

The worm endosymbionts in tabulate corals from the Silurian of Podolia, Ukraine

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Abstract. Two endosymbionts, *Chaetosalpinx sibiriensis* and *Coralloconchus bragensis*, occur in Silurian tabulate corals of Podolia. The endosymbiotic worms responsible for *C. sibiriensis* bioclaustrations in tabulates are found only in certain species: *Paleofavosites* cf. *collatatus*, *Heliolites* sp. A, *Heliolites* sp. B, *Heliolites* sp. C, *Favosites gothlandicus*, *Favosites* sp. A. One to six *C. sibiriensis*-infested tabulate species are known from Late Homeric to Ludfordian, in the reef-related community. *Chaetosalpinx sibiriensis* preferred certain tabulate species over the others, but showed no preference for the favositid or heliolitid type of morphology.

Key words: tabulate corals, *Chaetosalpinx*, endosymbiosis, Silurian, Podolia.

INTRODUCTION

Macroscopic worm endosymbionts are frequently found in recent corals (Ross & Newman 1973; Smith 1984; Hunte et al. 1990a, 1990b; Marsden & Meeuwig 1990; Nishi & Nishihira 1996, 1999), but were common also in the Palaeozoic (Richards & Dyson-Cobb 1976; Tapanila 2002, 2004, 2005; Tapanila & Copper 2002; Tapanila & Holmer 2006). The earliest endosymbiotic worm fossils are known from Late Ordovician rugose (Elias 1986) and tabulate corals (Tapanila 2004) and are preserved as bioclaustrations. Bioclaustrations are produced by the embedding of an endosymbiont within the growing skeleton of a living, host organism. As a result of this interaction, a cavity is produced within the host skeleton in which the endosymbiont lives (Tapanila 2005). Three species of endosymbiotic worms, *Chaetosalpinx ferganensis* Sokolov, 1948, *Chaetosalpinx sibiriensis* Sokolov, 1948 (= *Camptosalpinx estonicus* Klaamann, 1958), and *Coralloconchus bragensis* Vinn & Mõtus, 2008, are known in the Silurian tabulate corals of Baltica (Tapanila 2005; Vinn & Mõtus 2008). *Chaetosalpinx sibiriensis* has hitherto been reported from *Parafavosites germana* (Wenlock, NE Russia, Sokolov 1948) and *Paleofavosites balticus* (Llandover, Estonia, Klaamann 1958). The specimens of *Favosites pseudoforbessi muratsiensis* containing *C. sibiriensis*, from an Ordovician–Silurian erratic of the Netherlands (Stel 1976), could also be of Baltic origin.

Similarly to modern endosymbionts of scleractinian corals (Tapanila 2005), Palaeozoic bioclaustrations are common in particular host taxa, but entirely absent from the others. Like recent endosymbionts, Palaeozoic endosymbionts appear to have preferred colonial corals with a massive, cerioid (e.g. favositids) to coenenchymal (e.g. heliolitids and sarcinulids) structure, and are more rarely found in solitary rugosans (Tapanila 2005). Palaeozoic bioclaustrations are hitherto unknown in cateniform, fasciculate, and auloporoid tabulate corals (Tapanila 2005).

The Silurian rocks (Wenlock–Pridoli) of Podolia (Ukraine) are exposed in an approximately 80 km wide area along the Dniester River and its tributaries (Fig. 1). The Silurian deposits were formed in variable conditions from the normal-marine to lagoon facies (Tsegelnjuk et al. 1983). The massive coral–stromatoporoid–algal bioherms (Grytsenko 2007) from Lower to Upper Ludlow of Podolia are characteristic of a shallow shelf environment (Fig. 2).

The aim of this paper is to test the following hypotheses: (1) the endosymbiotic worms occurred only in certain host species; (2) the infestation rates are host-specific; (3) endosymbionts preferred a certain type of tabulate morphology (heliolitid versus favositid); (4) the number of infested tabulate species in the coral reef and reef-related community changes over time; (5) the infestation rate of coral species changes with time.

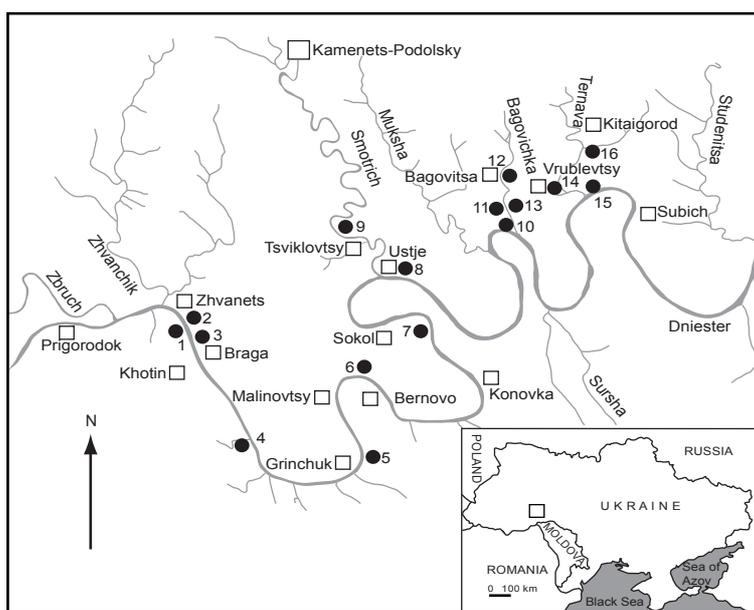


Fig. 1. Location map of the study area in Podolia. Rectangles mark the settlements and black dots mark localities. 1, Khotin; 2, Zhvanets; 3, Braga; 4, Babshin; 5, Grinchuk; 6, Malinovetskaya Sloboda; 7, Sokol; 8, Ustje; 9, Tsviklevtsy; 10, Ustje Bagovitsy; 11, Bagovitsa C; 12, Bagovitsa A; 13, Bagovitsa B; 14, Vrublevtsy; 15, Ustje Ternavy; 16, Kitaigorod. These are the localities visited by M.-A. Mõtus. The localities Grinchuk-27, Sokol-25, Tsviklevtsy-186, and Kitaigorod-96 of old collections from the early 1970s are assumed to be close to the others with the same name.

SERIES	Stage	Formation	Subformation
LUDLOW	Ludfordian	Rykhta	Grinchuk
	Gorstian	Tsviklevtsy	Bernovo
			Sokol
		Konovka	Shutnovtsy
			Goloskov
	Bagovitsa	Ustje	
WENL.		Homerian	Muksha

Fig. 2. Stratigraphical scheme of the study interval after Kaljo et al. (2007).

MATERIAL AND METHODS

A total of 182 tabulate specimens were collected from 20 Silurian outcrops of Podolia (Fig. 1). The following species were represented: *Cladopora* sp. (Homerian to Gorstian), *Cystihalysites* sp. (Ludfordian), *Heliolites* sp. A (Gorstian to Ludfordian), *Heliolites* sp. B (Gorstian to Ludfordian), *Heliolites* sp. C (Gorstian to

Ludfordian), *Heliolites* sp. D (Ludfordian), *Heliolites* sp. E (Ludfordian), *Favosites gothlandicus* Lamarek, 1816 (Gorstian to Ludfordian), *Favosites* sp. A (Gorstian), *Favosites* sp. B (Ludfordian), *Favosites* sp. C (Gorstian), *Favosites* sp. D (Gorstian), *Favosites* sp. E (Gorstian to Ludfordian), *Paleofavosites* cf. *collatatus* (Homerian to Gorstian), *Stelliporella* sp. (Ludfordian), *Syringopora* sp. A (Gorstian), *Syringopora* sp. B (Gorstian), *Syringopora* sp. C (Sheinwoodian), and *Thecia* sp. (Sheinwoodian). A number of widely distributed species are found in this collection of the Silurian of Podolia. We followed the stratigraphy by Kaljo et al. (2007) (Fig. 2). The material was collected from the carbonate rocks of reef and reef-related shelf facies. Several longitudinal and transverse sections were made from each tabulate corallum. Coral endosymbionts were searched under a binocular light microscope. Digital calipers (accurate to 0.01 mm) were used to measure the diameter of endosymbiont shafts in thin sections.

RESULTS

Two endosymbiotic worms were present in the Silurian tabulate corals of Podolia. The common ichnofossil

Chaetosalpinx sibiriensis Sokolov, 1948 (Table 1, Fig. 3) was found in 45 tabulate coralla and a rare cornulitid *Coralloconchus bragensis* Vinn & Mõtus, 2008 (Fig. 4) in two coralla of *Heliolites* sp. (Vinn & Mõtus 2008).

The infestation pattern of tabulate corals by *C. sibiriensis* is not random. The worms responsible for *C. sibiriensis* bioclaustrations were capable of infesting certain tabulate species: *Paleofavosites* cf. *collatatus*, *Heliolites* sp. A, *Heliolites* sp. B, *Heliolites* sp. C, *Favosites gothlandicus*, *Favosites* sp. A (6 of the 19 species studied). One of these species was infested both in the Late Homeric and Gorstian, one in the Gorstian as well as in the Ludfordian, one in the Ludfordian, and three infestations occurred in the Gorstian (Tables 1 and 2). The infestation rates of *P. cf. collatatus* changed only moderately over time (Table 3).

Chaetosalpinx sibiriensis preferred the tabulates *P. cf. collatatus* (71% of the specimens infested) over *Heliolites* sp. B (25% infested) and *Favosites gothlandicus* (11% infested) in the Gorstian, however, no preference was observed concerning the favositid (infestation rates from 11% to 71%) or heliolitid (infestation rates from 25% to 42%) type of tabulate morphology. The multiple peaks on the histogram of the *C. sibiriensis* diameter (Fig. 5) in most infested *P. cf.*

collatatus indicate that worms responsible for the bioclaustration could have had more than one distinct growth type.

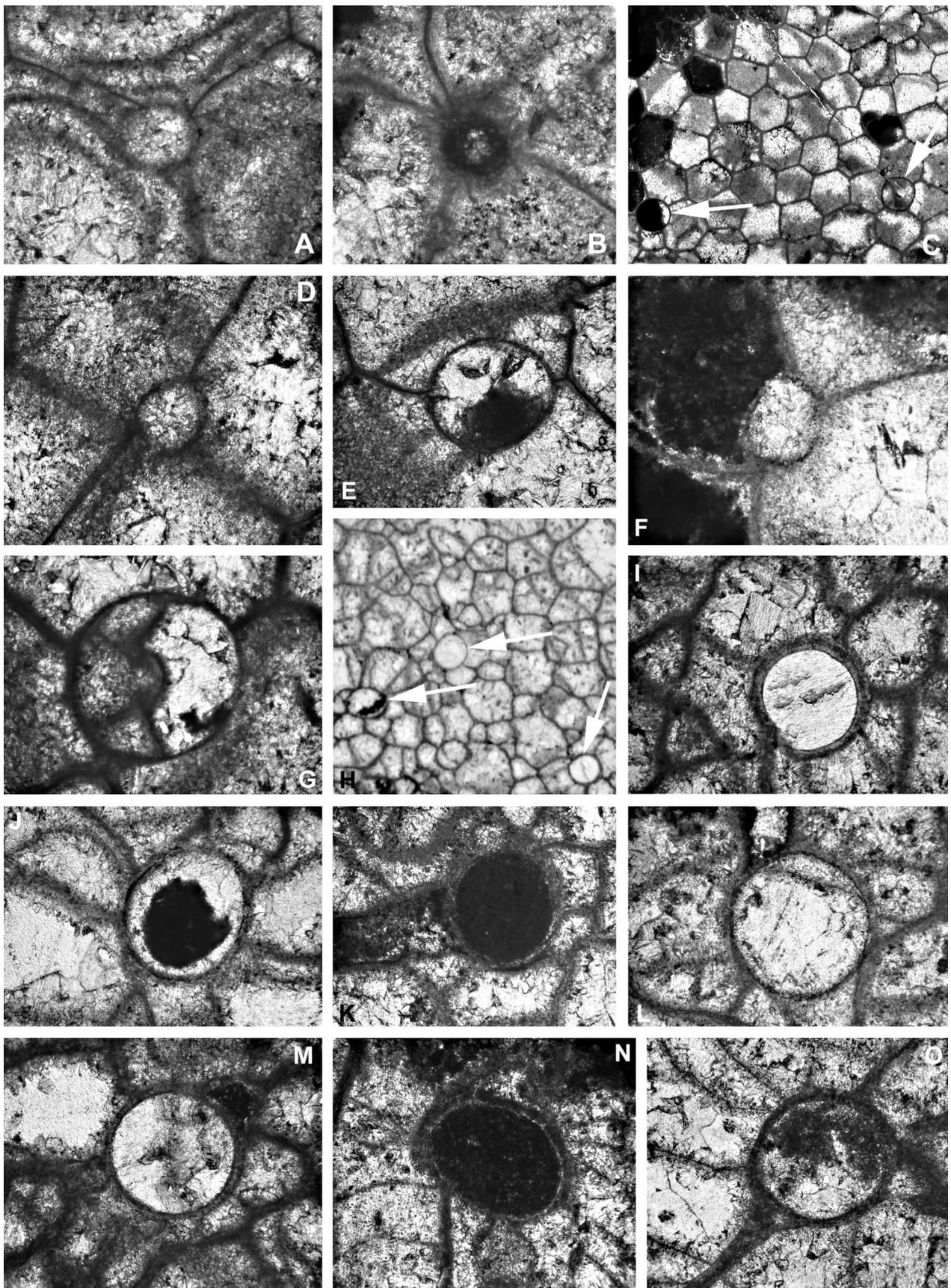
DISCUSSION

The number of infested tabulate species in the Silurian of Podolia increases from one in the Late Homeric to five in the Gorstian, and decreases to two in the Ludfordian (Table 2). However, these numbers are based on relatively small samples, while different results can be obtained from larger samples.

It is not possible to detect on the fossil material whether variations in the infestation rates in the Gorstian (Table 3) result from active larval selectivity by the worms or simply indicate their success of colonization. The environmental differences in worm infestation rates could be an alternative way to explain the species-specific percentage of infested specimens, if the infested corals lived in different environments. All studied tabulates were collected from shallow shelf facies and we believe that all our *C. sibiriensis*-infested corals were living in a similar environment.

Table 1. Stratigraphic and locality information of *Chaetosalpinx sibiriensis*-infested tabulate species. The first number in parentheses shows the number of the studied samples, the second number in parentheses – the number of infested tabulate specimens

Tabulate species	Late Homeric	Gorstian	Ludfordian
<i>Paleofavosites</i> cf. <i>collatatus</i>	Bagovitsa area (39; 19) Vrublevtsy (5; 1) Ustje Bagovitsy (3; 3)	Ustje (2; 1) Sokol (3; 3) Tsviklevtsy (2; 1)	
<i>Heliolites</i> sp. A		Ustje (1; 0) Tsviklevtsy (2; 0) Grinchuk-27 (1; 1) Grinchuk (1; 0)	Braga (2; 1) Babshin (1; 1) Zhvanets-39 (16; 6)
<i>Heliolites</i> sp. B		Tsviklevtsy-186 (1; 1) Tsviklevtsy (7; 2) Grinchuk (1; 0) Grinchuk-27 (1; 0) Ustje (1; 0) Sokol (1; 0)	Babshin (1; 0) Zhvanets (8; 0)
<i>Heliolites</i> sp. C		Sokol (1; 0) Ustje (2; 0) Tsviklevtsy (1; 0) Tsviklevtsy-186 (1; 0)	Zhvanets (2; 1)
<i>Favosites gothlandicus</i>		Sokol-25 (10; 0) Tsviklevtsy-186 (6; 1) Ustje (2; 1) Sokol (1; 0)	Grinchuk-27 (11; 0) Malinovetskaya sloboda (1; 0)
<i>Favosites</i> sp. A		Ustje (2; 1) Tsviklevtsy-186 (1; 1)	



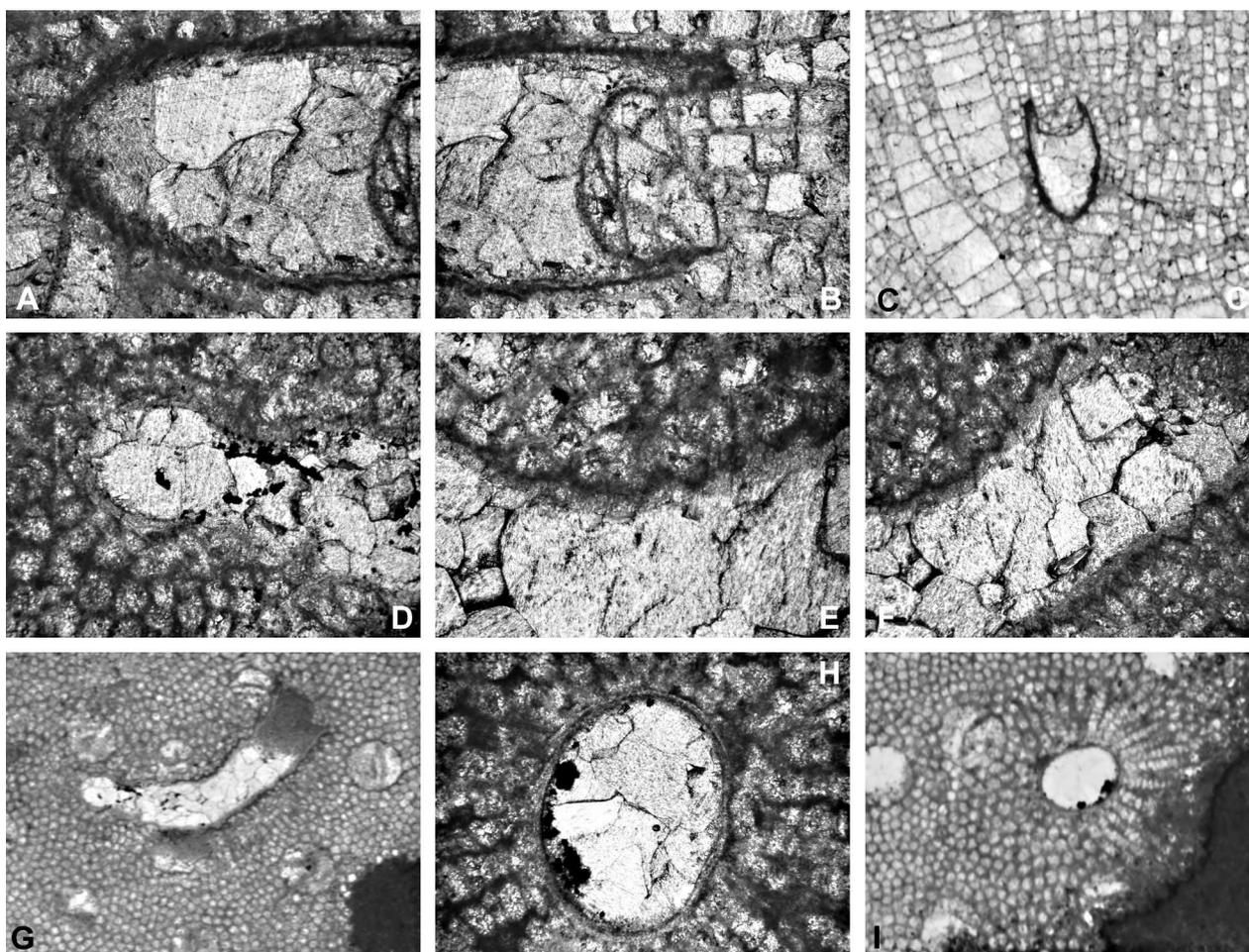


Fig. 4. Photographs of *Coralloconchus bragensis* Vinn & Mõtus, 2008 in thin sections of tabulate corals. **A–C**, *C. bragensis* in *Heliolites* sp. B, GIT 534-2-1, Zhvanets, Grinchuk Subformation; A, $\times 25$, B, $\times 25$, C, $\times 7$. **D–G**, *C. bragensis* in *Heliolites* sp. D, GIT 534-1-2, Zhvanets, Grinchuk Subformation; D, $\times 25$, E, $\times 40$, F, $\times 25$, G, $\times 7$. **H, I**, *C. bragensis* in the same specimen of *Heliolites* sp. D as in D–G, GIT 534-1-1 (holotype); H, $\times 25$, I, $\times 8$.

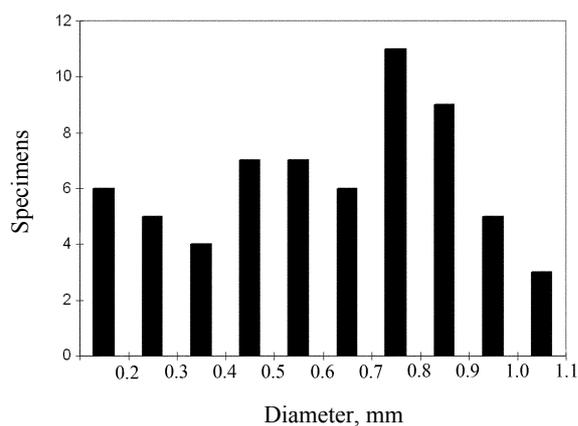
Table 2. Infestation (X) of tabulate corals by *Chaetosalpinx sibiriensis* in the Silurian of Podolia

Tabulate species	Late Homerian	Gorstian	Ludfordian
<i>Paleofavosites</i> cf. <i>collatatus</i>	X	X	
<i>Heliolites</i> sp. A		X	X
<i>Heliolites</i> sp. B		X	
<i>Heliolites</i> sp. C			X
<i>Favosites gothlandicus</i>		X	
<i>Favosites</i> sp. A		X	

Fig. 3. Photographs of *Chaetosalpinx sibiriensis* Sokolov, 1948 in thin sections of tabulate corals. **A, B**, *C. sibiriensis* in *Favosites* sp. A, GIT 440-13, Tsviklevtsy, Goloskov Subformation; A, $\times 35$, B, $\times 56$. **C**, *C. sibiriensis* in *Favosites gothlandicus* Lamarck, 1816, GIT 440-508, Ustje, Goloskov Subformation, transverse section, the arrows point to *C. sibiriensis*, $\times 4$. **D**, *C. sibiriensis* in *Favosites* sp. A, GIT 440-428, Ustje, Goloskov Subformation, $\times 38$. **E–G**, *C. sibiriensis* in *Favosites gothlandicus*, GIT 440-508, Ustje, Goloskov Subformation; E, $\times 25$, F, $\times 40$, G, $\times 39$. **H–J**, *C. sibiriensis* in *Paleofavosites* cf. *collatatus* Klaamann, 1961, GIT 481-65, Bagovitsa A, Muksha Subformation; H, transverse section, the arrows point to *C. sibiriensis*, $\times 7$, I, $\times 27$, J, $\times 27$. **K**, *C. sibiriensis* in *Paleofavosites* cf. *collatatus*, GIT 481-75, Bagovitsa A, Muksha Subformation, $\times 25$. **L**, *C. sibiriensis* in *Paleofavosites* cf. *collatatus*, GIT 481-70, Bagovitsa A, Muksha Subformation, $\times 27$. **M–O**, *C. sibiriensis* in *Paleofavosites* cf. *collatatus*, GIT 481-73, Bagovitsa C, Muksha Subformation; M, $\times 27$, N, $\times 27$, O, $\times 27$.

Table 3. Infestation rates of the tabulate coral species by *Chaetosalpinx sibiriensis* in the Silurian of Podolia

Tabulate species	Late Homerician	Gorstian	Ludfordian
<i>Paleofavosites</i> cf. <i>collatatus</i>	(n = 47) 49%	(n = 7) 71%	
<i>Heliolites</i> sp. A			(n = 19) 42%
<i>Heliolites</i> sp. B		(n = 12) 25%	
<i>Favosites gothlandicus</i>		(n = 19) 11%	

**Fig. 5.** Distribution of *Chaetosalpinx sibiriensis* diameters (63 specimens) in transverse sections of *Paleofavosites* cf. *collatatus* (27 specimens) from the Late Homerician to Gorstian of Podolia. Note three maxima on the graph.

Chaetosalpinx has been interpreted as a tabulate parasite, considering its position between the corallites, perforation of the host's skeleton and soft tissue, modification of its phenotype and possible inhibition of its growth (Zapalski 2007). Thus, some of the uninfested tabulate species could have evolved active means of protection against infestation by *C. sibiriensis*. On the other hand, as we did not find any adverse effects of *Chaetosalpinx* on the neighbouring coral skeleton (Fig. 3), we suggest that the relationship was commensal. In Palaeozoic endosymbiosis it is possible that the particular tabulate coral taxa which tend to contain bioclastrations may have been among the community's least aggressive or toxic corals (Tapanila 2005). Three peaks on the histogram of *C. sibiriensis* diameter in *P. cf. collatatus* (Fig. 5) could be explained by the presence of three distinct morphotypes. Thus, there may have been more than one species of endosymbiotic worms responsible for *C. sibiriensis* in *P. cf. collatatus*. We did not find any correlation between the growth form of the corals and the occurrence of *Chaetosalpinx* bioclastrations.

In Palaeozoic tabulate corals bioclastrations are preferentially found in common host taxa that span

millions of years of geologic time, e.g. *Favosites* (Tapanila 2005). Our observations on the Silurian tabulates from Podolia support this opinion. We found the highest infestation rates in *P. cf. collatatus*, which is a common tabulate species in the Muksha Subformation (Mõtus & Grytsenko 2007) and ranges from the Late Homerician to the Gorstian (Table 1). Common and long-ranged species had sufficient abundance in space and a long exposure time for their potential symbionts, increasing so the probability of the development of an endosymbiotic relationship as compared to short-ranged and less common coral species.

In Baltica *Chaetosalpinx* has hitherto been reported from *Favosites vicinalis* (Stel 1976), *Heliolites* sp. (Stel 1976), *Parafavosites germanica* (Sokolov 1948), and *Paleofavosites balticus* (Klaamann 1958), and probably also from *Favosites pseudoforbesei* (Stel 1976) and *Thecia swindereniana* (Stel 1976). Our new data from Podolia show that *Chaetosalpinx* was infesting many more coral species in the Silurian of Baltica, and besides favositids, also heliolitids were common hosts. *Chaetosalpinx* is hitherto known from eight species of favositids (Tapanila 2005; our data), three species of heliolitids (our data), and one species of *Thecia* (Stel 1976). Thus, in the Silurian favositid corals could have had the highest number of *Chaetosalpinx*-tolerant species as compared to the rest of tabulates. However, among the *Chaetosalpinx*-tolerant corals no preference of favositids over heliolitids is observed as both the highest and lowest infestation rates characterize favositids (Table 3). The scanty data on the occurrences of *Chaetosalpinx* outside Baltica do not allow analysing the palaeobiogeographic distribution patterns of the genus in the Silurian.

CONCLUSIONS

In Palaeozoic tabulate corals bioclastrations are mainly found in common host taxa spanning millions of years of geologic time, e.g. *Favosites* (Tapanila 2005). We established the highest infestation rates in *P. cf. collatatus*, possibly because this species is a common tabulate in the Muksha Subformation.

Among the *Chaetosalpinx*-tolerant corals, favositids show no preference over heliolitids. Both the highest and lowest infestation rates are associated with favositids.

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Siluri endosümbiootilised ussid Podoolia (Ukraina) tabulaatsetes korallides

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Podoolia Siluri-aegsetest tabulaatidest (Homerian–Ludfordian) on leitud kaks endosümbiootilist ussi *Chaetosalpinx sibiriensis* ja *Coralloconchus bragensis*. Neid endosümbionte on leitud vaid järgmistest tabulaadi liikidest: *Paleofavosites cf. collatatus*, *Heliolites* sp. A, *Heliolites* sp. B, *Heliolites* sp. C, *Favosites gothlandicus* ja *Favosites* sp. A. *Chaetosalpinx sibiriensis* eelistas teatud tabulaadi liike teistele. Endosümbiontide sisalduse suuruses favositiidides ja helioliitiidides ei ole vahet, kuna favositiidid sisaldavad helioliitiididest nii vähem kui ka rohkem endosümbionte.