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TOLYPAMMINA VAGANS (FORAMINIFERIDA) AS INHABITANT OF  
THE OXFORDIAN SILICEOUS SPONGES

**Abstract.**— An argillaceous, monothalamous foraminifera *Tolypammina vagans* (Brady) adapted to live in sponges, was found in the water system of numerous siliceous sponges collected from Oxfordian marls and limestones of Central and Southern Poland. Individual variability of *T. vagans* was traced and it was found that most species of *Tolypammina* Rhumbler should be classified within this species. The occurrence of *T. vagans* in sponges was commensal in character and dependend on: 1) dynamics of water circulation in sponges, 2) presence of sufficient quantity of terrigenous quartz in silt fraction in water. The role of occurrence of *T. vagans* in successively changing sponge assemblages for the reconstruction rate of silt sedimentation in the Oxfordian Basin of Poland is pointed out.

## INTRODUCTION

Biotic associations of sponges with various invertebrates and algae long attracted the students of recent marine communities. Foraminifera, however, belong to rarities among variable groups of organisms inhabiting or encrusting contemporary sponges. Hence the frequent occurrence of agglutinated foraminifera in skeletons and mummies of siliceous Oxfordian sponges is particularly interesting. The primitive, monothalamous foraminifera determined as *Tolypammina vagans* (Brady), the recent representatives of which are known as adherent forms (Brady, 1879) is worth of mention here. The specimens of this species occurring in the Oxfordian sponges exhibit many characters proving their adaptive connections with their hosts. Analysis of those connections allows to make a reconstruction of many details of ecology of tolypamminas, and throws a light on the dynamics of the water systems of Jurassic sponges and gives some information about the character of the sedimentation in the epicontinental Oxfordian Basin.

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#### MATERIAL AND METHODS

Tolypamminas were extracted from the siliceous sponges collected from Oxfordian marls and limestones. These rocks crop out in many sites of the Cracov-Częstochowa Jurassic Belt and along the southwestern border zone of the Holy Cross Mts.

Sampling sites:

- a) Krzeszowice (Cracov district), outcrops near the "Nowa Krystyna" mine. Sponges were collected from marls and marly limestones 1.40 m thick of cordatum and placatilis zones of the Oxfordian (Różycki, 1953).
- b) Wrzosowa (suburb of Częstochowa). Sponges were collected from marls and marly limestones 2.5-3.0 m thick belonging most probably to mariae-plicatilis zones of the Oxfordian (Różycki op.cit.).
- c) Kłobuck (vicinity of Częstochowa). Sponges are very abundant in marls 1.60 m thick of cordatum-plicatilis zones of the Oxfordian (Różycki, 1953).
- d) Korzecko and Bolmin (Kielce district). Sponges and their fragments were collected from very hard, poorly or non-stratified limestones, commonly known as "rocky limestones" of variable thickness from few to a dozen of meters of probable Upper Oxfordian age (Świdziński, 1931; Kutek, 1968).

Altogether 100 sponges of various shape and size were analysed. The following genera of siliceous sponges (mainly *Triaxonina*) were identified: *Pachyteichisma* Zittel, *Sporadopyle* Zittel, *Pachyascus* Schrammen, *Caesaria* Quenstedt, *Cypellia* Zittel, *Craticularia* Zittel, *Feifelina* Schrammen. In few calcareous sponges occurring with the siliceous ones (mainly ?*Pero-nidella* sp.) neither tolypamminas nor other agglutinated foraminifera were noted.

The spicular sponge skeletons out of which the tolypamminas have been extracted, only in few cases were completely preserved and partly in fragmentary primary siliceous form. Most sponges are preserved in mummified form, with the primary opal of the spiculae replaced by calcium carbonate.

Tolypamminas were prepared by dissolution of sponges in hydrochloric acid (see also Feifel, 1930). Prior to this process the sponges were carefully cleaned, and the specimens with hard stoppers of sediment in their cloacas had to be cut along their growth axis. A part of the sponges prepared in this way were then dissolved completely in order to find the total number of tolypamminas which occur in the particular morphological sponge types. Other sponges were treated in phases which allowed to determine in detail the mode of occurrence of tolypamminas in the skeletal and water system of sponges. This was done by serial transversal sections of the sponges as well. The obtained thin plates were then treated with HCl. Together with thin sections this allowed to investigate the distribution of tolypamminas in the various growth stages of sponges.

#### MORPHOLOGY AND TAXONOMY OF TOLYPAMMINA VAGANS

##### *Species problem in the genus Tolypammina*

The genus *Tolypammina* was distinguished by Rhumbler (1895) from the genus *Hyperammina* Brady with a type species *Hyperammina vagans* Brady. A basis for the new genus was various attitude to the substratum in the representatives of both taxa: freely benthic mode of life for *Hyperammina*, and adherent to the substratum in *Tolypammina*. Such subdivision makes the separation of the representatives of both genera easy in taxonomic practice. Specific identification of *Tolypammina* representatives is much more difficult. They are known from the Silurian till recent times, and many of them were established on the basis of very fragmentary materials. Simple, tubular tests of *Tolypammina* do not offer good diagnostic features thus the species are described either on the basis of secondary morphological features, or on the basis of considerable chronological differences in their appearance.

Species assigned: *T. tortuosa* Dunn, 1942 — Silurian; *T. helicina* Cressin, 1961 — Upper Devonian; *T. nexuosa* Cressin, 1961 — Upper Devonian; *T. extenda* Ireland, 1956 — Pennsylvanian; *T. nodosa* Ireland, 1956 — Pennsylvanian; *T. polyverta*, Ireland, 1956 — Pennsylvanian; *T. rugosa* Ireland, 1956 — Pennsylvanian; *T. serpens* Ireland, 1956 — Pennsylvanian; *T. delicatula* Cushman & Waters, 1928 — Pennsylvanian; *T. permiana* (Paalzov, 1935) — Permian; *T. jurensis* Franke, 1936 — Lower Jurassic; *T. contorta* (Haeusler, 1890) — Upper Jurassic; *T. vagans* (Brady, 1879) — recent.

*T. jurensis* and *T. helicina* should be excluded from the above list. The former because its branching tests do not fit the definition of *Toly-*

*pammina* and the latter one — with its unattached test with tightly coiled initial portion of tubular chamber should be classified to *Ammovertella* Cushman or *Lituotuba* Rhumbler. Barnard (1958) suggested that *T. delicatula* should be transferred to *Ammovertella* because of its coiled initial portion. *T. nexuosa* and *T. permiana* have been established on the basis of very fragmentary material which does not justify their separatness. Differences between other species described on the basis of better materials do not justify, at least in the light of the individual variability of *tolypamminas* from sponges, full separatness of those taxa. Phenotypical character of their variability devaluates most of diagnostic criteria used so far for *Tolypammina* species. For instance, morphological features of tests taken by Ireland (1956) as a basis for diagnoses of five species of *Tolypammina* from the Pennsylvanian of the Mississippi Basin such as: broadening of tubes toward aperture (*T. extenda*), recurring swellings and narrowings (*T. nodosa*), various degree of bending of tubes (*T. polyverta*) and insignificant differences in tube thickness or size of grains building tests (*T. rugosa* and *T. serpens*) — occur frequently in one specimen of *Tolypammina* in a sponge (see chapter "Variability").

As the best described and oldest *Tolypammina* species is *T. vagans* (Brady), it should be regarded most probably as the only one valid (monotype), and the remaining ones — as its younger synonyms. Such a concept of *T. vagans*, because of great time span of its occurrence (Silurian — Recent), would be too broadly meant chronospecies. Nevertheless, the morphology of the tests of the discussed primitive foraminifera does not give grounds to maintain the validity of the species established so far. It should be mentioned here that the author's opinion about the time span of *T. vagans* is not an isolated one. The *tolypamminas* found in analogous sponge facies in the Oxfordian of Switzerland and Germany were also most frequently identified with recent *T. vagans* (Haeusler, 1890, Feifel, 1930; Frenzen, 1944; Oesterle, 1968; Schairer, 1971).

### Morphology

Test in form of irregularly bent, monothalamous imperforate tube. Oval or spherical proloculus occurs in initial part, from which a considerably longer second chamber protrudes, terminating with undifferentiated aperture. No diaphragma occurs inbetween the proloculus and second chamber. Test shows point traces of attachment to the substratum, but without characteristic flattenings of tube at points of attachment. Tube section usually annular, less frequently elliptical. Most tests exhibit irregularly scattered deeper or shallower narrowings which in some cases may form regularly spaced beads, say every 0.18—0.25 mm. Generally the tube dia-

meter increases gradually toward distal part but deviations from this rule occur frequently. Internal tube walls are obviously smoother than the external ones and in some cases show traces of indistinct growth bands (see Pl. XXIII, Figs 1 and 3). Tubes occur single as a rule but aggregations in form of irregularly tangled masses (Pl. XIX, Fig. 1) or interweaved sets (Pl. XIX, Fig. 2) are frequent.

Dimensions:

Length of tubes: 5—12 mm

Tube diameter: 0.09—0.40 mm, most specimens within 0.15—0.25 mm.

Wall thickness: 0.008—0.025 mm, usually 0.010—0.015 mm.

*Dimorphism.* — Majority of the specimens prepared from sponges show preserved proloculi among which two types maybe distinguished: 1) spherical proloculi 0.10—0.15 mm in diameter, and 2) ellipsoidal proloculi, which are considerably larger than the former, 0.29—0.33 mm long with largest diameter 0.14—0.23 mm (see Pl. XXII, Figs 1—8).

Distinct differences both in size and shape of proloculi in *T. vagans* clearly show that micro- and megalospherical forms are represented in the investigated material. It is difficult to find out, however, to which extent the proloculi dimorphism corresponds to sexual and asexual generations in tests of recent specimens of this species. Specimens with small proloculi form about 60-70 per cent of all specimens with preserved proloculi. A tendency to tight screwing of the initial part of tube is to be observed in those specimens (Pl. XXII, Figs 1—3) what makes them similar to some species of the genus *Lituotuba* Rumbler. Among specimens with large proloculi the second chamber stretches straight or (less frequently) is bent at angle of no more than 90°—100° from the growth axis of proloculus.

*Composition and source of test material* — The tubes are build of quartz grains 2—12  $\mu$  in size, most frequently within two fractions: 2—5  $\mu$  and 8—12  $\mu$ . These fractions correspond to medium clay to very fine silt range according to Wentworth's (1922) classification. Mineralogical identification of grains was not possible by optical method because of too fine fraction. Comparative X-ray analyses were done of powdered tests coming from very pure Oxfordian limestones and of siliceous spiculae in order to find out whether those tests were build of disintegrated spiculae of siliceous sponges, or of secondarily silicified limestone detritus. The analyses carried out by Debye-Scherrer method showed much higher degree of crystallization of grains building tests of *Tolypamminae* (quartz) than of spiculae (chalcedony). The shape of the grains in tests is angular to subrounded (roundness class after Pettijohn, 1957). Grains are densely packed (see Pl. XXIII, Fig. 2) and cemented probably with silica with considerable admixture of organic substance, the latter being observable, after dissolving of tubes in fluoric acid, as mucosubstance.

*Variability.* — A rich material of *T. vagans* prepared out of sponges reveals considerable morphological differentiation the causes of which are

explained farther on in the text. These variations are observable not only in shape and size of the test of different individuals but also may be traced in the particular tests. A tube may show longer straight sectors, then some narrowings may occur in it as well as some swellings and the growth direction is subject to many changes (see Pl. XXI, Fig. 3). The tube diameter is highly variable as well. As an example, fragments of tubes belonging to three different specimens are presented in Pl. XX. The thickest one is over four times larger than the thinnest one. The degree of bending of the particular individuals is also highly variable — from almost straight (Pl. XX, Fig. 1; Pl. XXI, Figs 3—6) to worm — like bent of loose coils (Pl. XXI, Fig. 1), and tightly interweaved bundles (Pl. XIX, Fig. 2), or tangled aggregates (Pl. XIX, Fig. 1, Pl. XXI, Fig. 2).

#### TOLYPAMMINA — SPONGE INTERRELATIONSHIP

Observation of *T. vagans* — siliceous sponges association allows to reconstruct at least in part the factors which were of importance in mode and frequency of settling of sponges by these foraminifera. These factors are first of all: a) organisation and dynamics of the sponge water system and b) character and terrigenous sedimentation rate in a basin. No connection was noted between appearance of tolypamminas with definite species or genera of siliceous sponges.

#### *Distribution of T. vagans in the channels of the sponge water system*

The system of water channels in sponges of leuconoid organization, as it is the case in the siliceous sponges under consideration, consists of three zones: 1) external inhalant, 2) central choanosomal, and 3) internal exhalant zones. The interrelations of the channels in these zones may be modified in various way depending on the organization degree of a particular sponge (Hyman, 1940). Tolypamminas are most frequent in the channels of the inhalant zone, i.e. subdermal spaces and incurrent canals. Some tolypamminas grow out of inhalant zone and encrust dermal sponge surfaces (Text-fig. 1). Tolypamminas were not found in choanosomal zone (in choanocyte chambers). They occur again in the exhalant zone where they penetrate very thin channels leading to choanocyte chambers through larger canals and excurrent canals (aphoduses and apopyles). Rather large quantities of these foraminifera are to be observed in some cases on cloaca walls and near osculum.

As it might be reckoned from the position of a dozen specimens with preserved proloculi prepared in situ, tolypamminas grew in sponges usually against the current of water flowing through a sponge (see Text-fig.

1). In some cases, however, particularly so in case of irregularly bent individuals, determination of the growth direction was impossible.

A direct connection exists between the shape and size of tolypamminas and the diameter and shape of canals in sponges occupied by them. The

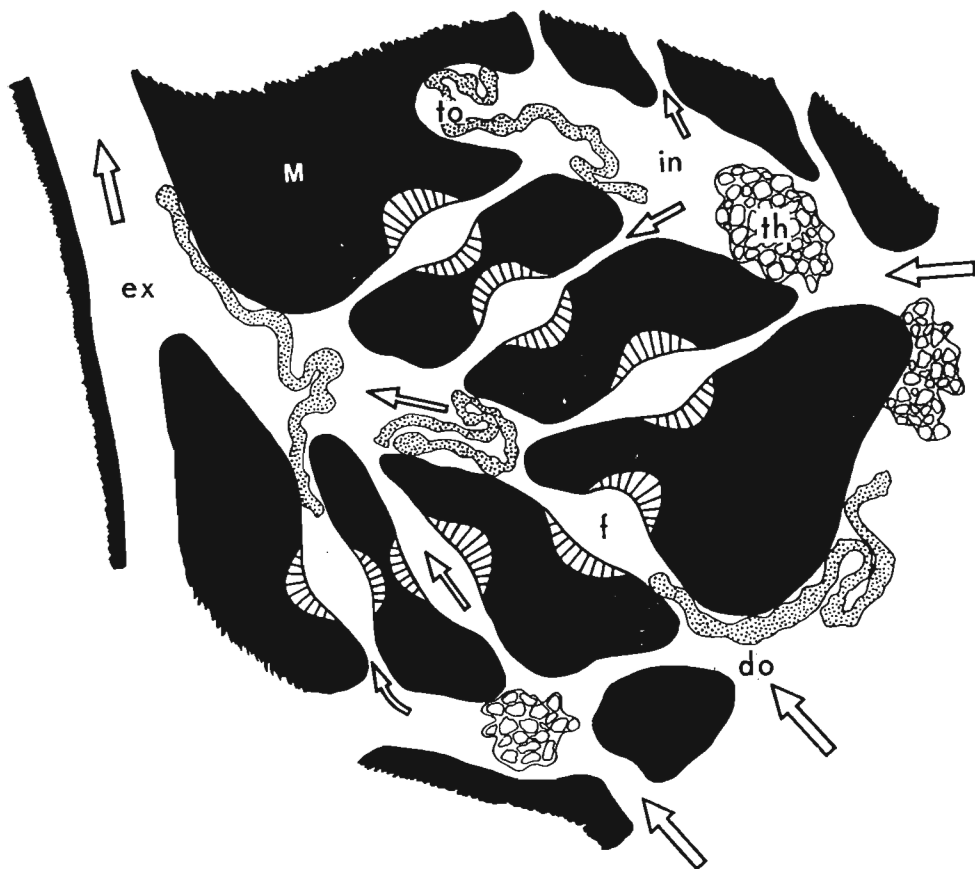


Fig. 1.—Distribution of tests of *T. vagans* in canals of water system of leuconoid sponge. (Scheme of sponge structure after Hyman, 1940): *to* tests of *T. vagans*, *th* tests of *Thurammina* sp., *do* dermal ostia, *f* flagellate chambers, *in* incurrent canals, *ex* excurrent canals, *M* sponge body; arrows point flow direction of water in sponge; not to scale.

diameter of water canals in inhalant and exhalant zones of sponges diminishes considerably toward the chaonocyte chambers, thus tolypamminas inhabiting them also show smaller dimensions. Hence the largest tolypamminas occur in subdermal spaces and larger subcloacal canals. Also in such places tolypamminas had enough room to form large tangled aggregates consisting of many individuals (Pl. XIX, Fig. 1). Smaller and less bent tubes of tolypamminas occur in incurrent and excurrent canals, in which they formed bundles of parallel growing individuals, in result

of lack of free space (Pl. XIX, Fig. 3). The thinnest specimens of these foraminifera are to be found in systems of fine canals (propyles and apopyles), leading directly to the choanocyte chambers. As these canals are strongly bent and armored with spiculae, the foraminifers had to push through them during their growth. Thus the specimens extracted from such broadening and narrowing passages show, aside of bent tubes, numerous narrowings and swellings (the so called "Einschnürungen" of Seibold & Seibold, 1960) which correspond as a rule to the spaces of meshes in spiculae network which is characteristic of each taxonomical group of sponges.

The dependence of the tube morphology of *Tolypammina vagans* on the shape of inhabited type of sponge canal is frequently visible in tubes of individual specimens, in straight sectors or sectors bent to various degree (Pl. XXI, Figs 3 and 5).

#### *Dynamic of water circulation in sponges and Tolypammina settlement*

The quantity of water flowing through a sponge depends on the quantity and activity of choanocytes and organization of a system of water canals, their diameter and total length. These parameters are decisive in sponges of leuconoid structure to which belong the analysed siliceous sponges with tolypamminas, that the effectiveness of the water system is maximal (Hyman, 1940, Barrington, 1967). Two types of currents form this system: namely the slower one bringing water into the choanocyte chambers, and a much quicker current which expells the water out of a sponge. This difference in water current velocity is of particular importance preventing a sponge from impurities such as sediment particles etc., both coming into the inhalant zone and falling on the sponges. The measurements of the water current velocity in the particular types of canals that were carried out on recent sponges by Parker (1914) and Bidder (1923) have revealed that this velocity of water flowing in through dermal ostia to incurrent canals decreases along the penetration into thin subchoanal canals (propyles). Minimal velocity was noted just before entering choanocyte chambers and in the chambers proper. After leaving the choanocyte chambers the velocity increases quickly and attains its maximum near osculum.

The ability of a sponge to transport grains of a definite fraction is closely connected with the velocity of water flowing through it. This pertains to grains settling in closets vicinity of sponge or being in suspension in case of very small fraction. Canals of inhalant zone are the only entrance for sediment as the water velocity thrown out of osculum is sufficiently great (4 and more mm per sec — Parker, 1914), and a whirl-

ling motion of water exists around the sponge (Text-fig. 2). As it was already mentioned the velocity of incurrent is insignificant (according to Bidder, 1923 — 100 to 150 times smaller than that of oscular stream), its transporting power is also small. Thus regardless of the grain size settling on a sponge or near it (within re-entrant vortex zone — see Text-fig. 2), the upper fraction limit of grains which may be pumped into a sponge

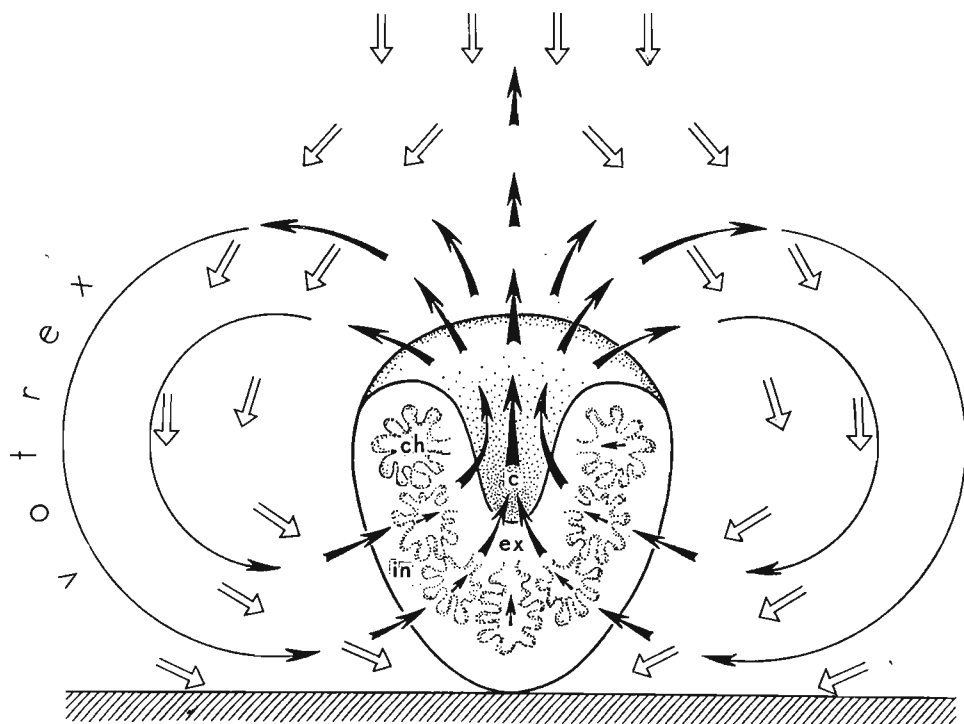


Fig. 2. — Diagram illustrating water circulation in sponge (black arrows) and direction of particle settling in re-entrant vortex zone (white arrows). (After Bidder, 1923, modified). Current velocity in the particular zones of water system in sponge and re-entrant vortex is proportional to the thickness of black arrows; *in* incurrent zone, *ch* chaenosomal zone (choanocyte chambers), *ex* excurrent zone, *c* cloaca.

is already determined. The observations on mode of distribution of tolypamminas and other agglutinated foraminifera in sponges fully confirm this reasoning. Upper limit of terrigenous quartz grain fraction of which the tubes of *T. vagans* are built is  $12\ \mu$ . Only in subdermal spaces and in some cases on sponge surface other agglutinated foraminifera occur frequently together with tolypamminas (e.g. *Thurammina* sp. — see Text-fig. 1), the tests of which are built of much larger ( $30\text{--}40\ \mu$ ) well selected quartz grains. These largest grains occurring inside sponges determine the maximal transporting ability of incurrent in the outermost zone. Further inside current velocity decreased and tolypamminas living in canals of subchoanal zone have built their tests of finer fraction of  $2\text{--}7\ \mu$ . Only

the finest material was transported through the choanocyte chambers, nevertheless, its quantity was sufficient for existence of numerous tolypamminas of the exhalant zone. Their tubes consist of grains of 2—5  $\mu$  fraction of very high degree of selection.

The size of dermal ostia might have been another factor limiting quartz grain size entering sponges. This factor which is of no importance in the case of large ostia of siliceous sponges made impossible the settlement of agglutinated foraminifera in calcareous sponges occurring in small quantities in assemblages of siliceous ones in the Oxfordian sediments. Dermal ostia of calcareous sponges as intracellular pores are so small (Hyman, 1940, Barrington, 1967) that neither sediment suitable to test construction nor young foraminifera (zygote) can penetrate the sponge.

Small (young) sponges exhibited probably too weak incurrent thus tolypamminas are seldom found in them. Smaller quantity of choanocytes prevented to develop such a current which would be able to introduce to sponge canals a quantity of material sufficient to build tests of foraminifera.

Shape of sponges, which according to Bidder (1923) plays an important role in the effectiveness of their water system, did not influence the settlement of the Oxfordian sponges by tolypamminas.

#### *Role of sedimentation in the occurrence of T. vagans in sponges*

Existence of grains suitable to test construction in the water pumped by a sponge was a basic prerequisite in settlement of tolypamminas in the siliceous sponges. The tests of the investigated *T. vagans* are composed of terrigenous quartz grains of a definite fraction, thus frequency of occurrence of tolypamminas in sponges may serve as an indicator of sedimentation rate of those fractions in the various parts of sponge facies of the Oxfordian. This is of particular importance in case of fewness of terrigenous material in sponge limestones. Identification of such terrigenous quartz is usually impossible in practice because it occurs together with abundant spiculae of siliceous sponges. The terrigenous material in tolypamminas is much more concentrated than in the surrounding sediment.

Because of a fine fraction (argillaceous) used by tolypamminas these foraminifera are more frequently found in marly sediments than in pure limestones (the so called "rocky"). Nevertheless, too clayey deposition inhibited sponge development by choking water canals. It is remarkable as well that even when the terrigenous material was in excess no increase in tolypamminas quantity beyond sponge interior was observed. *T. vagans* as ecological adherent type of benthonic foraminifer needed hard substratum to adhere even with its proloculus. Intensive sedimentation of fine fraction could not furnish such a substratum. Thus no specimens

of *T. vagans* were prepared out of sediment surrounding the sponges, despite of dissolving in hydrochloric acid. The species is mentioned neither by Garbowska (1970) in her elaboration of the Oxfordian and Lower Kimmeridgian foraminifera of the Cracow-Częstochowa area, nor by Wiśniewska-Żelichowska (1971) in her list of microfossils derived from Upper Oxfordian sponge bioherms from the vicinity of Częstochowa.

### *Discussion of the biotic character of Tolypammina-sponge association*

The association of tolypamminas and sponges was already noted by Haeusler (1890). He first observed irregular tubes of these foraminifera on surface of Hexactinellida and treated them as rhizoids of these sponges but later classified them to *Hyperammina* (*Tolypammina*) *vagans* Brady. Kolb (1910) finding frequently agglutinated foraminifera in Upper Jurassic sponges including tolypamminas, regarded them as having flown into sponges together with sediment directly after sponge death.

It was Feifel (1930) who claimed association of tolypammina and other agglutinated foraminifera with the Upper Jurassic sponges. He treated sponges with hydrochloric acid, and pointed out active mode of growth of tube-like tests of tolypammina in sponge skeleton and described this association as commensalism, not excluding, however, their negative influence on water circulation in sponges, which is particularly the case if they occur in sponges in plenty. This may lead after him to premature death of a sponge. Seibold & Seibold (1960) were of the same opinion when analysing specific content of foraminifera from Upper Jurassic sponges of southern Germany. These authors cite 16—21 species of agglutinated foraminifera in average from sponges, but they dealt neither with the mode and frequency of occurrence nor with detail explanation of biotic connections between those two organisms.

The present author agrees with the opinion of Feifel (1930) that tolypammina — sponge association was a typically commensalic. As foraminifera found shelter in sponge canals and water current produced by sponge brought them food, thus such a variety of commensalism should be named inquilinism. Such commensalism is grounded on an association of a passive filtrator with a considerably larger active filtrator and is most common among recent water organisms. There are many examples of associations of invertebrates with recent sponges (see among others: Santucci, 1922; Pearse, 1932, 1950; Laubenfels, 1950; Riedl, 1968). Strikingly, there is lack of information on the occurrence of agglutinated foraminifera as permanent inhabitants-commensals in sponges everywhere good conditions exist. Known are foraminifera (Trochammididae, Rotaliidae, Homotremidae) encrusting living sponges, cirripedes, hydroids and bryozoans

(Riedl, 1968), there is no information, however, about forms living in water system of sponges.

This makes explanation of causes of universal infection of tolypamina and other foraminifera in Upper Jurassic sponges difficult. No such phenomenon was noted in sponges of other geological periods. Somewhat similar association was observed in Upper Maastrichtian of Denmark. Arenaceous, adherent foraminifera (*Bdelloidina vincentovnsensis*) encrusted around pores of a boring sponge (*Entobia cretacea*) pierced in oyster shell (Bromley & Nordmann, 1971). The same foraminiferan species was noted by Voigt (1970) encrusting outlets of small, vertical canals on the surface of Upper Maastrichtian hard-ground. He regarded these canals as possible borings of Phoronoidea. In both cases the association was classified to commensalism caused by attractive nourishing possibilities for foraminifera (water movement near *Entobia*) or shelter (phoronid tentacles).

It is not quite clear whether such commensalism turned out to spacial parasitism in case of partial or even complete choking the water canals of sponges by tolypamminas. This might lead to premature death of sponge as it was already noted by Feifel (1930). In the present author's opinion it was rather not the case because decrease of water current in sponge probably discouraged foraminifera to settle any more in it.

That there was no feeding competition between sponges and tolypamminas may be reckoned from diet of recent representatives of both groups of organisms. Basic if not only food of sponges are bacteria (Hyman, 1940, Barrington, 1967, Riedl, 1966), whereas that of foraminifera consists of larger organisms such as copepods, caprellids, cumaceans and nematodes, not mentioning unicellular algae, naupli, diatoms and ciliates (Sandon, 1932, *fide* Hedley, 1964).

Foraminifera played a preventing role from choking of canals catching large part of coarser terrigenous material flowing into a sponge, and building their tests with it.

Early stages of sponge colonization by tolypamminas are not clear. The foraminifera penetrated into sponges being flown in by incurrent probably as young ameboid schizonts or gamonts. These amoebas attached with their pseudopodia to the canal walls of sponges, most preferably to a spicular skeleton and quickly constructed an argillaceous proloculus. Presence of tolypamminas in canals of exhalant zone, to which they might have enter only through choanocyte chambers, proves that young foraminifera were not captured by flagella of the choanocytes. During their farther growth in sponges tolypamminas took advantage of tube-like shape second chamber, showing tremendous morphological ability to adapt themselves to complicated system of sponge water canals. Attractiveness of life in sponges was so great that their tubes were repetitively used by subsequent generations of tolypammina, which formed characteristic "tube-in-tube" aggregations (see Text-fig. 3, Pl. XXIV, Figs 1—2).

Although *T. vagans* is an adherent foraminifer, the individuals living in sponges could adhere to spiculae surrounding or sticking in water canals in points only. Thus, contrary to usually unilaterally flattened tests

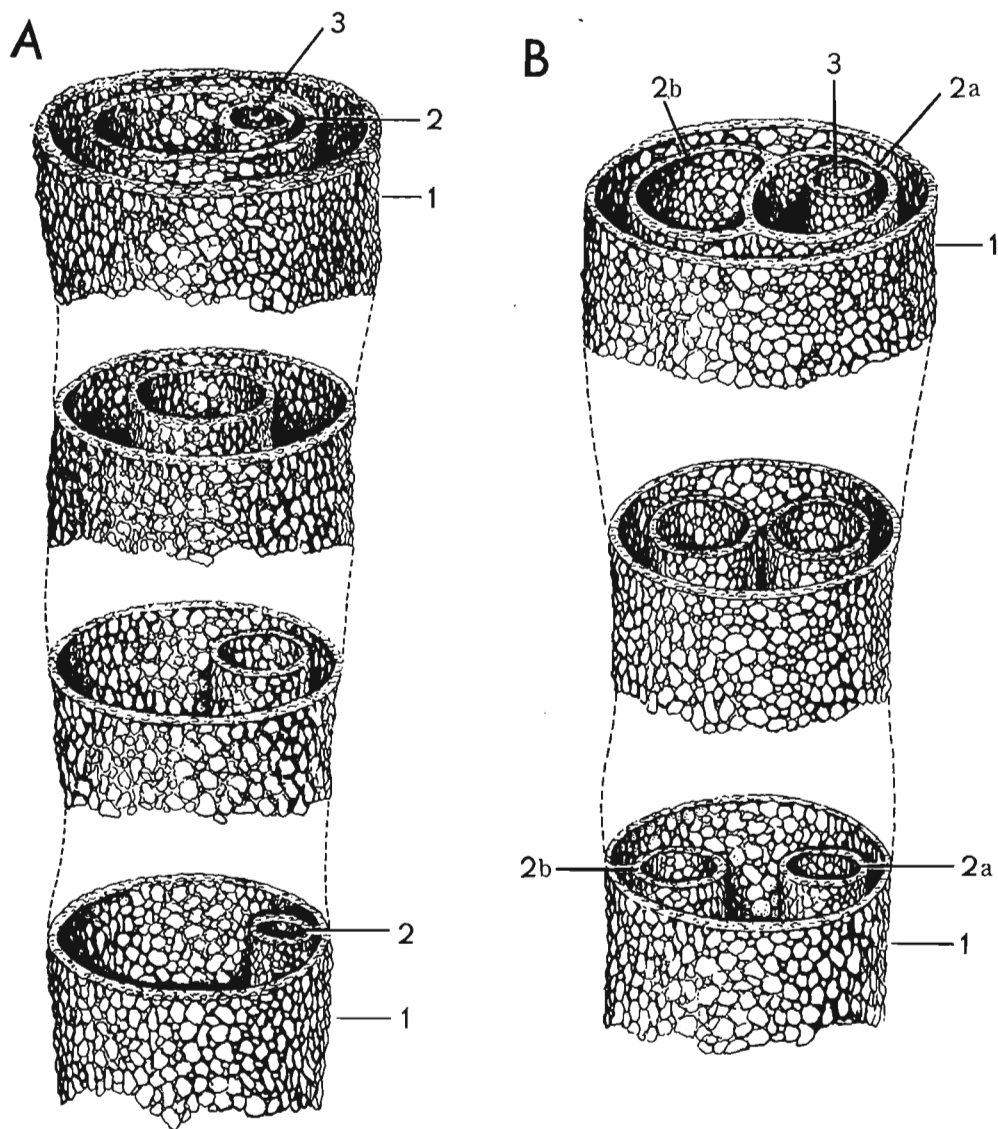


Fig. 3. — "Tube-in-tube" aggregations of *T. vagans* tests in three dimensional serial transversal sections;  $\times 500$ . 1, 2, 3—successive generations of *T. vagans*.

of adherent foraminifera, tolypaminas associated with sponges exhibit almost ideally circular tube sections.

Seldom occurrence of *T. vagans*, beside Oxfordian sponges, may be probably explained by its extraordinary environmental requirements

which are: hard substratum, water motion (= inflow of food) and character and rate of sedimentation. A mass development of siliceous sponges over vast areas of the epicontinental Oxfordian basin of Central and Western Europe with large food base and source of argillaceous material opened a new, very attractive ecological niche for these foraminifera. Due to favourable life conditions this niche was quickly colonized by them. Similar environmental situation did not repeat in a long history of this species. Secular fortuity of this association excluded probably a possibility of turning loose, facultative relations into a more specific cooperation.

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TOLYPAMMINA VAGANS (FORAMINIFERIDA) JAKO KOMENSAL  
OKSFORDZKICH GĄBEK KRZEMIONKOWYCH

Streszczenie

W wielu oksfordzkich gąbkach krzemionkowych z Jury Krakowsko-Częstochowskiej i południowo-zachodnich Gór Świętokrzyskich stwierdzono występowanie aglutynujących, jednokomorowych otwornic *Tolypammina vagans* (Brady). Bliższa analiza morfologii i sposobu rozmieszczenia tych prymitywnych otwornic w gąbkach wykazała, że posiadały one szereg przystosowań do życia w kanałach systemu wodnego żywych gąbek.

Sposób rozmieszczenia i ilościowe występowanie *T. vagans* w gąbkach krzemionkowych, pochodzących z różnych poziomów oksfordu, zbadano przy zastosowaniu stopniowego nadtrawiania gąbek w kwasie solnym. Ponieważ rurki *T. vagans* zbudowane są z ziaren kwarcu terrygenicznego frakcji drobnomulowcowej scementowanych substancją krzemionkowo-organiczną, łatwo można je było preparować HCl ze zwykle kompletnie zdesylikowanych mumii gąbek.

Najwięcej rurek *T. vagans* stwierdzono w kanałach inhalacyjnych i na powierzchni gąbek w sąsiedztwie por dermalnych. Dostępnie pojawiają się też tolypamminy w kanałach ekshalacyjnych oraz na ściankach kloak. Mimo, że tak w strefie inhalacyjnej jak i ekshalacyjnej tolypamminy stwierdzono nawet w najcieńszych kanalikach subchoanalnych, nigdy nie napotkano ich w komorach choanocytowych.

Wyraźny jest związek morfologii i wielkości rurek *T. vagans* z konfiguracją i rozmiarami zajmowanych przez nie kanałów wodnych gąbek. Najgrubsze rurki tolypammin zanotowano w przestrzeniach subdermalnych i większych kanałach ekshalacyjnych, gdzie również najczęściej występują duże agregaty złożone z wielu osobników. W cieńszych odcinkach kanałów inhalacyjnych i ekshalacyjnych tolypamminy są drobniejsze z licznymi rozdęciami i przewężeniami na rurkach odpowiadającymi kolejnym oczkom sieci spikul gąbki, przez które otwornice musiały przeciskać się w trakcie wzrostu.

Głównymi czynnikami determinującymi osiedlanie się *T. vagans* w gąbkach były: (a) dynamika cyrkulacji wody w gąbkach i (b) obecność w wodzie pompowanej przez gąbki odpowiedniej frakcji osadu terrygenicznego. Szybkość prądu inhalacyjnego gąbki określała maksymalną wielkość ziaren kwarcu, jakie mogły być wciągnięte do kanałów wodnych gąbki. Ziarna te były w sposób selektywny wykorzystywane przez *T. vagans* i inne otwornice aglutynujące osiedlone w gąbce.

Bardzo ograniczona sedymentacja terrygeniczna lub brak odpowiedniej dla tolypammin frakcji ziaren osadu ograniczał również zasiedlanie gąbek przez te otwornice. Stąd też, analiza częstości występowania *T. vagans* w powtarzających się w profilach oksfordu zespołach gąbkowych, może być dobrym wskaźnikiem tempa sedymentacji terrygenicznej w okresach rozwoju facji gąbkowych oksfordu.

Stowarzyszenie *T. vagans* z gąbkami krzemionkowymi ma charakter komensalizmu, w jego szczególnej odmianie określanej inkwilinizmem. Otwornica znajdowała schronienie w gąbce, a będąc pasywnym filtratorem korzystała jednocześnie z pokarmu napędzanego w jej kierunku przez aktywnego filtratora — gąbkę. Ponieważ gąbki i otwornice odżywiały się różnym pokarmem, brak konkurencji pokarmowej byłby dodatkowym argumentem potwierdzającym komensaliczny charakter stowarzyszenia obydwu partnerów. Przy masowym pojawianiu się tolypammin w gąbkach mogło dochodzić do częściowego pasożytnictwa przestrzennego polegającego na utrudnianiu cyrkulacji wody w gąbce. Ten typ konfliktu pomiędzy otwornicą i gąbką nie osiągnął jednak nigdy drastycznych rozmiarów. Przeciwnie, otwornice przechwytyując znaczną część grubszej frakcji osadu wpływającego z prądem inhalacyjnym do gąbek i układając ten osad w sposób uporządkowany w swoich testach, pomagały gąbkom uchronić się przed powstawaniem korków z osadu zatykających kanały wodne.

Tolypamminy wnikały przypuszczalnie do gąbek poprzez pory dermalne w postaci nagich, amebowatych, niedojrzałych schizontów bądź gamontów, które przyczepiały się pseudopodiami do ścian kanałów wodnych lub fragmentów spikul. Następnie szybko obudowywały osadem komorę prolokularną i wytwarzały długą, rurkowatą drugą komorę, przeciskającą się zwykle w kierunku doprądowym przez zawiłe systemy kanałów gąbki. *T. vagans* wykazuje doskonałą adaptację do życia w kanałach wodnych gąbek, wyrażającą się olbrzymią plastycznością morfologiczną rurek poszczególnych osobników. Rurki obumarłych *T. vagans* zasiedlane były często przez następne generacje tolypammin, świadcząc dobitnie o atrakcyjności środowiska, jakim było dla nich wnętrze gąbek.

Masowe pojawienie się *T. vagans* w gąbkach oksfordzkich jest zjawiskiem bez precedensu. Poza oksfordem bowiem, inkwilinizmu otwornic w gąbkach tak kopalnych jak dzisiejszych nie stwierdzono. Także występowanie przedstawicieli rodzaju *Tolypammina* Rhumbler jest poza facją gąbkową oksfordu rzadkie. Zjawisko to można tłumaczyć szczególnymi wymogami środowiskowymi tych otwornic. Jako formy bentoniczne, przyrastające do podłoża, tolypamminy wymagają twardego podłoża, przy jednoczesnym ruchu wody (= dopływ pokarmu) i niezbyt szybkiej akumulacji materiału, który byłby odpowiedni do nadbudowywania testów. Masowy rozwój gąbek krzemionkowych w oksfordzie, przy obecności odpowiedniego materiału terrygenicznego deponowanego w zbiorniku, otworzył dla *T. vagans* bardzo atrakcyjną niszę ekologiczną, szybko przez ten gatunek skolonizowaną.

Bardzo duża zmienność stwierdzona u *T. vagans* stowarzyszonej z gąbkami, mająca niewątpliwie charakter fenotypowy, każe powątpiewać o poprawności kryteriów diagnostycznych stosowanych dotychczas dla gatunków rodzaju *Tolypammina* Rhumbler. Większość tych gatunków, w tym także niektóre opisane z paleozoiku, należy przypuszczalnie uznać za młodsze synonimy *T. vagans*.

ЮЗЕФ КАЗЬМЕРЧАК

TOLYPAMMINA VAGANS (FORAMINIFERIDA) КАК КОММЕНСАЛ  
ОКСФОРДСКИХ КРЕМНЕВЫХ ГУБОК

## Резюме

Во многих оксфордских кремневых губках, распространенных на территории Краковско-Ченстоховской Юры и в юго-западной части Свентокшиских гор, встречаются агглютинированные однокамерные фораминиферы *Tolypammina vagans* (Brady). Детальный анализ морфологии и способа расположения этих простых фарминифер показал, что они обладали рядом приспособлений для обитания в каналах ирригационной системы живых губок.

Исследование фораминифер *T. vagans* в кремневых губках производилось путем последовательного травления губок в соляной кислоте. Так как трубки *T. vagans* сложены зернами терригенного кварца мелкоалевролитовой фракции, сцементированными кремнистым органическим веществом, они легко выщелачивались соляной кислотой из скелетов губок, как правило полностью обескремнелых.

Самые многочисленные скопления трубок *T. vagans* наблюдались в каналах приводящей системы и на поверхности губок, вблизи дермальных пор. В довольно большом количестве представлены толипаммины и в отводящих каналах, а также на стенках клоак. Несмотря на то, что так в приводящей, как и в отводящей системах толипаммины встречаются в тончайших субхоанальных каналах, то в хоаноцитовых камерах они полностью отсутствуют.

Отчетливо проявляется зависимость морфологии и величины трубок *T. vagans* от конфигурации и размеров ирригационных каналов губок, в которых они обитали. Самые крупные трубки толипаммин наблюдались в субдермальном пространстве и в больших отводящих каналах, в которых чаще всего присутствуют также крупные агрегаты, сложенные несколькими особями. В пережимах приводящих и отводящих каналов встречаются более мелкие толипаммины, характеризующиеся многочисленными раздувами и сужениями на трубках, соответствующими последовательным отверстиям в системе спикул губки, через которые фораминиферы проникали во время своего роста.

К основным факторам, определявшим поселение *T. vagans* в губках, относятся: а) динамика циркуляции воды в губках, б) наличие в воде, перекачиваемой губками, терригенного материала соответствующей фракции.

Величина частиц кварца, поступавшего в ирригационные каналы, зависела от силы приводящего водотока в губке. Эти частицы селективно использовались *T. vagans* и другими агглютинирующими фораминиферами, поселившись в губке.

В условиях ограниченного количества терригенного материала, осаждавшегося в губках, или при несоответствующей фракции этого материала, поселение

фораминифер в губках происходило тоже в ограниченном количестве. В связи с этим детальный анализ распространения *T. vagans* в сообществах губок, представленных в разрезах оксфорда, может дать критерии, характеризующие темпы терригенного осадконакопления в периодах развития губковых фаций оксфорда.

Симбиоз *T. vagans* с кремневыми губками имеет характер комменсализма в его особом проявлении, называемом инквилинизмом. Фораминиферы находили в губках безопасное убежище и, кроме того, будучи пассивным фильтратором, потребляли пищу, поставляемую в их направлении активным фильтратором — губкой. Фораминиферы и губки питались разным веществом и безконфликтность в этом отношении является дополнительным доказательством комменсального характера симбиоза этих организмов. Массовые поселения толипаммин в губках могли вызывать частично пространственный паразитизм, состоящий в замедлении циркуляции воды в губке. Однако, этот конфликт между фораминиферой и губкой не достигал никогда критического момента. Наоборот, фораминиферы перехватывали крупные минеральные частицы, попадавшие в губку с приводящим потоком, распределяли их закономерно в конструкциях своих трубок и, таким образом, предотвращали возможность образования скоплений, закупоривающих каналы ирригационной системы.

Толипаммины проникали в губки вероятно через дермальные поры в виде незрелых, амёбовидных шизонтов или гамонтов, которые прикреплялись ложноножками к стенкам водных каналов или к спикулам. После этого они быстрыми темпами окружали свой пролокулом минеральной стенкой и приступали к наращиванию длинной, трубкообразной второй камеры, проникавшей сквозь сложную систему каналов губки, как правило в направлении течения. *T. vagans* прекрасно приспосабливалась к образу жизни в водных каналах губок, что выражалось в исключительной пластичности формы трубок отдельных особей. Трубки отмирающих фораминифер *T. vagans* заселялись часто следующими генерациями толипаммин, что является выразительным доказательством весьма благоприятных условий для их обитания внутри губок.

Массовое появление *T. vagans* в оксфордских губках представляет исключительное явление, так как инквилинизм фораминифер в губках не наблюдался больше ни в ископаемых, ни в современных условиях. Кроме того, представители рода *Tolypammina* Rhumbler встречаются редко вне оксфордской губковой фации. Это объясняется, по-видимому, особенными требованиями этих фораминифер в отношении среды обитания. Как бентонные формы, толипаммины требуют для прикрепления прочного основания в условиях подвижных вод (привнос пищи) и довольно медленной аккумуляции материала пригодного для сооружения трубок. Массовое развитие кремневых губок в оксфорде и осадконакопление соответствующего терригенного материала в водоеме создавали весьма благоприятную экологическую среду для массового развития этого вида.

Очень сильная изменчивость, наблюдающаяся у *T. vagans*, обитающих в симбиозе с губками, ставит под сомнение достоверность диагностических критериев,

характеризующих виды рода *Tolypammina* Rhumbler. Большинство этих видов, в том числе и некоторые палеозойские виды, следует, по всей вероятности, рассматривать в качестве младших синонимов *T. vagans*.

## EXPLANATION OF PLATES

### Plate XIX

#### *Tolypammina vagans* (Brady)

- Fig. 1. Aggregate of tangled tests prepared out of subdermal space of ?*Sporadopyle* sp. (Z. Pal. F. XVI/1); Korzecko (Holy Cross Mts), Upper Oxfordian;  $\times 25$ .  
 Fig. 2. A bundle of tangled tests prepared out of incurrent canal of ?*Sporadopyle* sp. (Z. Pal. F. XVI/2); Korzecko (Holy Cross Mts), Upper Oxfordian;  $\times 25$ .  
 Fig. 3. A fragment of test encrusted over a large monaxone of siliceous sponge (from subdermal space) (Z. Pal. XIV/3); Bolmin (Holy Cross Mts), Upper Oxfordian;  $\times 25$ .  
 Fig. 4. Megalospheric proloculus with a fragment of second chamber from subdermal space of *Craticularia* sp. (Z. Pal. F. XVI/20); Bolmin (Holy Cross Mts), Upper Oxfordian;  $\times 40$ .

### Plate XX

#### *Tolypammina vagans* (Brady)

- Figs. 1—3. Three fragments of tests illustrating variability in thickness and shape of tubes within various canals of siliceous sponge water system: 1 — specimen from subchoanal canal (Z. Pal. F. XVI/4), 2 — specimen from incurrent canal (Z. Pal. F. XVI/5), 3 — specimen from subdermal space (Z. Pal. F. XIV/6); Bolmin (Holy Cross Mts), Upper Oxfordian; all figures  $\times 30$ .

### Plate XXI

#### *Tolypammina vagans* (Brady)

- Figs. 1—2. Two irregularly bent test fragments numerous narrowings and swellings (prepared out of subdermal spaces of *Ceasaria* sp.) (Z. Pal. F. XVI/7 and 8); Kłobuck (Częstochowa district), Middle Oxfordian;  $\times 20$ .  
 Figs. 3, 5—6. Various test fragments from incurrent (Figs 5—6) and excurrent canals (Fig. 3) of *Cypellia* sp. illustrating morphological variability versus canal shape of sponges (Z. Pal. F. XVI/9, 11 and 12); Kłobuck (Częstochowa district), Middle Oxfordian;  $\times 25$ .  
 Fig. 4. A test fragment with well visible narrowings corresponding to spaces in spiculae network (prepared out of inhalant zone of *Pachyascus* sp.) (Z. Pal. F. XVI/10); Krzeszowice — „Nowa Krystyna” mine (Cracov district), Middle Oxfordian;  $\times 40$ .

# Plate XXII

## *Tolypammina vagans* (Brady)

Figs 1—3. Three specimens with microspherical proloculi (Z. Pal. F. XVI/13, 14 and 15); Krzeszowice — „Nowa Krystyna” mine (Cracov district), Middle Oxfordian;  $\times 50$ .

Figs 4—8. Specimens with megalospherical proloculi (Z. Pal. F. XVI/16 to 20); Figs 4—5 — Krzeszowice — „Nowa Krystyna” mine (Cracov district), Figs 6—7 — Kłobuck (Częstochowa district) Middle Oxfordian; Fig. 8 — Bolmin (Holy Cross Mts), Upper Oxfordian;  $\times 50$ .

# Plate XXIII

## *Tolypammina vagans* (Brady)

(Stereoscan micrographs at 20 Kv)

Fig. 1. A fragment of broken second chamber. Smooth internal wall with indistinct growth bands (Z. Pal. F. XVI/23); Korzecko (Holy Cross Mts), Upper Oxfordian;  $\times 450$ .

Fig. 2. Enlarged fragment of external surface of the same tube;  $\times 1000$ .

Fig. 3. Enlarged fragment of internal surface of the same tube,  $\times 1000$ .

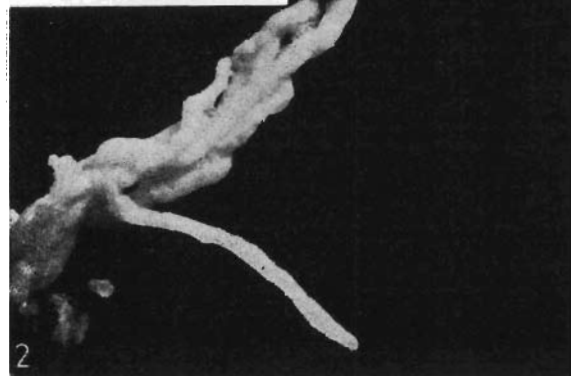
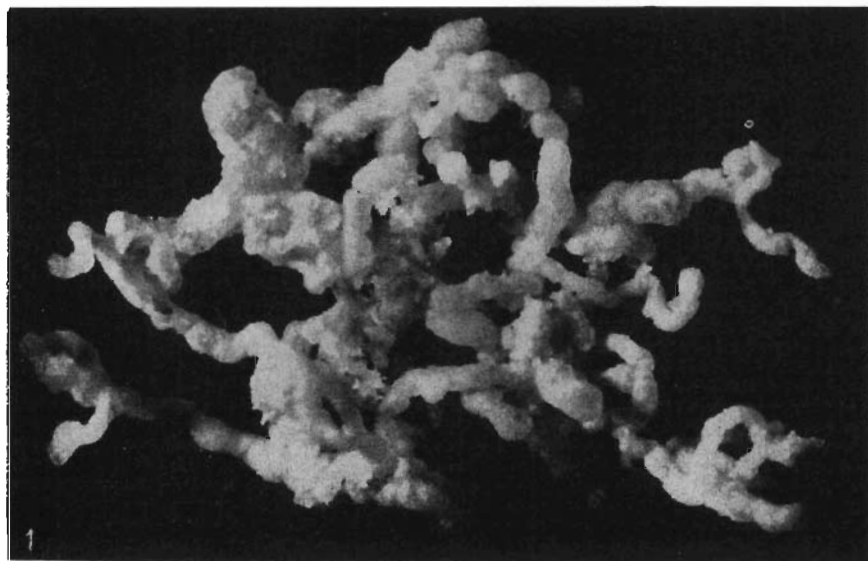
# Plate XXIV

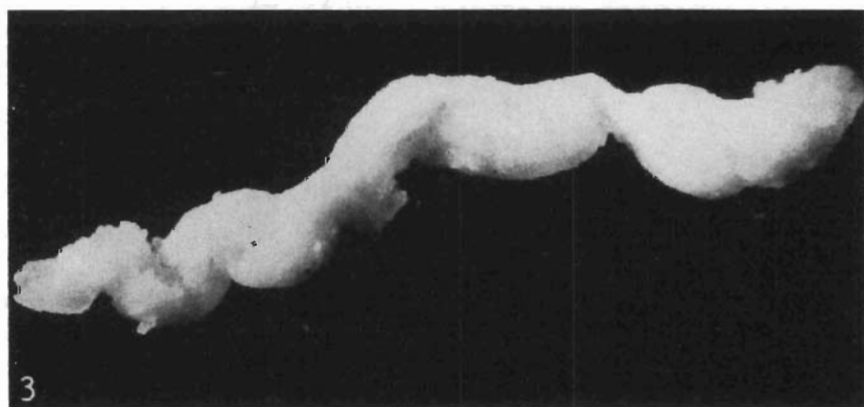
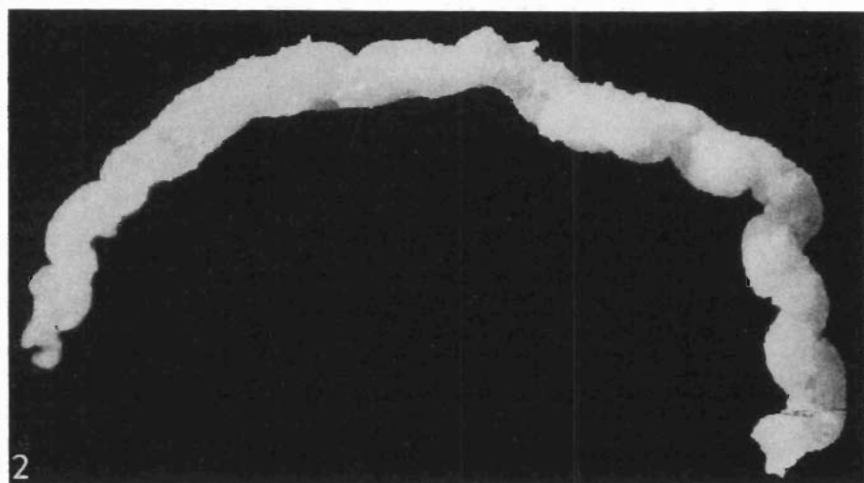
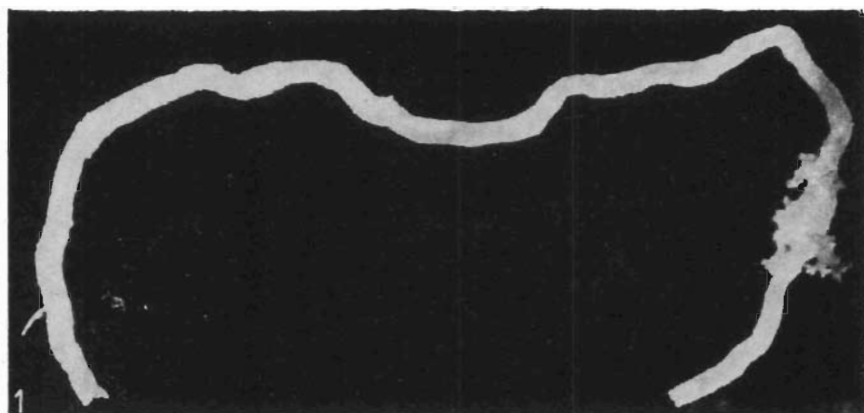
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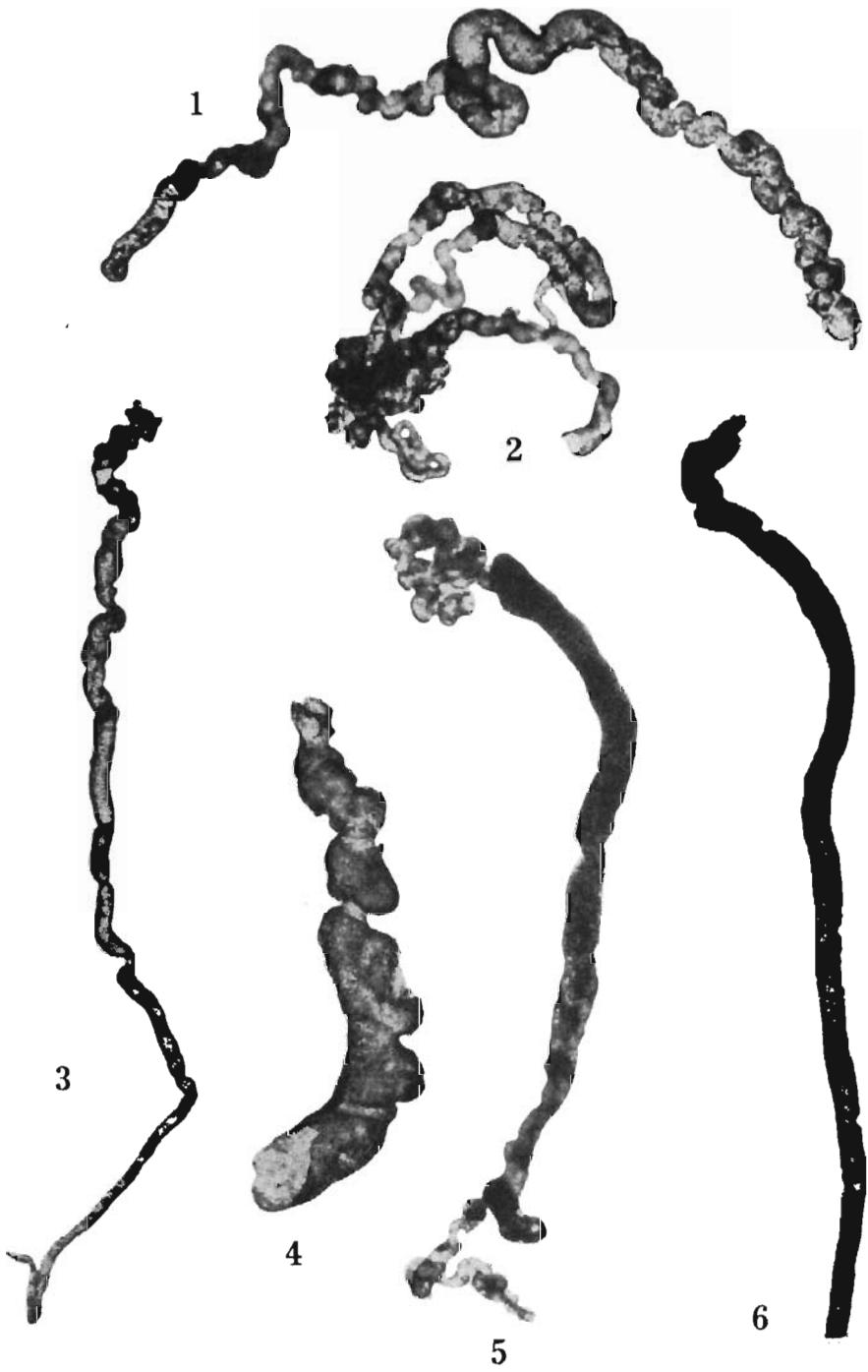
Fig. 1. A fragment of two generations of tests in “tube-in-tube” aggregation (prepared out of excurrent canal of *Feifelina* sp.) (Z. Pal. F. XVI/21); Krzeszowice — „Nowa Krystyna” mine (Cracov district), Middle Oxfordian;  $\times 100$ .

Fig. 2. A fragment of test bundle with two multi-generation “tube-in-tube” aggregations (prepared out of excurrent canal of *Feifelina* sp.) (Z. Pal. XVI/21); Krzeszowice — „Nowa Krystyna” mine (Cracov district), Middle Oxfordian;  $\times 80$ .

Fig. 3. A fragment of dermal surface of *Pachyascus* sp. slightly corroded by HCl. Radial incurrent canals and foraminifera tubes protruding from them are visible. (Z. Pal. F. XVI/22); Wrzosowa (suburb of Częstochowa), Middle Oxfordian;  $\times 5$ .









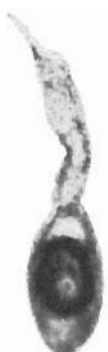
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