the purposes of taxonomy of this group (Stearn, 1966; St. Jean, 1967; Sleumer, 1968, 1969).

The results of studies on astrorhizae made on the basis of an abundant and varied material of the Stromatoporoidea, collected from the Devonian (Givetian-Frasnian) of the Holy Cross Mountains, are described in the present paper. The data concerning the problem of astrorhizae in the Ordovician and Silurian Stromatoporoidea have been taken from published works. About 500 complete and fragmentary colonies, on part of which astrorhizae occur only superficially, and about 600 thin slides with cross sections of astrorhizae have been examined. Valuable information concerning the frequency of occurrence of astrorhizae in the colonies of stromatoporoids was obtained by looking through hundreds of polished plates of Devonian stromatoporoid limestones stored at the Building Stone Dressing Plant in Kielce. These plates, made of Givetian limestone, hewn out at the "Panek" quarry in Bolechowice near Kielce, are commonly used in Poland as a decorative stone slab facing.

This paper has been prepared at the Palaeozoological Institute (abbreviated Z. Pal.) of the Polish Academy of Sciences in Warsaw, where the specimens described are housed.

The present writer's cordial thanks are extended to Prof. Z. Kielan-Jaworowska, Director of the Palaeozoological Institute of the Polish Academy of Sciences, for her scientific patronage and a many-sided help in the preparation of the work. He also feels indebted to Prof. R. Kozłowski (Palaeozoological Institute of the Polish Academy of Sciences, Warsaw) and Docent A. Urbanek (Palaeozoological Laboratory of the Warsaw University) for an extensive discussion and valuable remarks concerning the text. Separate thanks are due to Miss D. Kościelska, laboratory assistant at the Palaeozoological Institute, who prepared thin sections of stromatoporoids.

MORPHOLOGICAL CHARACTERISTICS OF ASTRORHIZAE

The term "astrorhiza", introduced to literature by Carter (1880) to replace his previous definition "stellate venation", was generally accepted. Carter's definition determines astrorhizae as stellate systems of canals marked on the surface and in deeper parts of coenosteum of stromatoporoids. The term "astrorhiza", referring to "hydrorhiza", was intended to emphasize a homology between these structures which existed according to Carter. Carter's definition was subsequently supplemented by descriptions of astrorhizae presented by many authors (including Nicholson, 1886; Kühn, 1927, 1939; Lecompte, 1951, 1952; Yavorsky, 1955; Galloway & St. Jean, 1957; Flügel, 1959; Nestor, 1964, 1966; Bogoyavlenskaya, 1965).

In the present paper, citing examples of relationships between astrorhizae and definite morphological types of coenosteum, the writer purposely confines himself to the determination of a genus as a taxonomic category relatively easy to distinguish among the Stromatoporoidea in contradistinction to a species, which happens to be ununivocally understood. His negative attitude towards most species of the Stromatoporoidea, erected so far, will be justified in a separate paper devoted to the taxonomic value of the morphology of the skeletal tissue and its microstructure.

Shape of astrorhizae

An astrorhiza is a structure formed as a result of superposition of a certain number of growth stages, marked by more or less regularly distributed tabulae and cysts. It consists of a system of stellate canals branching off from a centrally situated point or area. Lateral canals of astrorhizae, frequently diverging dichotomously, are disposed parallel, obliquely or, less frequently, perpendicularly to the laminae of coenosteum. In extreme cases, all the manners of disposition of lateral canals may be found in one astrorhiza (Pl. V, Figs. 1-2). This fact renders doubtfull the classification of astrorhizae, according to which a regular manner of disposition of lateral canals in relation to the plane of laminae of coenosteum is assumed (Bogoyavlenskaya, 1968). The present writer also does not agree with Lecompte's (1956) view that the tendency to a vertical position of lateral canals is a character of astrorhizae which, according to that author, is the most distinct in the Mesozoic forms (Sphaeractinoidea) derived from Palaeozoic stromatoporoids. In the representatives of the genera *Hermatostroma* and *Stromatoporella*, examined by the present writer, bundles of vertical canals are clearly visible next to horizontal and oblique canals (Pl. V, Figs. 1-2; Pl. VIII, Fig. 2). Principal morphological features of all astrorhizae, observed on the surface of coenosteum, are similar even in such stromatoporoids which considerably differ from each other in the architecture of their skeletons. A considerable differentiation of astrorhizae is, however, revealed by spatial observation.

Previous descriptions of astrorhizae distinguish simple forms consisting only of stellate, horizontal canals occurring on the surface of coenosteum and complex forms, composed of several superposed, simple astrorhizae connected with each other by a common axial canal (or, according to Galloway, 1957 — astrorhizal cylinder). In simple astrorhizae, a small depression or, *vice-versa,* elevation occurs at central point. An opening which corresponds to an outlet of the axial canal or, in the case of a bundle of axial canals, several openings are observed in the central part of superposed astrorhizae (Pl. I, Figs. 1-3; Pl. II, Fig. 2; Pl. VIII, Fig. 1).

Lateral canals of astrorhizae may be straight, not branched or branched singly, dichotomously or many times. There also occur anastomozing lateral canals. In the systems of superposed astrorhizae, differences are observed in the length of lateral canals which at certain levels are short and at others considerably longer (Pl. IV, Fig. 4).

Despite their usually stellate structure, astrorhizae do not display symmetry. Traces of hexametric symmetry which may be observed in some astrorhizae seem to be fortuitous.

In addition to astrorhizae with a stellate system of lateral canals, some other types occur. So some Ordovician and Silurian stromatoporoids have a vertical canal with a cross section mostly larger than that of galleries of skeleton tissue and having short, irregular lateral branching. Such astrorhizae are considered to be a primitive initial type of strongly branched ones (Galloway, 1957; Nestor 1964). According to Lecompte (1951, 1956), vertical canals with few, short, lateral branchings and which are axially or excentrically situated in digitiform and ramose stromatoporoids (as, for instance, in the genera *Idiostroma, Dendrostroma, Amphipora* and *Stachyodes*), should be also assigned to astrorhizae. In many specimens of the genus *Hermatostroma* from the Devonian of the Holy Cross Mountains, strongly concentrated astrorhizae display an irregular pattern of structure and a lack of a definite orientation in relation to the skeletal tissue (Pl. VI, Figs. 1-2; Pl. VII, Figs. 1-2).

Astrorhizal canals are usually round or suboval in transverse section. They may be also more irregular in outline.

Size of astrorhizae

The size range of astrorhizae is very extensive. The spacing of terminal ends of lateral astrorhizal canals may vary within limits of 2 and 30 mm (Galloway, 1957), the smallest of them being recorded in Ordovician and Silurian stromatoporoids (e.g. *Stromatocerium rugosum* Hall), and the largest in Devonian ones (e.g. *Stromatoporella eifeliensis* Nicholson). Astrorhizae with the spacing of their lateral canals exceeding 50 mm (Pl. I, Figs. 1-2) have been found by the present writer in Devonian forms from the Holy Cross Mountains, belonging to *Stromatoporella* sp. and *Hermatostroma* sp. Accurate measurements of the spacing of lateral canals on the surface of coenosteum or in tangential sections are more difficult in the case when canals are obliquely disposed in relation to laminae. On the other hand, with measurements taken in vertical sections, it is difficult to place the plane of section in the axis of an astrorhiza.

In regard to size, astrorhizae may be divided into the following two groups: 1) small, with lateral canals spaced 1—8 mm apart, averaging

4—6 mm; 2) large, with lateral canals spaced 15—50 mm apart, averaging 20—30 mm.

Each of these groups is related to a definite type of the structure of coenosteum and differs from the other in its relation to the skeletal tissue (see below).

The diameter of the transverse section of lateral and axial canals is in principle proportional to the size of the entire astrorhizal structure, but sometimes astrorhizae happen to have long and narrow axial and thick lateral canals.

The superposed astrorhizae continue to run in coenosteum over a space of a few to some scores of laminae. Their length, measured along the axis, varies from a few mm to 4 cm and even more. Systems of superposed astrorhizae are represented in both size groups. The degree of ramification of lateral canals of superposed astrorhizae frequently varies within particular "floors".

The concurrence of large astrorhizae of two types: larger ones with canals set about 50 mm apart, and lateral canals about 1 mm in transverse section, and smaller ones with canals set about 15—20 mm apart, and lateral canals about 2.5 mm in transverse section, have been observed by the present writer on the surface of a few colonies of *Hermatostroma* sp. The central zone of the former is of the nature of a broad depression, and that of the latter — of an elevation on which the outlets of a bundle of axial canals are visible (Pl. I, Fig. 1). Lateral canals of both types of astrorhizae do not join each other.

Relationship of astrorhizae to the surrounding skeletal tissue

It was proved by Carter (1879, 1880) and Nicholson (1886) that astrorhizal canals have not proper walls and that the space they occupy is bounded by elements of coenosteum. These observations were later confirmed by Steiner (1932), Kühn (1927, 1939), Lecompte (1951, 1956), Yavorsky (1955), Galloway (1937) and others. Characterizing astrorhizae, Nicholson (1886, p. 53) maintains that they are fully connected with pores of the skeletal tissue (according to Galloway, 1957 — galleries). According to this author, lateral canals of an astrorhiza, bifurcating many times, with an increase in distance from the center of the astrorhiza, gradually decrease their thickness and finally freely interlace with pores (galleries) of the skeletal tissue. Such a manner of a connection between astrorhizae and the skeletal tissue has so far been accepted without reservation.

It is, however, clear from the present writer's studies that the free connection of astrorhizal canals with the skeleton may occur only in a few morphological groups of the skeletal tissue, whereas in other groups astrorhizal canals are isolated from the skeletal tissue and do not join it at all, or at least, if there is any connection between them, it is considerably limited. Depending on the degree of connection with the skeletal tissue, the present writer distinguishes the following two groups of astrorhizae: 1) *integrated type,* 2) *separated type.*

Characteristics

1) The canals of astrorhizae of the *integrated* type are marked by a free connection with the galleries of skeleton and occur, for example, in the representatives of such genera as *Actinostroma, Densastroma, Tienodictyon, Ecclimadictyon, Clathrodictyon* or *Atelodictyon.* Lateral canals of astrorhizae of the *integrated* type are usually arranged parallel to the surface of the laminae of coenosteum, and their thickness does not exceed a single interlaminar space. The boundaries of canals of such astrorhizae are usually indistinct and the canals themselves gradually pass into pores (galleries) of the skeletal tissue (Pl. III, Figs. 1,3; Pl. IV, Fig. 3). In vertical sections, astrorhizae of the *integrated* type are marked only in the form of more or less distinct turbulences in the trace of laminae, which sometimes leads to the formation of mamelons on the surface of coenosteum. Tabulae intersecting the canals of such astrorhizae are on the whole oriented parallel to the trace of laminae (Pl. III, Fig. 2; Pl. IV, Figs. 2,3; Pl. VI, Fig. 3). In regard to size, almost all astrorhizae of the *integrated* type belong to the group of small forms. They are related to what is known as an "open" type of the structure of coenosteum (Tripp, 1928, 1932) (for further explanation see p. 510).

2) The canals of astrorhizae of the *separated* type are marked by their being separated from the skeletal tissue or by a very small degree of connection with it. They occur, for example, in the representatives of such genera as *Stromatopora, Hermatostroma, Parallelopora, Trupetostroma, Stromatoporella* etc. The trace of lateral canals of astrorhizae of this type is only rarely in line with the arrangement of laminae in coenosteum. Usually, it is oblique or even perpendicular (Pl. V, Figs. 1-2) and the thickness of such canals is mostly several times as large as a single interlaminar space. The canals are usually tightly encased by a skeletal substance (Pl. I, Fig. 3 Pl. II, Figs. 1-2; Pl. V, Figs. 1-2). The ends of lateral canals do not join galleries and in relation to the thickness of an entire canal are only slightly contracted, or, on the contrary, frequently are even bulbously extended (Pl. VII, Figs. 1-2; Pl. VIII, Fig. 2). The canals of astrorhizae of the *separated* type are also intersected by irregularly distributed, flat, concave or convex tabulae. Calcareous lamellae of the nature of cysts are also fairly frequent. However, in contradistinction to the astrorhizae of the *integrated* type, here tabulae are arranged discordantly to the laminae, mostly obliquely or even perpendicularly (Pl. VII, Figs. 1-2). In regard to size, the astrorhizae of the *separated* type belong mostly to the group of large astrorhizae and are related to what

is known as a "closed" type of the structure of coenosteum (Tripp, 1928, 1932) (for further explanation see p. 510).

Mamelons. — Nodules and nipples called mamelons (Galloway, 1957) frequently occur on the surface of coenosteum of the astrorhizae of both types. They are formed as a result of a series of laminae being bent upwards in the neighbourhood of an astrorhiza (Pl. IV, Figs. 1-2). Their height amounts, on the average, to from a few to a dozen or so mm, with a basal diameter reaching 10 mm. Many astrorhizae are, however, devoid of mamelons and no turbulence is observed in the trace of laminae (Pl. IV, Figs. 3-4). Mamelons were also formed when the skeletal tissue overgrew foreign organisms settled on the surface of a colony (e.g. tubes of polychaetes, corallites of Tabulata), particles of sediment or spontaneously as a reponse to a change in abiotic factors of the environment (e.g. an increase in the deposition of sediment). The outlets of axial canals of astrorhizae are situated on the apical surface of mamelons, but frequently excentrically in relation to the mamelon axis (Lecompte, 1956; Galloway, 1957).

Changes in skeleton in the zone of astrorhizae. — In almost all astrorhizae, particularly those of the *separated* type, a thickening of the skeleton with a simultaneous partial or complete decay of the lamina-pilla system, typical of a given colony, occurs in the contact area with the skeleton (Pl. IV, Fig. 3; Pl. VI, Fig. 2). A thin sheath of a skeletal substance of the nature of a pseudo-wall frequently occurs in the astrorhizae of the *separated* type in the area where the skeleton contacts astrorhizal canals. As seen in thin sections, this substance is usually darker than the rest of the skeleton (?organic substance) (Pl. VI, Fig. 2; Pl. VII, Figs. 1-2). Likewise, the skeletal substance which fills narrow spaces between lateral canals and bundles of axial canals in the systems of superposed astrorhizae is structureless and darker (Pl. V, Figs. 1-2; Pl. VIII, Fig. 1). A considerable concentration of astrorhizae in coenosteum may lead to a complete deformation of the system of the skeletal network typical of a given form.

The distribution of astrorhizae in coenosteum

The astrorhizae are distributed in coenostea at random. A concentration of astrorhizae in the zone of latilaminae was observed by Lecompte (1951, 1956). This is confirmed by the observation of the specimens from the Holy Cross Mountains. The present writer does not agree with Kühn's (1939) statement that astrorhizae do not appear in early development stages of the colonies of stromatoporoids. In the material under study, there are many specimens in which normally developed astrorhizal canals occur within some first laminae of coenosteum.

Astrorhizae are not constantly related to the specimens of a definite species or genus of the Stromatoporoidea. It is clear from Flügel's (1959) studies on a considerable number of the species of *Actinostroma* that astrorhizae occur in 65 per cent of the species of this genus, some of them (e.g. *A. verrucosum*) displaying an abnormally high degree of concentration of astrorhizae. Galloway (1957) found that, in the colonies he examined, astrorhizae occurred on the average in one specimen out of every ten. Of 85 species, described by Galloway and St. Jean (1957), astrorhizae occurred only in 55. According to these authors, out of 18 species of the genus *Anostylostroma* only 3 had astrorhizae, of *Stromatoporella* — about a half of the entire number of species and of *Stromatopora* and *Syringostroma* — all species. These data contradict a previous statement of Kühn (1939) that astrorhizae occur in all species of the Stromatoporoidea. It is clear from the present writer's studies that astrorhizae almost identical with each other in morphology and size occur in colonies of different genera (e.g. *Actinostroma* and *Atelodictyon* or *Hermatostroma* and *Stromatoporella*).

A REVIEW OF PREVIOUS INTERPRETATIONS OF ASTRORHIZAE

The views of only those authors who, discussing the function of astrorhizae, took a now commonly accepted standpoint that stromatoporoids should be assigned to the Coelenterata (Hydrozoa), are discussed below. Other views, assuming the relationship of stromatoporoids to other taxonomic groups and being at present of a purely historical importance, are discussed in detail in the works by Dehorne (1920), Lecompte (1951, 1956) and Galloway (1957).

All previous interpretations of the function of astrorhizae were based on the assumption that astrorhizae are traces left by soft parts of colonies related anatomically to the rest of coenosarc.

View I

Astrorhizae are homologous to coenosarcal stolons (hydrorhizae) of the Hydroida and Milleporina; the budding of zooids of a colony took place in their centres.

Discussion. — This view, formulated by Carter (1880), was subsequently maintained by Nicholson (1886), Steiner (1932) and Yavorsky (1955). Such an interpretation is, however, contradicted by the organization of a hydrorhiza and of the asexual reproduction of the Recent Hydroida which develop coenosteum at the base of a colony (Tripp, 1928; Hyman, 1940: Braverman & Schrandt, 1966; Vervoort, 1966, and others). The stellate arrangement of astrorhizal canals is absolutely incomparable to the irregular network of basal stolons in the Recent Gymnoblastina (e.g. *Hydractinia).* Likewise, in the Recent Hydroida no increase is observed in the thickness of stolons in the budding area of a new zooid, whereas the astrorhizal canals frequently exceeds several times the dimensions of the galleries of coenosteum. The canals of astrorhizae are intersected by tabulae and cysts, which are not recorded in the zone of basal stolons of the Hydroida or Milleporina. The fact that this conception cannot be used to elucidate the sporadicalness of the occurrence of astrorhizae or even its lack in many coenostea, is the most important objection to this interpretation.

View II

The system of astrorhizal canals correspond to branched systems of stolons in skeletal spines and humps of some Recent Gymnoblastina (e.g. *Hydractinia echinata*).

Discussion. — This view, expressed by Tripp (1928), was subsequently criticized by Kühn (1939) who correctly remarked that the spines of Recent *Hydractinia* only superficially resemble the mamilliform structures, which sometimes occur on the surface of coenosteum of stromatoporoids and which not always are related with the occurrence of astrorhizae. On the contrary, sometimes astrorhizae are situated in distinct depressions of coenosteum. In contradictinction to the spines of *Hydractinia* which function for a short time and then degenerate in the skeleton, astrorhizae usually continue through a dozen or so successive laminae of coenosteum. Tripp's conception is only a completion of view I and all proofs, quoted above, testify against it.

View III

Astrorhizal canals are traces of special tubes which contained reduced zooids. These zooids, which performed a function homologous to gonophores (blastostyles) of the Recent Hydroida, were connected with a hydrorhiza by a system of stellate stolons.

Discussion. — This view, based to a considerable extent on the observations of previous authors, was expressed by Kühn (1929, 1939) without a detailed analysis of morphological characters of astrorhizae. He assumed that some important, soft elements of the colony, most likely fulfilled a function of reproductive organs, were bound to occur in the place of astrorhizae. The structure and distribution of gonophores (blastostyles) in Recent Hydroida (Hyman, 1940; Naumov, 1960) does not, however, entitle one to compare them with astrorhizae. Gonophores do not ever substantially differ in size from the remaining zooids in a colony and frequently are smaller than they. Judging by the dimensions of the skeletal tissue of coenosteum, the size of possible zooids in stromatoporoidal colonies was bound to correspond approximately to an average size of zooids in the Hydroida. The dimensions (in some cases quite large) of axial canals of astrorhizae, which were believed by Kühn to contain gonozooids, would indicate vast disproportions in the size of individuals in a colony (Pl. V, Figs. 1-2). Kühn's hypothesis also does not explain how to interpret the character of the gonozooid, referred to above, in the case in which astrorhizae have not an axial canal or are formed by a bundle of axial canals. Astrorhizae are structures fixed in coenosteum, whereas in the Hydroida, developing a basal skeleton, gonophores are not marked in this skeleton and do not take part in its development either (Tripp, 1928). No marked thickening of stolons and a system of stellate connections with a hydrorhiza are observed in the Recent Hydroida with hydrorhizal budding of gonophores, whereas they are clearly visible in the system of astrorhizal canals. In the skeleton of *Hydractinia* with which the coenosteum of stromatoporoids is most frequently paralleled (Tripp, 1928), gonophores bud not from stolons but on modified hydranths (gonozooids). The shape of reproductive organs and frequency of their occurrence in the colonies of the Recent Hydroida are on the whole constant characters, whereas astrorhizae are ephemeral structures, frequently differing in shape and size within a colony.

Kühn's (1929, 1939) conception was modified by Galloway (1957) who tried to explain the lack of astrorhizae in some specimens of the same species by the phenomenon of a sexual dimorphism of a colony of stromatoporoids. He believed that astrorhizal structures might be traces of female gonozooids. According to his interpretation, the colonies with astrorhizae would be female ones and those devoid of astrorhizae — male or sexless ones. Although we cannot preclude the possibility that the colonies of stromatoporoids were dioecious, but astrorhizae do not seem likely to indicate this phenomenon. Galloway himself emphasized that his presumptions were not confirmed by any species described so far and that nobody succeeded in finding pairs of dimorphic coenostea corresponding to each other. Within the range of the Recent Hydroida described so far, producing a basal skeleton, the forms in which female and male gonophores would be differently disposed in relation to coenosteum are unknown (Hyman, 1940; Naumov, 1960).

Referring to Nicholson's (1886) guesses, Galloway (1957) did not also preclude the possibility of interpreting astrorhizae as organs whose function is similar to that of ampullae of the Recent Hydrocorallina. The present writer believes that comparing these two types of structure is baseless. Spherical spaces scattered within the skeletal tissue of some stromatoporoids and believed by Nicholson (p. 63, Fig. 8) to be an equivalent of ampullae, seem to be nothing else but transverse sections of lateral astrorhizal canals intersected by many tabulae (Pl. VII, Figs. 1-2; Pl. VIII, Fig. 2).

A NEW INTERPRETATION OF ASTRORHIZAE

According to the present writer's opinion, all characters of astrorhizae indicate that these structures may be considered as traces left by organisms, which during their life time were associated with colonies of stromatoporoids. This interpretation is based on the following facts:

1) astrorhizae occur in coenostea irregularly, from considerable concentrations up to a complete lack;

2) astrorhizae are differentiated morphologically within one and the same colony;

3) lateral and axial canals of astrorhizae frequently display disproportions in size as compared with skeletal galleries;

4) the arrangement of lateral astrorhizal canals is usually discordant with the course of laminae of coenosteum;

5) tabulae and cysts, occurring in axial and lateral astrorhizal canals, are usually arranged discordantly to the direction of laminae of coenosteum;

6) astrorhizae display a differentiated manner of relationship to the skeletal tissue of coenosteum (*integrated* and *separated* types of astrorhizae);

7) in the zone of astrorhizae, the skeletal tissue of coenosteum frequently displays disturbances and deformations.

The main reason why astrorhizae have not so far been interpreted as traces of foreign organisms were, on the one hand, too superficial studies of these structures and, on the other, until recently a poor knowledge of the phenomena of symbiosis (*sensu* Allee *et al.*, 1949) between particular marine invertebrates, sometimes only slightly related systematically.

Many authors (including Carter, 1879, 1880; Nicholson, 1886; Clarke, 1907, 1921; Flügel, 1956; Galloway, 1957) described such organisms, encrusted by stromatoporoids, as tabulates, solitary tetracorals or tubes of polychaetes which, without more detailed studies, were considered as commensals or parasites. In contradistinction to astrorhizae, all these forms have their own skeletons, clearly outlined in coenosteum and their relationships to the stromatoporoids are more or less accidental or facultative. The fact that they commonly occurred independently in stromatoporoidal assemblages or encrusted skeletons of dead colonies, shows how loosely were they related to the stromatoporoids.

MORPHOLOGICAL INTERPRETATION OF THE ASTRORHIZA-STROMATOPOROID SYSTEM

The lack of proper walls in the canals of astrorhizae, which would separate these structures from the skeletal tissue, allows one to suppose that the organism which developed them was a skeletonless form. This lack may be also indicative of a closer relationship of both associates than it is the case of the anthozoans and polychaetes mentioned above.

The two types of astrorhizae *integrated* and *separated* distinguished by the present writer, are related with one of the two fundamental types of the construction of the skeletal tissue in the stromatoporoids, separated by Tripp (1928, 1932).

Astrorhizae of the *integrated* type occur primarily in the coenostea with what is known as "open" ("offene Bauweise") manner of depositing the skeleton (e.g. in *Actinostroma*), observed by Tripp (*op. cit.*) in the Recent *Hydractinia echinata*. The laminae of these forms are built of a homogenous layer of the skeletal substance deposited only on the bottom side of the hydrorhizal stolons and which, with the growth of a colony, successively shifts to higher levels. A relatively thin mat was here formed by the coenosarc.

Astrorhizae of the *separated* type are related to coenostea with what is known as a "closed" manner of building ("geschlossene Bauweise") the skeletal tissue, characterized by laminae consisting of two layers each (e.g. in *Stromatoporella*), observed by Tripp in, among other species, *Podocoryne carnea*. The skeletal substance is here deposited simultaneously on all sides of hydrorhizal stolons so that, as result of apposition of stolons, bipartite laminae are formed with a median line. The whole of the coenosarc has here the form of a loose network, some stolons being situated within the skeleton. The layer of coenosarc is thicker than in the former case.

Accepting two fundamental types of the organization of the skeletogenous hydrorhizal zone in the stromatoporoids, suggested by Tripp, one may attempt to elucidate on this basis how an astrorhizal guest could be related to its host. In the present writer's opinion, an organism corresponding to an astrorhiza of the *integrated* type settled in the host's coenosarc and was probably metabolically dependent on it, which in turn compelled it to be shifted upwards together with the coenosarc. Owing to the fact that the skeleton was deposited only by the lower layer of the hydrorhiza (Tripp's "open" type), the canals of the astrorhiza contacted it to a very limited extent only. Such an interpretation clearly explains a presently observed free connection between the canals of astrorhizae and galleries of coenosteum, vague outlines of these canals and a small thickness of lateral canals, which does not exceed the zone of coenosteum limited by two successive laminae (Pl. III, Fig. 2*a*; Pl. VI, Fig. 3).

Quite different was the relationship of an astrorhizal guest to the colonies of stromatoporoids which represented Tripp's "closed" type of the structure of skeleton and in which the layer of coenosarc was correspondingly thicker and its lowermost parts (stolons) were situated within the skeleton. An organism, corresponding to an astrorhiza of the *separated* type and metabolically dependant on its host, during the growth of the latter was here contacting for some time the stolons situated within the skeleton and was gradually walled up by the skeletal substance they secreted. Such an interpretation allows one to explain a presently observed isolation of astrorhizae of this type from coenosteum, a considerable thickness of their lateral canals which usually exceeds the width of the zone of coenosteum limited by two successive laminae, as well as the dimensions of entire astrorhizal structures — as a rule generally large — as compared to the dimensions of coenosteum (Pl. I, Figs. 1-3; Pl. V, Figs. 1-2).

In the case of astrorhizae of the *separated* type, it might well be that the organism, which settled on a stromatoporoid, was not metabolically dependent on it, but only used its host as a substratum. Such an interpretation, is, however, testified against by a usually strongly ramified network of lateral astrorhizal canals, particularly so in Devonian forms, in which astrorhizae frequently penetrate a considerable part of the capacity of coenosteum (Pl. I, Fig. 1).

GROWTH RELATIONS IN AN ASTRORHIZA-STROMATOPOROID SYSTEM

A foreign organism, which settled a colony of a stromatoporoid, had to adapt the rate of its growth to that of its host. This was caused, on the one hand, by the necessity to keep in contact with the host's coenosarc and, on the other, the guest was exposed to the danger of being stifled by the growing skeleton of the stromatoporoid. It is clear from the observations of relationships between astrorhizae and coenosteum that the partner of the stromatoporoid was well-adapted to keep itself in the surface zone of the colony the most advantageous for it. The superposed systems of astrorhizae, continuing through a few to several scores of laminae, give ample evidence that an organism associated with a stromatoporoid did not for a long time change its position within the colony, except for its upward displacement caused by the growth of the latter. A variable length of systems of superposed astrorhizae indicates that the relative lifetime of organisms lodged in them was considerably differentiated and varied even in the case of forms, which occurred within one and the same colony. The functioning of simple astrorhizae with canals restricted to one interlaminar space only, was very brief. A steady direction of the growth of astrorhizal structures in the skeletons of stromatoporoids is one more proof against interpreting them as traces left by the zooids of stromatoporoids. It is clear from the studies on the growth of the colonies of the Hydroida which produce coenosteum (e.g. Bougenvillidae) that the zooids are short-lived structures which, with the growth of coenosteum, become subject to resorption ("eingeschmolzen", Tripp, 1928, 1932) and new ones bud in a mosaic-like manner at different points of the colony (Mackie, 1966).

The length of lateral astrorhizal canals, variable at different "floors" of the systems of superposed astrorhizae, was closely correlated with the rate of growth of a stromatoporoid (Pl. IV, Figs. 3-4; Pl. V, Fig. 2). Longer lateral canals are usually observed in astrorhizae in the zone of latilaminae which corresponds to the slowing down of the growth of the skeleton caused by a deterioration in living conditions. Due to the fact that, in such cases, coenosarc kept itself on one and the same level for a longer time than usually, the guest could penetrate the host's tissue much deeper than usually. With a normal growth of the host, there was no possibility of a considerable lateral expansion of the guest and, if such was the case, the lateral canals were very short and only the vertical axial canals of astrorhizae were clearly marked (Pl. IV, Fig. 3; Pl. V, Fig. 2).

The process of growth of a guest in stromatoporoid colonies was combined with the deposition, on the bottom side, of many tabulae and cysts. These are thin (ca. 0.02 mm), structureless calcareous lamellae which do not differ microscopically from the rest of the skeletal tissue of coenosteum. Their irregular distribution in astrorhizal canals also shows that the rate of the guest's growth was not uniform and depended on an increase in the host's skeleton. More densely distributed tabulae usually occur, therefore, in those parts of astrorhizae in which the lateral canals are strongly developed (Pl. IV, Fig. 3; Pl. V, Fig. 2).

The discordance in the arrangement of tabulae and cysts in relation to the laminae of coenosteum, particularly clearly marked in astrorhizae of the *separated* type (Pl. V, Figs. 1-2; Pl. VII, Figs. 1-2), shows that they were formed rather independently of the skeleton of a stromatoporoid. Tabulae and cysts make up a permanent character of astrorhizal structures in contrast to bent calcareous lamellae, mostly called dissepiments, which sometimes occur in the coenostea of stromatoporoids.

Conclusions concerning growth relations of both organisms associated with each other may also be drawn on the basis of the manner of arranging laminae in the zone of astrorhizae. In the present writer's opinion, a relatively rapid growth of the stromatoporoid resulted in an upturning tendency of laminae in the neighbourhood of an astrorhiza and, consequently, in the formation on the surface of a colony of mamillary elevations (Pl. IV, Figs. 1-2), called by most authors mamelons (cf. Galloway, 1957). With a uniform growth of both organisms the course of laminae was not disturbed (Pl. IV, Figs. 3-4; Pl. VI, Fig. 3), whereas with the slower growth of the host's skeleton laminae surrounding an astrorhiza were slightly bent downwards and a small depression was formed on the surface of coenosteum.

ORIGIN AND BIOLOGICAL CHARACTER OF AN ASTRORHIZA-STROMATOPOROID SYSTEM

In the light of the interpretation, discussed above, we may attempt to explain the appearance of astrorhizae in the history of stromatoporoids.

The first astrorhizae appeared in stromatoporoids in the Upper Ordovician, while the oldest stromatoporoids have already been known since the Middle Ordovician (Galloway, 1957; Galloway & St. Jean, 1961; Nestor, 1964). The first astrorhizae were small and consisted of a single axial canal and simple lateral canals. Besides, they occurred relatively rarely (Galloway, 1957; Nestor, 1964). However, it is already during the Silurian that a considerable increase is marked in their dimensions, degree of ramification of lateral canals and frequency of their occurrence in coenostea (Nestor, 1964, 1966). This process reached the summit of its development in the Devonian forms. The astrorhiza-stromatoporoid association is, therefore, an example of a gradual invasion of the guest with a clearly progressive adaptation to an increase in cooperation with its host, i.e. the stromatoporoid. The first associations of both organisms were probably accidental and facultative in character and the guest's interest in the host resulted primarily from the attractivity of the substratum, formed by a hard and stable stromatoporoid colony. Initial epibionts (epizoites) could subsequently pass to a closer cooperation with the host. A considerable density of population of stromatoporoid assemblages was an important factor favourable to the formation of a partnership of such type. Frequently, the stromatoporoid colonies occupied an entire surface of the bottom, almost completely displacing other benthonic organisms from their biotic niche. Such a situation was probable stimulative to several displaced organisms compelling them in turn to their own attempts at a settlement on the surface of stromatoporoid colonies. In regard to population density, stromatoporoid communities are only comparable to Recent reef communities, which are marked by precisely such a variety of biotic associations between species living in them.

Having at one's disposal skeletons as an only available material, it is difficult to determine accurately the nature of the astrorhiza-stromatoporoid association in the categories used by ecologists in the studies of this type. We may only assume one of the following two categories of symbiosis:

1) a *commensalism*: the guest used the stromatoporoid as a substratum only; astrorhizal canals would correspond to more or less specialized anchoring organs of the guest;

2) a *mutualism*: the guest used the stromatoporoid as a substratum, but also participated in its host's metabolic processes; in addition to the anchoring function, astrorhizal canals would increase the area of contact with the host.

On the other hand, since no traces of a destructive effect of astrorhizae on the growth of coenosteum are observed even when they occur in great concentrations, we may preclude the possibility of a parasitic nature of the guests of stromatoporoids. Likewise, there are no symptoms of the host's defensive responses which would occur in the form of pathogenic degenerations of the skeletal tissue in the neighbourhood of astrorhizae.

Assuming that an astrorhiza-stromatoporoid association might fluctuate between commensalism and mutualism, attention should simultaneously be paid to the fact that the two types of astrorhizal structures distinguished in the present paper, i. e. *integrated* and *separated*, must not be interpreted as two separate categories of biotic association. These terms are only morphological in character and serve to explain the position of the guest in relation to the skeleton of the stromatoporoid.

The irregular occurrence of astrorhizae in coenostea indicates that the relationships of both organisms were facultative in character on the part of the host, but — if we take into account the guest's high degree of specialization — they might be obligate on the part of the latter. Although some of the astrorhizae seem to be permanently associated with certain morphological groups of coenosteum, no distinct specifity is observed in the relation of the guest to the host.

ASTRORHIZAE AS STROMATOPOROID SYMBIONTS

An organism inhabiting astrorhizae cannot be reconstructed without the knowledge of the organization of its soft parts. It is also among Recent biotic associations that we do not know a system identical with that consisting of an astrorhiza and a stromatoporoid. The present astrorhizal structure does not even allow one to state for certain whether an organism associated with a stromatoporoid was a solitary or a colonial form. On the other hand, we may state that astrorhizae are a product of non-skeletal organisms and that most likely they make up traces of their variously specialized anchoring organs (rhizoids). The rest of the body of these organisms might be more or less elevated above the coenosarc of the stromatoporoid. A similar shape of astrorhizae allows one to believe that the organisms, which developed them, belonged to one and the same systematic group and differed from each other only in the adaptation to the symbiotic mode of life with stromatoporoids.

An approximate reconstruction of the systematic position of astrorhizal organisms may be carried out on the basis of examples of biotic associations observed in Recent marine communities. A comparison may be only made of such Recent organisms whose morphological organization and habitat are similar to those of stromatoporoids. Such organisms are primarily the Recent sponges and coelenterates. In the present writer's opinion, based on examples of some of the forms associated with sponges and coelenterates, the astrorhiza-stromatoporoid system may be examined as: 1) a plant-animal association, or 2) an animal-animal association.

1) *Astrorhizae as plant traces*

Algae are among the most common symbionts of sponges and coelenterates. In addition to a well-known phenomenon of an endosymbiosis of the last-named organisms with unicellular algae (cf. Droop, 1963; McLaughlin & Zahl, 1966), also known are associations of sponges and coelenterates with thallophyte algae with a higher degree of organization such as primarily those of the group of red algae (Rhodophyceae), rarely green algae (Chlorophyceae) and brown algae (Phaeophyceae) (cf. Buchner, 1953; Füller, 1958; Fritsch, 1959, 1961; Droop, 1963). Some epi- and endozoic thallophyte algae produced structures similar to astrorhizal canals.

Among the red algae (mostly of the Florideae) associated with sponges both epi- and endozoic forms are known which range from typically parasitic, through commensal up to mutualistic (Carter, 1878; Kuckuck, 1897; Darbishire, 1899; Weber-Van Bosse, 1910; Howe & Hoyt, 1916; Chemin, 1928; De Laubenfels, 1950, and others). The thalli of endozoic algae are subject to considerable changes which result in a conspicuous reduction of the vegetative part and development of rhizoid parts. In extreme cases of this process (e.g. in *Marchesettia spongioides, Ceratodictyon spongioides, Jania* sp.) the thallus of an alga very densely penetrates the entire scleroderma of a sponge so that only its fructifying branches are exposed outside (Hauck, 1889; Zanardini, 1878 — cf. Fritsch, 1959). In most cases, the sponge-alga associations are of the nature of epibionts with a tendency to the penetration of rhizoids into the host's tissue without, however, any close relationship to it.

Red algae of the group Florideae also occur as epizoic (e.g. *Rhodochorton membranaceum*) and, partly, endozoic (e.g. *Acrochaetium, Colaconema*) forms on benthonic coelenterates (mostly the Hydroida), to which they are attached by means of radially spread simple rhizoids or modified attachment organs in the form of dichotomous ramifications, or what is called haptera, gathered in bundles.

Tangled, filamentous thalli of green algae (Chlorophyceae) abundantly occur in the coenenchyme and skeletons of reef corals, i.e. hydrocorals (*Millepora*), octocorals and, primarily, in most hexacorals (Odum & Odum, 1955). These algae were previously interpreted as parasitic forms (Duerden, 1905), but later they turned out to be mutualistically related to corals and to play an important role in their metabolic processes (Odum & Odum, (*l.c.*).

It is clear from this brief review of the symbiosis of algae with sponges and coelenterates that there is a possibility of comparing radial, frequently dichotomously ramified attachment organs of these algae with astrorhizal structures. Since most associated algae may lead an independent life and only some of them, extremely parasitic forms which lost their capability of assimilation, are obligate in relation to their hosts, the algal character of astrorhizae may also serve as an explanation of their irregular occurrence in stromatoporoids. Algae may occur in sponges and coelenterates as individuals markedly separated from each other or in the form of an irregular, tangled mass of the branches of thalli. Quite similar is the behaviour of astrorhizae in coenostea. Among epi- and endozoic algae, there are both annual and perennial forms which, growing older, successively shift their rhizoids or hapters upwards (e.g. *Phyllophora* in the shells of pelecypods; Fritsch, 1959). A similar principle could explain a variable length of the systems of superposed astrorhizae, as well as repeated extensions of lateral astrorhizal canals periodically, occurring at various levels of the skeleton of stromatoporoids. Algae symbiotic with stromatoporoids might unite with each other by their rhizoid parts, which could elucidate the existence of connections between lateral canals of zone of the astrorhizae (Nicholson, 1886, Pl. 4, Fig. 2; Galloway, 1957, Pl. 36, Fig. 4). One colony of a stromatoporoid might be settled by two different algae which may serve as an explanation of the concurrence of morphologically different astrorhizae in one and the same coenosteum (Pl. I, Fig. 1).

An insufficient extent of knowledge of growth processes in algae associated with sponges and coelenterates does not allow one to state for certain, whether or not the lower parts of thallus are, in the course of growth, capable of developing calcareous lamellae homologous to tabulae and cysts of astrorhizal canals. A considerable percentage of green and red algae are capable of encrusting thalli with calcium carbonate and other mineral substances and, therefore, it might well be that, under the conditions of symbiosis with a steadily growing stromatoporoid, the terminations of algal rhizoids periodically deposited tabulae. Such tabulae might be also deposited, in particular in astrorhizal canals of the *integrated* type, by low disposed parts of coenosarc of a stromatoporoid which were in contact with algae.

2) *Astrorhizae as animal traces*

Among a great number of invertebrates living in various forms of biotic association with Recent sponges and coelenterates (cf. Carter, 1878; Pearse, 1932; Hyman, 1940; De Laubenfels, 1950; Dales, 1957, 1966; Hopkins 1957; Füller, 1958, and others), attention is attracted by some of the non-skeletal coelenterates.

Frequent associations of sponges with polyps of the Zoanthidea were observed by Carter (1878). They occur in sponges as single or double polyps, as well as gathered to form larger assemblages. Their occurrence may be limited to the surface of a sponge, but they may be also more or less sunk in its scleroderma. Among the polyps of the Zoanthidea, Carter (*cit. op.*) distinguished forms which are isolated from the scleroderma of the sponge ("marginated") and those which are connected with it ("...circumference of the polyp defined but not marginated"). Some of these associations are to a considerable extent specific, e.g. *Epizoanthus* which occurs only with some of the Hexactinellida (Hyman, 1940). The size of the polyps of the Zoanthidea, which settle sponges, amounts to 1.5—8.0 mm. The relationship of the Zoanthidea to sponges was provisionally determined by Carter as parasitic but, as shown by recent studies, most of them are epibionts and commensals. Some of the Zoanthidea settle on juvenile sponges from the early larval stages which, according to Carter (1878), is indicative of an advanced cooperation of both organisms.

The same forms of the Zoanthidea (e.g. *Palythoa fatua* Schultze), which occur in sponges, were found by Carter (1878) in coenosarc of some Gymnoblastina (e.g. *Podocoryne* sp.).

In addition to the Zoanthidea, the polyps of the Hydroida, which in contrast to the former penetrate the body of a sponge to a much larger depth, were observed by Carter. These hydroids (e.g. *Spongicola fistularis* Schultze) form concentrations of tangled tubes (?stolons) which penetrate parenchyma of a sponge and have a common external outlet. Some of these hydroids are very small (0.25 mm) with strongly ramified branchlets of the body in parenchyma. Hydroids associated with sponges are also considered by Carter as parasites. However, he does not accurately explain their relationships to the host.

Many hydroids are known as epibionts or semi-parasites of gorgonians and pennatulids (Stechow, 1909; Broch, 1924), as well as of many other invertebrates and fishes (cf. Dales, 1957; Hopkins, 1957).

Despite the universality of the associations, discussed above, no closer information is available on morphological relationships of both partners. Likewise, there are no detailed descriptions and illustrations of structures, formed in the body of a host as a result of its being settled by a foreign organism and which could be fully compared with astrorhizae of the Stromatoporoidea.

The explanation of the presence of tabulae and cysts in astrorhizal canals is easier on the assumption that the polyps of zoantids, hydroids or other systematically closely related animals were organisms, which caused the formation of astrorhizae than in the case of algae since identical structures are known in Recent and fossil anthozoans. With such interpretation, the astrorhizal canals would correspond to modified rhizoids of non-skeletal polyps, which successively shift with the growth of a stromatoporoid. The arrangement of tabulae in astrorhizal canals is, in some cases, very similar to that in the Tabulata. In the present writer's opinion, it might well be that the symbionts of stromatoporoids derived from coelenterates similar to the Tabulata, in which, as a result of the passage to a cooperative mode of life, a complete reduction of the skeleton took place, with the exception of tabulae that could be useful to the shifting body.

SYSTEMATIC VALUE OF ASTRORHIZAE

Attempting to interpret astrorhizae, several authors tried to determine the importance of these structures to the taxonomy of the Stromatoporoidea. Most of them shared the standpoint that astrorhizae were an important taxonomic element whose rank was, however, not higher than specific (Carter, 1879, 1880; Nicholson, 1886; Galloway, 1957; Nestor, 1964; Bogoyavlenskaya, 1965, 1968, and others). Many species were erected only on the basis of astrorhizae despite the fact that the morphology of their skeletons did not differ from identical forms devoid of astrorhizae. Such doings contributed to a considerable extent to a confusion in the taxonomy of the Stromatoporoidea. Recent attempts at a classification of astrorhizae (Nestor, 1964; Bogoyavlenskaya, 1965, 1968), which are aimed at a yet more extensive application of these structures to the taxonomy of the stromatoporoids, are frequently purely formal in character and do not explain the biological relationships between taxa in which astrorhizae occur.

Some other authors assumed that none of the previous interpretations was sufficient to explain the significance of astrorhizae occurring in stromatoporoids and, therefore, omitted these structures as diagnostic feature (Dehorne, 1920; Lecompte, 1951—52; Sleumer, 1968, and others).

Interpreting astrorhizae as traces of foreign organisms associated with stromatoporoids, we may eliminate them completely as systematic characters of this group. As a result of a revision of most species, it may turn out, however, that some astrorhiza-stromatoporoid associations are very specific and, if such would be the case, these structures might serve as a secondary diagnostic feature.

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June 1969

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JÓZEF KAŹMIERCZAK

NOWA INTERPRETACJA ASTRORIZ U STROMATOPOROIDEA

Streszczenie

W pracy przedstawione są wyniki badań nad morfologią, funkcją i znaczeniem systematycznym astroriz u paleozoicznych Stromatoporoidea, przeprowadzonych na materiale zebranym z dewonu (żywet-fran) Gór Świętokrzyskich. Mimo, że astrorizy opisywane były wielokrotnie od drugiej połowy XIX wieku, autorowi udało się poczynić wiele nowych obserwacji, które umożliwiły nową interpretację funkcji i charakteru tych struktur.

W przeciwieństwie do dotychczasowych poglądów, w których bez powodzenia doszukiwano się podobieństwa astroriz do struktur, wytworzonych przez stolony cenozarkalne bądź specjalne zooidy stromatoporoidów, autor dochodzi do wniosku, że są one śladami po organizmach stowarzyszonych przyżyciowo ze stromatoporoidami. Za taką interpretacją astroriz przemawiają następujące fakty:

1) astrorizy występują w stromatoporoidach nieregularnie: bywają liczne lub ich brak,
2) astrorizy zróżnicowane są morfologicznie w obrębie jednej kolonii,
3) kanały boczne i osiowe astroriz są często nieproporcjonalnie duże w stosunku do por tkanki szkieletowej,
4) układ kanałów bocznych astroriz jest zwykle niezgodny z przebiegiem lamin cenosteum,

5) denka i cysty występujące w kanałach bocznych i osiowych mają zazwyczaj przebieg niezgodny z przebiegiem lamin cenosteum,
6) tkanka szkieletowa cenosteum w strefie astroriz wykazuje często zaburzenia i deformacje.

Na podstawie sposobu powiązania astroriz z tkanką szkieletową, autor wyróżnił dwa typy astroriz: *integrata* i *separata*. Pierwszy z nich cechuje się swobodnym połączeniem kanałów bocznych z porami tkanki szkieletowej, w drugim zaś kanały astrorizalne nie łączą się z porami szkieletu, bądź w sposób bardzo ograniczony.

Astrorizy typu *integrata* są zwykle strukturami małymi (2—8 mm), *separata* zaś dużymi (15—50 mm).

Astrorizy typu *integrata* występują przede wszystkim w stromatoporoidach o tzw. „otwartym" sposobie odkładania szkieletu (Tripp, 1928, 1932), którym charakteryzują się na przykład przedstawiciele rodzajów *Actinostroma, Densastroma, Actinodictyon*. Astrorizy typu *separata* związane są natomiast ze stromatoporoidami o tzw. „zamkniętym" sposobie budowy tkanki szkieletowej, reprezentowanym między innymi u przedstawicieli takich rodzajów jak *Stromatoporella, Hermatostroma, Trupetostroma*.

Średnica kanałów bocznych w astrorizach typu *integrata* nie przekracza jednej przestrzeni międzylaminarnej, w typie *separata* zaś jest często kilkakrotnie od niej większa.

Zdaniem autora, występowanie u Stromatoporoidea dwóch typów wspomnianych astroriz wskazuje na różne położenie organizmów zasiedlających kolonię w stosunku do strefy szkieletotwórczej cenozarku stromatoporoidów. Astrorizy typu *integrata* mogły powstać w przypadkach ograniczonego kontaktu gościa ze szkieletem gospodarza, zaś *separata* — gdy był on pogrążony w szkielecie i stopniowo przez niego obrastany.

Z analiz powiązań morfologicznych i stosunków wzrostowych w układach astroriza — stromatoporoid wynika, że stowarzyszenie obu organizmów mogło mieć charakter:

1) *komensaliczny* — gość korzystał ze stromatoporoida jedynie jako podłoża; kanały astrorizalne odpowiadałyby wówczas organom czepnym gościa;
2) *mutualistyczny* — gość korzystał również ze stromatoporoida jako podłoża, lecz jednocześnie był z nim związany tkankowo i uczestniczył w jego procesach metabolicznych; kanały astrorizalne powiększałyby powierzchnię kontaktu obu partnerów.

Nieregularne występowanie astroriz w stromatoporoidach świadczy, że związek obu organizmów miał charakter fakultatywny. Przykładów wyraźnej specyficzności w układach astroriza — stromatoporoid nie obserwuje się.

Organizmy stowarzyszone ze stromatoporoidami były przypuszczalnie początkowo epibiontami, które przeszły następnie do ściślejszej kooperacji z gospodarzem. Ta progresywna adaptacja do symbiotycznego trybu życia widoczna jest w historii rozwoju Stromatoporoidea. Rzadkie i proste w budowie astrorizy u stromatoporoidów górno-ordowickich i dolno-sylurskich, powiększały stopniowo swoje rozmiary i rozgałęzienie kanałów bocznych, wyrażone w pełni u form dewońskich.

Rekonstrukcję przynależności systematycznej symbiontów stromatoporoidów przeprowadzić można w sposób przybliżony na podstawie przykładów związków biotycznych, obserwowanych u współczesnych gąbek i jamochłonów. Przyjmując, że kanały astrorizalne są śladami po organach czepnych (ryzoidach) organizmów bezszkieletowych, należących przypuszczalnie do jednej grupy systematycznej, układ astroriza — stromatoporoid można rozpatrzeć jako: 1) stowarzyszenie roślina—zwierzę, 2) stowarzyszenie zwierzę—zwierzę. W pierwszym przypadku istnieje możliwość algowej interpretacji natury symbiontów stromatoporoidów, przedyskutowana na podstawie przykładów stowarzyszeń alg plechowych (krasnorostów i zielenic) z gąbkami i koralowcami. Algi te mogą występować jako formy epi- i endozoiczne i charakteryzują się zbliżonym do astroriz układem ryzoidów, którymi łączą się z ciałem gospodarza. W drugim przypadku uwagę zwracają niektóre bezszkieletowe jamochłony (Zoanthidea i Hydroida), wchodzące w różnorodne związki biotyczne z gąbkami i jamochłonami. Zdaniem autora, nie jest wykluczone, że astrorizalnymi symbiontami stromatoporoidów mogły być jamochłony zbliżone do Tabulata, u których w wyniku przejścia do kooperatywnego trybu życia nastąpiła redukcja szkieletu z zachowaniem zdolności do odkładania denek w trakcie wzrostu.

Interpretacja astroriz jako śladów po organizmach symbiotycznych eliminuje te struktury jako cechę diagnostyczną w badaniach taksonomicznych Stromatoporoidea. Stwarza to jednocześnie konieczność rewizji tych gatunków i rodzajów stromatoporoidów, które zostały wydzielone jedynie na podstawie występowania tych struktur.

ЮЗЭФ КАЗЬМЕРЧАК

НОВОЕ ОБЪЯСНЕНИЕ АСТРОРИЗ У STROMATOPOROIDEA

Резюме

В статье изложены результаты исследования морфологии, природы и систематического значения астрориз у палеозойских Stromatoporoidea, проведенного на материале из девона (живетского и франского ярусов) Свентокшиских Гор.

Несмотря на то, что, начиная со второй половины XIX века, астроризы были описываны многократно, автору удалось произвести новые наблюдения, которые дают возможность иначе объяснить функцию и характер этих структур, чем это делалось до сих пор.

Вопреки принятым взглядам, согласно которым астроризы сходны со структурами ценосаркальных столонов или являются местом обитания зооидов строматопороидей, автор приходит к выводу, что астроризы являются следами орга-

низмов, прижизненно связанных со строматопороидеями. Такое объяснение подтверждают следующие факты:

1) астроризы встречаются в колониях нерегулярно: в одних они многочисленны, в других их почти нет,
2) в одной и той же колонии астроризы часто различаются между собой своим строением,
3) боковые и осевые каналы áстрориз часто непропорционально крупны по сравнению с галлереями скелета,
4) расположение боковых каналов астрориз обычно не согласуется с направлением ламин ценостеума,
5) ориентировка днищ и пузырьков в астроризальных каналах обычно не согласуется с расположением ламин ценостеума,
6) скелетная ткань в зоне астрориз проявляет волнения и деформации.

По способу сочленения астрориз с галлереями скелета автор выделил два типа астрориз: *integrata* и *separata*. В первом типе боковые каналы астрориз с галлереями скелета сочленяются свободно, во втором они вообще с ними не сочленяются или сочленяются очень ограниченно.

Астроризы типа *integrata* обычно малы (2—8 мм), а *separata* — большие (15—50 мм).

Астроризы типа *integrata* характерны прежде всего для строматопороидей с „открытым" способом образования скелета (Tripp, 1928, 1932), свойственным, например, представителям родов *Actinostroma, Densastroma, Actinodictyon* и др. На оборот, астроризы типа *separata* связаны с „закрытым" способом строения скелета, характерным для родов *Stromatoporella, Hermatostroma, Trupetostroma.*

Согласно мнению автора наличие двух типов астрориз указывает на различное положение симбиотических организмов по отношению к образующей скелет зоне ценосарка строматопороидей. Астроризы типа *integrata* возникали в случаях ограниченного контакта гостей со скелетом хозяина, а *separata* — когда гости были погружены в скелет и постепенно через него прорастали.

Из анализа морфологических и возрастных отношений в системе астрориза-строматопороидея следует, что связь обсих организмов могла иметь характер:

1) *комменсализма* — гость использовал колонию только как субстрат; в таком случае астроризальные каналы отвечали органам прикрепления гостя,
2) *мутуализма* — гость использовал колонию также как субстрат, но одновременно участвовал в метаболических процессах хозяина; боковые астроризальные каналы увеличивали поверхность контакта обоих партнеров.

Нерегулярное присутствие астрориз у строматопороидей свидетельствует о том, что связь обоих организмов имела факультативный характер. Примеров четкой специфичности в системах астрориза-строматопороидея не наблюдается.

Организмы, связанные со строматопороидеями, были по всей вероятности в начале сожительства квартирантами, которые потом перешли к более тесной кооперации с хозяином. В истории развития Stromatoporoidea видна прогрессивная адаптация этих организмов к симбиотической жизни. Редкие и простые астроризы у верхнеордовикских и нижнесилурийских строматопороидей постепенно увеличивали свои размеры и разветвления боковых каналов, которые были резко выражены у девонских форм.

Понять систематическую принадлежность симбионтов строматопороидей можно памятуя о биотических связях, наблюдаемых сейчас у губок и кишечнополостных. Принимая астроризальные каналы за следы органов прикрепления (ризоидов) бесскелетных организмов, которые повидимому принадлежали к одной систематической группе, систему астрориза-строматопороидея можно рассматривать как: 1) связь растение-животное, 2) связь животное-животное. В первом случае возможен водорослевый характер симбионтов строматопороидей, на подобие того как у некоторых слоевищных водорослей с губками и кишечнополостными. Эти водоросли являются эпи- или эндозоическими и обладают близкой к астроризам системой ризоидов, которой они соединяются с телом хозяина. Во втором случае мыслимы некоторые бесскелетные кишечнополостные (Zoanthidea, Hydroida), входящие в различные биотические связи с губками и кишечнополостными. По мнению автора не исключено, что астроризальными симбионтами строматопороидей могли быть кишечнополостные близкие к Tabulata, у которых в результате перехода к кооперативной жизни произошла редукция скелета с сохранением способности к выделянию днищ во время роста.

Симбиотическое объяснение астрориз исключает эти структуры из ряда систематических признаков Stromatoporoidea. В связи с этим возникает необходимость в ревизии видов и родов строматопороидей, которые были установлены только на основании наличия этих структур.

PLATES

Plate I

Fig. 1. Two different astrorhizae of the *separated* type on the surface of a colony of *Stromatoporella* sp. In addition to the large astrorhiza, another, much smaller one and with a different structure of its central part is visible in bottom right corner of the photograph (Z. Pal. St. I/100 J); nat. size.

Fig. 2. A large astrorhiza of the *separated* type on the surface of a colony of *Hermatostroma* sp. (Z. Pal. St. I/101 J); nat. size.

Fig. 3. An astrorhiza of the *separated* type in a tangential section through a colony of *Hermatostroma* sp. Lateral canals markedly isolated from skeletal tissue and running discordantly to the plane of laminae. Many tabulae and cysts irregularly distributed in canals (Z. Pal. St. I/102 J); ×4.

Jurkowice, Givetian

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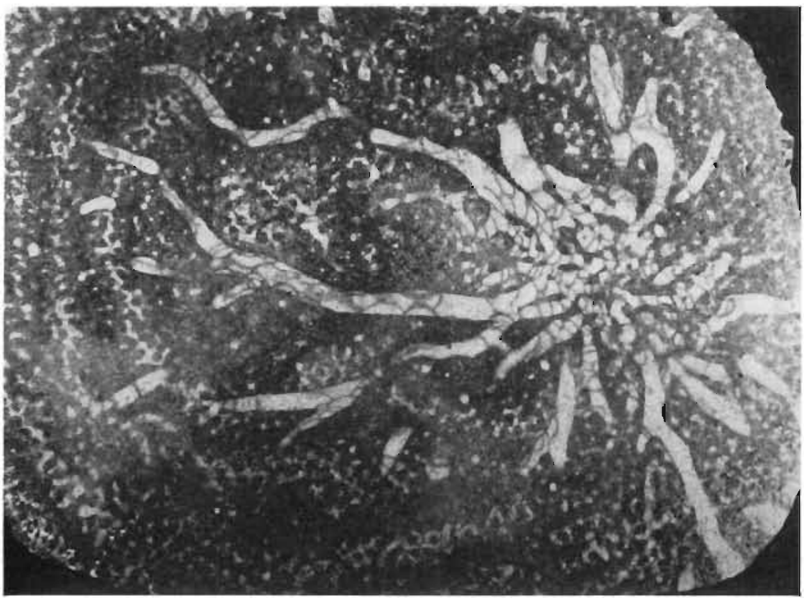
2



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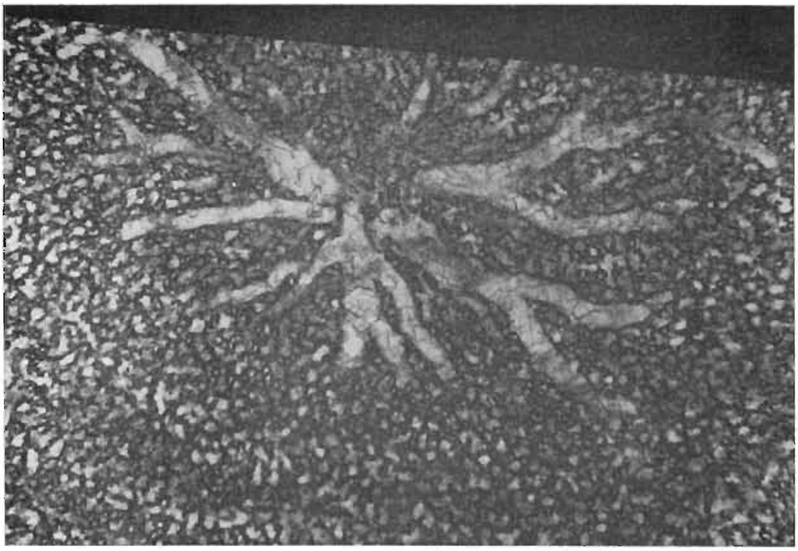

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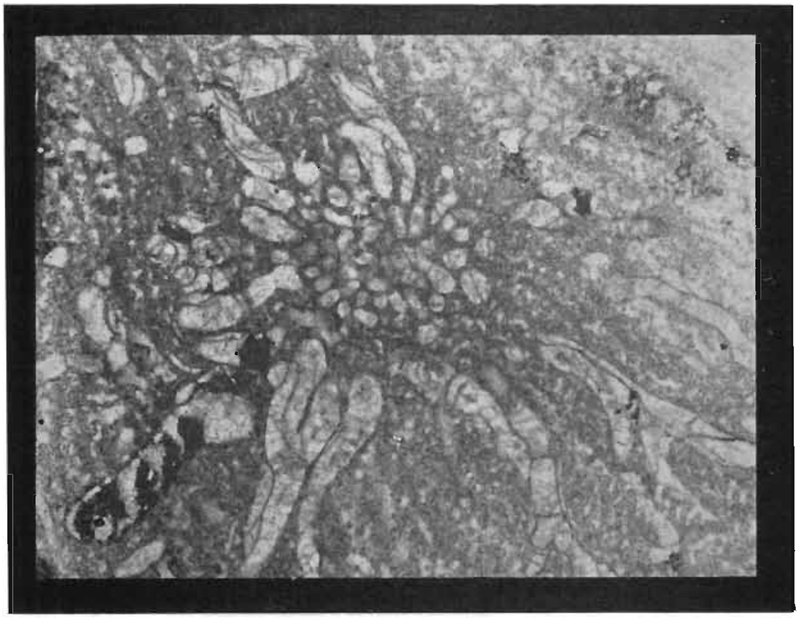

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Plate II

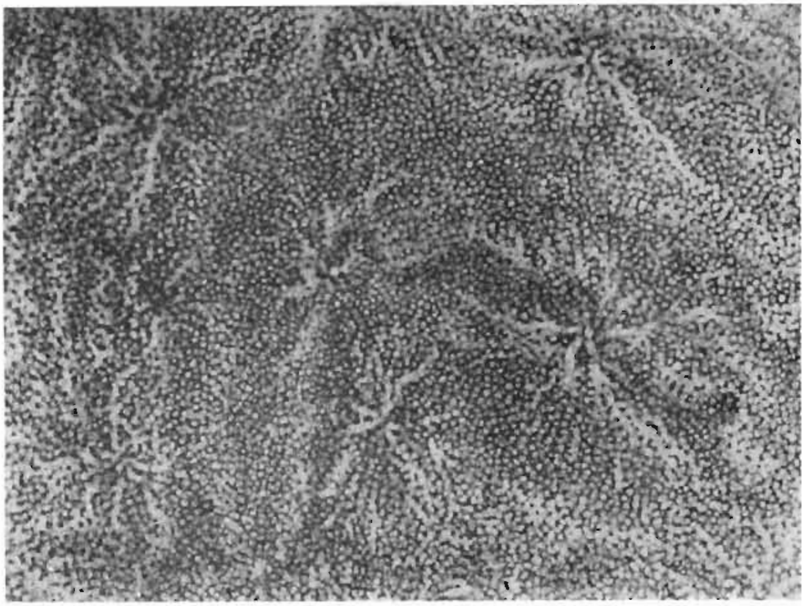
Fig. 1. An astrorhiza of the *separated* type in a tangential section through a colony of *Parallelopora* sp. Lateral canals dichotomously ramified, axial canal lacking. Strongly recrystallized tabulae in canals (Z. Pal. St. I/200 Ł), Radkowice (Sołtysia Góra), Givetian; ×8.

Fig. 2. Another astrorhiza of the *separated* type in a tangential section through a colony of *Hermatostroma* sp. A strongly developed system of lateral canals and a bundle of axial canals with tabulae are visible. Sitkówka (Z. Pal. St. I/300 L), Sitkówka ("Bełkowa" quarry), Givetian; ×6.

Plate III

Fig. 1. Astrorhizae of the *integrated* type in a tangential section through a colony of *Actinostroma* sp. Lateral canals freely communicating with the skeletal tissue of coenosteum, consequently their outlines are very indistinct; the axial zone of astrorhizae poorly outlined (Z. Pal. St. I/400 K), Kowala (railway cut), Frasnian; ×5.

Fig. 2. Astrorhizae of the *integrated* type from a colony of *Actinostroma* sp.: *a* vertical section through coenosteum with lateral canals slightly separated from the skeletal tissue and a blurred axial zone, *b* tangential section through coenosteum with indistinct outlines of lateral canals and a slight turbulence in laminae in the zone of astrorhizae (Z. Pal. St. I/301 L), Sitkówka "Bełkowa" quarry), Givetian; ×10.



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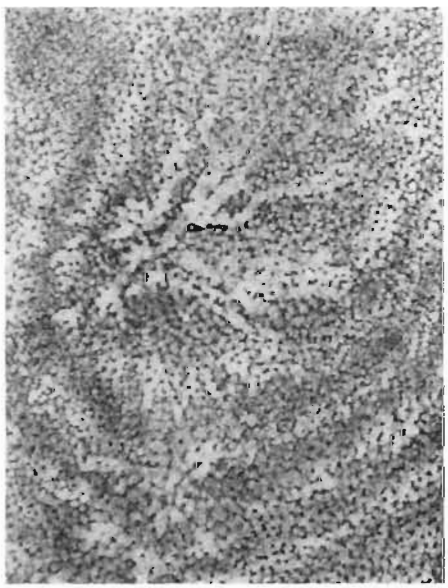

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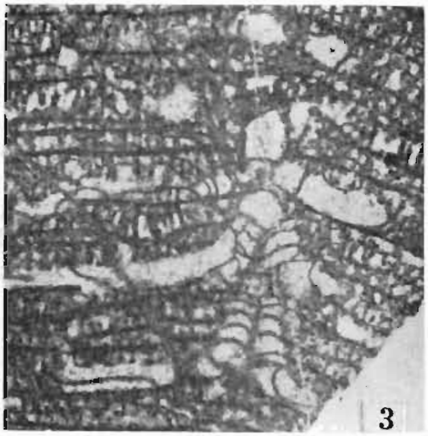

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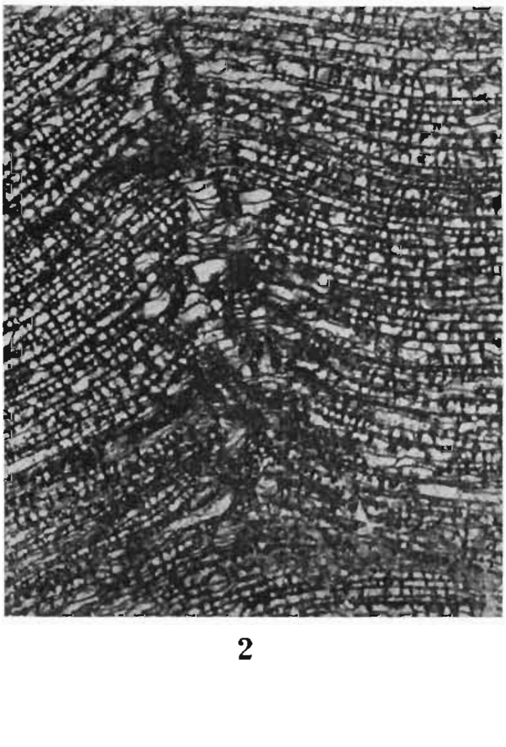

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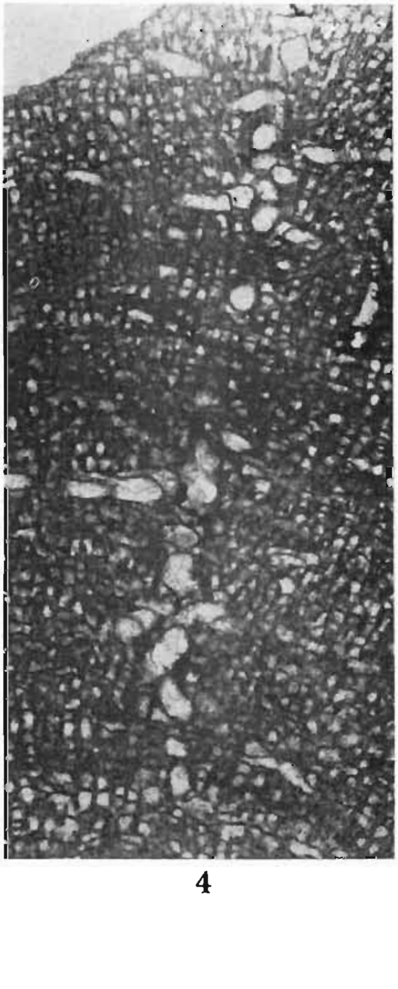

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Plate IV

Fig. 1. A fragmentary colony of *Atelodictyon* sp. seen in vertical section. A strong curve of laminae of the nature of a nipple (mamelon) visible near an astrorhiza (Z. Pal. St. I/500 B), Bolechowice ("Panek" quarry), Frasnian; ×8.

Fig. 2. A superposed astrorhiza of the *integrated* type seen in a vertical section through a colony of *Atelodictyon* sp. The curve of laminae near the astrorhiza much slighter than that in Fig. 1; skeletal tissue in the astrorhizal zone markedly thickened; many tabulae visible in astrorhizal canals (Z. Pal. St. I/501 B), Bolechowice ("Panek" quarry), Frasnian; ×6.

Fig. 3. A superposed astrorhiza of the *integrated* type seen in a vertical section through a colony of *Atelodictyon* sp. A convergent arrangement of canals with many cysts is visible; the thickness of canals does not exceed the width of one interlaminar space (Z. Pal. St. I/201 Ł), Radkowice (Sołtysia Góra), Givetian; ×8.

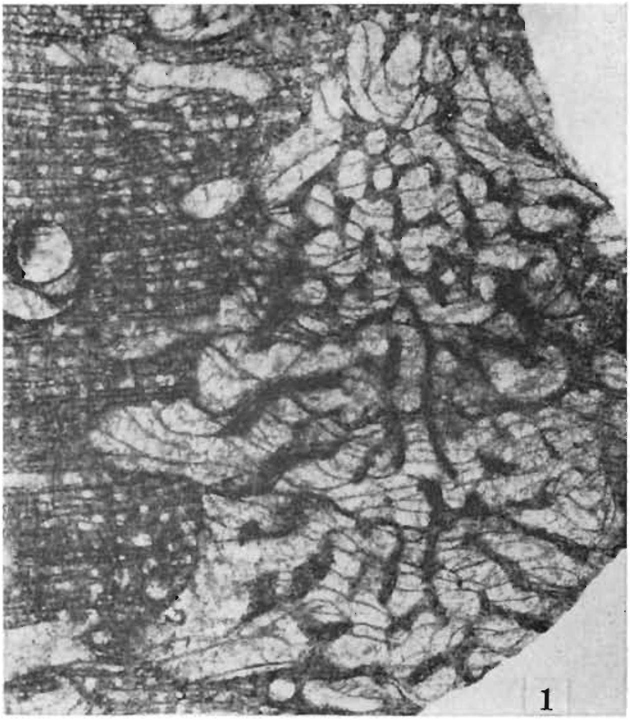
Fig. 4. A superposed astrorhiza of the *separated* type seen in a vertical section through a colony of *Stromatopora* sp. A long axial canal with horizontal lateral canals detaching themselves from it at irregular intervals are visible, tabulae irregularly distributed in canals (Z. Pal. St. I/202 Ł), Radkowice (Sołtysia Góra), Givetian; ×8.

Plate V

Fig. 1. An astrorhiza of the *separated* type seen in a vertical section through a colony of *Stromatoporella* sp. Lateral canals are clearly distributed obliquely to the laminae of coenosteum and gathered in a bunch. A very wide axial zone of the astrorhiza consists of a thick bundle of axial canals. Many straight and bent tabulae occur in canals (Z. Pal. St. I/302 L); ×8.

Fig. 2. Another astrorhiza of the *separated* type seen in a vertical section through a colony of *Stromatoporella* sp. A thick bundle of axial canals and long, horizontal, lateral canals are visible; the thickness of astrorhizal canals is several times as large as the width of a single interlaminar space. Many, round, transverse sections of lateral canals of other astrorhizae are visible in the skeletal tissue. The skeletal substance in the zone of the astrorhiza is clearly darker than in the rest of the skeleton. In the contact area with the astrorhiza, laminae are slightly bent (Z. Pal. St. I/303 L); ×8.

Sitkówka ("Bełkowa" quarry), Givetian



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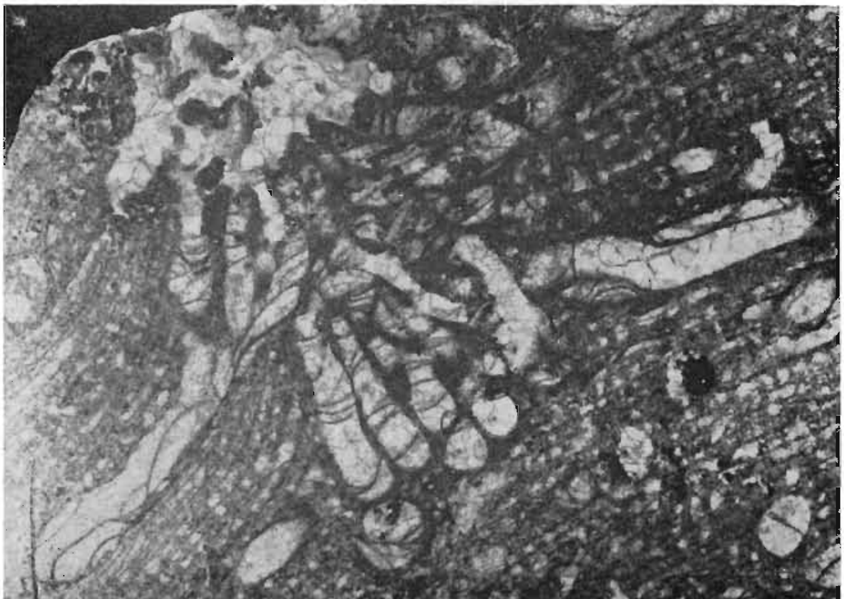

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Plate VI

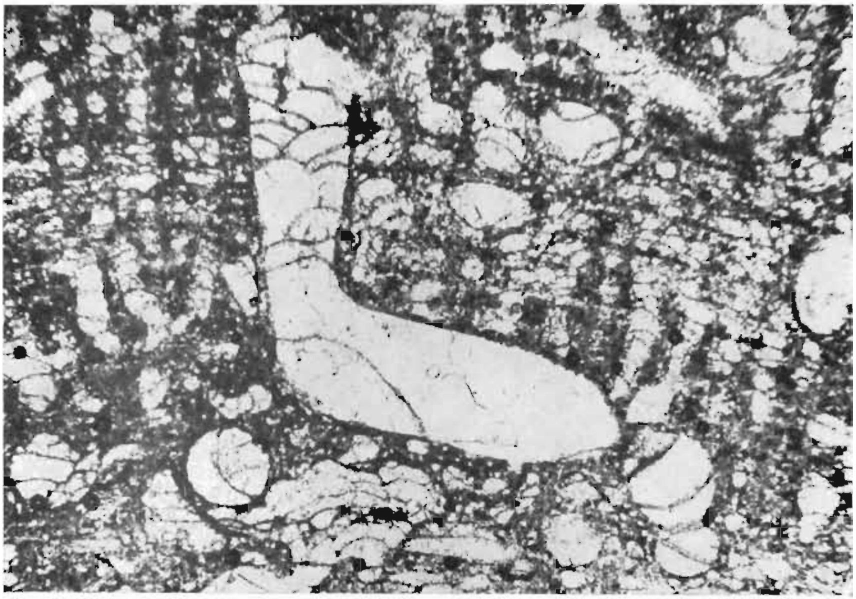
Fig. 1. An astrorhiza of the *separated* type seen in a tangential section through a colony of *Hermatostroma* sp. Astrorhizal canals are not arranged radially but in a coronary manner and they are irregularly anastomozing; many tabulae and cysts in canals (Z. Pal. St. I/104 J), Jurkowice, Givetian; ×6.

Fig. 2. Fragmentary canals of astrorhizae of the *separated* type seen in a vertical section through a colony of *Stromatoporella* sp. Canals, irregularly penetrating the entire skeletal tissue of the stromatoporoid, deform the lamina-pilla system. Tabulae and cysts distributed very irregularly (Z. Pal. St. I/502 B), Bolechowice ("Panek" quarry), Frasnian; ×6.

Fig. 3. Two astrorhizae of the *integrated* type seen in a vertical section through a colony of *Actinostroma* sp. The presence of astrorhizae in the skeletal tissue is marked only by the thickening of vertical elements of skeleton in the zone of astrorhizae and by the occurrence of very thin tabula (Z. Pal. St. I/401 K), Kowala (railway cut), Frasnian; ×10.

Plate VII

Figs. 1-2. Fragmentary canals of astrorhizae of the *separated* type seen in vertical sections through a colony of *Hermatostroma* sp. Canals are sharply separated from the skeletal tissue by a sort of a pseudowall; many irregular tabulae are arranged mostly discordantly to the trace of laminae. Terminal ends of some canals are swollen in a bulblike manner. Many round and oval transverse sections of lateral canals are also visible (Z. Pal. St. I/105 J), Jurkowice, Givetian; ×15.



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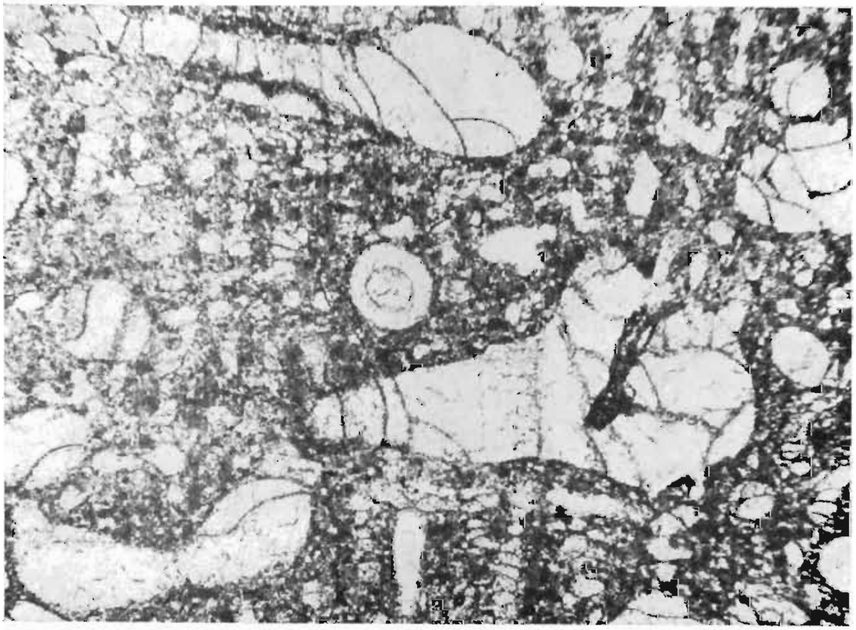
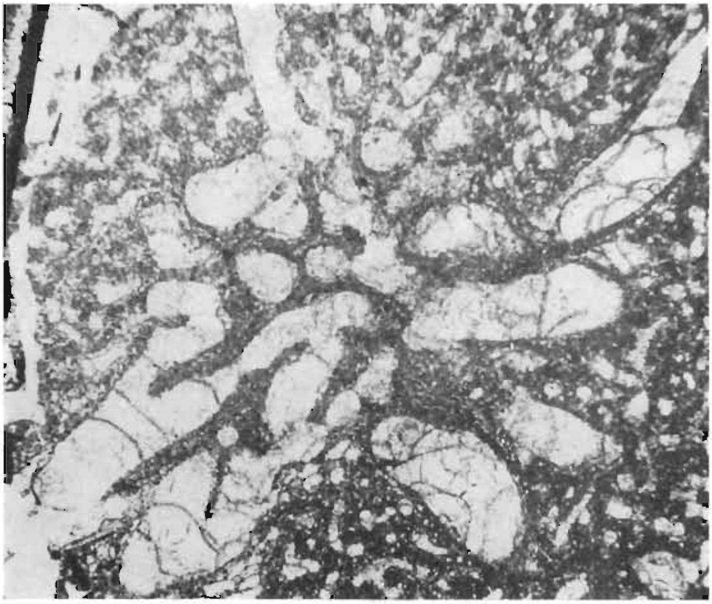


2



1

2

Plate VIII

Fig. 1. A central part of an astrorhiza of the *separated* type seen in a tangential section through a colony of *Hermatostroma* sp. A transverse section through a bundle of axial canals and fragmentary lateral canals are visible (Z. Pal. St. I/105 J), Jurkowice, Givetian; ×15.

Fig. 2. A fragmentary astrorhiza of the *separated* type seen in a vertical section through a colony of *Stromatoporella* sp. A bundle of axial canals and a swollen terminal end of a lateral canal are visible; many straight and bent tabulae occur in canals (Z. Pal. St. I/303 L), Sitkówka ("Bełkowa" quarry), Givetian; ×15.