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Some aspects of the biology of fossil solid-branching demosponges, exemplified by *Reiswigia ramosa* gen. n., sp. n., from the Lower Oxfordian of Poland

ABSTRACT: A new demosponge, *Reiswigia ramosa* gen. n., sp. n., recognized in the Lower Oxfordian deposits of the Polish Jura Chain and analysed in terms of its taxonomy and biology, represents the solid-branching type of sponge morphology. The functional analysis of various sponge-morphological types permits a determination of their significance for current-energy analysis. The very nature of sponge dependence upon current energy consists in (*i*) resistance of sponges to destructive activities of currents, and (*ii*) relationship of both the diameter and angle of supply of sponges to currents. The evolutionary transition of solid-encrusting sponges into the solid-branching ones is discussed in the light of current-induced flow through sponges and life conditions in a boundary layer near the bottom surface.

INTRODUCTION

The investigated new fossil demosponge, *Reiswigia ramosa* gen. n., sp. n., whose biology appears instructive for the other demosponges, occurs commonly in the Lower Oxfordian deposits of the Polish Jura Chain. It was recorded in the localities Zalas, Nowa Krystyna, Wysoka, Ogrodzieniec, and Wrzosowa (Text-fig. 1) where the Lower Oxfordian is represented by interbedded limestones, marly limestones, and marls (*cf.* Różycki 1953, Malinowska 1963, Kutek & *al.* 1977). These deposits comprise an abundant and diverse assemblage of both siliceous (Zittel 1880, Siemiradzki 1913, Fibich 1975, Moczydłowska & Paruch-Kulczycka 1978) and calcareous sponges (Siemiradzki 1913, Hurcewicz 1975). Similar sponge assemblages are also well known to occur in the Upper Jurassic sponge facies of Svabia and Franconia, as well as France and Switzerland (Quenstedt 1878; Zittel 1878; Oppliger 1897, 1907, 1915, 1926; Kolb 1911; Schrammen 1937).

Fig. 1
Lower Oxfordian outcrops yielding the new demosponge, *Reiswigia ramosa* gen. n., sp. n., within the occurrence zone *(hachured)* of Upper Jurassic deposits in the Polish Jura Chain; inset shows position of the area in Poland

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TAXONOMY OF THE INVESTIGATED SPONGE

Class **Demospongea** Sollas, 1875

Order **Spirosclerophora** Reid, 1963

Suborder **Rhizomorina** Zittel, 1878

Family uncertain

Genus *REISWIGIA* gen. n.

Type species: **Reiswigia ramosa** sp. n.
Derivation of the name: in honor of Dr. H. M. Reiswig, Montreal, an outstanding student of modern sponges.
Species assigned: the type species only.

Diagnosis: Branching form lacking cloaca or distinct canal system, covered with cortex of the *"Deckschicht"*-type. Subcircular and irregular pores of 0.1 to 0.5 mm in diameter scattered at the surface. The skeleton composed of rhizoclones of 0.4 to 0.7 mm in size. The rhizoclones covered with sharply ended processes. Some spicules resemble tetraclones.

Remarks. — The morphology of *Reiswigia* gen. n. is unique for the Jurassic Rhizomorina. Some genera morphologically close to *Reiswigia* occur, however, among the Cretaceous Rhizomorina. The genus *Bolidium* Zittel, 1878, differs from *Reiswigia* in its rhizoclones being covered with peculiarly rounded lumps; moreover, it lacks any spicules resembling tetraclones. On the other hand, *Bolidium* is variable, mostly nodular in shape, whereas *Reiswigia* is always of the branching type.

The genus *Reiswigia* resembles also some genera of the family Astroboliidae de Laubenfels, 1955, the oscules of which however, are always surrounded by a stellate pattern of radiating grooves. The genus *Reiswigia* appears also close to some genera of the tetracladid family Astrocladiidae Schrammen, 1910; the resemblance is most conspicuous in the case of *Astrocladia* Zittel, 1878, and *Ingentilotus* de Laubenfels, 1955, comprising not only desmas of tetraclone type but also ones resembling rhizoclones. In the Astrocladiidae, however, the oscules are also always surrounded by a stellate pattern of grooves.

Reiswigia ramosa sp. n.
(Text-fig. 2 and Pls 1—3)

Holotype: specimen in Pl. 1, Fig. 1.
Type horizon: Cardioceras cordatum Zone, Lower Oxfordian.
Type locality: Zalas near Cracow, Cracow Upland (Polish Jura Chain, Central Poland).
Derivation of the name: Lat. *ramosa* — branched, after the branching structure of the species.
Material: some 150, mostly fragmented specimens (*see* Pl. 1, Figs 1—11); a thousand spicules preserved in their original (siliceous) form (*see* Pl. 3).
Diagnosis: as for the genus.

Description. — The form is branching in structure; the branches are circular, oval, or elliptic in cross section and range from 4 (in juveniles) to 20 mm in diameter with the modal value at some 10 mm; they are straight or slightly undulate (*see* reconstruction in Text-fig. 2) with the diameter more or less constant all over a branch but decreasing distally, that is upwards (Pl. 1, Fig. 3); the branch ends are rounded. There is a cortex (Pl. 1, Figs 2, 11) of the "*Deckschicht*"-type, attaining in adults a millimeter in thickness. Circular and irregular pores (Pl. 2) ranging from 0.1 to 0.5 mm in size are scattered at the surface. There is no cloaca or any distinct canal system. The spicules are arranged in such a way as to form some irregular free spaces visible in both transversal and longitudinal section (Pl. 1, Figs 2, 4, 10). Just below the cortex, the skeletal lattice is dense but it becomes more loose inwards. The skeleton consists of the rhizoclones, variable in both their shape (Pl. 3) and size (0.4 to 0.7 mm). Some spicules resemble tetraclones (Pl. 3, Figs 6, 11—12). The mode of spicule interconnection is typical of the Rhizomorina, *i.e.* the spicules do not fuse one with another. The mode of the sponge attachment to substrate is unknown, as no basal part was found (*see* Pl. 1, Fig. 1, and reconstruction in Text-fig. 2).

Remarks. — The Polish Oxfordian sponges attributed by Siemiradzki (1913) to *Jerea cracoviensis* Siemiradzki and *Bolospongia jurassica* Siemiradzki may actually represent the new species *Reiswigia ramosa;* any more detailed comparison appears, however, impossible because of the inadequate illustrations given by that author.

Occurrence. — Cardioceras cordatum Zone at Wysoka (*cf.* Łacwik 1970), Zalas (*cf.* Giżejewska & Wieczorek 1977), Nowa Krystyna (*cf.* Szulczewski 1968), Wrzosowa and Ogrodzieniec (Dr. B. A. Matyja, *pers. communication*); possibly also the lowermost part of the Perisphinctes plicatilis Zone at Nowa Krystyna and Ogrodzieniec (Dr. B. A. Matyja, *pers. communication*).

BIOLOGY AND ECOLOGY

ORGANIZATIONAL TYPE OF *REISWIGIA RAMOSA*

The sponge genus *Reiswigia* represents that morphological type called as the "solid-branching organizational type of Demospongiae architecture" (Reiswig 1975). This is indicated by the following characteristics of the investigated form: the lack of cloaca and apical oscule, the occurrence of numerous oscules all over the surface close to the ostia, and the branching structure. As a present-day morphological counterpart of *Reiswigia,* one may indicate for example a common and widely distributed species *Microciona prolifera* (Ellis & Solander).

PROBLEM OF CURRENT-INDUCED FLOW IN SPONGES

Vogel & Bretz (1972) and Vogel (1974, 1977, 1978) recently discovered a phenomenon of current-induced flow through sponges (*cf.* also

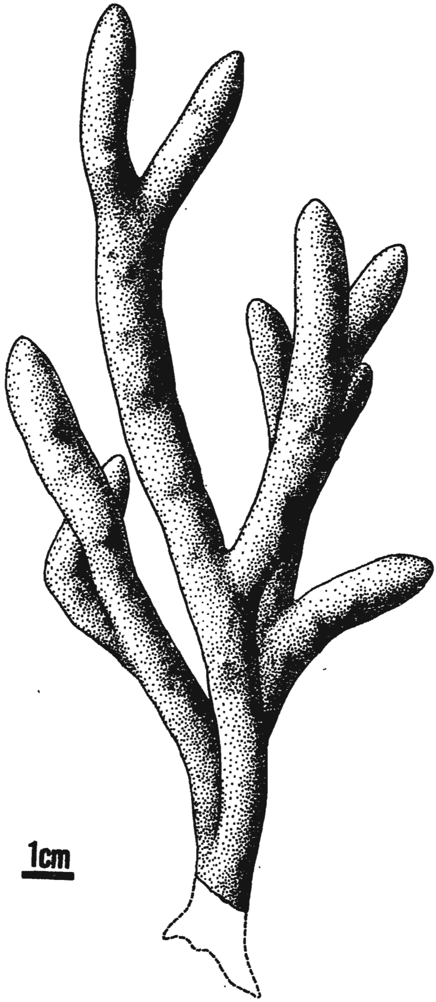

Fig. 2. Reconstruction of the new demosponge, *Reiswigia ramosa* gen. n., sp. n., from Lower Oxfordian deposits of the Polish Jura Chain; drawing taken by Dr. J. Dzik

Hill 1976), which Vogel (1977) claims to be widespread among sponges. Actually, however, a passive flow was found to occur in tubular sponges with apical oscules, round sponges, and flat ones (Vogel 1977); whereas such solid-branching forms as *Reiswigia ramosa* or *Microciona prolifera* may be inadapted to use an ambient current-induced flow. In fact, the mechanisms reported by Vogel & Bretz (1972) to induce such a flow through sponges with apical oscules or flat ones, appear unable to induce such a flow through solid-branching forms. Were this supposition true, one may draw the following conclusion.

The solid-branching sponges derive from the solid-encrusting forms (Reiswig 1975) adapted to exploit passive flows. Due to their evolutionary achievement of the erect mode of life, they lost ability to exploit current-induced flows; in exchange, however, they became able to exist in the main stream instead of having been restricted to a boundary layer close to the substrate where much weaker currents prevailed (*cf.* Wainwright & Koehl 1976). It was already shown by Bidder (1896) that the main stream some 10 to 20 cm above the bottom surface is evidently the most suitable habitat for sponge development.

SPONGES AS TURBULENCE INDICATORS

The terms *angle of supply* and *diameter of supply* introduced by Bidder (1923) for tubular sponges will be used herein. According to Bidder (1923) and Barrington (1967), the *angle of supply* is the angle between the intake and outflow currents of a sponge (see *A* in Text-fig. 3). Between the two currents a re-entrant vortex is established, the diameter of which was called by Bidder (1923) as the *diameter of supply* (see *D* in Text-fig. 4). Tubular sponges display either a large angle of supply, or a large diameter of supply, in both the cases the previously filtered water being hindered from re-entering the ostia (Bidder 1923). Thus, those sponges are able to efficiently separate the inhalant and exhalant streams without any dependence upon the external-water movement.

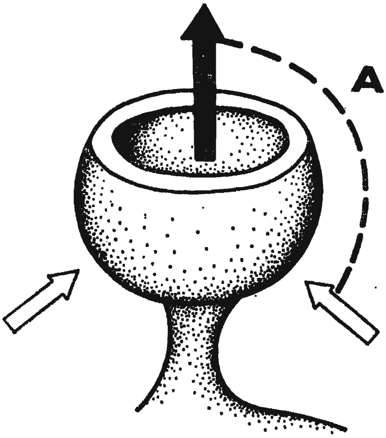

Fig. 3
Diagram illustrating inhalant *(blank arrows)* and exhalant *(haevy arrow)* streams of a tubular euryproct sponge; **A** — angle of supply. Adopted from Barrington (1967)

Following Bidder (1923), one may also apply the above terminology to solid sponges displaying numerous oscules distributed all over the surface. The ostia surrounding an oscule occur very closely to it and at the same plane. The angle of supply is therefore equal to 0, and the diameter of supply is very small for each oscule. Hence, solid sponges are unable to live in quiet-water habitats, as they would filter all the same water under such conditions. Their inhalant and exhalant streams can be efficiently separated only owing to a continuous movement of the surrounding water.

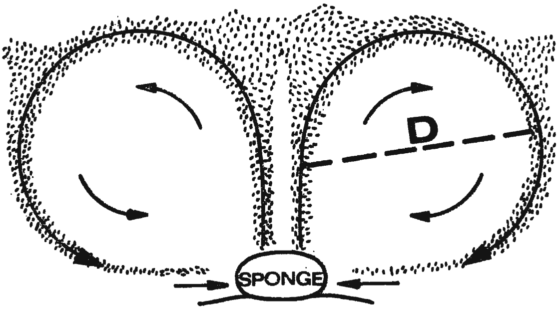

Fig. 4
Diagram illustrating inhalant and exhalant streams *(arrowed)* of a bath sponge; between the two streams the re-entrant vortex appears; **D** — diameter of supply. Adopted from Barrington (1967)

Consequently with the above statements, one may conclude that the investigated solid sponge *Reiswigia ramosa* was unable to assure itself an adequate separation of the inhalant and exhalant streams under quiet-water conditions, as its diameter of supply was too small. It was inadapted to live in even temporarily quiet water. On the other hand, it was unable to resist destructive activities of highly turbulent waters because of its erect mode of life. Similarly to the present-day species *Microciona prolifera* (cf. Reiswig 1975), the investigated sponge *R. ramosa* could flourish only under slow- and constant-current conditions; hence, its ocurence is indicative of such environments.

Previous authors, such as de Laubenfels (1957), Nestler (1961), Wagner (1963), Rützler (1965), Ulbrich (1974), and others, related the sponge shape to water turbulence, they considered encrusting or amorphous sponges as indicative of high turbulence, while regular sponges were regarded as typical of quiet water.

With the above discussion (*cf.* also Bidder 1923, Reiswig 1975) taken into account, this relationship of sponge shape to water turbulence can be investigated in more details. The relationship consists actually in (*i*) the ability of sponges to resist destructive activities of currents, and (*ii*) their diameter of supply and angle of supply. All these characteristics depend strongly upon the shape and organizational type of a sponge, as follows:

(*1*) Solid-encrusting sponges are adapted to live in highly turbulent waters, since they are very resistant to destruction by current energy. They are, however, unable to persist in very quiet waters, as they require a continuous water movement because of their very small diameter of supply.

(*2*) Solid-cylindrical and solid-branching sponges are endangered by overturning and burial under high-turbulence conditions (*cf.* Arndt 1928, Reiswig 1973), because of their erect mode of life. On the other hand, they require some water movement to live, as their diameter of supply is very small just as in solid-encrusting sponges. They are, however, able to live within somewhat quieter habitats than solid-encrusting sponges because their erect position places them in the main stream above the bottom surface; by this way, they exploit the strongest currents available in their environment.

(*3*) Tubular sponges are able to live in very quiet waters, as they can separate their inhalant and exhalant streams by themselves, without any dependence upon the external water movement. This is the case with both finger-like sponges with apical oscules (tubular stenoproct types of de Laubenfels 1955) and vase-shaped

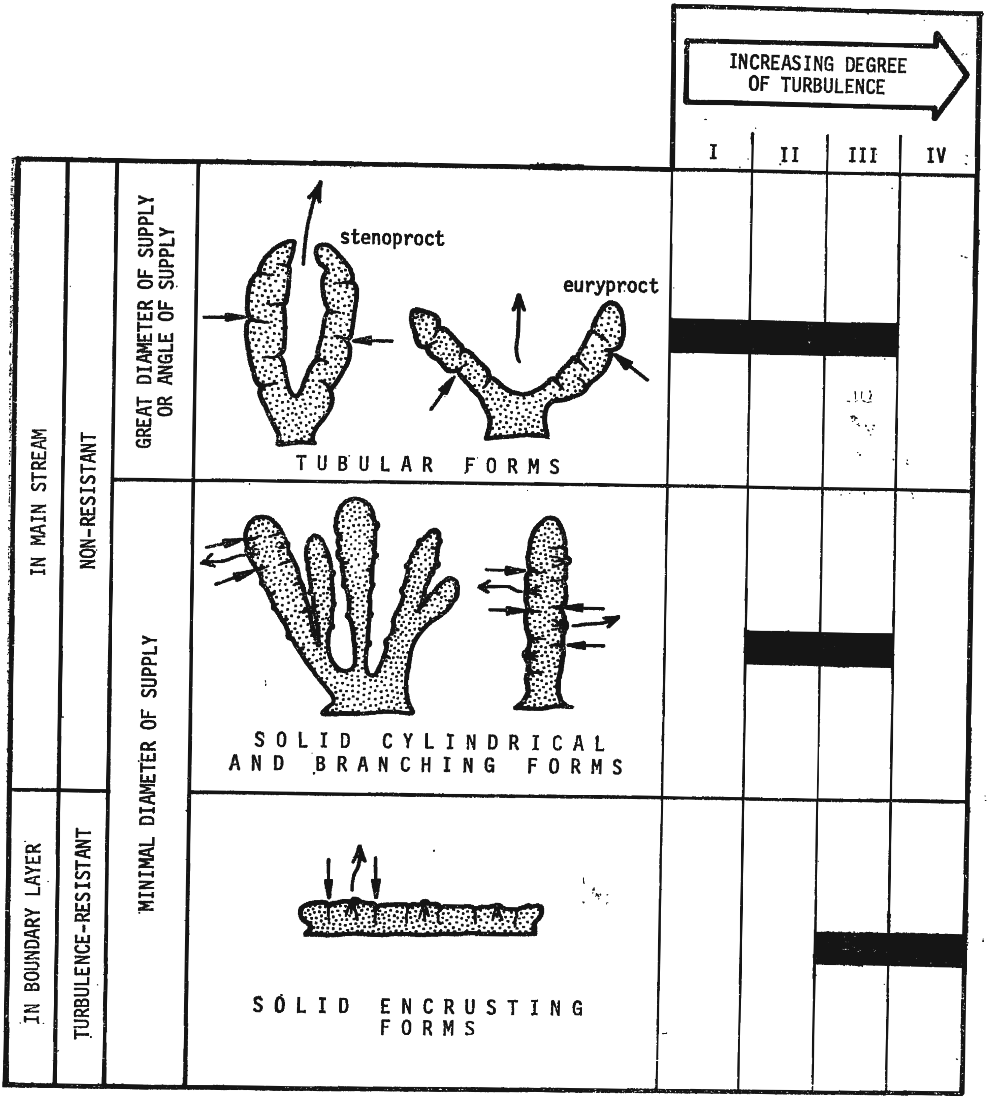

Fig. 5. Dependence of different organizational types of sponges upon the zones (*I—IV*) of diverse turbulence within a sedimentary basin domiciled by the sponges; arrows indicate the mode of water circulation in particular types of sponges; detailed explanation in the text

forms (tubular eury-and amblyproct types of de Laubenfels 1955). The latter sponges display a smaller diameter of supply than do the stenoproct ones, but their angle of supply is large making possible an efficient separation of intake and outflow currents (*cf.* Bidder 1923, Barrington 1967). Because of their erect mode of life, tubular sponges are strongly endangered by complete damage in highly-turbulent habitats.

On the basis of distributional pattern of the organizational types of sponges, one may therefore distinguish within a basin four distinct zones variable in water turbulence (Text-fig. 5). The zone *I* is characterized by very weak water circulation, temporarily stopped at all; it is settled exclusively by tubular sponges. Water turbulence is slightly higher in the zone *II*; the currents are there sufficiently strong to permit proliferation of those solid sponges which exploit the main stream. This zone is therefore characterized by occurrence of tubular with solid-cylindrical and solid-branching sponges. Water currents are still stronger in the zone *III*, assuring efficient separation of the inhalant and exhalant streams of solid-encrusting sponges living in the boundary layer; the currents are, nevertheless, too weak to damage non-resistant for turbulence erect sponges. Hence, all the sponge organizational types co-occur in this zone. The water is highly turbulent in the zone *IV* and hence, only solid-encrusting sponges are able to cope with the environment, while all the other organizational types would be easily overturned. The boundary between the zones *III* and *IV* is the sharpest one in this spectrum, as there is a rapid increase in environmental energy.

EVOLUTIONARY PROBLEMS

Individual variability within some flexible, both modern, and ancient sponge species depends on current energy among others (*cf.* e.g. Grant 1825, Storr 1976). For example, the present-day species *Halichondria panicea* (Pall.) is high-shaped in quiet habitats, whereas it is low in high-turbulence environments (de Laubenfels 1949, Vogel 1978). The Cretaceous species *Jereica polystoma* (Roemer) is high and slender in quiet-water deposits, while it is low and globular in turbulent-water sediments (Ulbrich 1974). The considerable height of those species in quiet waters reflects probably their drive to reach the main stream and thus, to exploit the strongest currents available in a given biotope.

One may claim that a similar shift took place during the evolutionary transition of solid-encrusting sponges into solid-branching ones. In fact, the organizational type of solid-branching sponges appears as the final effect of a successful settlement of low-turbulence habitats by sponges derived from some ancestors of solid-encrusting type.

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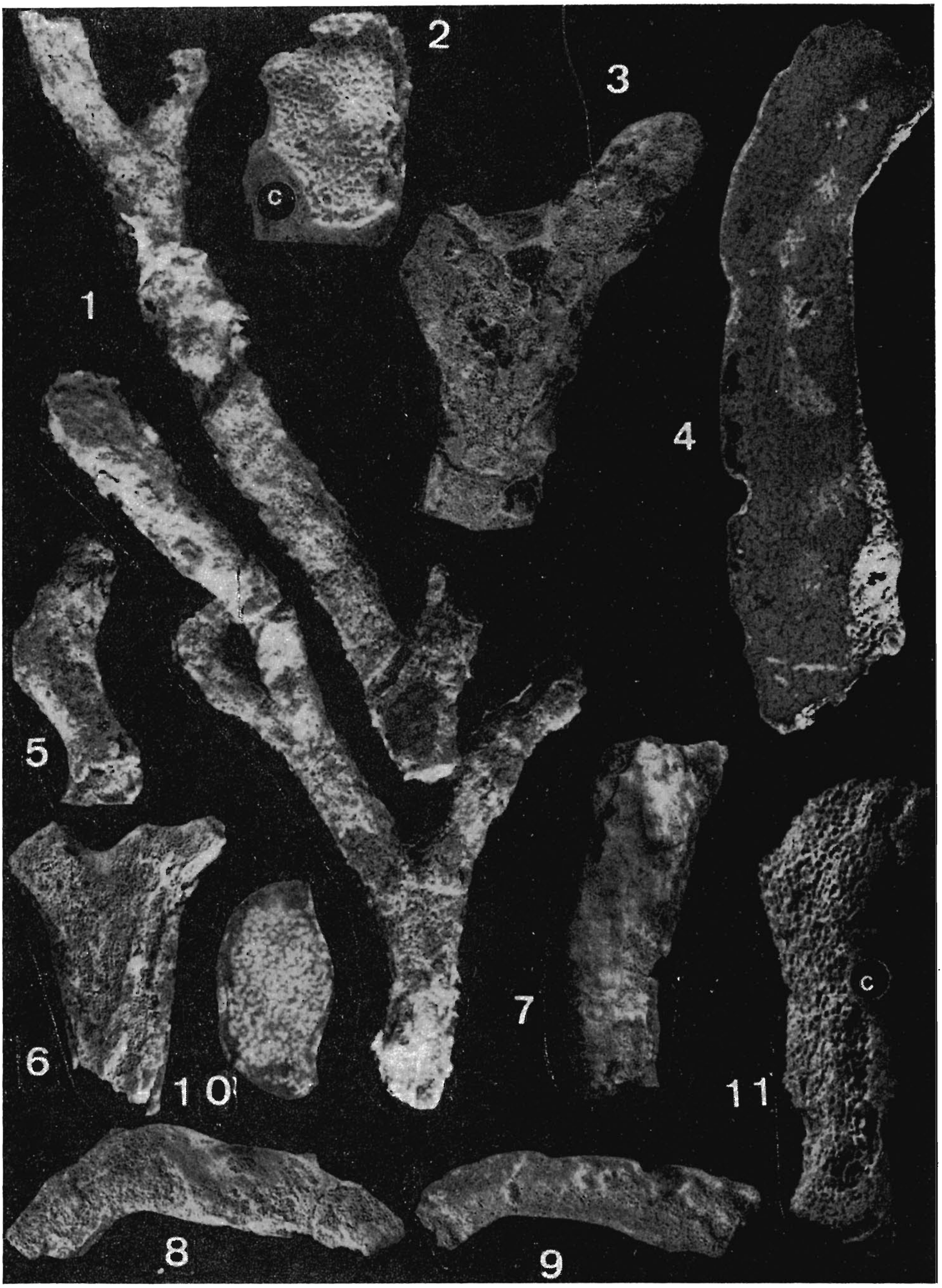
J. TRAMMER

CHARAKTERYSTYKA BIOLOGICZNA GĄBKI *REISWIGIA RAMOSA* GEN. N., SP. N. Z DOLNEGO OKSFORDU POLSKI

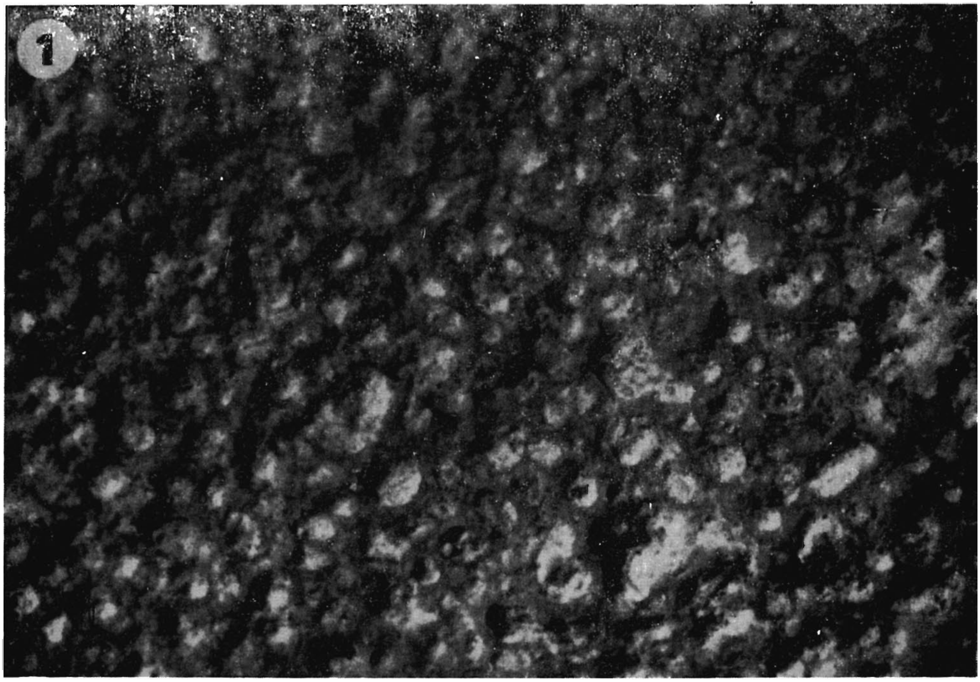
(Streszczenie)

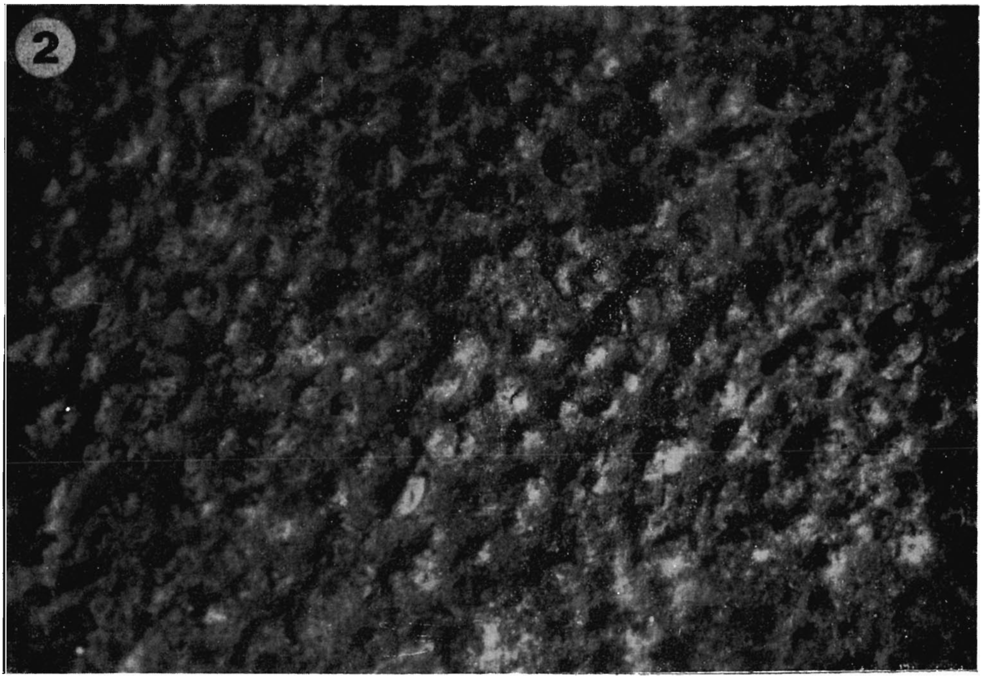
Przedmiotem pracy jest analiza gąbek reprezentujących nowy rodzaj i gatunek, *Reiswigia ramosa* gen. n., sp. n., a należących do gromady Demospongea Sollas, 1875. Gatunek ten (*patrz* fig. 2 oraz pl. 1—3) jest częsty w utworach dolnego oksfordu Jury Polskiej (*patrz* fig. 1), zwłaszcza w odsłonięciach Zalas, Nowa Krystyna i Ogrodzieniec. Wykazano, że gatunek ten reprezentuje typ budowy, który w literaturze dotyczącej gąbek współczesnych określa się jako *"solid branching"* (*por.* Reiswig 1975). Na podstawie analizy funkcjonalnej przeprowadzonej dla różnych typów gąbek, omówiono znaczenie tych typów jako wskaźników siły prądów (fig. 5). Zwrócono uwagę, że istota zależności gąbek od siły prądu polega (*1*) na ich odporności na niszczącą działalność prądu, oraz (*2*) jest uwarunkowana wielkością średnicy dopływu i kąta dopływu danej formy (*"diameter of supply"* i *"angle of supply"*; *por.* Bidder 1923, oraz fig. 3—4). Na tle problemu zewnętrznie wzbudzonego przepływu przez gąbki (*por.* Vogel & Bretz 1972) oraz zagadnienia życia w warstwie granicznej przepływu w pobliżu powierzchni dna, przedyskutowano proces ewolucyjnego przejścia gąbek *"solid encrusting"* w formy *solid branching"*.



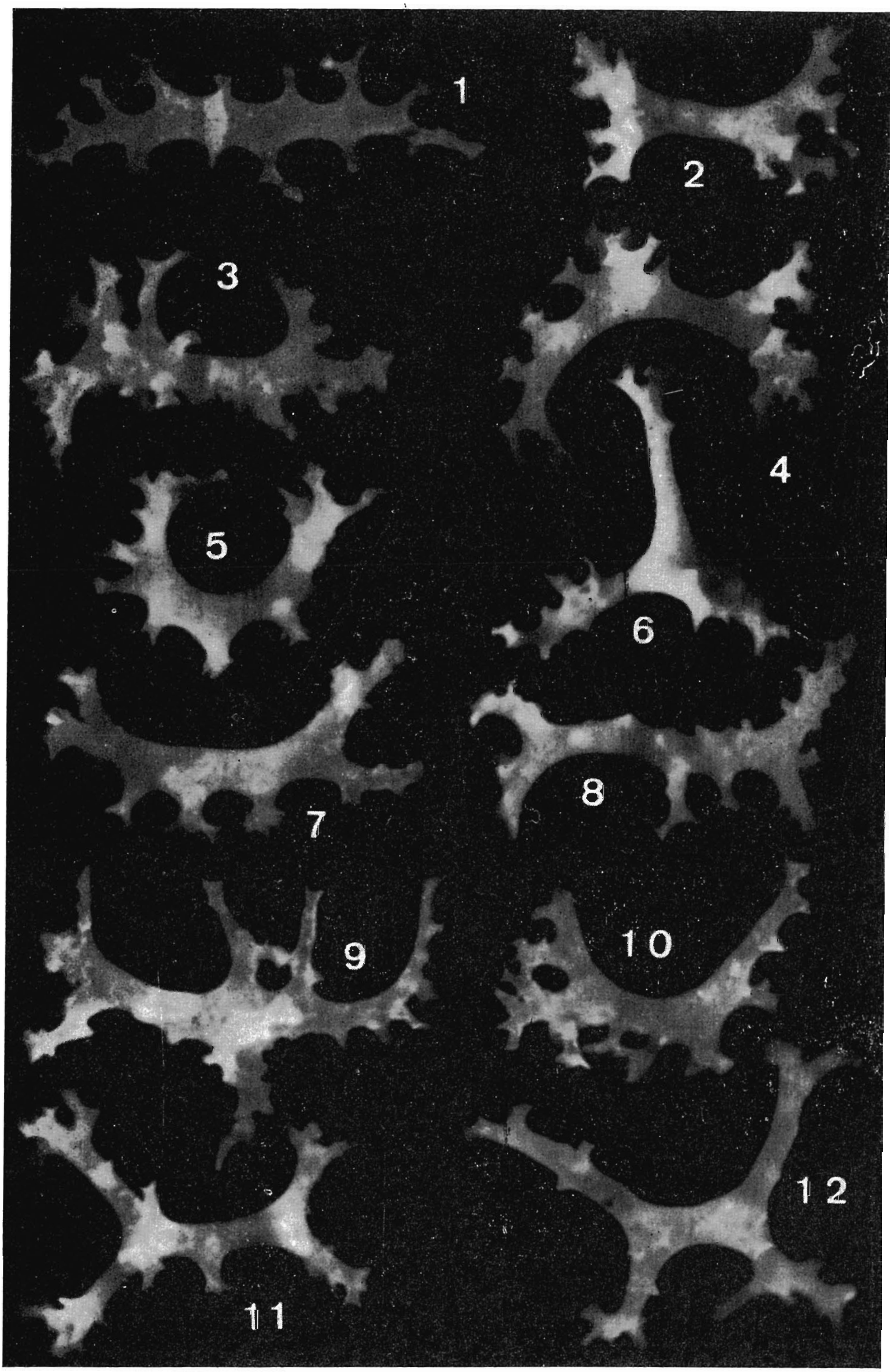
Demosponge *Reiswigia ramosa* gen. n., sp. n.; Lower Oxfordian, locality Zalas in the Polish Jura Chain

1 Holotype; almost complete specimen, nat. size; **2** Transverse section through the weathered branch; structure of the skeleton and the cortex (c) around it are visible (note a lack of the axial cloaca); × 2; **3** Distal fragment of the branch; nat. size; **4** Longitudinal section through the branch; internal structure of the skeleton is visible; polished cut, × 2; **5—9** Fragments of branches as the most common material to be found in the exposure; **10** Transverse section through the branch; internal structure of the skeleton is visible (note a lack of the axial cloaca); polished cut, × 2; **11** Weathered fragment of the branch; in places the cortex (c) is preserved, × 2





1—2 Pores on the cortex surface of the demosponge *Reiswigia ramosa* gen. n., sp. n.; magn. × 22, taken by L. Łuszczewska, M. Sc.



1—12 Spicules of the demosponge *Reiswigia ramosa* gen. n., sp. n.; most of the specimens are rhizoclones, except of those (Figs 6 and 11—12) resembling the tetraclones; all magn. × 100, taken by L. Łuszczewska, M. Sc.