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SCLEROSPONGE NATURE OF THE LOWER HAUTERIVIAN
„BRYOZOAN” *NEUROFORA PUSTULOSA* (ROEMER, 1839)
FROM WESTERN GERMANY

Abstract. — A former bryozoan *Neuropora pustulosa* (Roemer, 1839) from the Lower Hauterivian northwestern Germany is redescribed as a ceratoporellid sclerosponge. The systematic replacement of *N. pustulosa* is justified by the discovery of monaxonid spicules entrapped in its calcareous skeleton. The relation of *N. pustulosa* to recent and fossil sclerosponges is discussed. New order Muraniida including one new family Muraniidae based on the recently established genus *Murania* Kaźmierczak is here proposed.

INTRODUCTION

During preparation of a monograph of the Lower Hauterivian bryozoans from northwestern Germany by one of the authors (G. H.) holotypes of Roemer (1839) were found among which the type specimen of *Neuropora* (*recte: Chrysaora*) *pustulosa* was encountered. Preliminary morphological evaluation of this material (Hillmer, 1971, p. 97) has shown that its assignment to bryozoans of the family Heteroporidae Waters 1880 suggested by Bassler (1953) is doubtful. Detailed investigations of *Neuropora pustulosa* done by the first author (J. K.) based on large quantity of thin sections have shown the existence of vestigially preserved spicules in the skeleton of the type specimen and in some other specimens of the same species. These spicules are a critical proof of affinity of *N. pustulosa* to a very interesting group of modern sponges with mixed calcareous-siliceous skeleton, which was recently distinguished as a separate class Sclerospongiae Hartman & Goreau, 1971. Although the first representatives of recent sclerosponges were discovered rather early (Lister, 1900; Kirkpatrick, 1909; Hickson, 1911), a more detailed knowledge about that group was possible with the moment of discovery of numerous new forms in underwater caves on the Jamaica coast and islands of Micronesia (Hartman, 1969; Hartman & Goreau, 1966, 1970a, b, 1972). These discoveries renewed an old discussion initiated already by Kirkpatrick (1912a, b)

on possible sclerosponge affinities of some problematic fossils such as stromatoporoids, tabulates and chaetetids (Hartman & Goreau, 1966, 1970a, b, 1972; Stearn, 1972). Because no representatives of these fossil groups were found with traces of spiculation, the problem of their affinity to sclerosponges is still open. Farther discoveries of larger quantities of fossil sclerosponges would allow to make this question more precise.

MATERIAL

The material has been collected from the biogenic Lower Hauterivian marl, the so called "Pharetronenfazies" of northwestern Germany (Weigelt 1923, p. 42). The sediments and fauna within this relatively narrow area of the eastern region of the "Braunschweiger Bucht" are characteristic of the shallow sublittoral zone. Although not a single specimen is preserved in whole, all of them (the type specimen included) exhibit perfectly preserved details of external morphology such as, e.g., calicular depressions and stellate veinules. Elements of microscopic skeletal structure are not so well preserved which may be explained by destructive influence of replacement of primary aragonite by calcite, and by partial silification of some specimens. Thus traces of the primary microstructure of calcareous skeleton and spiculation are preserved only in few specimens. Spicules occur entirely as calcite pseudomorphs after primary opaline silica. Their pseudomorphic character was proved by negative result of solution of skeletal fragments containing spicules in a weak hydrochloric acid.

The material described here is stored under the following Catalog Nos in the collection of Geological-Palaeontological Institute of the University of Hamburg (SGPIH) and the collection of ROEMER—PELIZAEUS—Museum Hildesheim (SRPMHi).

Catalog No	Locality	number of thin sections	spicules
SRPMHi 15	Schöppenstedt	4	preserved
SGPIH 1708	Schandelah	1	preserved
SGPIH 1709	Schandelah	1	not preserved
SGPIH 1710	Schöppenstedt	2	not preserved
SGPIH 1711	Schandelah	3	not preserved
SGPIH 1712	Achim	2	preserved
SGPIH 1713	Schandelah	2	not preserved
SGPIH 1714	Schandelah	—	not sectioned
SGPIH 1715	Grube Hannöversche Treue b. Salzgitter	—	not sectioned
SGPIH 1716	Schöppenstedt	—	not sectioned
SGPIH 1717	Grube Hannöversche Treue b. Salzgitter	—	not sectioned
SGPIH 1718	Achim	—	not sectioned
SGPIH 1719	Achim	1	not preserved

SGPIH	1720	Schöppenstedt	1	preserved
SGPIH	1721	Schöppenstedt	1	not preserved
SGPIH	1722	Grube Hannöversche Treue b. Salzgitter	3	not preserved
SGPIH	1723	Schöppenstedt	3	preserved
SGPIH	1724	Achim	1	preserved
SGPIH	1725	Grube Hannöversche Treue b. Salzgitter	2	preserved
SGPIH	1726	Achim	—	not sectioned
SGPIH	1727	Grube Hannöversche Treue b. Salzgitter	—	not sectioned

DESCRIPTION

Class **Sclerospongiae** Hartman & Goreau, 1970
 Order **Ceratoporellida** Hartman & Goreau, 1972
 Family **Ceratoporellidae** Hartman & Goreau, 1972
 Genus *Neuropora* Bronn, 1825

Type species: Chrysaora spinosa Lamouroux, 1821; Upper Bathonian, Calvados, France.

Stratigraphic range: — Hettangian — Upper Cretaceous.

Discussion. — The genus *Neuropora* was recently revised by Walter (1969), who selected a neotype and prepared a list of synonyms of the type species *N. spinosa*. He also suggested that two Cretaceous genera: *Filicava* d'Orbigny and *Neuroporella* Hennig are probably younger synonyms of *Neuropora*. Brood (1971) in the subsequent attempt of revision of the systematic position of *Neuropora* referred it tentatively to Stromatoporoidea. He also regarded two other Upper Cretaceous genera as younger synonyms of *Neuropora* namely: *Neuroporella* Hennig and *Spinopora* Blainville. As the congeneric character of *Neuropora* and *Neuroporella* rises no doubts, the existence of thick mural spines in *Spinopora* justified in present authors' opinion, the validity of this genus. Very similar but much smaller mural spines occur in closely related to *Spinopora* genus *Acanthopora* d'Orbigny. In longitudinal sections of those fibro-lamellar spines a distinct accentuation of conically superposed growth lines is visible erroneously interpreted by some authors as a peculiar type of microstructure (e.g. "cone-in-cone" pattern of Brood, 1971, 1972), of important diagnostic value.

The authors are aware that proving sclerosponge nature of one species of *Neuropora* does not implicate sclerosponge affinity of all other forms described so far within this genus and related genera. A detailed microscopic revision of abundant museal materials should clarify this problem soon. Finding of spicules in type specimens is of particular importance

here. This would allow to define a revised diagnosis of *Neuropora*. It is quite obvious that shifting of the representatives of *Neuropora* to sclerosponges is connected with a change of terminology of those forms and a reevaluation of the functions of the particular skeletal elements. The terminology applied in this paper is that (with few exceptions) of Hartman (1969) and Hartman & Goreau (1970a, b, 1972) used by those authors in descriptions of recent sclerosponges.

Neuropora differs from modern genera of the family Ceratoporellidae by presence of radially distributed ridges, the so called stellate veinules (or "nervation" of other authors) on the surface of skeleton, and by bizonal structure of the rised parts of skeleton.

Neuropora pustulosa (Roemer, 1939)

(Pl. II—V; Text-fig. 1)

1839 *Chrysaora pustulosa* Roemer; F. A. Roemer, p. 13, Pl. 17, Fig. 18.

1971 *Neuropora (Chrysaora) pustulosa* Roemer; G. Hillmer, p. 97, Pl. 22, Figs 8—9.

Locus typicus: Schöppenstedt (northwestern Germany)

Stratum typicum: Lower Hauterivian (biogenic marl)

Revised diagnosis. — Sclerosponge with an encrusting-arborescent calcareous skeleton composed in branching parts of: (a) tubular axial zone, and (b) massive periaxial zone bearing on the surface calicular depressions with mean diameter 80 μm to 100 μm . Monaxonid spicules (? acanthostyles) entrapped in the calcareous skeleton with mean lengths of 128 μm to 141 μm , and mean widths — 6.6 μm to 7.6 μm .

Dimensions¹⁾ (in microns):

Calices:

distance from center to center	105—152
internal diameter	80—105
depth	150—185
thickness of wall	41—62

Axial tubules:

length	1200—1350
max. diameter	72—98
wall thickness	
(a) near axis	32—45
(b) near periaxial zone	54—72
thickness of tabules	13—15

Description. — Calcareous skeleton in its basal part encrusting, unilamellar, up to 3 mm thick. Encrusted objects are mainly pelecypod shells. From the basal part branches 1—7 mm thick grow dichotomously or irregularly giving the skeleton an arborescent appearance (Pl. II, Fig. 1a).

¹⁾ Only mean values are given.

In cross-section the branches are circular or oval. In some cases irregularly distributed mamelons up to 4 mm high appear on some branches and on the basal layer. These are most probably rudimentary branches (Pl. II, Fig. 2).

The surface of the skeleton is pitted with shallow calicles, circular, oval or irregularly polygonal in cross-section. Calicles are separated one from another by walls terminated at top with small knobs (Text-fig. 1). Characteristic stellate veinules with prominent tubercle in the middle part are irregularly scattered on skeleton surface. Near the central tubercle veinules are thick and protrude strongly over the level of calicles; more outwardly they gradually become thinner to join finally the intercalicular walls (Pl. II, Figs 1b and 5—6). Average spread of branches of those stellate structures is 2.5 mm, but the largest ones attain 4 mm whereas the smallest ones are hardly larger than central tubercle. Stellate veinules were probably formed in a result of a dense calcareous secretion beneath excurrent channels of the sponge near its oscular region. In this interpretation the central tubercle would correspond to a place in which osculum was situated. Various dimensions and shapes of stellate veinules as well as their irregular distribution on the surface of skeleton make them less diagnostic.

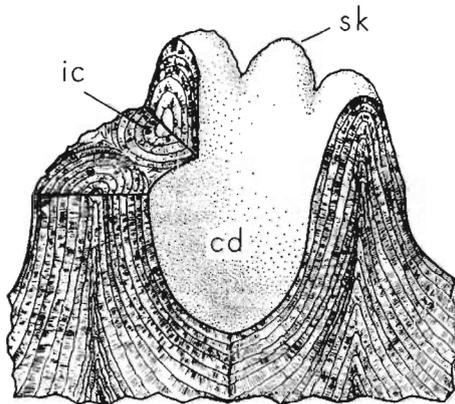


Fig. 1—*Neuropora pustulosa* (Roemer): diagrammatic sketch of a calice (without spicules); cd calicular depression, ic palisade of intramural columns, sk surficial knobs; approx. $\times 500$

The skeleton of the branches shows clearly bizonal structure. Its middle part, about a half of the section of branches is occupied by upward radiating bundles of narrow-conical tubules with irregularly polygonal less frequently circular cross-sections (Pl. III, Figs 1a, b; Pl. IV, Figs 1—3).

Tubular axial zone passes into a massive (dense) periaxial skeleton terminating on the sponge surface with calicular depressions (Pl. III,

Figs 1a, b; Pl. IV, Figs 1—3). In longitudinal section it may be observed that the periaxial zone is built of densely adhering columnal skeletal units perpendicular to the growth axis of the branches. The columns thin out on the surface of skeleton and form walls surrounding calicles.

Solid periaxial skeleton was formed as a result of filling the calicles with calcareous substance during growth of the sponge. This interpretation is supported by the presence of more or less abundant hemispheric empty spaces flat at top, scattered within the skeleton. These spaces were not filled during the growth of calicles (Pl. III, Fig. 1b; Pl. IV, Figs 1a, 3b). Hemispheric voids occur in some cases in a form of superposed rows, interspaced by a sort of thick tabules and are a good indicator of growth periodicity of the periaxial skeleton (Pl. IV, Figs 5a, b).

Primary microstructure of the calcareous skeleton is strongly changed (probably as a result of replacement of aragonite by calcite). Microscopically the skeletal substance has irregularly granular appearance. (Pl. V, Figs 1—3). On some better preserved specimens one can observe that the columns building the periaxial skeleton exhibit fibro-normal structure with cone-like overlapping growth lines. Such a type of skeletal microstructure is commonly known among Anthozoa (see Kato, 1963).

The monaxonid spicules of a style type (? acanthostyles) are always more or less corroded (Pl. III, Figs 2—5). They occur both in the axial and in the periaxial zone of the skeleton. These spicules are always calcite pseudomorphs after primary silica. In all cases spicules are entrapped in the calcareous skeleton and oriented with their longer axes in the growth direction of the skeleton.

Discussion. — *Neuropora pustulosa* is a second nondisputable fossil sclerosponge after recently discovered *Murania lefeldi* Kaźmierczak from the Lower Cretaceous of the Slovakian Tatra Mts (see Kaźmierczak, 1974). These two sclerosponges differ so much in structure of their calcareous skeleton and mode of distribution and shape of spicules that they should be classified to two different orders: *N. pustulosa* to Ceratoporellida Hartman & Goreau, and *Murania lefeldi* to the here proposed new order Muraniida (see Addendum, p. 449).

N. pustulosa differs from the recently revised (Walter, 1969) Jurassic *Neuropora spinosa* (Lamouroux) by its arborescent skeleton, bizonal structure of its branching parts, usually more massive skeleton and much smaller dimensions of calicles. A comparison with other species of *Neuropora* (e.g. *N. socialis* Dumortier or *N. mamillata* de Fromentel) is impossible because of inadequate description or poor preservation of specimens of the latter (see also Walter, 1969, pp. 181—182). A representative of *Acanthopora* d'Orbigny — *A. lamourouxi* Haime from the Lower and Middle Jurassic of France show very similar structure of calcareous skeleton to *N. pustulosa* (Walter, 1969, Pl. 18, Figs 9—10). As

in *N. pustulosa* branches of those forms show distinct bizonal structure and their periaxial zone is also very massive. The main difference is lack in *N. pustulosa* of intercalicular spines which are characteristic for the representatives of *Acanthopora*. It seems very probable that the spines of *Acanthopora* have developed from modified and enlarged intramural columns that occur in *N. pustulosa*. This might suggest close relationship of *Neuropora* and *Acanthopora* as well as *Spinopora* which has the thickest surficial spines. Such a conclusion must be first supported by the existence of spicules in the representatives of the two last mentioned genera.

Among contemporary sclerosponges *Ceratoporella nicholsoni* (Hickson) seems to be closest to *N. pustulosa* by similar although larger calicular depressions below which a very solid basic calcareous skeleton is deposited within which acanthostyle spicules are entrapped. Similarly as in *N. pustulosa*, *C. nicholsoni* shows thin vertical columns within intercalicular walls which are visible on skeleton surface as spines (see Hartman & Goreau, 1972, Fig. 7). The species described differs, however, distinctly from *C. nicholsoni* in its arborescent shape and by existence of stellate veinules on its surface. Counterparts of them in *C. nicholsoni* seem to be the radiating impressions of excurrent channels with mamelons at sites of oscules observable on surfaces of some skeletons (see Hartman & Goreau, 1970a, Fig. 6).

Considerable similarity of *N. pustulosa* to *C. nicholsoni* sufficiently proves classification of the described species into ceratoporellid sclerosponges. This group would have had a long history as it comes from the recent discovery of not yet named new form from the Triassic of the Dolomites (Cuif, 1973), the affinity of which with *Ceratoporella* despite of non preserved spicules, but only traces of their insertion, seems to be evident.

A discussion concerning the importance of *N. pustulosa* and other fossil sclerosponges for recent attempts to connect systematically the Stromatoporoidea with sclerosponges (Hartman & Goreau, 1966, 1970a, b, 1972) or generally with sponges (Stearn, 1972) will be done in a separate paper.

ADDENDUM

Order **Muraniida** ordo nov.

Fossil sclerosponges with a compound skeleton composed of a basal calcareous skeleton formed of juxtaposed fibrous columnal units and siliceous spicules (monaxons) embedded in their axial parts.

Range: Known at present only from the Lower Cretaceous (Aptian) Muran Limestone of the Sub-Tatric Succession of the Slovakian Tatra Mts.

Families: A single family, the Muraniidae fam. nov. with one genus (type-genus) *Murania* Kaźmierczak. For diagnosis of the family (= diagnosis of the type-genus) see Kaźmierczak, 1974.

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O SKLEROGĄBKOWEJ NATURZE „MSZYWIOLA” *NEUROFORA PUSTULOSA*
(ROEMER, 1839) Z DOLNEGO HOTERYWU ZACHODNICH NIEMIEC

Streszczenie

W pracy zrewidowana została, w oparciu o materiał typowy, pozycja systematyczna gatunku opisywanego dotychczas jako mszywiol *Neuropora pustulosa* z dolnego hoterywu północno-zachodnich Niemiec. Odkrycie u kilku okazów tego gatunku monaksonowych spikul (stylu) w obrębie szkieletu wapiennego jest dowodem przynależności tych form do rzadkiej grupy dzisiejszych gąbek, o mieszanym wapienno-krzemionkowym szkielecie, wydzielonych niedawno w nową gromadę Sclerospongiae Hartman & Goreau, 1970. *N. pustulosa* jest dopiero drugą, po *Murania lefeldi* Kaźmierczak, 1974, sklerogąbką kopalną z dobrze, chociaż pseudomorficznie, zachowanymi spikulami. Opisany gatunek wykazuje znaczne podobieństwo do dzisiejszego gatunku *Ceratoporella nicholsoni* (Hickson), typowego przedstawiciela rzędu Ceratoporellida Hartman & Goreau, 1972. Odkrycie spikul w szkielecie *N. pustulosa* każe przypuszczać, że sklerogąbkami są także inne gatunki rodzaju *Neuropora* Bronn pospolite w osadach jurajskich i kredowych, jak również formy zaliczane do bliskich *Neuropora* rodzajów: *Acanthopora* d'Orbigny i *Spinopora* Blainville. Zaproponowany został nowy rząd sklerogąbek Muraniida zawierający jedną nową rodzinę Muraniidae z rodzajem typowym *Murania* Kaźmierczak, 1974.

Odkrycie bezdyskusyjnych sklerogąbek kopalnych ma duże znaczenie dla rozpoczętej w ostatnich latach dyskusji (Hartman & Goreau, 1966, 1970a, b. 1972; Stearns, 1972) nad ewentualnymi związkami tych organizmów z takimi kopalnymi grupami jak stromatoporoidy, chetetydy czy niektóre tabulaty.

О СКЛЕРОГУБКОВОЙ ПРИРОДЕ „МШАНКИ” *NEUROPORA PUSTULOSA*
(ROEMER, 1839) ИЗ НИЖНЕГО ГОТЕРИВА ЗАПАДНОЙ ГЕРМАНИИ

Резюме

В работе пересматривается на основании типового материала систематическая принадлежность мшанки *Neuropora pustulosa* из нижнего готерива северо-западной Германии. Наблюдавшиеся у некоторых особей этого вида монактиновые спикулы (стили) в известковом скелете являются показателем принадлежности этих форм к редкой группе современных губок со смешанным известково-кремнистым скелетом, выделенных недавно в виде нового класса *Sclerospongiae* Hartman & Goreau, 1970. *N. pustulosa* представляет вторую, после *Murania lefeldi* Kaźmierczak, 1974, склерогубку с хорошо, хотя и псевдоморфически, сохраненными спикулами. Описанный вид проявляет большое сходство с современным видом *Ceratoporella nicholsoni* (Hickson) — типичным представителем отряда *Ceratoporellida* Hartman & Goreau, 1972. Выявление спикул в скелете *N. pustulosa* позволяет предполагать, что к склерогубкам относятся и другие виды рода *Neuropora* Bronn, распространенные в юрских и меловых отложениях, как и формы, относящиеся к близким *Neuropora* родам *Acanthopora* d'Orbigny и *Spinopora* Blainville. Предлагается новый отряд склерогубок *Muraniida*, включающий одно новое семейство *Muraniidae* с типичным родом *Murania* Kaźmierczak, 1974.

Открытие достоверных ископаемых склерогубок имеет важное значение для обсуждающейся в последнее время проблемы (Hartman & Goreau, 1966, 1970a, 1972; Stearn, 1972) связи этих организмов с такими ископаемыми группами как строматопороидеи, хететиды или некоторые табуляты.

EXPLANATION OF PLATES

Plate II

Neuropora pustulosa (Roemer)

Figs 1a-b. General view: (a) of the type specimen (SRPMH 15), $\times 3$; (b) enlarged surface of the same specimen densely pitted with calicular depressions and ornamented with stellate veinules, $\times 12$; Schöppenstedt.

Fig. 2. Basal part of a skeleton with irregularly distributed prominent mamelons in top view (SHPIH 1713), locality Schandelah, $\times 1.5$.

- Figs 3—4. Two fragments of arborescent skeletons in side view (SGPIH 1714 and SGPIH 1726), localities Schandelah and Achim; $\times 1.5$.
- Fig. 5. A fragment of skeletal surface with calicles and richly branching thick stellate veinules (SGPIH 1727), locality Grube Hannöversche Treue; $\times 25$.
- Fig. 6. An example of an indistinct stellate veinule with large central knob (SGPIH 1726), locality Achim; $\times 25$.

Plate III

Neuropora pustulosa (Roemer)

- Figs 1a-b. (a) Transversal and (b) longitudinal axial sections through a skeletal branch of the type specimen (SRPMHi 15) showing bizonal structure of the skeleton and shallow callicular depressions on the surface; Schöppenstedt; $\times 16$.
- Figs 2—5. Examples of monaxonid spicules (? acanthostyles): 2—SGPIH 1712, locality Achim; $\times 500$; 3 and 5—SGPIH 1724, locality Achim; $\times 450$; 4—SGPIH 1723, locality Schöppenstedt; $\times 450$.

Plate IV

Neuropora pustulosa (Roemer)

- Fig. 1. Longitudinal axial section through a dichotomously ramified skeletal branch; rare and irregularly distributed empty spaces in the massive periaxial zone are clearly visible (SGPIH 1720), locality Schöppenstedt; $\times 12$.
- Fig. 2. A fragment of axial section of a skeletal branch with very massive periaxial zone (SGPIH 1721), locality Schöppenstedt; $\times 12$.
- Figs 3a-b. Longitudinal axial sections through a fragment of a skeletal branch showing rows of superposed hemisphaerical spaces within the periaxial zone (SGPIH 1724), locality Achim; a— $\times 12$, b— $\times 30$.
- Fig. 4. Transversal section of a skeletal branch; very massive periaxial skeleton and axial tubes are clearly visible (SGPIH 1722), locality Grube Hannöversche Treue; $\times 12$.

Plate V

Neuropora pustulosa (Roemer)

- Fig. 1. Longitudinal axial section through a skeletal branch showing tabules crossing the axial tubes; hemisphaerical spaces within the periaxial skeleton are also visible (SGPIH 1724), locality Achim; $\times 50$.
- Fig. 2. Longitudinal axial section through a skeletal branch of the type specimen (SRPMHi 15) showing tabules crossing some axial tubes; locality Schöppenstedt; $\times 50$.
- Figs 3a-b. Transversal sections through (a) periaxial zone showing granular character of the mural calareous substance and centripetally infilled calicular depressions, and (b) axial tubes showing their coarse granular structure (SGPIH 1723), locality Schöppenstedt; $\times 150$.

