

Gregarines (Apicomplexa: Eugregarinida) of Chilopoda and Diplopoda in Slovenia

Dušan Devetak¹, Katarina Mihelak² & Ivan Kos³

¹ Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, 2000 Maribor, Slovenia; E-mail: dusan.devetak@guest.arnes.si

² Škale 83, 3320 Velenje, Slovenia

³ Department of Biology, Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, 1000 Ljubljana, Slovenia

Abstract: Gregarines (Apicomplexa: Eugregarinida) are relatively large protozoan parasites of the intestines and body cavities of marine, freshwater and terrestrial invertebrates. Between June 2013 and September 2014, guts of centipedes (Chilopoda) and millipedes (Diplopoda) originating from Slovenia were eviscerated and inspected for the presence of gregarines. During this study, we identified eight gregarine species belonging to the genera *Trichorhynchus*, *Echinomera*, *Grebnickiella*, *Stenophora* and *Cnemidospora*. Brief morphological and standard morphometric data as well as illustrations are presented for the identified species. Difference in the ratio DL : DWM confirms that two closely related *Echinomera* species (*E. hispida* and *E. horrida*) are clearly differentiated.

Key words: Eugregarines, Alveolata, centipedes, millipedes

Introduction

Gregarines are obligate unicellular parasites infecting intestines and other organs of invertebrates living in terrestrial, freshwater and marine habitats. Gregarines within Apicomplexa belong to the alveolates (Alveolata), which are a major line of protists. The subdivision of the gregarines is based on trophozoite morphology, host range and habitat. Traditionally, the gregarines have been divided into three major subgroups: eugregarines, archigregarines and neogregarines (GRASSÉ 1953, LEANDER 2008, LEVINE 1971, RUECKERT & LEANDER 2008). Archigregarines occur only in marine invertebrates. Eugregarines are known in marine, freshwater and terrestrial hosts. Neogregarines are found only in terrestrial invertebrates. Eugregarines contain most of the known gregarine species and a great number of them are the most important unicellular parasites in arthropods, especially in insects. Despite recent molecular studies (e.g. CLOPTON 2009, SIMDYANOV et al. 2017), the delineation of superior taxa is unstable because of our poor understanding of the ac-

tual diversity and phylogenetic relationships in the group (RUECKERT & LEANDER 2009, SIMDYANOV et al. 2017). Based on molecular phylogenetic analyses, neogregarines have been incorporated into the Eugregarinida (SIMDYANOV et al. 2017).

Although numerous papers have been published on European gregarine species (see DESPORTES & SCHRÉVEL 2013) and there are several monographs (e.g. LIPA 1967, GEUS 1969), our knowledge of the diversity and distribution of the European gregarine fauna is still poor. Many eugregarine species have been described from Chilopoda (centipedes) and Diplopoda (millipedes). These parasite species belong to the families Monoductidae, Cnemidosporidae, Dactylophoridae, Stenophoridae, Trichorhynchidae, Actinocephalidae and Monocystidae (GEUS 1969, DESPORTES & SCHRÉVEL 2013). One neogregarine species is recorded in a millipede (TUZET & MANIER 1958).

In this study, gregarines from centipedes and millipedes in Slovenia are listed for the first time.

Materials and Methods

Centipedes and millipedes collected between June 2013 and September 2014 in Slovenia were eviscerated and their alimentary canals dissected in insect Ringer's solution (LAUGHTON et al. 2011: 128 mM NaCl, 18 mM CaCl₂, 1.3 mM KCl, 2.3 mM NaHCO₃, 1 l dH₂O, pH 7.2). Their guts were examined microscopically at 40, 100, 200 and 400-times magnifications. Gregarines were photographed and measured using a Nikon E 800 microscope with a mounted digital camera Nikon DN100 and Eclipse Net software v. 1.16.3. The following standard gregarine trophozoite and gamont metrics (LIPA 1967, CLOPTON 2004) are reported (in µm): total length, length of epimerite, length of protomerite, length

of deutomerite, maximum width of protomerite, width of deutomerite at equatorial axis and maximum width of deutomerite. We followed the nomenclature and taxonomy of Myriapoda proposed by Fauna Europaea, v. 2017.06 (ENGHOFF 2018). A list of Myriapoda hosts is presented in Table 1.

Results

Guts of centipedes and millipedes were studied and eight gregarine species were recorded. They are listed below, with data on their hosts, some morphological characters, host ranges and distribution.

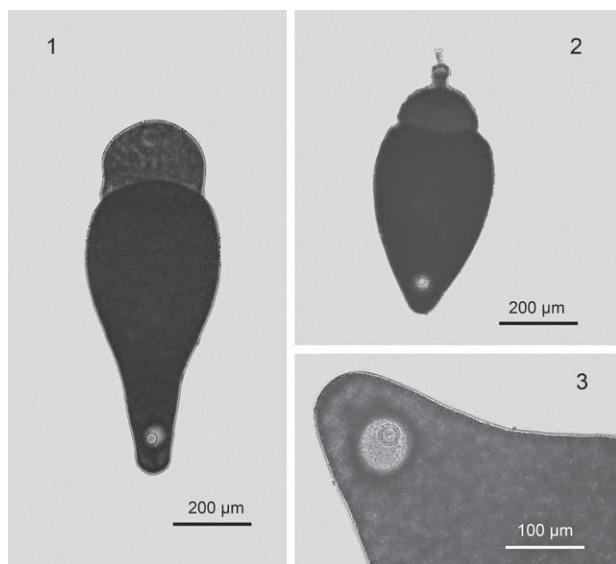
ORDER EUGREGARINIDA

FAMILY TRICHORHYNCHIDAE

Genus *Trichorhynchus* Schneider, 1882

Table 1. List of centipedes (Chilopoda) and millipedes (Diplopoda) species studied for the presence of gregarines. Legend: n = number of infected host individuals; N = number of studied host individuals.

Host species	Locality, coordinates, date, n/N	Gregarine species
CHILOPODA		
<i>Scutigera coleoptrata</i> (Linnaeus, 1758)	Maribor, 46.566235, 15.654314, 29.IX.2014, 1/6; Velenje (Šmartno), 46.364819, 15.122664, 31.V.2014, 0/1	<i>Trichorhynchus pulcher</i> Schneider, 1882
<i>Lithobius forficatus</i> (Linnaeus, 1758)	Velenje: Škale, 46.391713, 15.093449, 12.IV.2014, 1/1	<i>Echinomera hispida</i> (Schneider, 1875)
<i>Lithobius parietum</i> Verhoeff, 1899	Velenje: Škale, 46.391713, 15.093449, 17.III.2014, 1/2; 18.III.2014, 1/1; 12.IV.2014 1/1; 13.VIII.2014, 1/1	<i>Echinomera hispida</i> (Schneider, 1875) <i>Echinomera horrida</i> (Léger, 1899)
<i>Lithobius punctulatus</i> C. L. Koch, 1847 (= <i>Lithobius validus</i> Meinert, 1872)	Velenje: Škale, 46.391713, 15.093449, 17.III.2014, 1/1; 18.III.2014, 1/1; 12.IV.2014, 1/1; 11.VIII.2014, 1/1; Spodnje Hoče, Pivola, 46.505075, 15.622092, 4.VI.2014, 1/3	<i>Echinomera hispida</i> (Schneider, 1875) <i>Echinomera horrida</i> (Léger, 1899)
<i>Lithobius</i> sp.	Velenje: Škale, 46.391713, 15.093449, XI.2013, 1/1; Spodnje Hoče, Pivola, 46.505075, 15.622092, 7.I.2014, 1/1; Maribor, 46.566308, 15.654459, 26.V.2013, 1/2	<i>Echinomera hispida</i> (Schneider, 1875) <i>Echinomera horrida</i> (Léger, 1899)
<i>Cryptops anomalans</i> Newport, 1844	Maribor, 46.566308, 15.654459, 10.V.2014, 0/2; 26.V.2013 0/2	-
<i>Cryptops</i> sp.	Maribor, 46.566308, 15.654459, 10.V.2014, 0/3	-
<i>Scolopendra cingulata</i> Latreille, 1829	Rakitovec, 45.469995, 13.971727, 29.V.2014, 2/2	<i>Grebniackiella gracilis</i> (Grebniacki, 1873)
<i>Geophilomorpha</i> gen. sp.	Maribor, 46.566308, 15.654459, 10.V.2014, 0/2	-
<i>Clinopodes flavidus</i> C. L. Koch, 1847	Maribor, 46.566308, 15.654459, 4.V.2014, 0/1	-
<i>Dicelophilus carniolensis</i> (C. L. Koch, 1847)	Maribor, 46.566308, 15.654459, 4.V.2014, 0/2	-
<i>Geophilus</i> sp.	Maribor, 46.566308, 15.654459, 12.V.2014, 0/1	-
DIPLOPODA		
Julidae gen. sp.	Maribor: Kamnica, 46.577234, 15.599724, 4.VI.2014, 5/9; Spodnje Hoče, Pivola, 46.505075, 15.622092, 4.VI.2014, 5/5; Velenje: Črnova, 46.325792, 15.181002, 15.III.2014, 1/2; Velenje: Škale, 46.391713, 15.093449, 13.XI.2013 1/1; 12.IV.2014, 1/1	<i>Stenophora robusta</i> Ellis, 1912 <i>Stenophora julipusilli</i> (Leidy, 1853) <i>Stenophora rauchallesi</i> Levine, 1976
<i>Polydesmus</i> sp.	Maribor: Kamnica, 46.577234, 15.599724, 4.VI.2014, 0/1; ; Spodnje Hoče, Pivola, 46.505075, 15.622092, 7.I.2014, 1/1; 4.VI.2014, 1/1	<i>Cnemidospora</i> cf. <i>lutea</i> Schneider, 1882



Figs. 1-3. Individuals of *Trichorhynchus pulcher*. Fig. 1. Individual without epimerite. Fig. 2. Individual with epimerite. Fig. 3. Caudal part of deutomerite containing nucleus.

***Trichorhynchus pulcher* Schneider, 1882**

(Figs. 1-3)

Host: *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda).

Epimerite clearly seen (Fig. 2), often prolonged. Measurements of an individual (gamont) with epimerite are given in Table 2.

Literature records: Ultrastructure of this species was described by ORMIÈRES et al. (1977), MARQUÈS et al. (1978). *Trichorhynchus pulcher* was reported from the following centipede species: *Scutigera coleoptrata*, *S. forceps*, *Thereuonema clunifera*, *T. tuberculata* (ELLIS 1913, WATSON 1916, HOSHIDE 1959, GEUS 1969, DESPORTES & SCHRÉVEL 2013).

General distribution: France, USA, Japan (summarised from GEUS 1969 and DESPORTES & SCHRÉVEL 2013).

FAMILY DACTYLOPHORIDAE

Genus *Echinomera* Labbé, 1899

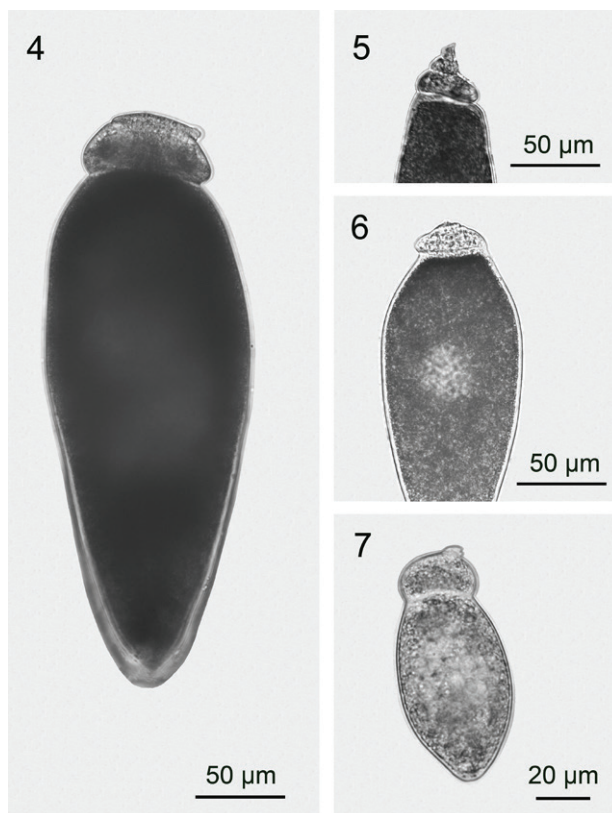
***Echinomera hispida* (Schneider, 1875)**

(Figs. 4-7)

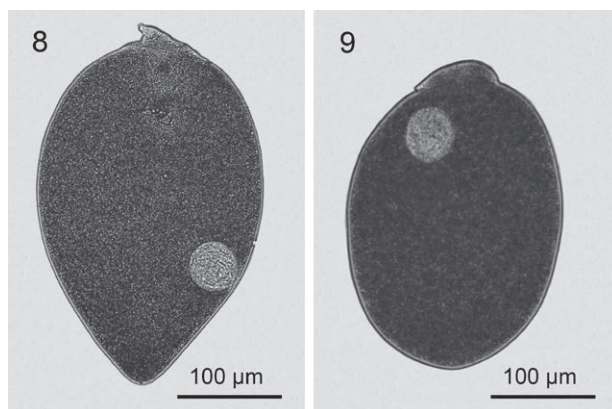
Hosts: *Lithobius forficatus* (Linnaeus, 1758); *L. parietum* Verhoeff, 1899; *L. punctulatus* C. L. Koch, 1847 and *Lithobius* sp. (Chilopoda).

Gamont: epimerite with a shape of an irregular cone. Trophozoite: epimerite with a corona of eight digitiform rhizoids, not clearly seen in observed individuals. Measurements of gamonts are given in Table 2. In *E. hispida* gamonts, the ratio DL : DWM was 2.0–2.7, mean 2.4 (n=24).

Literature records: Life-cycle of this species was described by SCHELLACK (1907). *Echinomera*



Figs. 4-7. Solitary individuals of *Echinomera hispida*. Fig. 4-6. Gamonts. Fig. 7. Trophozoite.



Figs. 8-9. Solitary individuals of *Echinomera horrida*.

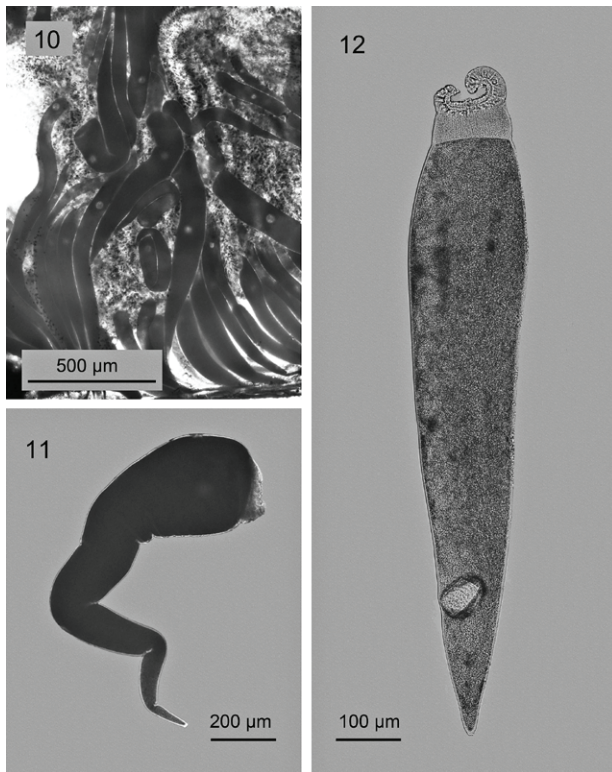
hispida was reported from the following centipede species: *Lithobius calcaratus*, *L. forficatus*, *L. muticus*, *L. piceus*, *Nadabius coloradensis* (= *Lithobius coloradensis*) (WATSON 1916, GEUS 1969, DESPORTES & SCHRÉVEL 2013).

General distribution: Europe – France, Germany, Great Britain, Russia: Kaliningrad), USA (summarised from GEUS 1969 and DESPORTES & SCHRÉVEL 2013).

***Echinomera horrida* (Léger, 1899)**

(Figs. 8-9)

Hosts: *Lithobius parietum* Verhoeff, 1899,



Figs. 10-12. *Grebnickiella gracilis*. Fig. 10. Mass occurrence in the host. Fig. 11. Individual with lobeless epimerite. Fig. 12. Individual with epimerite composed of two prominent lobes.

L. punctulatus C. L. Koch, 1847 and *Lithobius* sp. (Chilopoda).

Measurements of gamonts are given in Table 2. In *E. horrida* gamonts, the ratio DL : DWM was 1.0–1.9, mean 1.5 (n=9).

Literature records: *Echinomera horrida* was reported from the following centipede species: *Lithobius calcaratus* and *L. mutabilis* (WATSON 1916, GEUS 1969, DESPORTES & SCHRÉVEL 2013).

General distribution: Europe – France, Germany (summarised in GEUS 1969; DESPORTES & SCHRÉVEL 2013).

Genus *Grebnickiella* Bhatia, 1938

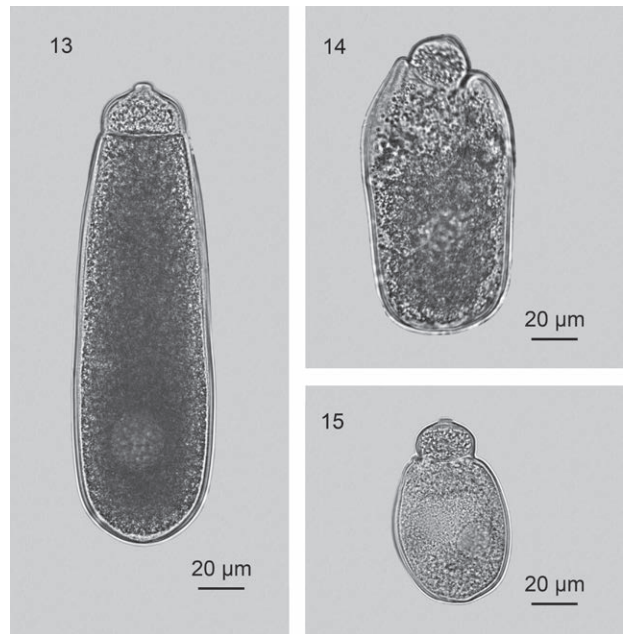
***Grebnickiella gracilis* (Grebnicki, 1873)**

(Figs. 10-12)

Host: *Scolopendra cingulata* Latreille, 1829 (Chilopoda).

Protomerite spreads out with numerous filamentous rhizoids, made up of two long horizontal lobes turned up spirally at the end (Fig. 12). Deutomerite elongate. Large gregarines with maximum length of trophozoites 1.7 mm (Table 2). In both host individuals, a mass infection with more than 100 gregarines per individual was found (Fig. 10).

Literature records: *Grebnickiella gracilis* was reported from the centipedes *Scolopendra cingu-*



Figs. 13-15. *Stenophora*: Fig. 13. Gamont of *Stenophora julipusilli*. Fig. 14. *Stenophora rauchallesi*. Fig. 15. Trophozoite of *Stenophora robusta*.

lata and *S. morsitans* (GEUS 1969, DESPORTES & SCHRÉVEL 2013).

General distribution: Europe – France and Bulgaria; North Africa (GEUS 1969, GOLEMANSKY & LIPA 1991, DESPORTES & SCHRÉVEL 2013, GOLEMANSKY 2015).

FAMILY STENOPHORIDAE

Genus *Stenophora* Labbé, 1899

In *Stenophora* spp., epimerite is rarely observed even in young trophozoites (DESPORTES & SCHRÉVEL 2013). An epimerite with digitiform processes has been observed in *Stenophora levinei*.

***Stenophora julipusilli* (Leidy, 1853)**

(Fig. 13)

Hosts: Julidae gen. sp. (Diplopoda).

Measurements of gamonts are given in Table 2.

Literature records: *Stenophora julipusilli* was reported from a number of millipede species of the families Craspedosomatidae, Julidae and Parajulidae (GEUS 1969, DESPORTES & SCHRÉVEL 2013).

General distribution: Europe – France, Germany, Slovakia; USA (GEUS 1969, VALIGUROVÁ & MATIS 2001, DESPORTES & SCHRÉVEL 2013).

***Stenophora rauchallesi* Levine, 1976**

(Fig. 14)

Syn. *Stenophora orthomorphae* Lipa, 1967, preoccupied.

Hosts: Julidae gen. sp. (Diplopoda).

In some individuals, protomerite somewhat sunk into the front part of deutomerite. Measurements of gamont are given in Table 2.

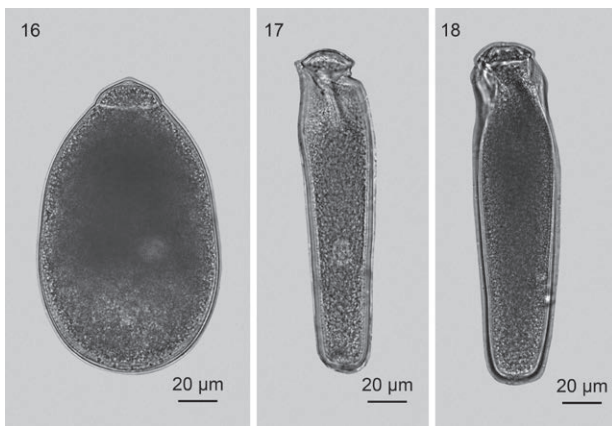


Fig. 16-18. 16. Gamont of *Stenophora robusta*; 17-18. Solitary individuals of *Cnemidospora* cf. *lutea*.

Literature records: *Stenophora rauchallesi* was reported from two millipede species (LIPA 1967, VALIGUROVÁ & MATIS 2001): *Oxidus (Orthomorpha) gracilis* and *Ommatoiulus sabulosus*.

General distribution: Europe – Poland, Slovakia (LIPA 1967, VALIGUROVÁ & MATIS 2001, DESPORTES & SCHRÉVEL 2013).

Remarks: DESPORTES & SCHRÉVEL (2013) clarified a confusion concerning the species name “*orthomorphae*”. Three species were named *Stenophora orthomorphae* by HOSHIDE (1952), LIPA (1967) and Rauchalles in GEUS (1969). LEVINE (1976) renamed the species described by LIPA (1967) as *Stenophora rauchallesi*. DESPORTES & SCHRÉVEL (2013) renamed the third species (de-

Table 2. Measurements of gregarines in centipedes and millipedes (in µm). Legend: TL – total length; EL – epimerite length; PL – length of protomerite; PL* – length of protomerite without epimerite; DL – length of deutomerite; PWM – maximum width of protomerite; PWE – width of protomerite at equatorial axis; DWM – maximum width of deutomerite; DWE – width of deutomerite at equatorial axis; n – number of individuals.

<i>Trichorhynchus pulcher</i> , gamont									
Individual	TL	EL	PL	PWM	PWE	DL	DWM	DWE	
1	695	36	188	215	185	507	337	300	
<i>Echinomera hispida</i> , gamonts									
n=24	TL	EL	PL	PL*	PWM	PWE	DL	DWM	DWE
Mean	265.8	10.9	28.7	17.8	46.2	38.5	237.1	98	91.9
Standard deviation	70.96	5.9	8.2	7.4	14	15.8	67.9	38.9	35.6
Minimum	140.3	3.5	15.9	8.3	28	16.8	119.4	43.6	39.1
Maximum	414.5	26.1	44.3	36.3	78.6	75.2	392.3	199.6	195.7
<i>Echinomera horrida</i> , gamonts									
Individual	TL	EL	PL	PL*	PWM	PWE	DL	DWM	DWE
1	390.2	4	23.4	19.4	83.6	62.7	366.8	240.4	234
2	213.2	3.4	28.8	25.4	69.4	62.8	184.4	186.7	175.2
3	292.7	/	35.2	/	47.4	44.2	257.5	164.4	162.3
4	237.3	/	36.7	/	55.3	52	200.6	119.9	109.9
5	278.7	/	27.9	/	75.2	64.7	259.8	220.4	218.7
6	301	/	16.7	/	65.2	40.4	284.3	196.5	189.9
7	332	12.3	30.5	18.1	68.8	29.7	301.5	158.3	144.6
8	343.1	15.7	24	8.3	69.9	29.9	319.1	215	214.8
9	282.7	/	9.8	/	36.4	/	272.9	149.8	132.8
<i>Grebniackiella gracilis</i> , trophozoites									
n=26	TL	EL	PL	PL*	PWM	PWE	DL	DWM	DWE
Mean	915.4	50.6	89.4	39.5	91.1	79.9	822.6	120.9	87.6
Standard deviation	355.4	19.1	25.5	19.7	30.6	34.3	342.9	38.1	32
Minimum	318.7	14.6	37.1	15.8	45.9	25.5	201.6	68.4	44
Maximum	1726	78.2	156.8	105	145.8	142.6	1637	193.7	153.2
<i>Stenophora julipusilli</i> , gamonts									
n=18	TL	PL	PWM	PWE	DL	DWM	DWE		
Mean	157	21.3	30.2	28.6	135.7	53.8	53.4		
St. deviation	32.1	3.5	7.3	7.1	30.6	13.5	13.2		
Minimum	107.6	16.3	19.1	18.4	87.7	27.3	27.3		

Table 2. Continuation.

Maximum	233.1	31.3	40.8	38.1	213.9	73.3	72.6
<i>Stenophora rauchallesi</i> , gamont							
Individual	TL	PL	PWM	PWE	DL	DWM	DWE
1	129	22	26	24.5	112	65	60
<i>Stenophora robusta</i> , trophozoites							
Individual	TL	PL	PWM	PWE	DL	DWM	DWE
1	87.5	15	19	18.5	72.5	38.5	37.5
2	73	15	18	17	58	33.5	32
3	80	18.5	26	25.5	61.5	48.5	48
4	96.5	15.5	19.5	19	81	48	47
5	94.5	17	25	24.5	77.5	40	40
6	78.5	14.5	18	17	64	35.5	35.5
7	101	17	26.5	24	84	47.5	47.5
<i>Stenophora robusta</i> , gamonts							
n=23	TL	PL	PWM	PWE	DL	DWM	DWE
Mean	151.9	19.5	31.9	30.2	132.5	79.2	76.9
St. deviation	30.1	4.4	4.8	4.8	27	16.2	15.2
Minimum	120.5	9.6	19.3	18.8	103.5	49.7	47.8
Maximum	228.7	28.8	43.5	42.3	199.9	122.3	111.1
<i>Cnemidospora cf. lutea</i> , gamonts							
Individual	TL	PL	PWM		DL	DWM	DWE
1	158.6	31.3	33.4		127.3	35.5	30
2	110.3	15.5	24.7		94.8	28.6	27.7
3	160.5	15.1	27.2		145.4	39.2	31.5
4	257.5	28.5	42.2		229	63.7	55.1
5	225.7	12.8	42.7		212.9	61.1	60
6	252.3	17	42.2		235.3	60.7	56.7
7	116.2	7.8	23.1		108.4	26.7	26.5
8	114.4	18.6	21.4		95.8	29.1	26.2
9	162.5	17.2	26.3		145.3	34.8	31.6

scribed by Rauchalles in GEUS 1969) as *Stenophora levinei*.

***Stenophora robusta* Ellis, 1912**

Hosts: Julida gen. sp. (Diplopoda).

The most abundant gregarine species in Diplopoda in Slovenia (Figs. 15-16). Measurements of trophozoites and gamonts are given in Table 2.

Literature records: *Stenophora robusta* has been reported from the following millipedes: Diplopoda: Polydesmida (Paradoxosomatidae), Julida (Parajulidae) (ELLIS 1912, GEUS 1969, DESPORTES & SCHRÉVEL 2013).

General distribution: Europe – Bulgaria, Germany; Guatemala; USA (ELLIS 1912, 1913, GEUS 1969, GOLEMANSKY et al. 2009, DESPORTES & SCHRÉVEL 2013, GOLEMANSKY 2015).

FAMILY CNEMIDOSPORIDAE

Genus *Cnemidospora* Schneider, 1882

In millipedes, four named species of this genus have been described (CLOPTON 2002, DESPORTES & SCHRÉVEL 2013).

***Cnemidospora cf. lutea* Schneider, 1882**

(Figs. 16-18)

Hosts: *Polydesmus* sp. (Diplopoda: Polydesmidae).

In a couple of *Polydesmus* individuals, a number of gamonts of a species resembling *Cnemidospora lutea* were found (Figs. 17-18). However, it could be a new, undescribed species. A sucker-like or dome-shaped protomerite is characteristic for gamont (for *C. lutea*, see also DESPORTES & SCHRÉVEL 2013). Measurements of gamonts are given in Table 2.

Discussion

In terrestrial arthropods, the highest diversity of gregarines has been reported in insects and myriapods (centipedes and millipedes). A review of current knowledge on the gregarines in myriapods is presented by DESPORTES & SCHRÉVEL (2013) and many species have been described in Europe. Among

European countries with comprehensive studies of gregarines in myriapods are France, Germany, Poland, Slovakia and Bulgaria (for reviews, see LIPA 1967, GEUS 1969, VALIGUROVÁ & MATIS 2001, DESPORTES & SCHRÉVEL 2013, GOLEMANSKY 2015). In the recent decades, a series of papers was published by Golemansky, who explored the gregarines in myriapods in Bulgaria; among them, there are also hosts living in caves – troglomorphic or troglomorphic species (GOLEMANSKY 1973a, 1973b, 2010, 2015, GOLEMANSKY & TASCHEV 1973, GOLEMANSKY & LIPA 1991, GOLEMANSKY & BONNET 1994).

The knowledge on the occurrence of the gregarines in arthropods in Slovenia is poor. Till now, gregarines have been reported in the country only from insects (DEVETAK et al. 2013, DEVETAK 2014, RUECKERT & DEVETAK 2017). In this paper, the first survey of the gregarines from Myriapoda occurring in Slovenia is presented.

In a polydesmid host, a few gamonts of a *Cnemidospora* species resembling *C. lutea* were detected (Figs. 17-18). *Cnemidospora lutea* has been reported from the diplopod family Glomeridae (*Glomeris* sp.) (ELLIS 1912, WATSON 1916, LIPA 1967, GEUS 1969, DESPORTES & SCHRÉVEL 2013) and the species is noted for Croatia, France, Germany and Poland (LIPA 1967, GEUS 1969). We found a presumably undescribed *Cnemidospora* sp. in *Polydesmus*. Two further species of this genus, *C. rhyodesmi* Hoshide, 1957 and *C. takanaensis* Hoshide, 1957, were found in a polydesmid host in Japan (HOSHIDE 1958).

Two *Echinomera* species from Slovenia differed according to the standard gregarine gamont metrics. Differences in the ratio DL : DWM revealed that the two closely related species could be clearly differentiated – for *E. hispida*, the mean ratio was 2.4, and for *E. horrida*, the mean ratio was 1.5. When comparing these values with the data of the measurements in GEUS (1969), the differences for both species are very similar (in GEUS 1969, for *E. hispida*, the mean ratio DL : DWM is 2.5, min 2.1, max 3.6, n=10, and for *E. horrida*, the mean ratio DL : DWM is 1.7, min 1.4, max 2.2, n=10). Furthermore, in *E. hispida* individuals originating from Slovenia, two additional host species (*Lithobius parietum* and *L. punctulatus*) are found.

Taking into account that only a small number of centipedes and millipedes have been examined in this study, new findings of gregarines in the Myriapoda from Slovenia could be expected in future.

Acknowledgements: This study was supported by the Slovenian

Research Agency and the Research Programme Computationally Intensive Complex Systems (P1-0403).

References

- CLOPTON R. E. 2002. Phylum Apicomplexa Levine, 1970: Order Eugregarinorida Léger, 1900. In: LEE J. J., LEEDALE G., PATTERSON D. & BRADBURY P. C. (Eds.): Illustrated Guide to the Protozoa. 2nd ed. Lawrence, Kansas: Society of Protozoologists, pp. 205–288.
- CLOPTON R. E. 2004. Standard nomenclature and metrics of plane shapes for use in gregarine taxonomy. *Comparative Parasitology* 71: 130-140.
- CLOPTON R. E. 2009. Phylogenetic relationships, evolution, and systematic revision of the septate gregarines (Apicomplexa: Eugregarinorida: Septatorina). *Comparative Parasitology* 76: 167-190.
- DESPORTES I. & SCHRÉVEL J. 2013. The Gregarines. The Early Branching Apicomplexa. Treatise on Zoology – Anatomy, Taxonomy, Biology. Leiden, Boston: Brill. 781 p.
- DEVETAK D., OMERZU M. & CLOPTON R. E. 2013. Notes on the gregarines (Protozoa: Apicomplexa: Eugregarinorida) of insects in Slovenia. *Annales Series Historia Naturalis* 23: 73-89.
- DEVETAK D. 2014. Host diversity and seasonality of *Hyalospora hemerobii* (Apicomplexa: Eugregarinorida: Hirmocystidae) infections in lacewings. *Biologia* 69: 1585-1592.
- ELLIS M. M. 1912. Five polycystid gregarines from Guatemala. *Zoologischer Anzeiger* 39: 680-689.
- ELLIS M. M. 1913. A descriptive list of the cephaline gregarines of the New World. *Transactions of the American Microscopical Society* 32 (4): 259-296.
- ENGHOFF H. 2018. Fauna Europaea: Myriapoda. Fauna Europaea version 2017.06, <https://fauna-eu.org>. Accessed on 5 February 2018.
- GEUS A. 1969. Sporentierchen, Sporozoa: die Gregarinida der land- und süßwasserbewohnenden Arthropoden Mitteleuropas. In: DAHL F. (ed.): Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise. Jena: Gustav Fischer Verlag. 608 p.
- GOLEMANSKY V. 1973a. *Stenophora beroni* n. sp. (Gregarinida: Stenophoridae) – une nouvelle eugregarine du Diplopode troglophile *Balkanopetalum armatum* Verhoeff (Diplopoda: Lysiopetalidae). *Zoologischer Anzeiger* 191 (1/2): 151-156.
- GOLEMANSKY V. 1973b. *Stenophora bulgarosomae* n. sp. – une nouvelle grégarine (Gregarinida, Stenophoridae) de diplopode troglobie *Bulgarosoma bureschi* Verhoeff. *Zoologischer Anzeiger* 190 (3/4): 159-166.
- GOLEMANSKY V. 2010. Septate gregarines (Apicomplexa: Eugregarinorida) of the alien invasive millipede *Oxidus gracilis* C. L. Koch, 1847 from Bulgaria. *Acta Zoologica Bulgarica* 62 (2): 193-199.
- GOLEMANSKY V. 2015. Checklist of Gregarines (Apicomplexa: Eugregarinorida and Neogregarinorida) from Bulgaria. *Acta Zoologica Bulgarica* 67 (2): 149-157.
- GOLEMANSKY V. & BONNET L. 1994. Protozoa. In: JUBERTHIE C. & DECU V. (Eds.): Encyclopaedia biospeologica I, Moulis and Bucarest: Société de Biospeologie, pp. 23–33.
- GOLEMANSKY V. & LIPA J. J. 1991. Gregarines (Apicomplexa: Eugregarinorida) from cave and terrestrial arthropods in Bulgaria. *Acta Protozoologica* 30: 201-208.

- GOLEMANSKY V., PILARSKA D., GEORGIEV G., TAKOV D., TODOROV M. & PILARSKI P. 2009. Protozoan parasites and pathogens of forest pest arthropods. *Silva Balcanica* 11 (1): 67-72.
- GOLEMANSKY V. & TASCHEV D. 1973. Recherches sur les Grégarines (Gregarinida: Stenophoridae) du Diplopode troglobie *Typhloiulus bureschi* Verhoeff en Bulgarie. *International Journal of Speleology* 5: 87-94.
- GRASSÉ P.-P. (1953): Classe des grégarinomorphes (Gregarinomorphia, N. nov., Gregarinae Haeckel, 1866; Gregarinidea Lankester, 1885; grégarines des auteurs). In: GRASSÉ P.-P. (ed.): *Traité de Zoologie*. Paris: Masson, pp. 590–690.
- HOSHIDE K. 1952. Studies on three new Gregarines from Diplopods in Yamaguchi Prefecture in Japan. *Yamaguchi Journal of Science* 3: 1-14.
- HOSHIDE K. 1958. Studies on the cephaline Gregarines of Japan. II. 1. Description of those belonging to the families Lecudinidae, Polyrhadinidae, Cephalophoridae and Szenophoridae. *Bulletin of the Faculty of Education, Yamaguchi University* 6: 97-157.
- HOSHIDE K. 1959. Studies on the cephaline Gregarines of Japan. II. 3. Description of the members belonging to the families Didymophyidae, Actinocephalidae, Acanthosporidae, Stylocephalidae, Dactylophoridae. *Bulletin of the Faculty of Education, Yamaguchi University* 8: 35-101.
- LAUGHTON A. M., BOOTS M. & SIVA-JOTHY M. T. 2011. The ontogeny of immunity in the honey bee, *Apis mellifera* L. following an immune challenge. *Journal of Insect Physiology* 57: 1023-1032.
- LEANDER B. S. 2008. Marine gregarines—evolutionary prelude to the apicomplexan radiation? *Trends in Parasitology* 24: 60–67.
- LEVINE N. D. 1971. Taxonomy of Archigregarinorida and Selenidiidae (Protozoa, Apicomplexa). *Journal of Protozoology* 18: 704–717.
- LEVINE N. D. 1976. Some nomenclatural corrections among septate gregarines (Protozoa, Apicomplexa). *Proceedings of the Zoological Society Calcutta* 29: 21-28.
- LIPA J. J. 1967. Studies on gregarines (Gregarinomorphia) of arthropods in Poland. *Acta Protozoologica* 5: 97-179.
- MARQUÈS A., ORMIÈRES R. & PUISSÉGUR C. 1978. Scanning electron microscopy of some stages of *Trichorhynchus pulcher* Schneider, 1882, eugregarine parasite of *Scutigera coleoptrata* L. (Myriapoda: Chilopoda). *Annales des Sciences Naturelles, Zoologie, Paris, 12e serie* 20 (1): 27-36.
- ORMIÈRES R., MARQUÈS A. & PUISSÉGUR C. 1977. *Trichorhynchus pulcher* Schneider, 1882, eugregarine parasite of *Scutigera coleoptrata* L. Cycle, ultrastructure, systématique. *Protistologica* 13: 407-417.
- RUECKERT S. & DEVETAK D. 2017. Gregarines (Apicomplexa, Gregarinasina) in psocids (Insecta, Psocoptera) including a new species description and their potential use as pest control agents. *European Journal of Protistology* 60: 60-67.
- RUECKERT S.I. & LEANDER B. S. 2008. Gregarina. Gregarines. Version 23 September 2008. <http://tolweb.org/Gregarina/124806/2008.09.23> In: The Tree of Life Web Project, <http://tolweb.org/>
- RUECKERT S. & LEANDER B. S. 2009. Molecular phylogeny and surface morphology of marine Archigregarines (Apicomplexa), *Selenidium* spp., *Filipodium phascolosomae* n. sp., and *Platyproteum* n. g. and comb. from North-Eastern Pacific Peanut Worms (*Sipuncula*). *Journal of Eukaryotic Microbiology* 56: 428–439.
- SHELLACK G. 1907. Über die Entwicklung und Fortpflanzung von *Echinomera hispida* (A. Schn.). *Archiv für Protistenkunde* 9: 297-345.
- SIMDYANOV T. G., GUILLOU L., DIAKIN A. Y., MIKHAILOV K. V., SCHRÉVEL J. & ALEOSHIN V. V. 2017. A new review on the morphology and phylogeny of eugregarines suggested by the evidence from the gregarine *Ancora sagittata* (Leuckart, 1860) Labbé, 1899 (Apicomplexa: Eugregarinida). *PeerJ* 5:e3354; DOI 10.7717/peerj.3354.
- TUZET O. & MANIER J. F. 1958. Parasites et inquilins d'un Spirostreptidae Malgache: *Spirostreptus madagascariensis* Gerv. *Mémoires de l'Institut Scientifique de Madagascar Série A* 12: 1-6.
- VALIGUROVÁ A. & MATIS D. 2001. Nálezy gregarín (Eugregarinida, Apicomplexa) vo viacnôžkach (Myriapoda) na území Slovenska. *Folia faunistica Slovaca* 6: 1-8.
- WATSON M. E. 1916. Studies on Gregarines. Including descriptions of twenty-one new species and a synopsis of the Eugregarine records from the Myriapoda, Coleoptera and Orthoptera of the World. *Illinois Biological Monographs* 2 (3): 214-468.

Received: 15.02.2018

Accepted: 11.04.2018