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COLONY STRUCTURE AND SYSTEMATIC ASSIGNMENT OF  
*CLADOCHONUS TENUICOLLIS* McCOY, 1847 (HYDROIDEA)

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Colony and corallite structure of *Cladochonus tenuicollis* such as: the lack of tabulae and septal apparatus, presence of diaphragms between corallites, as well as the sympodial mode of budding, are different than in tabulates. These features make *Cladochonus* close to Hydroidea. Analysis of structure of the Carboniferous species *C. parasitica* Vassiljuk proves that it is a junior synonym of *C. tenuicollis* McCoy.

**Key words:** Hydroidea, systematics, colony structure, corallite structure.

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INTRODUCTION

A topotype material of *Cladochonus parasitica* Vassiljuk, 1947 from the Bashkhirian Stage ( $C_2^1$ , Carboniferous) of the Donetz Basin (USSR) has been investigated, which constitutes an element of a poor fauna composed mostly of the tabulates and chaetetids (Vassiljuk 1974). An analysis by the Rg diaphractometr showed that the skeleton of these specimens is composed of low-Mg-calcite; a small amount of dispersed silica (1—2%) is responsible for their good preservation. The corallite structure was studied by means of serial sections.

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of Sciences, Warszawa) made the photographs. The material is housed at the Geological Museum, Donetsk Polytechnical Institute, Donetsk (abbreviated as GMDPI). The SEM photographs were taken at the Laboratory for the Electron Microscopy, Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warszawa.

#### SYSTEMATIC POSITION OF *CLADOCHONUS* McCOY, 1847

The genus *Cladochonus* has been erected by McCoy and described by him as a form close to the genus *Aulopora* (Tabulata) but differing from the latter in: ascending, non-encrusting colonies, thick-walled corallites and their zigzag arrangement, and the angular, regular mode of budding. The type species, *C. tenuicollis* McCoy, 1847, comes from the Lower Carboniferous Dunvegan Shales, New South Wales, Australia. Hill and Smyth (1938) made the most detailed studies of colony structure within *Cladochonus* basing on *C. tenuicollis* of Australia and *C. crassus* of the Carboniferous of Great Britain. They noticed the presence of the diaphragms between corallites as well as the lack of tabulae and of the septal apparatus, which, in their opinion, was the strong argument against the assignment of *Cladochonus* to the Tabulata. Hill and Smyth (1938) stated that *Cladochonus* "belongs to a suborder of the Zoantharia distinct from the Tabulata, Rugosa and the Hexacoralla". Sokolov (1959) erected a new family Cladochonidae within the order Auloporida to include *Cladochonus* and *Bainbridgia* Ball, 1933. The latter genus was described in detail by Ball (1933) and by Ball and Grove (1940); it was compared by these authors with the auloporids. These authors did not determine, however, the systematic position of *Bainbridgia*, but suggested its possible relationship with the Bryozoa or Hydrozoa, emphasizing its most close resemblance to *Cladochonus*. In 1963 Sokolov assigned *Cladochonus* and *Bainbridgia* (as well as *Amniopora* Sokolov, 1955) to the Moniloporidae, the family erected by Grabau (1899) for *Monilopora* Nicholson et Etheridge, 1879. According to Girty (1925) and Hill and Smyth (1938), *Monilopora* was a junior synonym of *Cladochonus*. Sokolov (1955) noted that *Cladochonus* differs from all other auloporids in the mode of budding and in the shape of calices.

The *Cladochonus* species have been described from strata ranging from the Devonian to Permian. It seems that the zigzag shape of colony, resulting from the alternation of corallites, is overestimated as the generic criterion. This is why representatives of other genera, which have quite different types of structure, are assigned to *Cladochonus*. The undoubted *Cladochonus* is known from the Carboniferous; the generic assignment of the species described so far as *Cladochonus*, especially of the Devonian ones, should be revised. For example, a colony described as

a representative of *Cladochonus* by Laub (1972) from the Devonian of the New York State exhibits all the characters of *Grabaulites* Sokolov, 1962 (= *Ceratopora* Grabau, 1899). The typical features of *Grabaulites* are: the presence of vesicular tabulae and of the septa sunk in the wall; the ends of septa protrude toward corallite cavity in the form of rows of spines; budding in *Grabaulites* is of the same type as in *Aulopora* (Stasińska 1974).

Basing on the wall microstructure in a Carboniferous representative of *Cladochonus* from Algeria and its comparison with the wall structure in some Permian species, Lafuste (1979) stated that these species lack a characteristic internal layer; he was of the opinion that these species may represent genera other than *Cladochonus*. The differences between *Cladochonus* and the morphologically closest group of Tabulata — the Auloporida, lie in a different structure of the corallites, colonies and in a different wall microstructure. In the Auloporida colonies, as in other Tabulata, the corallites have transverse elements — tabulae; in the living colonies, the polyps rested on the last tabula, the remaining portion of corallite being dead. The septal apparatus may be more or less developed in the Auloporida; microstructure of the wall investigated by the present author (Stasińska 1974) is radial (in: *Aulopora serpens minor*, *A. serpens maior*, *A. liniformis*, *A. lataeformis*, *A. lata*, *Mastopora spicata*) or concentric (in representatives of *Grabaulites*). The contact between corallites broke in the Auloporida after a daughter corallite had budded.

There are no horizontal elements (tabulae) in *Cladochonus* and the septal apparatus is lacking as well. The corallites which appear successively are joint with the parental corallites by a narrow channel running from the place of budding and broadening distally toward the corallite cavity. The contact between the corallites of the successive generations does not break. At the budding spot, there is a diaphragm present, the structure peculiar to *Cladochonus*, which separates parental corallite from the daughter corallite. The diaphragm is pierced by some *canaliculi* which joint the calicular cavity of the parental corallite and a central canal of the daughter corallite. This structure suggests that an individual consisted of a polyp and peduncle similarly as it is in the hydrozoan polyp. The sympodial, alternating mode of the colony growth in *Cladochonus*, resulting in the zigzag shape of a colony, is unknown in the Tabulata, occurring however in the recent Hydrozoa. Occurrence of the pillow-like structures in some calices may be interpreted as a manifestation of the polymorphism. The wall is composed of the proper wall, which has a fibrous radial structure and of the epitheca in the Tabulata, while of the three layers in *Cladochonus* (Lafuste 1979): the fibrous external layer, lamellar medial layer and the internal layer consisting of peculiar elongated rods (*grindulae*) the surface of which is covered by grooves and sharp spines. In the Lafuste's opinion, that kind of structure is peculiar to *Cladochonus* being unknown in the Anthozoa.

The structure of *Cladochonus* skeleton, as well as the relations between the individuals within a colony, do not allow to maintain that genus within Anthozoa. It should be added here that some Silurian organisms, having the chitinous skeletons provided with the very peculiar diaphragms unknown in the recent organisms, were interpreted by Kozłowski (1959) as representatives of an extinct group of the Hydroidea. According to the present author's opinion, peculiarities of the *Cladochonus* structure make also that genus most close to the Hydroidea.

#### SYSTEMATIC PART

##### Subclass **Hydroidea**

Family **Cladochonidae** Hill, 1942

Genus *Cladochonus* McCoy, 1847

*Cladochonus tenuicollis* McCoy, 1847

(pls 19, 20, 21, 22)

1847. *Cladochonus tenuicollis* McCoy: 227

1938. *Cladochonus tenuicollis* McCoy; Hill and Smyth: 128, pls. 22, 23

1974. *Cladochonus parasitica* Vassiljuk: 63, pl. 11: 1—18.

*Revised diagnosis.*—Colony in form of ascending branches diverging from a ring; budding sympodial; hydrocorallites pipe-like, with broad calices, alternating, what results in zigzag shape of a colony; average corallite length 10 mm, width 1.5—2.0 mm, average calice diameter 3 mm; wall three-layered, internal layer built of *grundulae*, wall thickness up to 0.6 mm.

*Material.*—Thirty fragments of the *C. parasitica* Vassiljuk topotype colonies (GMDPI 15/101) including two stages described earlier as "*Monilopora*" Nicholson and Etheridge, 1879 and *Cladochonus* McCoy, 1847.

*Description.*—Preserved fragments of the branched part of a colony attain 2 cm in height. The hydrocorallites are pipe-like, alternatively arranged what results in the zigzag shape of the colony (pl. 19: 1) The parental and daughter corallites are separated by the oval diaphragms (pl. 19: 2, 3) built of the ribs between which occur rows of the oval openings (pl. 19: 4). Two round openings larger than the others are placed side by side in the central part of the diaphragm. The budding place occurs on the dorsal side of the calice. In the longitudinal section through the parental calice and the budding daughter calice, the calicinal cavity is visible which bifurcates: each of the two ramifications passes through one of the two large central openings in the diaphragm to join each other behind the diaphragm, forming the calicinal cavity of the daughter hydrocorallite (pl. 19: 5; 20: 6). Such is the mode of the contact between calices of all the individuals within a colony. The pillow-like convexities occur in some calices, which are located on the floor of calice close to its edge (pl. 21: 1, 2). They are built of the vesicular tissue which contains some oval structures (pl. 20: 2—4) and could be due to the polymorphism connected with the sexual reproduction. The septal structures and tabulae lack. Wall has three-layered structure typical of *Cladochonus* (comp. p. 61).

*Remarks.*—*Cladochonus parasitica* Vassiljuk, 1974 is here considered as the junior synonym of *C. tenuicollis* McCoy, 1847 because it exhibits the same size and structure and supposedly it had the same life habit.

*Occurrence.*—Australia, New South Wales: Lower Carboniferous, Dunvegan Shales; USSR, Donetz Basin: Bashkhirian (C<sub>1</sub><sup>1</sup>).

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ANNA STASIŃSKA

BUDOWA KOLONII I PRZYNALEŻNOŚĆ SYSTEMATYCZNA CLADOCHONUS  
TENUICOLLIS MCCOY, 1847

## Streszczenie

Praca niniejsza przynosi rezultaty badań gatunku typowego rodzaju *Cladochonus* — *C. tenuicollis* McCoy, 1847, który był dotychczas zaliczany do koralowców Tabulata. Materiał do badań pochodził z piętra baszkirskiego (C<sub>2</sub><sup>1</sup>) karbonu basenu donieckiego. Brak tabul i aparatu septalnego, obecność diafragm między koralitami, jak również sympodialny typ pączkowania, mikrostruktura wewnętrznej warstwy ściany, obecność w niektórych kielichach poduszczkowatych utworów (wskazująca

na polimorfizm) nie pozwalają na zaliczenie *Cladochonus* ani do Tabulata ani do żadnych innych Anthozoa. Wymienione cechy zbliżają natomiast ten rodzaj do Hydroidea. Analiza topotypowego materiału *C. parasitica* Vassiljuk, 1974, przeprowadzona w niniejszej pracy, udowodniła że powyższa nazwa gatunkowa jest młodszym synonimem *C. tenuicollis* McCoy.

## EXPLANATION OF THE PLATES 19—22

## Plate 19

*Cladochonus tenuicollis* McCoy

1. External view of colony,  $\times 10$  D. P. I. 15/102.
2. Fragment of corallite; diaphragm visible,  $\times 6.5$ . D. P. I. 15/103.
3. Fragment of colony; visible: diaphragm, transversely striated epitheca, longitudinal ribs,  $\times 6.5$ . D. P. I. 15/104.
4. Longitudinal section through diaphragm with two openings in medial part and rows of oval openings between ribs,  $\times 22$ , D. P. I. 15/105.
5. Cross-section of calice at the diaphragm; visible: epitheca and two layers of wall, as well as part of calicular cavity of parent corallite invading diaphragm,  $\times 23$ . D. P. I. 15/106.

## Plate 20

*Cladochonus tenuicollis* McCoy

- 1—4. Cross-sections of corallites; ribs visible.  $\times 20$ . D. P. I. 15/107—110.
5. Longitudinal section through corallite divided by diaphragm,  $\times 12$ . D. P. I. 15/111.
6. Cross-section of parental corallite and budding daughter corallite; visible diverging calicular cavity at the diaphragm,  $\times 23$ . D. P. I. 15/112.

## Plate 21

*Cladochonus tenuicollis* McCoy

1. Inside of calice with a pillow-like structure,  $\times 23$ . D. P. I. 15/113.
2. Cross-section through calice of parent corallite with the pillow-like structure and peduncle of daughter corallite,  $\times 12$ . D. P. I. 15/114.
3. Section of the reticulous pillow-like structure; visible rows of oval bodies,  $\times 40$ . D. P. I. 15/115.
4. Cross-section of calice at the pillow-like structure, diaphragm and diverging calicular cavity,  $\times 23$ . D. P. I. 15/116.
5. Cross-section of calice; visible epitheca and two layers,  $\times 20$ . D. P. I. 15/117.

## Plate 22

*Cladochonus tenuicollis* McCoy

- 1—3. SEM photographs showing microstructure of internal wall formed of grundulae. D. P. I. 15/118. 1.  $\times 1000$ , 2.  $\times 1200$ , 3.  $\times 2400$ .









